Tylochromis, Relationships and the Phylogenetic Status of the African Cichlidae

MELANIE L. J. STIASSNY[1]

ABSTRACT

The anatomy and relationships of the African cichlid genus *Tylochromis* are investigated. While morphological innovation within the genus has been notably muted, an impressive array of morphological characters attests to the monophyly of the tylochromine clade. The monophyly of the "African Cichlidae" is strongly corroborated by the presence of a suite of derived features of the cephalic and branchial musculature, epibranchial structure, and syndesmology of the suspensorium and associated structures. Evidence is presented in favor of a sister-group relationship between *Tylochromis* and the remaining "African Cichlidae."

INTRODUCTION

The genus *Tylochromis* comprises a moderately large assemblage of 18 morphologically similar species (fig. 1). *Tylochromis* adults are typically medium-size, deep-bodied cichlids bearing a superficial resemblance to the porgies, members of the marine family Sparidae. Taken as a whole the genus has an extensive geographical range with members found in the rivers, lakes, and coastal lagoons from Senegal to the Camerouns, and throughout the entire Zaire Basin (fig. 2). Interestingly, although represented in the Middle Ni- ger and Benue systems, the genus is absent from all other regions of the Nilo-Sudan. Similarly, while present in the upper reaches of the Kasai River and the Shaba region of Zaire, tylochromines are absent from the Zambesi and its entire drainage. In many important respects this distribution closely mirrors that of the hemichromine and pelmatochromine radiations recently reviewed by Greenwood (1985, 1987).

The little that is known of tylochromine ecology and ethology has been summarized

[1] Assistant Curator, Department of Herpetology and Ichthyology, American Museum of Natural History.
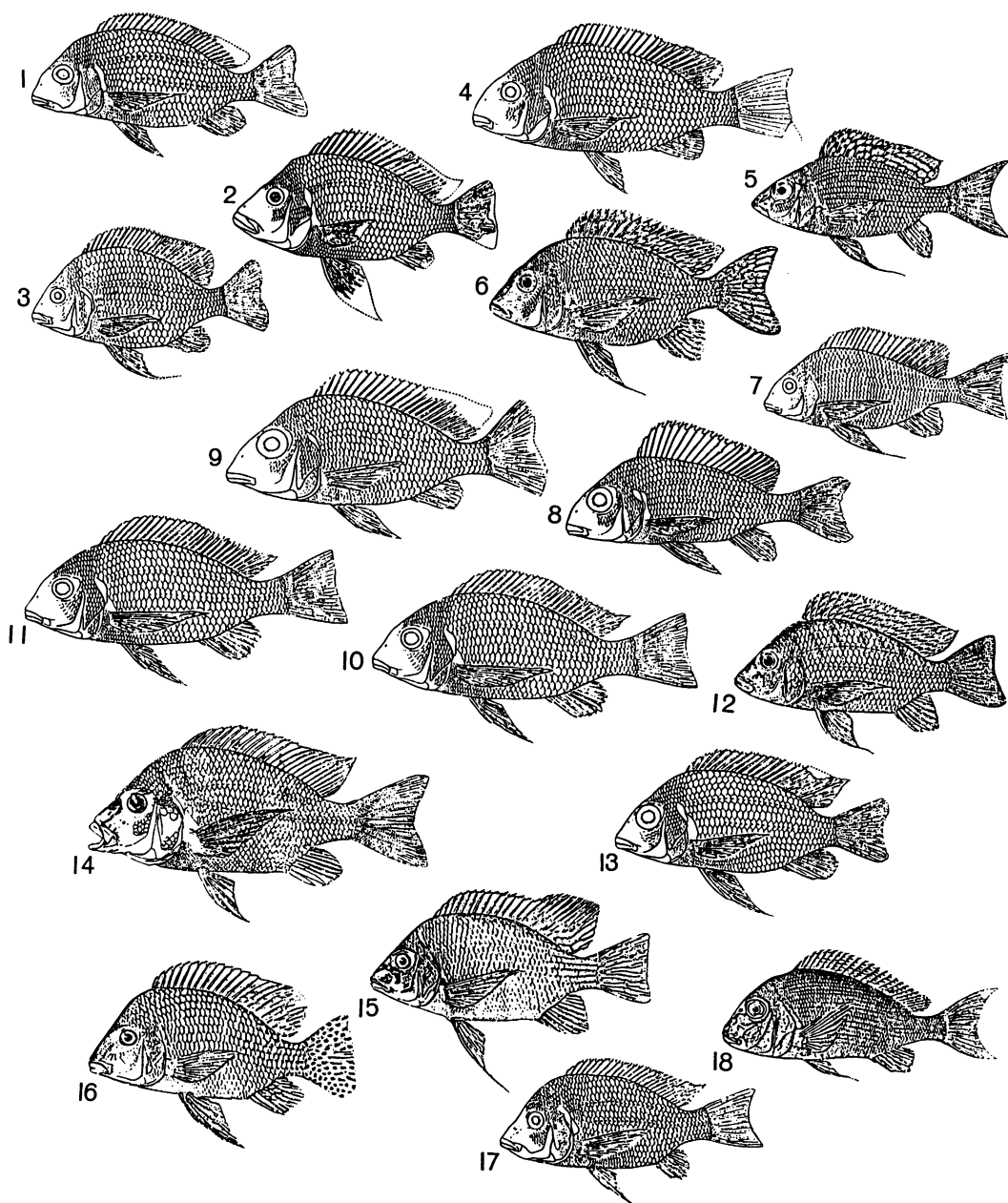
Fig. 1. The *Tylochromis* radiation: 1. *T. microdon* Regan, 1920, 2. *T. aristoma* Stiassny, 1989, 3. *T. pulcher* Stiassny, 1989, 4. *T. leonensis* Stiassny, 1989, 5. *T. intermedius* (Boulenger, 1916), 6. *T. jentinki* Steindachner, 1895, 7. *T. sudanensis* Daget, 1954, 8. *T. trewavasae* Stiassny, 1989, 9. *T. praecox* Stiassny, 1989, 10. *T. robertsi* Stiassny, 1989, 11. *T. elongatus* Stiassny, 1989, 12. *T. lateralis* (Boulenger, 1896), 13. *T. labrodon* Regan, 1920, 14. *T. mylodon* Regan, 1920, 15. *T. regani* Stiassny, 1989, 16. *T. variabilis* Stiassny, 1989, 17. *T. bangwelensis* Regan, 1920, 18. *T. polylepis* (Boulenger, 1900).

