



# A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes

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## Synopsis

Ethological evidence has cast some doubts on the phylogenetic validity of the tacitly accepted division of African cichlid genera into '*Haplochromis*' and '*Tilapia*' groups. This paper reviews the structure and morphology of the pharyngeal apophysis, the skull character on which the original two-group hypothesis was formulated. The revision shows that many of the original '*Tilapia*' group genera have a distinct apophyseal form and structure (the *Tropheus* type) which at least in some structural features, shows greater affinity with the '*Haplochromis*' type than with the '*Tilapia*' one, and that a fourth type (the '*Tylochromis*' one) must also be recognized. The only formally proposed subfamilial classification of African, Asian and American cichlids was based on the pharyngeal apophysis and must now be rejected.

## Abbreviations used in text figures

- b. Basioccipital buttress overlying parasphenoid
- bc. Articular surface for first vertebra
- boc. Basioccipital
- bocf. Facet-like region on basioccipital
- boc r-f. Ridge-like facet on basioccipital
- bof. Articular facet on basioccipital process
- bop. Ventrally directed basioccipital process
- exo. Exoccipital
- my. Myodomal groove in basioccipital
- pro. Prootic
- ps. Parasphenoid
- psf. Articular facet, or region, on parasphenoid
- s. Sutural surface interdigitating with the  $s_1$  process of parasphenoid

- s<sub>1</sub> Process of parasphenoid which interdigitates with s region of basioccipital  
 sg. Saccular groove  
 sgs. Septum between saccular groove of each side

## Introduction

Regan's now classic papers of 1920 and 1922 not only provided the first critical analysis of the African cichlid genera, but also appeared to offer a phylogenetic basis for their intrafamilial classification.

Using certain characteristics of the neurocranial apophysis with which the upper pharyngeal bones articulate (see p. 299), Regan brought together the genera into a *Tilapia* and a *Haplochromis* lineage, the lineages taking their names from the two genera whose apophyseal characters supposedly typified those of the related taxa contained in each group (Regan, 1920).

Some years later, Trewavas (1935), in a revision of the Lake Malawi cichlids, made a few slight modifications to Regan's basic scheme. As a result certain genera were reallocated, but the basic two-lineage concept remained.

Because subsequent workers were concerned mainly with revisions at the generic and specific levels (often paying scant attention to apophyseal characters), Regan's original division of the Cichlidae continued to be accepted, albeit informally as far as any higher classification was concerned, but still with implicit phyletic overtones.

In 1947, Hoedeman gave the two groups formal status by designating them as the subfamilies Tilapinae and Haplochrominae (see also Hoedeman, 1974). Hoedeman recognized a third subfamily, the Etroplinae (for the Asian genus *Etroplus* and the Malagasian genus *Paretroplus*), but did not discuss the nature of the pharyngeal apophysis in its constituent taxa, nor did he describe any but the most superficial of their anatomical features. This classification, put forward in handbooks written for aquarists, has been generally overlooked, or at least not utilized in the primary ichthyological literature.

The first serious doubts as to the phylogenetic validity of Regan's (1920) *Tilapia* and *Haplochromis* divisions were expressed by Wickler (1963), an ethologist studying the breeding behaviour of Lake Tanganyika cichlids. Wickler found that *Tropheus moorii*, a supposed member of the *Tilapia* lineage had, in fact, a typical *Haplochromis* type of breeding behaviour, a behaviour pattern associated with the presence of certain male secondary sexual characters (the anal ocelli) which are absent in species of the genus *Tilapia* (and in the closely related genus *Sarotherodon*). Wickler also suggested, but without experimental evidence, that the affinities of at least one other Tanganyika genus (*Petrochromis*) had been misinterpreted by Regan.

The uncertainty generated by Wickler's discovery was compounded by Trewavas' view (quoted in Burchard & Wickler, 1965) that *Tropheus moorii* did indeed have a *Haplochromis* type of pharyngeal apophysis and not, as Regan described it, one of the *Tilapia* type. As will be apparent later, I do not agree with either Trewavas or Regan on this point; *Tropheus* has neither a *Tilapia* nor a *Haplochromis* apophysis but represents a third apophyseal morphotype (see p. 302).

Fryer & Iles (1972 : 502–504), impressed by Wickler's findings, expressed their doubts regarding the value of the apophysis as an indicator of relationships in quite unequivocal terms, although they do not appear to have made a detailed examination of this structure themselves. In their opinion (Fryer & Iles, 1972 : 503), Regan gave too little weight to the phyletic value of other similarities shared by taxa whose apophyseal features placed them in different lineages. But, before the phyletic implications of these characters are accepted they will have to be subjected to a more detailed and critical analysis than was afforded them by Fryer & Iles in their proposed phylogenies of various Lake Tanganyika generic groups (1972 : 507, fig. 337).