by Stiassny (1989) who characterized the group as benthic macrophages, inhabiting the main channels of rivers and the open waters of lakes, although certain species are also found in association with small stream rapids (Reid, personal commun.). While it is true that most *Tylochromis* species occupy fluviatile habitats, the existence of a number of lacustrine species is known. However, unlike most other lacustrine cichlids, *Tylochromis* appears not to be ecologically tied to the lake proper and is usually also found in neighboring rivers and inundated forests.

All species exhibit pronounced sexual color dimorphism, and a feature characteristic of the genus is the presence, in sexually active females, of a flash of bright red on the cheek, likened by Jackson (1961) to " . . . an application of rouge hastily daubed on." *Tylochromis* species are advanced maternal mouthbrooders but beyond this little is known of the reproductive biology or ecology of the clade (Amon-Kothias, 1980; Loiselle, 1985).

Morphological innovation within *Tylochromis* has been notably muted. Attempts to fully resolve the species-level relationships of the genus have not been successful, although it is possible to define certain species groups. Despite such muted intrageneric differentiation, an impressive array of morphological characters attests to the monophyly of the genus. Stiassny (1989) briefly listed these, although no formal argumentation for their polarity was made and discussion was deferred to the present paper.

In that revisional study *Tylochromis* is considered to represent the sister group of the remaining African Cichlidae[2] (Stiassny, 1989; see also Stiassny, in press). By virtue of this position within the family the genus is of special importance to phylogeneticists interested in the resolution of relationships within the remaining African radiations. Most notably,
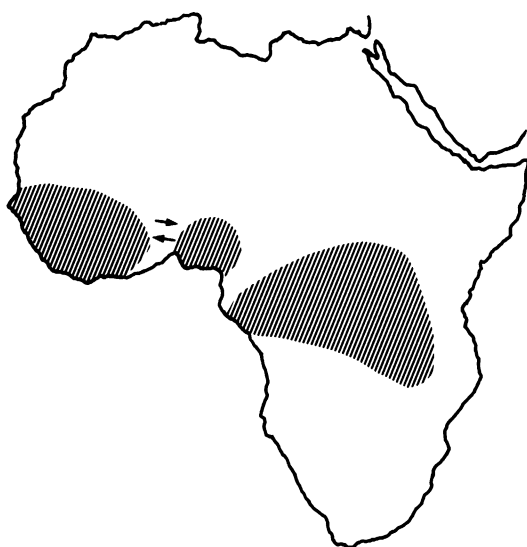

Fig. 2. Geographical distribution of *Tylochromis*. Shaded areas represent regions in which *Tylochromis* specimens have been collected. *T. sudanensis* has been collected on either side of the arrows and probably also occurs in the interconnecting unshaded region.

data derived from *Tylochromis* are of particular importance in the resolution of character polarities within the problematically plesiomorphous and phylogenetically basal lineages recognized in the ongoing studies of Greenwood (e.g., 1979, 1985, 1987) and Stiassny (in press). For this reason a more detailed explication of the phylogenetic status and relationships of the genus is presented here. It is hoped that the data presented herein will provide a useful baseline for further studies within the African assemblage.

METHODS

In this study a cladistic approach to character analysis has been adopted. Only those characters indicative of immediate common ancestry (synapomorphies) are accepted as admissible criteria for the recognition of monophyly. In estimating the relative polarities of characters, I have applied the outgroup method (Watrous and Wheeler, 1981; Maddison et al., 1984). In broad outline, figure 3 represents the current state of our knowledge regarding the high-level intrarelationships of the family. Selection of outgroup taxa has centered on representatives of

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[2] As discussed by Stiassny (1987), the Zairean genus, *Heterochromis,* appears to be the sister group to all other African and Neotropical cichlids, and as such is excluded from the (unnamed) residue of "other African" cichlids. See Oliver (1984) for a detailed anatomical study of *Heterochromis.* Throughout this paper "African Cichlidae" is restricted to imply that monophyletic entity incorporating all African cichlid taxa *except* the genus *Heterochromis.*

lineages and geographical groupings throughout the family, with particular emphasis on the examination of a range of Malagasy and Neotropical taxa, as well as the Zairean genus, *Heterochromis*.

The tylochromines appear to represent the ecological counterparts of certain phylogenetically (and geographically) disparate taxa [e.g., *Geophagus* (Neotropics), *Ptychochromis* (Madagascar), and *Lethrinops* (Africa)]. Because of the resulting convergence in many aspects of their morphology, I have included representatives of each of these lineages as interesting morphological "touchstones" in the present analysis.

MATERIAL EXAMINED

The informal grouping system adopted below follows that laid out by Stiassny (in press) who attempted to name a series of monophyletic subgroupings within the family.

Malagasy species

Ptychochromines: *Ptychochromis oligacanthus* (AMNH 88102, AMNH 88190)
Paratilapia polleni (AMNH 88101, AMNH 11687)
Etroplines: *Paretroplus polyactis* (AMNH 88708)

Neotropical species

Cichla ocellaris (AMNH 25831)
Crenicichlines: *Crenicichla saxitilis* (AMNH 39890)
Chaetobranchines: *Chaetobranchus* sp. (AMNH 47909); *Astronotus ocellaris* (AMNH 47910)
Geophagines: *Geophagus surinimamensis* (AMNH 54944); *Geophagus jurupari* (AMNH 15488); *Apistogramma steindachneri* (AMNH 73079); *Crenicara punctulata* (AMNH 33917)
Cichlasomine group A: *Acaronia nassa* (AMNH 52610); *Neetroplus nematopus* (AMNH 15639); "*Cichlasoma Archocentrus*" *nigrofasciatus* (AMNH 24435); "*C. Nandopsis*" *fredrichsthali* (AMNH 27821)
Cichlasomine group B: *Aequidens tetramerus* (AMNH 72938); *Bujurquina vittatus* (AMNH 22735); *Nannacara anomala* (AMNH 6352)

African species

Heterochromis multidens (AMNH 5963)
Tylochromines: *Tylochromis variabiis* (AMNH 57162); *Tylochromis lateralis* (AMNH 58041); *Tylochromis labrodon* (AMNH 6053)
Tilapiines: *Tilapia zilli* (AMNH 6120); *Tilapia*

tholleni (AMNH 47911); *Oreochromis aureus* (AMNH 39121); *Sarotherodon galileus* (AMNH 8900)
Hemichromines: *Hemichromis elongatus* (AMNH 5894); *Hemichromis lifalili* (AMNH 19704)
Chromidotilapines: *Chromidotilapia guntheri* (AMNH uncat.); *Pelvicachromis humilis* (AMNH 12317)
Others: *Pelmatochromis nigrofasciatus* (AMNH 5967); *Lethrinops longimanus* (AMNH 37902); *Lethrinops parvidens* (AMNH 31867); *Orthochromis polyacanthus* (AMNH 5854); *Astatotilapia burtoni* (AMNH uncat.); *Lamprologus mocguardii* (AMNH 5828).

ABBREVIATIONS IN ILLUSTRATIONS

A1, 2	adductor mandibulae 1, 2
AAP	adductor arcuus palatini
art.s	articular surface
Basio	basioccipital
CB3,4	ceratobranchial 3–4
Dil.Op	dilatator operculi
Dst.ExSc	distal extrascapular
ect	ectopterygoid
end	endopterygoid
Epax	epaxialis musculature
Epio	epiotic
Exo	exoccipital
fr	frontal
HBr3	hypobranchial 3
LAP	levator arcuus palatini
Lat.Eth	lateral ethmoid
Lev.Op	levator operculi
LPJ	lower pharyngeal jaw
Lat.Eth	lateral ethmoid
l.eth-pal	ethmopalatine ligament
l.pal-lac	palatolachrymal ligament
l.pal-mx	palatomaxillary ligament
l.pal-pal	palatopalatine ligament
Mes	mesethmoid
mx	maxilla
myo	myodome
NLP3–6	neurocranial laterosensory pore 3–6
Obl	obliquus ventralis
pal	palatine
Ph.Cl.ext	pharyngocleithralis externus
Ph.Cl.int	pharyngocleithralis internus
Pro	prootic
Prx.ExSc	proximal extrascapular
Psph	parasphenoid
Psph.ped	parasphenoid pedicel
Pst	posttemporal
Rec.vt	rectus ventralis
Semi.cir.lig	semicircular ligament
Sp.Cl	supracleithrum
Tv.ant	transversus ventralis anterior
vom	vomer

The following review is a partial account of the anatomy of the tylochromine clade. Only those structures that are found to yield characters suitable for phylogenetic analysis at the level of universality under consideration have been selected for description here. Reference should be made to Stiassny (1989) for a general review of the range of meristic and morphometric variation encompassed by the clade, as well as for details regarding the definition of species groups within the assemblage.

ANATOMICAL REVIEW

THE AFRICAN CICHLIDAE

The hypothesized monophyly of the African Cichlidae is strongly corroborated by the presence of a suite of unambiguously derived features of the cephalic and branchial musculature, epibranchial structure, and syndesmology of the suspensorium and associated structures (fig. 3, characters 1–5). Characters 1 to 4 are considered in some detail by Stiassny (in press), and additional discussion of some of these features is to be found in Cichocki (1976), Greenwood (1985), and Oliver (1984). In the course of the current investigation an additional feature of the ventral branchial musculature has been identified as lending further evidence to the hypothesis of African group monophyly (fig. 3, character 5).

Primitively among percomorphs, the transversus ventralis anterior muscle passes uninterrupted from its origin on the fourth ceratobranchial to its insertion of the contralateral element (see fig. 4 of Stiassny and Jensen, 1987), forming a muscle sling beneath the fifth ceratobranchial elements or lower pharyngeal jaw. In all Malagasy and Asian cichlids, in *Heterochromis,* and the great majority of Neotropical taxa, a component of the transversus ventralis anterior retains this plesiomorphic pattern of insertion, although some muscle fibers insert onto the keel of the medially situated lower pharyngeal jaw (e.g., fig. 4 C, D). In *Tylochromis* (fig. 4B) and the great majority of other African cichlids (e.g., fig. 4A; see also Stiassny and Jensen, 1987; fig. 4C) the transversus ventralis anterior is a bipartite muscle with fibers originating on each fourth ceratobranchial element and in-

serting onto the median keel of the lower pharyngeal jaw. Within some Neotropical clades a mosaic of derived and plesiomorphous configurations are expressed, for example among group A cichlasomines (sensu Stiassny, in press), *Acaronia* exhibits the derived transversus configuration while most other cichlasomines retain the plesiomorphous muscle sling. Similarly, the transversus ventralis configuration of *Cichla* mirrors that of the African clades, while that of its sister group, the crenicichlines, is of the plesiomorphous type (see Stiassny, 1982; Cichocki, 1976).

Despite these few anomalous occurrences within the Neotropical clade, I believe that it is reasonable to interpret their distribution as having had a derivation independent from that of the major African clade, and that the origin of a bipartite transversus ventralis anterior muscle in *Tylochromis* and the remaining African Cichlidae is an innovation unique to them and as such is additional evidence for their monophyletic origin.