Clearly there is a need to reconsider the phyletic relationships amongst the African cichlids, a vast task unlikely to be undertaken by a single worker. The notes and comments which comprise this paper are a contribution to that end. They do not by any means constitute a complete review of all the subtleties inherent in the question 'What value can be attached to the pharyngeal apophysis as an indicator of phyletic relationships?' But, as the first detailed and systematically wide-ranging review of apophyseal structure as a whole (and not just the articular surface as was used

by Regan), I believe they do provide grounds for invalidating the original evidence on which the *Tilapia-Haplochromis* dichotomy was based (see Regan, 1920).

### The structure and morphology of the apophysis

Although Regan (1920 : 34) remarks that 'The character of most importance in the classification is the *structure* of the apophysis that supports the upper pharyngials, . . .' [*italics mine*], his subsequent key and discussion are concerned only with part of the apophysis, its articular surface (see also Regan, 1922). Thus Regan's (1920 : 34) statements that the ' . . . apophysis is formed by the parasphenoid only (*Tilapia* type)' and ' . . . the apophysis is formed by the parasphenoid in the middle and the basioccipital at the sides (*Haplochromis* type)' are misleading since they do not refer to the entire structure but only to part of it. In fact, both types have the parasphenoid, the basioccipital and the prootic all contributing to the apophysis. Exceptional in this respect is the genus *Tylochromis* (formerly a member of the *Tilapia* group) where only the parasphenoid is directly involved.

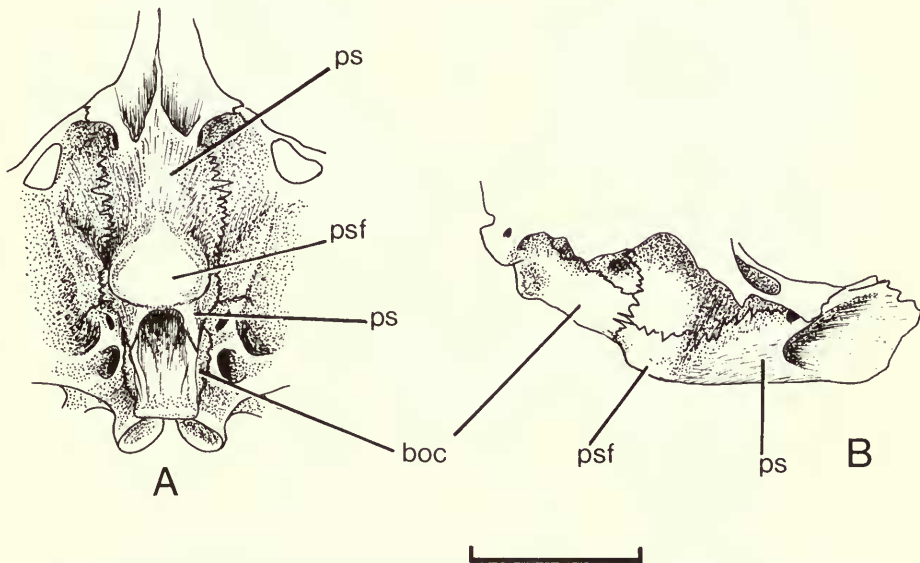


Fig. 1 *Tylochromis jentinki*. Apophysis in A: Ventral and B: Right lateral views. Scale = 5 mm.

If the interrelationships of these three bones, and their relative contributions to the body of the apophysis as well as to its articular surface, are taken into account, four apophyseal types can be recognized, viz. a *Tylochromis*, a *Tilapia*, a *Tropheus* and a *Haplochromis* type. There is possibly a fifth type, represented by *Chilochromis*, but this still requires confirmation (see p. 320).

The *Tylochromis* type is quite distinctive, but the boundaries between the *Tilapia* and *Tropheus* types on the one hand, and the *Tropheus* and *Haplochromis* types on the other, are less trenchant. However, the number of taxa showing intermediate types is relatively low and one is justified in recognizing the four modal categories, at least for descriptive purposes.

#### The *Tylochromis* type (Fig. 1)

When viewed laterally the apophysis appears as a slight ventral projection, its articular surface aligned in parallel with the ventral face of the basioccipital. The entire projecting part is formed by a localized hypertrophy of the parasphenoid. Although the articular surface is supported dorsally by the ventral margin of the prootic of each side, that bone does not, strictly speaking, contribute to the body of the apophysis.

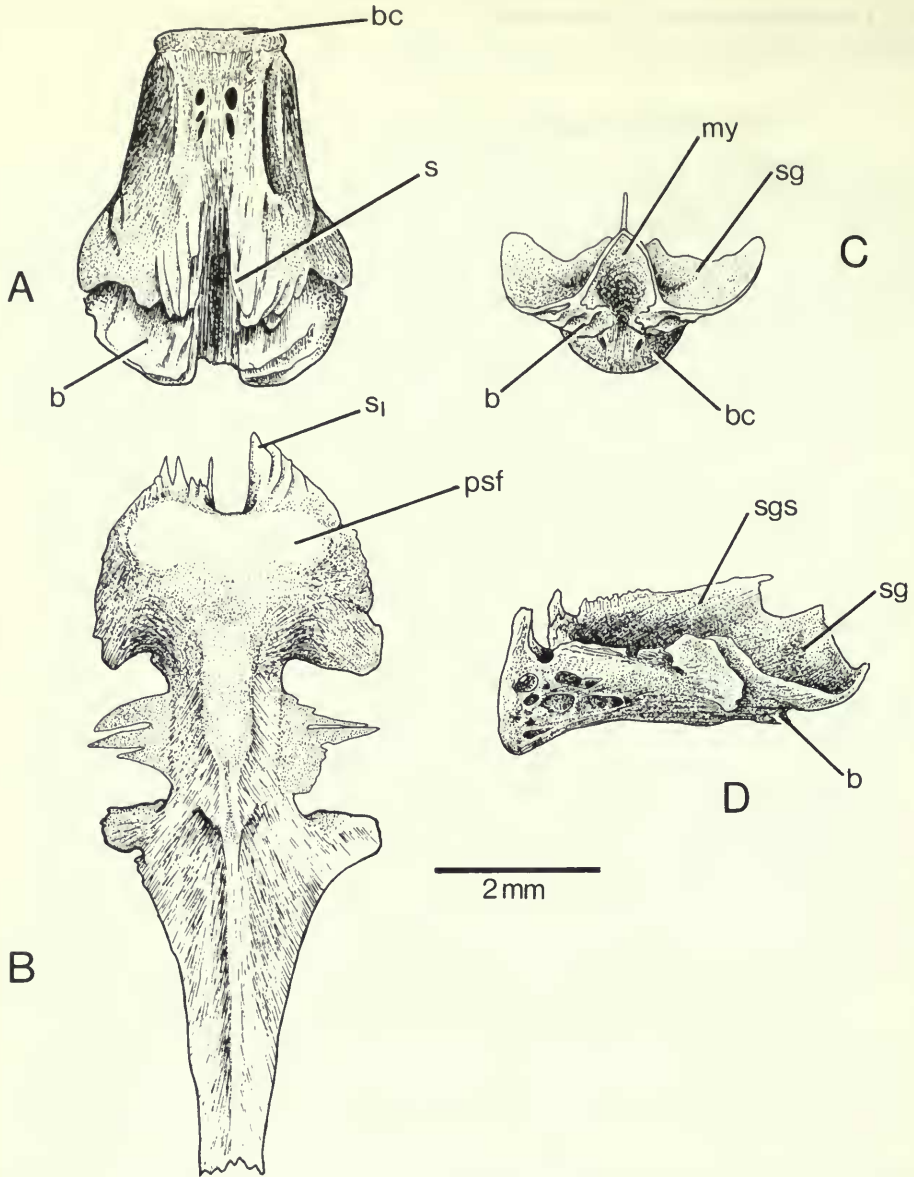


Fig. 2 *Tilapia* type apophysis (*Sarotherodon mossambicus*) disarticulated to show shape and inter-relationships of the bones. A. Basioccipital, ventral view. B. Parasphenoid (posterior part), in ventral view. C. Basioccipital, anterior view. D. Basioccipital in right lateral view.

The basioccipital also plays no part in the formation of the apophyseal body, but it does act as a posteriorly placed buttress to the articular surface; the parasphenoid and basioccipital meet in a strongly developed, interdigitating suture immediately behind the apophysis (see Fig. 1B).

The articular surface (Fig. 1A) is flat and expansive, triangular or subovate in outline, and not clearly divided into left and right facets (except in the specimen of *T. microdon* examined where there is a low median ridge partly dividing the surface).

This compound description is based on the apophysis as seen in specimens of *Tylochromis jentinki* (the type species), *T. polylepis*, *T. microdon* and *T. banguelensis*.

Structurally, the *Tylochromis* apophyseal type is the simplest encountered among the African Cichlidae. It would seem to represent an early stage in the evolution of an upper pharyngeal apophysis from the presumed ancestral one in which the upper pharyngeal bones merely abutted against the parasphenoid.

Identical apophyseal structure and virtually identical apophyseal morphology are found in the genera *Etroplus* (India and Sri Lanka) and *Paretroplus* (Malagasy). A structurally very similar apophysis is also found in at least some members of the Labridae (e.g. *Coris*), although in these fishes its gross morphology is quite unlike that in the cichlids.