TYLOCHROMINE MONOPHYLY

In addition to two characters considered in some detail (fig. 3, characters 1, 2), Stiassny (1989) listed five additional characters interpreted as evidence of tylochromine group monophyly but gave no formal argumentation as to their polarity, deferring discussion to the present paper. In the following section these five characters will be considered in further detail and a formal argumentation for their polarity presented.

Ventral branchial arch musculature

1. The fourth rectus ventralis muscles (fig. 3, character 8)

Primitively among percomorphs a single rectus ventralis (IV) muscle pair is present in the ventral branchial apparatus. The rectii originate on the fourth ceratobranchials and pass rostrad to insert onto a complex semicircular ligament system through which the ventral aorta passes en route to the gills (see fig. 4A, C, D). The configuration of the rectus ventralis IV and its association with the semicircular ligament system in cichlid fishes has been described in some detail by Vandewalle (1971), Anker (1978), Greenwood (1985), and
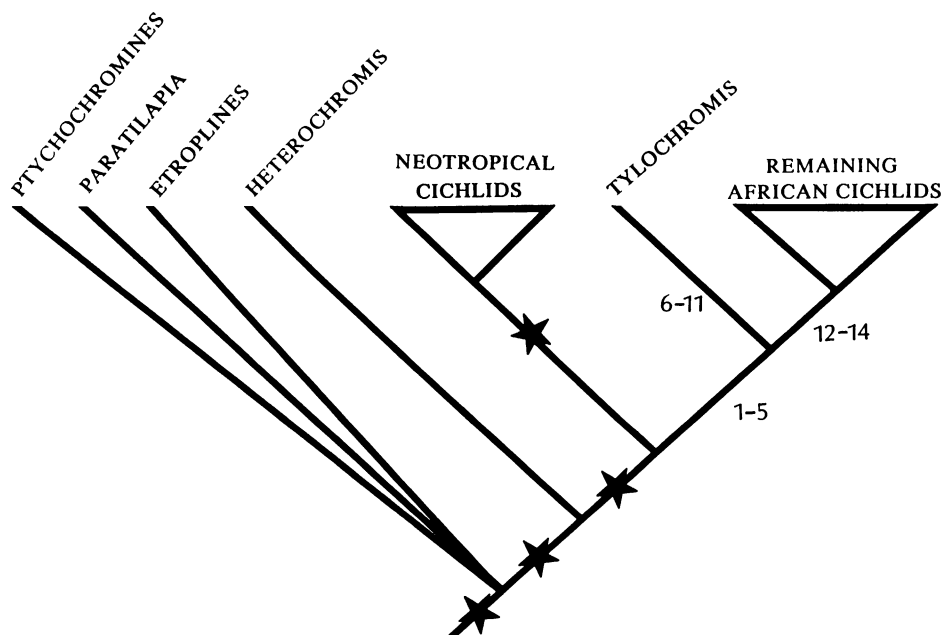
Fig. 3. Summary cladogram indicating intrafamilial relationships of cichlid fishes. For characters supporting the starred nodes see Stiassny, 1987, and Stiassny, in press. The numbers correspond to the following characters:

1. The adductor arcus palatini muscle (AAP) extends anteriad to insert onto the palatine bone in the region of the palatine fossa.
2. The anterior palatomaxillary ligament is well developed and straplike, and extends much of the length of the palatine prong.
3. The pharyngocleithralis internus muscle (PhCl.int.) inserts onto the lower pharyngeal jaw (LPJ) via a single, cordlike tendon.
4. The uncinate process of the first epibranchial (ep1) is oriented caudad and is considerably longer than the anterior arm of that element.
5. The transversus ventralis anterior muscle (Tv.ant.) is bipartite, with fibers originating on the fourth ceratobranchials and inserting onto the median horn of the LPJ (see p. 5).
6. Marked sexual dimorphism of buccal dentition (Stiassny, 1989).
7. Characteristic pattern of interdigitating "juvenile" bars in young fish (Stiassny, 1989).
8. Fourth rectus ventralis muscle (Rec.vt) is complex with a section originating from the median keel of the LPJ (see pp. 5–8).
9. A small epaxial muscle slip developed from the proximal extrascapular bone (see p. 8).
10. A distinct palatolachrymal ligament is lacking (see pp. 8–9).
11. A myodomal splint of bone is present on the basioccipital (see p. 9).
12. Loss of the posterior predorsal bone.
13. Presence of a well-developed and strongly pigmented opercular spot.
14. Pharyngeal apophysis with a major prootic and basioccipital contribution to the body of the apophysis (see pp. 10–11).

Stiassny (1987), and the condition in most of these fishes differs little from that found in most percomorph taxa (see Dietz, 1912,1914; Winterbottom, 1974; Stiassny, 1987; Stiassny and Jensen, 1987). *Tylochromis* forms a notable exception to this generalization, and the clade is readily characterized by an in-

teresting modification of the rectii ventralis IV muscles.