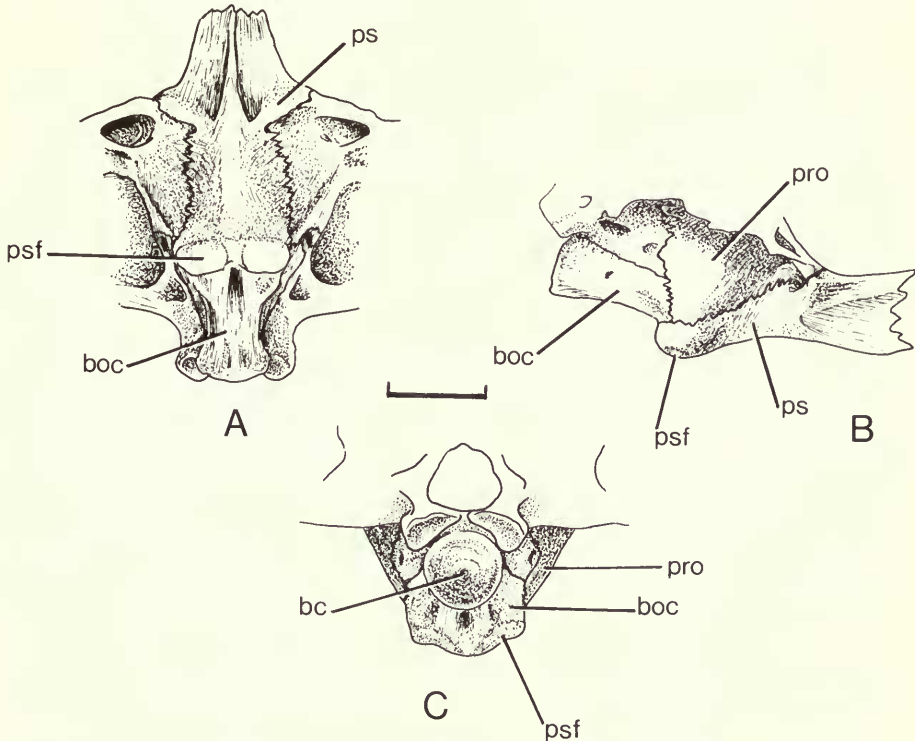


Fig. 3 *Sarotherodon shiranus*. Apophysis in A: Ventral view. B. Right lateral view. C. Posterior view. Scale = 5 mm.

### The *Tilapia* type (Figs 2 & 3)

This apophyseal type differs from *Tylochromis* mainly in having a definite prootic contribution to its lateral walls (which are, indeed, formed mainly from that bone) and in having the basioccipital extending further forward so that it contributes to the body of the apophysis as well as to the support of its articular surface. The latter is, however, still formed entirely from a thickened area of the parasphenoid which caps the ventral margins of the prootic and basioccipital contribution to the side walls; the anterior wall is formed from the parasphenoid alone. No part of the prootic or of the basioccipital extends ventrally to the level of the articular surface laterally or posteriorly.

In all but *Sarotherodon niloticus* of the ten *Tilapia* and *Sarotherodon* species examined, the basioccipital forms approximately the posterior third of the lateral apophyseal wall; in *S. niloticus* it contributes somewhat less than a third, but it still forms the posterior wall and does partly overlie the posterior part of the articular surface.

Since the basioccipital overlies the parasphenoid there is some appositional contact between the bones; their principal area of contact is, however, through a deep, vertically aligned suture

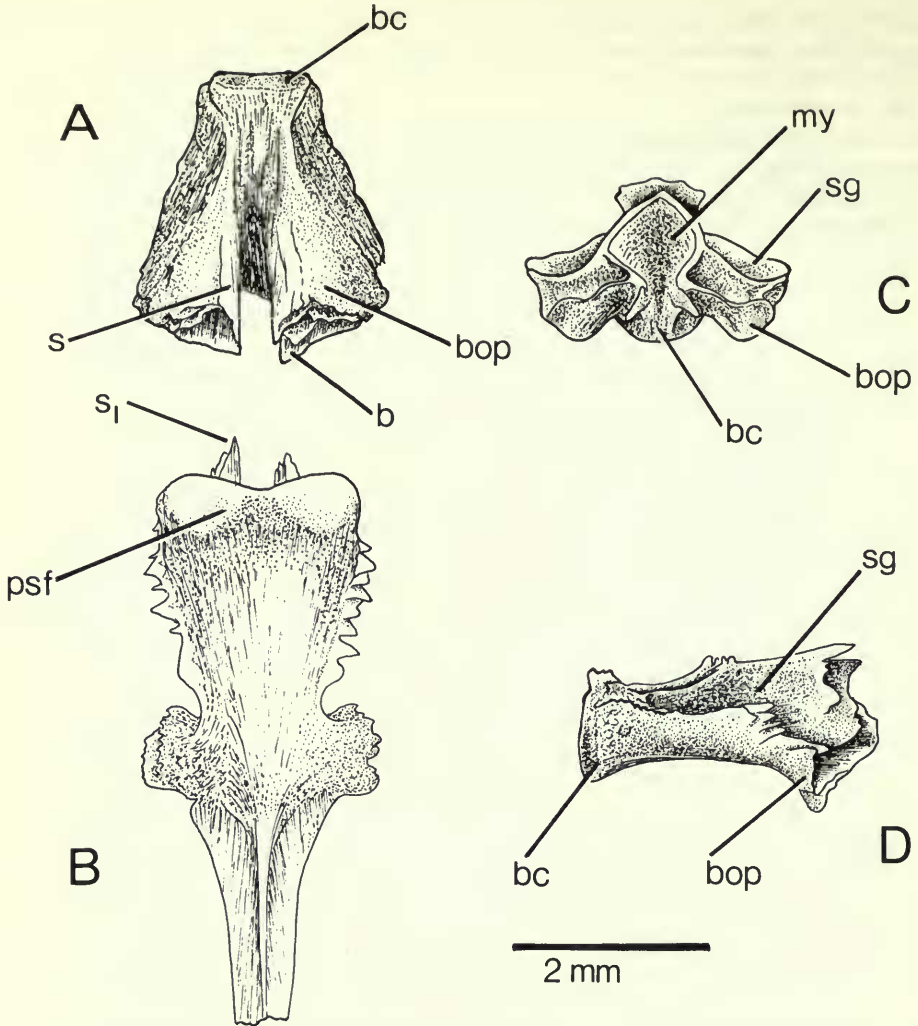


Fig. 4 *Tropheus* type apophysis (*Tropheus moorii*) disarticulated to show shape and interrelationships of the bones. A. Basioccipital, ventral view. B. Parasphenoid (posterior part) in ventral view. C. Basioccipital, anterior view, inclined slightly upwards. D. Basioccipital, right lateral view.

situated immediately behind the body of the apophysis (Fig. 2, s and s<sub>1</sub>). That part of the basioccipital overlying the parasphenoid (the anterior portion of the saccular groove of each side) is not noticeably produced into a pair of ventrally directed processes (cf. the *Tropheus* and *Haplochromis* types).

The articular surface on the parasphenoid is distinctly subdivided by a low medial ridge into two, near-circular facets.

This compound description of the *Tilapia* type apophysis is based on the structure as seen in *Tilapia zillii*, *T. guineensis*, *T. sparrmanii* (the type species), *Sarotherodon mossambicus*, *S. esculentus*, *S. variabilis*, *S. niloticus*, *S. shiranus*, *S. squamipinnis* and *S. tanganicae*.

#### The *Tropheus* type (Figs 4 & 8)

In general, the body of the typical *Tropheus* type apophysis is more inflated than that of the *Tilapia* type. The articular surface, like that in the *Tilapia* type, is formed entirely, or almost entirely, from the parasphenoid.

The body of the apophysis differs from that in the *Tilapia* type in having a greater basioccipital contribution to its side wall (often as much as half), in having a greater area of the articular surface (parasphenoid) overlain by the basioccipital, and by having the ventral margins of the basioccipital contribution to the apophysis almost, or actually reaching the level of the articular surface on the parasphenoid (which is relatively thinner than in the *Tilapia* type). Occasionally the prootic may reach that level as well.

No specimen I have examined has the ventral tip of the prootic wall incorporated into the articular surface, but posteriorly the ventral margins of the anterior basioccipital processes are often somewhat inflated and appear to form part of that surface (albeit a small and narrow part). Presumably it was this latter feature that led Trewavas to consider that *Tropheus moorii* had a *Haplochromis* type of apophysis (Trewavas *in litt.*, quoted by Burchard & Wickler, 1965; also see p. 308).

It is difficult to determine whether these small inflated areas of the basioccipital are functionally part of the articular surface. In many cases, however, the tip of the basioccipital is so orientated that it could not subserve that function. In others, dissections have shown that the upper pharyngeal bones cannot be moved far enough posteriorly or posterolaterally to contact the facet-like surface. Certainly the situation differs from that in a *Haplochromis* type apophysis where the basioccipital facets provide a significant (or even major) part of the articular surface. For the *Tropheus* type all that can be said with certainty is that the parasphenoid provides the major articulatory surface, and that the principal function of the basioccipital is to provide a foundation and a buttress for the expanded articular part of the parasphenoid.

As in the *Tilapia* type of apophysis, the basioccipital portion of the apophysis is derived from the anterior part of the floor to the saccular grooves (Fig. 4). In the *Tropheus* type this area is noticeably thickened, is spongy and is produced ventrally on each side to form a pair of slender projections (Fig. 4D). Contact between the basioccipital and parasphenoid is effected through the apposition of these processes with the upper side of the expanded articular surface of the parasphenoid, and through a vertical suture on either side of the myodomal groove. This sutural contact begins immediately above the articular surface (i.e. within the myodome) and extends for a short distance behind it. The area of appositional contact between the bones is quite extensive, covering about one half of the articular region anteroposteriorly, and about one third of its width on either side. The middle third is not overlain by the basioccipital, and forms the floor of the myodome posteriorly.

The articular surface of the parasphenoid is formed from relatively thick bone and generally has two subcircular or elliptical facets separated medially by either an elevated or a depressed area of variable width.

This description is based mainly on the apophyseal structure in *Tropheus moorii*, but is representative of many other species.