In *Tylochromis* the rectii ventralis IV are complex muscles (fig. 4B) and while a lateral component of the muscle retains its tendinous origin on the ventral aspect of the fourth ceratobranchial bone, medially the muscle is
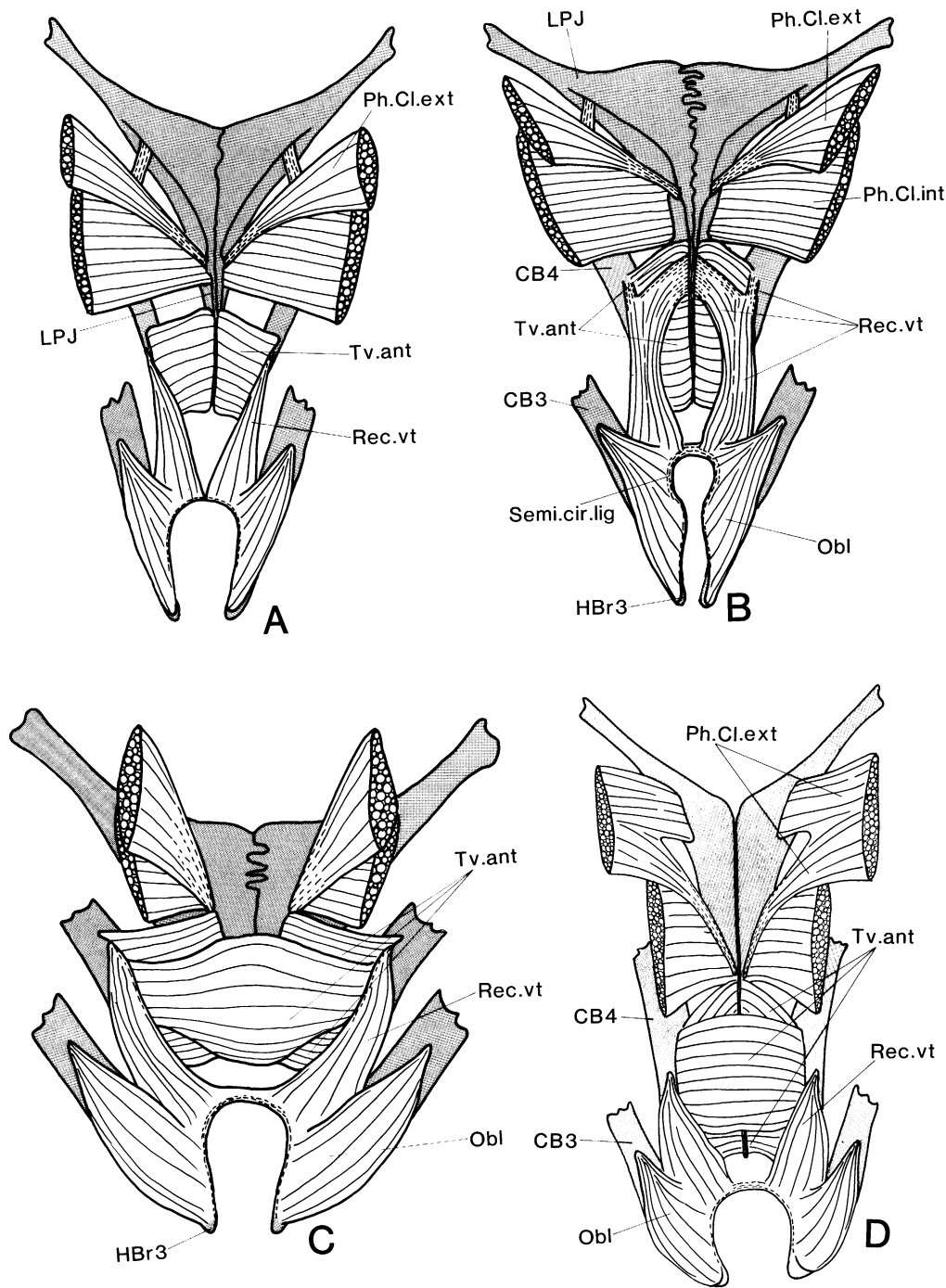
Fig. 4. Ventral branchial musculature in: A. *Lethrinops*, B. *Tylochromis*, C. *Heterochromis*, and D. *Geophagus*.
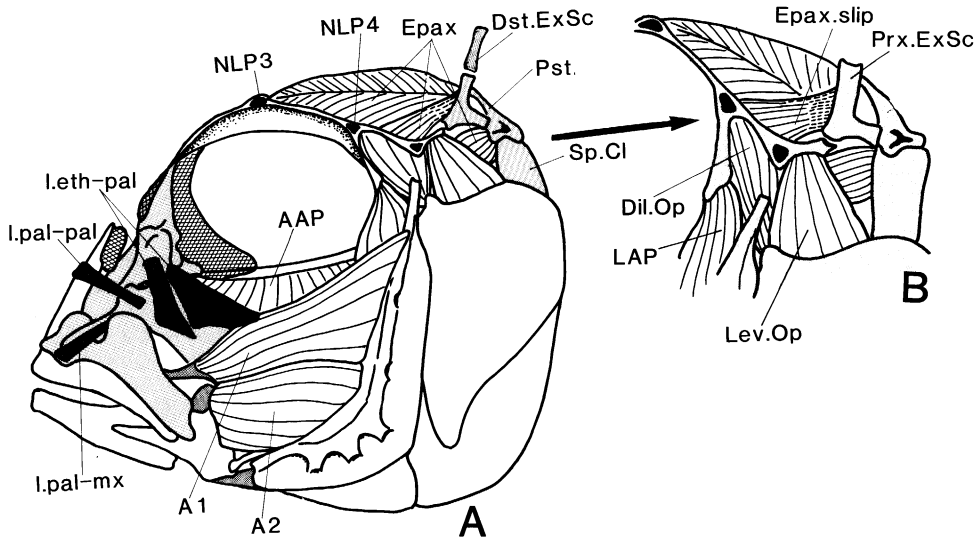
Fig. 5.   Superficial head musculature of *Tylochromis*: A. lateral view, B. detail of A to show insertion of epaxial muscle slip.

elaborated with a distinct section arising from the ventral keel of the lower pharyngeal jaw. This novel medial section of the rectus ventralis IV overlies the bipartite transversus ventralis anterior muscle described in the preceding section. The two sections of the rectus merge rostrally and insert onto the semicircular ligament system in the manner of the other cichlids examined. The peculiar elaboration of the rectii ventralis muscles of *Tylochromis* [which is present in all species examined by Stiassny (1989)] appears to be an unique feature of the genus and as such is correctly interpreted as evidence for group monophyly.