### The *Haplochromis* type (Figs 5 & 17)

As compared with the other types, the *Haplochromis* apophysis represents the ultimate stage in basioccipital involvement, both in the articular surface and in the body of the apophysis itself.

This structural involvement stems mainly from the increased development of the paired processes (Fig. 5D) on the anteroventral region of the basioccipital. The contribution of the basioccipital to the lateral walls of the apophysis differs little in the two types; it is usually somewhat greater in the *Haplochromis* type.

The principal difference between the *Tropheus* and *Haplochromis* apophyseal types is the nature of the articular surface. Whereas in the *Tropheus* type the expanded articular area of the parasphenoid completely or almost completely underlies the anterior end of the basioccipital, in a *Haplochromis* type most of the ventral face of the basioccipital process on each side is exposed. The bone thus becomes a major contributor to the articular surface, the parasphenoid contribution being restricted to the anterior and, generally, the posteromedial parts. The ventral face of each basioccipital process is, relatively speaking, so enlarged that the parasphenoid surface is still overlain by a substantial area of basioccipital and thus there is a considerable area of appositional contact between the two bones, an area larger, indeed, than that in the *Tropheus* type. Sutural

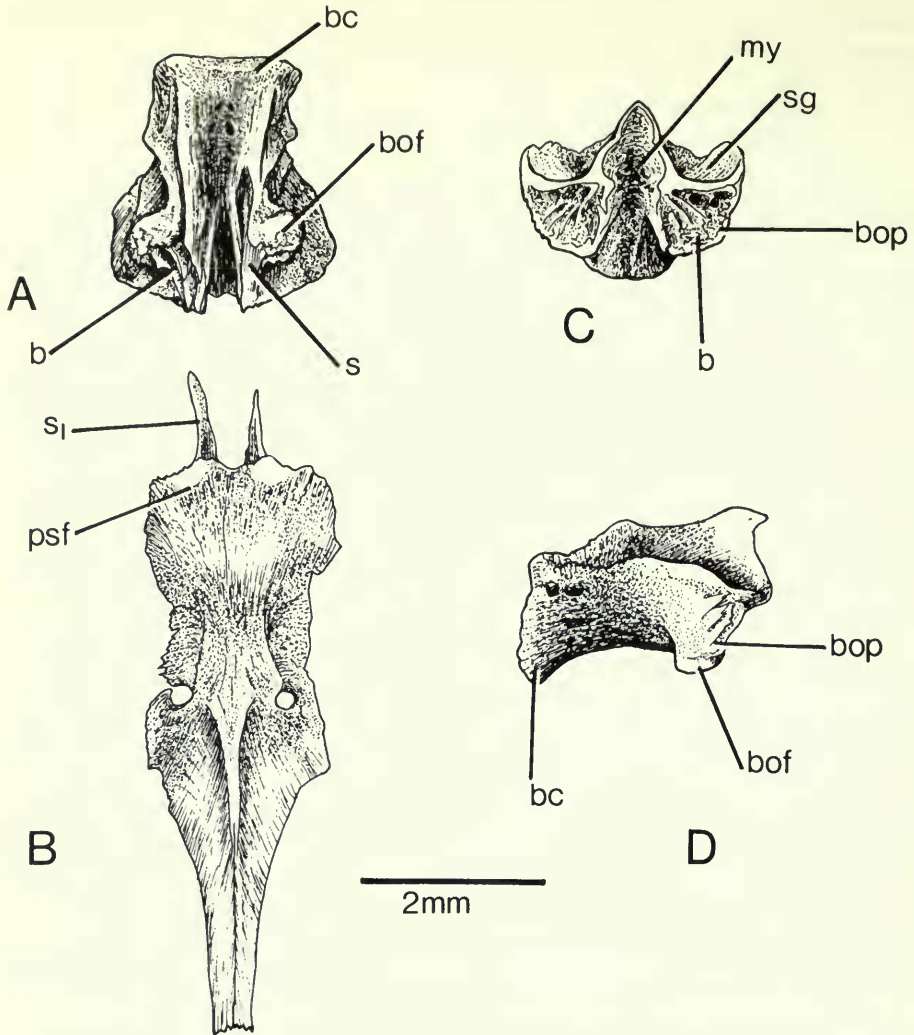


Fig. 5 *Haplochromis* type apophysis (*Haplochromis xenognathus*). A. Basioccipital, ventral view. B. Parasphenoid (posterior part) in ventral view. C. Basioccipital, anterior view, inclined slightly upwards. D. Basioccipital, in right lateral view.

contact between these bones, as in *Tropheus*, occurs below and posterior to the articular surface; it is relatively more extensive in many of the *Haplochromis* types I have examined.

Because the basioccipital invades the articular surface, the posterolateral margins of the parasphenoid are indented to accommodate the basioccipital facets. Posteromedially, the parasphenoid may extend between the facets, but when these are large and expanded medially the parasphenoid is excluded. A laterally indented parasphenoid articular surface is characteristic of a *Haplochromis* type apophysis, and is not seen in those *Tropheus* type apophyses where a part of the basioccipital extends to the level of the articular surface as a pseudofacet.