Epaxial musculature

2. **The extrascapular epaxial muscle slip (fig. 3, character 9)**

The epaxialis muscle forms the dorsal muscle mass of the body, and in percomorphs the epaxial muscle typically is expanded rostrally onto the dorsal head surface where various crests are developed in association with it. The degree of epaxial migration onto the head in cichlids varies somewhat (see Cichocki, 1976), but typically the epaxial musculature extends at least to the level of the NLF0 pores and medial canal, and frequently a little be-

yond this in most taxa (fig. 5A; see also Stiassny, in press).

The extrascapular series of laterosensory canal bearing bones usually overlies the epaxial muscle in the parietal region of the neurocranium where they are embedded in the dermis. In cichlids there are typically two extrascapular bones, a L-shaped proximal element and a tubular distal element (fig. 5A). In *Tylochromis* a small subdivision of the cephalic epaxialis is present connecting the rostral margin of the proximal extrascapular with the epiotic in the region between NLP4 and NLP5 (fig. 5B). A similar extrascapular muscle slip has not been found in any other cichlid (or percomorph) taxon examined, and its presence in all species of *Tylochromis* is clearly an additional indicator of the monophyly of the assemblage.

Palatine ligaments

3. **The palatolachrymal ligament (fig. 3, character 10)**

Primitively among cichlids a well-developed palatolachrymal ligament is present on the palatine bone (fig. 6A; see also Greenwood, 1985, Anker, 1978). In African cichlids the ligament originates close to the base of the palatomaxillary ligament, but is usu-
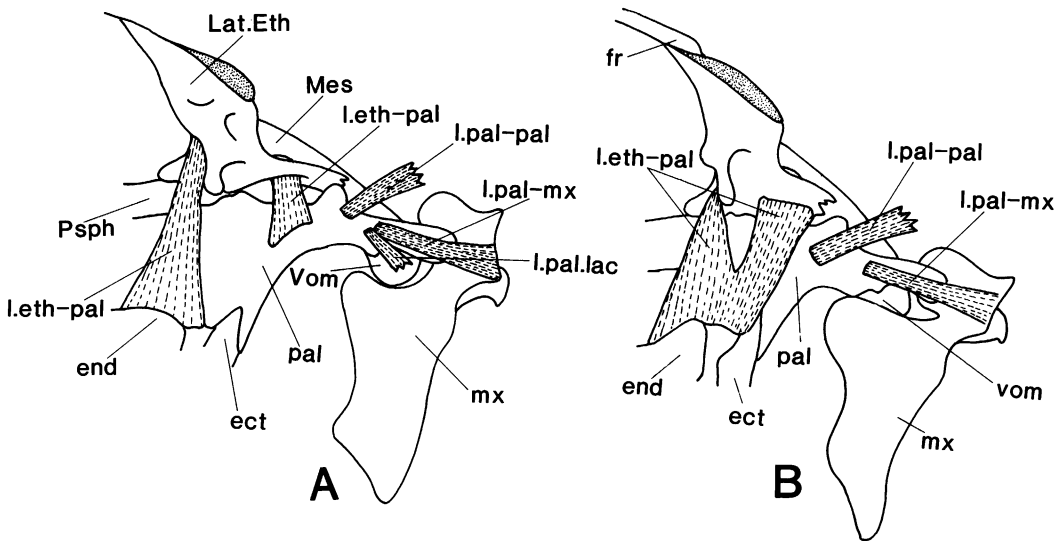
Fig. 6. Ethmovomerine region and associated ligaments in lateral view of: A. *Lethrinops,* and B. *Tylochromis.*

ally a distinct and separate structure (fig. 6A). The palatolachrymal ligament passes rostrad from the palatine to insert onto the mediorostral margin of the lachrymal bone. In *Tylochromis,* while a well-developed palatomaxillary ligament is present, the palatolachrymal ligament is usually completely lacking (fig. 6B). Although in some individuals examined a few connective tissue fibers are retained, a discrete ligament is invariably absent. Reinthal (personal commun.) has found a similar pattern of palatolachrymal ligament reduction to loss within certain of the Lake Malawi "mbuna" cichlid lineages. In view of the very distant relationship between *Tylochromis* and any Malawi taxon, I believe it is best to interpret the loss of the ligament in *Tylochromis* as being an independent event to that in the Malawian taxa, and as such may be considered as additional evidence of tylochromine group monophyly.

Basicranial morphology

4. The myodomal splint
   (fig. 3, character 11)

The posterior myodome of cichlid fishes is usually open (fig. 7B; see also figures in Greenwood, 1978), with emergent muscle variously extruded onto the basioccipital shaft. In *Tylochromis,* as in the majority of cichlid taxa, the basioccipital bone forms the posterior margin of the myodomal opening, but uniquely in this taxon a small splint of bone projects down from the basioccipital shaft (fig. 7A) and is embedded in the myodomal muscle mass. This myodomal splint, which is present in all *Tylochromis* species, has not been found in another cichlid (or percomorph) taxon and is apparently unique to the genus.

Apophyseal morphology

A fifth character noted by Stiassny (1989) was the presence of a distinctive apophyseal morphology described by Greenwood (1978) as a *Tylochromis* type apophysis (fig. 7A). This apophyseal type, which according to Greenwood (1978) is the simplest encountered among the African Cichlidae, differs from a *Tilapia* type (fig. 8A) in lacking a definite prootic contribution to its lateral walls, and in having no basioccipital contribution to the body of the apophysis or support for its articular surface.