There is considerable variation in the shape of the articular area as a whole, and also in the shape of its constituent facets. The entire apophyseal structure varies in shape from the inflated, near hemispherical, to the well-circumscribed truncated-conical.

This description is based on several *Haplochromis* species (including the type *H. obliquidens*) representing many different trophic specializations (see Greenwood, 1974).



## Discussion

Except for the *Tylochromis* type, all categories of apophyseal form and structure show slight departures from the modal conditions described above. The deviant forms will be discussed below when considering the distribution of apophyseal types amongst the cichlid genera of Africa.

Looked at from a developmental point of view, the four apophyseal types seem to form a continuous series, with the *Tylochromis* type as the basic one (see p. 299) and the *Haplochromis* type as the most derived form. The principal change involved in this transition series is an increased involvement of the basioccipital, both in the body of the apophysis and in its articular surface. However, I can find no characters which might argue against the possibility of the *Tropheus* type representing a 'regressional' trend from the *Haplochromis* condition rather than a 'progressive' one from the *Tilapia* type.

The value of the apophysis as an indicator of phyletic relationships will be discussed later (p. 321).

## A review of apophyseal structure in the African cichlid genera

Regan's opinion (1920 : 34) that the structure of the apophysis is the 'character of most importance in classification' referred to its value in providing a 'natural arrangement' of the genera which he defined mainly on the basis of oral and pharyngeal dentition (see Regan, 1920, 1921 & 1922).

The recognition of four rather than two apophyseal types necessitates a review of the apophysis in all cichlid genera as a first step towards re-evaluating its significance in cichlid phylogeny. The review which follows must be considered a preliminary one since skeletal material was not available for all species of every genus (especially those Lake Malawi species referred to the genus *Haplochromis*), nor for some of the fluviatile and crater-lake species of West Africa. The preliminary nature of this analysis was also enforced by the fact that it was rarely possible to examine more than one or two specimens of a species, and then only over a limited size range. Ontogenetic studies could well provide valuable information on the problem of the *Tropheus* apophysis and its relationship to the *Haplochromis* type (see p. 322).

Wherever possible I have examined a specimen of the generic type species; such specimens are indicated thus †. Also, wherever possible, I have utilized or at least examined the skeletal preparations used by Regan (1920, 1921 & 1922). Many of these are now in a poor state of preservation; where this is so, I have used newly prepared material instead.

Where, on the basis of its apophyseal structure, a species is now considered to belong to a group other than that in which it was placed by Regan, it is noted thus \*.

The neurocranial length (NcL), measured directly from the tip of the vomer to the posterior margin of the basioccipital, is given for all skulls examined.

A list of the material studied, quoting museum register numbers, or other cataloguing notations, is available in the Fish Section and the General Library of the British Museum (Nat. Hist.).

Since Regan's paper (1920) on the Tanganyika genera was published, Poll (1946 & 1956) has carried out two major revisions of the fishes from that lake. As a result several of Regan's genera have been sunk in synonymy, others subdivided and new genera erected. Because Poll does not take apophyseal characters into account, and because I am reviewing Regan's grouping of the taxa on these characters, I shall use Regan's nomenclature and classification, noting where relevant the subsequent taxonomic history of the taxon; where possible, however, Poll's new genera are described. For the same reasons I shall not use the revised taxonomy introduced for some species by Liem & Stewart (1976). This action must not be taken to infer my rejection of these workers' results nor as an implied criticism of them. A critical commentary on generic limits is beyond the scope of this paper.

For Lake Malawi I have used the classification and nomenclature proposed by Trewavas (1935). Trewavas followed Regan's (1921) grouping save for a few species which she transferred from the *Tilapia* to the *Haplochromis* group, and two genera (*Otopharynx* and *Cyrtocara*) which she synonymized with *Haplochromis*.

With a few exceptions, such as *Hemichromis*, *Pelmatochromis* (*sensu* Regan, 1922), *Chilotilapia* and *Tylochromis*, the entirely or predominantly fluviatile genera are not covered in this review.

## Lake Tanganyika

*TYLOCHROMIS* type (p. 299)

*Tylochromis polylepis* (Blgr.); NcL: 31 mm.

The apophysis does not depart in any significant way from that of the other *Tylochromis* species examined.

*TILAPIA* type (p. 301)

1 † *Sarotherodon tanganicae* (Günther); NcL: 34 mm.

This, the type species of Regan's (1920) genus *Neotilapia*, was placed in *Tilapia* by Poll (1956), but should now be included in the genus *Sarotherodon* as defined by Trewavas (1973a). Its apophysis is of a typical *Tilapia* type.