My own observations of apophyseal morphology among the Madagascan and Neotropical Cichlidae corroborate Greenwood's
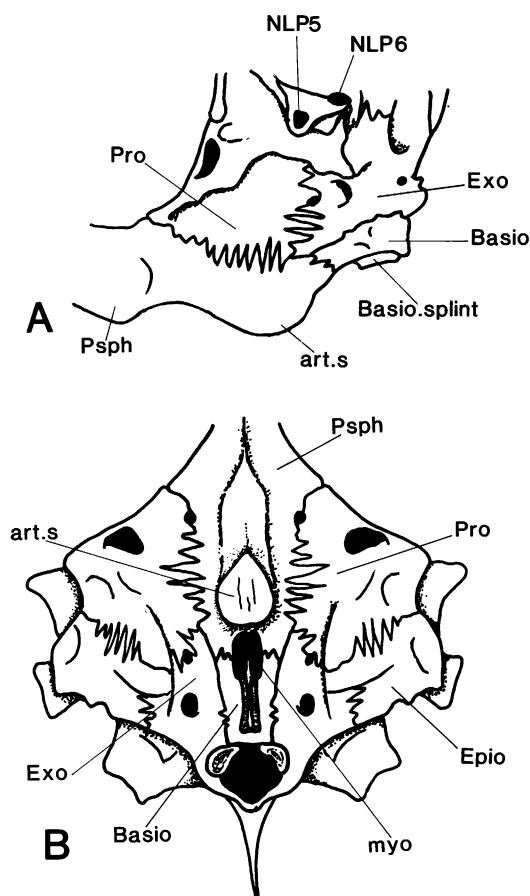
Fig. 7.   Basicranium and pharyngeal apophysis of *Tylochromis* in: A. ventral view, and B. lateral view.

basic conclusion regarding the plesiomorphic nature of the *Tylochromis* apophyseal type. Many Neotropical taxa have an apophyseal morphology which differs little from that described for *Tylochromis* by Greenwood (1978), although the articular apophyseal surface is usually borne on a strongly projecting parasphenoid process (fig. 8B). A similar morphology is also widespread among the Madagascan cichlids as well as in other labroids (see fig. 6 in Stiassny and Jensen, 1987). In view of the widespread occurrence of the *Tylochromis* type apophysis, I think it reasonable to suppose that this represents the plesiomorphic cichlid configuration and as such cannot be interpreted as evidence for tylochromine group monophyly. For this reason it is not included as a character in figure

3. However, the fact that the remaining African Cichlidae may all be characterized as having an apophyseal morphology phylogenetically advanced over that of the Madagascan/Asian, Neotropical, and tylochromine clades is a notion worthy of further consideration, and one that relates directly to the placement of *Tylochromis* as the sister group of the remaining African assemblage.

TYLOCHROMIS AND THE REMAINING AFRICAN CICHLIDAE

As noted in the introduction to this paper, *Tylochromis* is considered to represent the sister group of the remaining African Cichlidae, and Stiassny (in press) discusses two characters which lend support to this placement (fig. 3, characters 12 and 13). In addition to these two characters a feature of apophyseal morphology may be interpreted as further evidence for this placement (fig. 3, character 14).

Greenwood (1978), in his review of the pharyngeal apophysis in African cichlids, recognized four main categories of apophyseal type: a *Tylochromis* type, a *Tilapia* type, a *Tropheus* type, and a *Haplochromis* type. As noted previously, the *Tylochromis* type differs from the others in lacking a definite prootic contribution to the lateral walls of the apophysis and in having the basioccipital excluded from contributing to the body of the apophysis or its articular surface. As discussed above, the *Tylochromis* type apophysis is best interpreted as representing the plesiomorphic configuration within the Cichlidae. Given this, the remaining African Cichlidae may be characterized by the possession of a phylogenetically advanced configuration of the pharyngeal apophysis in which the prootic does contribute to the lateral walls of the apophysis, the basioccipitals extend rostrad to contribute to the body of the apophysis, and in the case of the *Haplochromis* type, the basioccipitals also contribute to the articular surface of the apophysis (see Greenwood, 1978, for a detailed consideration of each apophyseal type).

The situation in *Heterochromis* is anomalous as this taxon clearly has a *Tilapia* type apophysis with large prootic and basioccipital contributions to the body of the apoph-
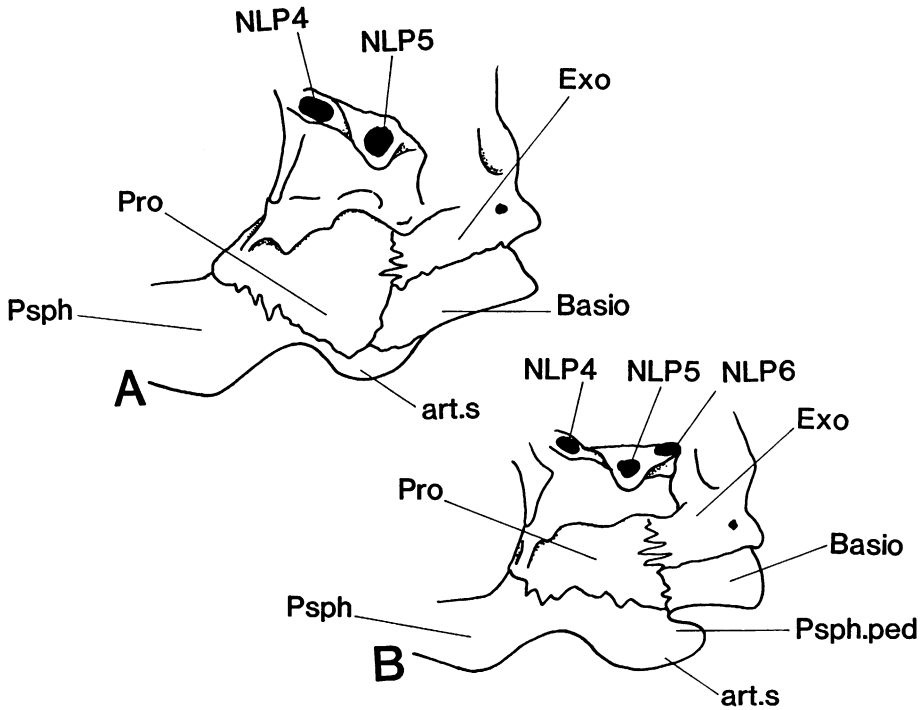
Fig. 8. Lateral view of pharyngeal apophysis of A. *Heterochromis,* and B. *"Cichlasoma Nandopsis."*

ysis (fig. 8A). In view of the supposed phylogenetic placement of *Heterochromis* (fig. 3), a *Tylochromis* type would be anticipated. Similarly, the Neotropical genus *Cichla* is problematical in that its apophyseal structure is clearly of a *Haplochromis* type, with large basioccipital contributions to the articular surface of the apophysis (Cichocki, 1976; see fig. 4 in Stiassny, 1982). Once again, given the phylogenetic placement of *Cichla* as a basal member of the Neotropical clade (Stiassny, 1987; Stiassny in press), a *Tylochromis* type apophysis would be expected to occur in this taxon.

Despite these few anomalous findings, the phylogenetic validity of a major grouping of African cichlids (excluding *Tylochromis*) is corroborated by the presence in those taxa of the derived apophyseal morphology detailed here (fig. 3, character 14).

INTRACLADAL DIVERSIFICATION

Perhaps one of the most striking features of this relatively speciose tylochromine ra-

diation is the limited degree of morphological divergence exhibited by its constituent species. Despite an impressively wide array of characters attesting to the monophyly of the lineage, morphological innovation within the clade has been muted and a highly conservative bauplan prevails (fig. 1). Although variation in combinations of meristic features appears to represent the primary means of differentiation at the species level, an array of pharyngeal modifications is represented [illustrated here by reference to the lower pharyngeal jaw (LPJ), fig. 9]. In fact, the degree of pharyngeal hyper- and hypotrophy encompassed by *Tylochromis* comes close to spanning the range of variation encountered within the family as a whole (see figures in Pellegrin, 1904; Kullander, 1986; Greenwood, 1984).

Typically among cichlids such pharyngeal modification is strongly correlated with trophic diversification (Fryer and Iles, 1972; Liem, 1973; Greenwood, 1974; Witte and Barel, 1976). Interestingly, surprisingly little trophic differentiation is evident among ty-
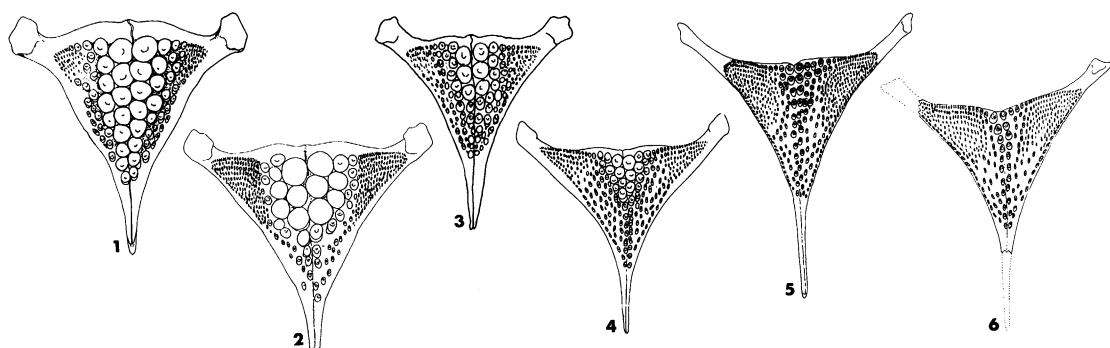
Fig. 9. Isolated LPJs of: 1. *T. mylodon*, 2. *T. labrodon*, 3. *T. lateralis*, 4. *T. pulcher*, 5. *T. microdon*, and 6. *T. aristoma*.

lochromines, and LPJ morphology is a rather poor predictor of diet. Although Stiassny's (1989) assessment of dietary regimes was based on the examination of the gut contents of specimens in museum collections, material from a wide range of localities collected at different times was incorporated in the study. All species may be characterized as opportunistic benthic macrophages feeding on an assortment of benthic invertebrates (larval and adult), vegetable matter, and detritus.

As with the haplochromine lineages investigated by Greenwood (e.g., 1974, 1984) it is possible to trace, among extant species, those gradual changes in anatomy that apparently underlie the acquisition of the highly specialized morphoclinal endpoints of pharyngeal hyper- and hypotrophy. Unfortunately however, little phylogenetically useful information is evident in the patterns of pharyngeal modification among tylochromines, and as in many other cichlid lineages, multiple (independent) acquisitions of markedly similar pharyngeal modifications have apparently occurred.

CONCLUSIONS

The systematic conclusions supported by data analyzed in this study may be summarized as follows:

1. The monophyly of the diverse and speciose "African Cichlidae" is strongly corroborated by the presence of a suite of derived features of the cephalic and branchial musculature, epibranchial structure, and syndes-

mology of the suspensorium and associated structures (fig. 3, characters 1–5).

2. The monophyly of the genus *Tylochromis* is established on the basis of a wide range of unambiguously derived morphological features of cranial osteology and myology, branchial musculature, dental anatomy, and coloration characteristics (fig. 3, characters 6–11).

3. Although far from overwhelming, the evidence currently available argues in favor of a sister group relationship between *Tylochromis* and the remaining African Cichlidae (fig. 3, characters 12–14).

In concluding a review of the current state of knowledge regarding the phylogenetics of the family Cichlidae, Stiassny (in press) noted that despite almost a century of intensive investigation we are still disappointingly far from a comprehensive understanding of the high-level intrarelationships of the group. Although quite remarkably speciose and ecologically diverse, as a group cichlids are notably conservative in underlying anatomical diversity. In the face of such muted morphological innovation, the problem of determining monophyletic lineages on the basis of shared derived morphological characters is particularly acute. In this context then, the fact that five rather "good" characters have been identified as supporting the hypothesis of "African" monophyly, is certainly strong corroboration. Similarly, the monophyly of *Tylochromis* appears well established. Regarding the placement of *Tylochromis* as the sister group of the remaining African assemblage, the evidence is less impressive. For

analysis at this level, the incorporation of molecular data into cladistic phylogeny construction may be particularly valuable.

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