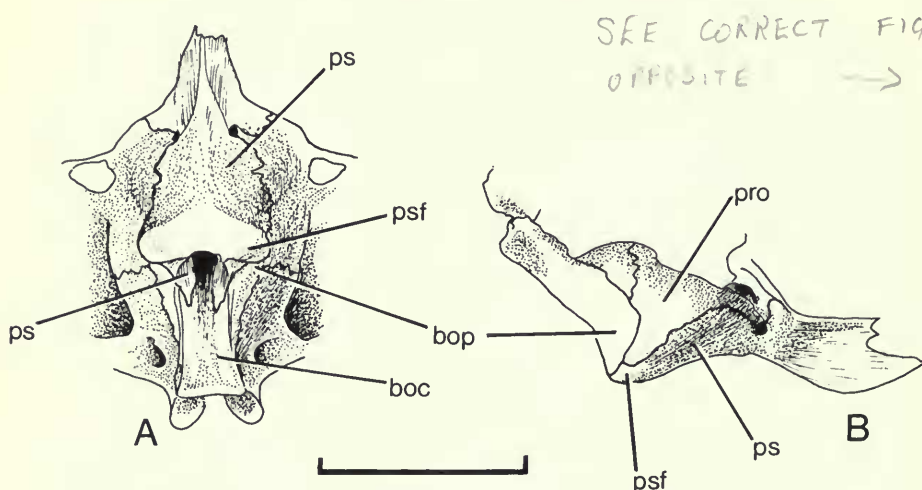


Fig. 6 *Boulengerochromis microlepis*. Apophysis in A: Ventral and B: Right lateral view. Scale = 5 mm.

2 † *Boulengerochromis microlepis* (Blgr.); NcL: 37 mm; Fig. 6.

The apophysis differs from the modal *Tilapia* type (p. 301) only in having a slightly thinner articular area of the parasphenoid; neither the prootic nor the basioccipital reaches the level of the articular surface, and both bones are capped by the parasphenoid in a typical *Tilapia* fashion.

3 † *Cyphotilapia frontosus* (Blgr.); NcL: 42 mm.

The apophysis is virtually identical with that in *Boulengerochromis microlepis*.

4 *Simochromis dardennii* (Blgr.); NcL: 40 and 48 mm; Fig. 7A & B.

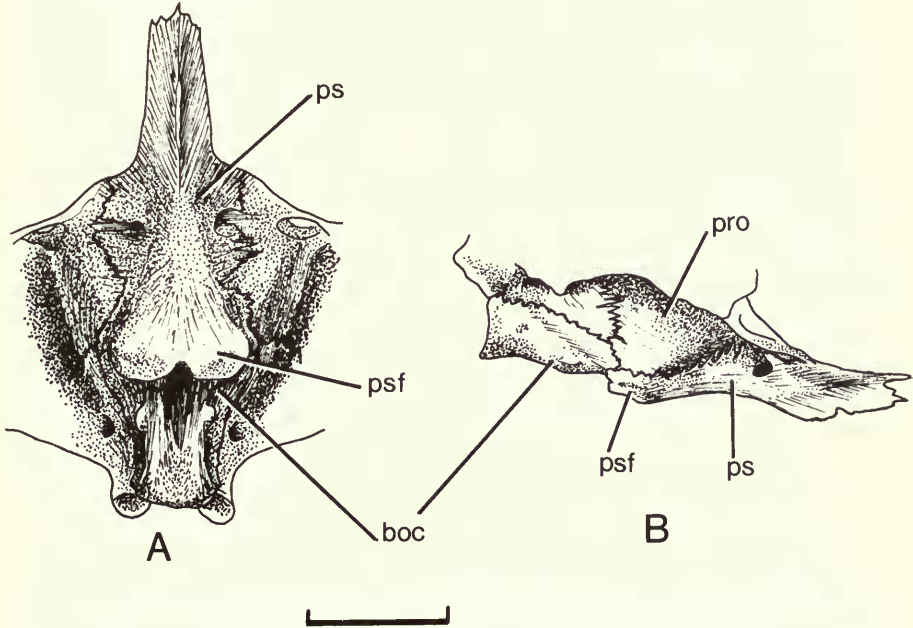
The apophysis is very similar to that in *Boulengerochromis* and *Cyphotilapia*, although the basioccipital forms rather more of the lateral walls in the former species.

The other species of *Simochromis* examined have an apophyseal structure and form approaching the modal *Tropheus* type (see p. 310).

5 † *Petrochromis polyodon* Blgr.; NcL: 23 and 33 mm.

In this species the apophysis could be classified either as a modified *Tilapia* or as a modified *Tropheus* type. The parasphenoid articular surface is relatively thinner than in the *Tilapia* type, the basioccipital contributes almost half of each lateral wall, and there are a pair of ventrally directed prominences on the anterior part of the basioccipital (see *Tropheus* type, p. 302). However, unlike the typical *Tropheus* condition, the basioccipital and prootic are capped ventrally by the parasphenoid in the characteristic *Tilapia* fashion, and do not reach the level of the articular surface.

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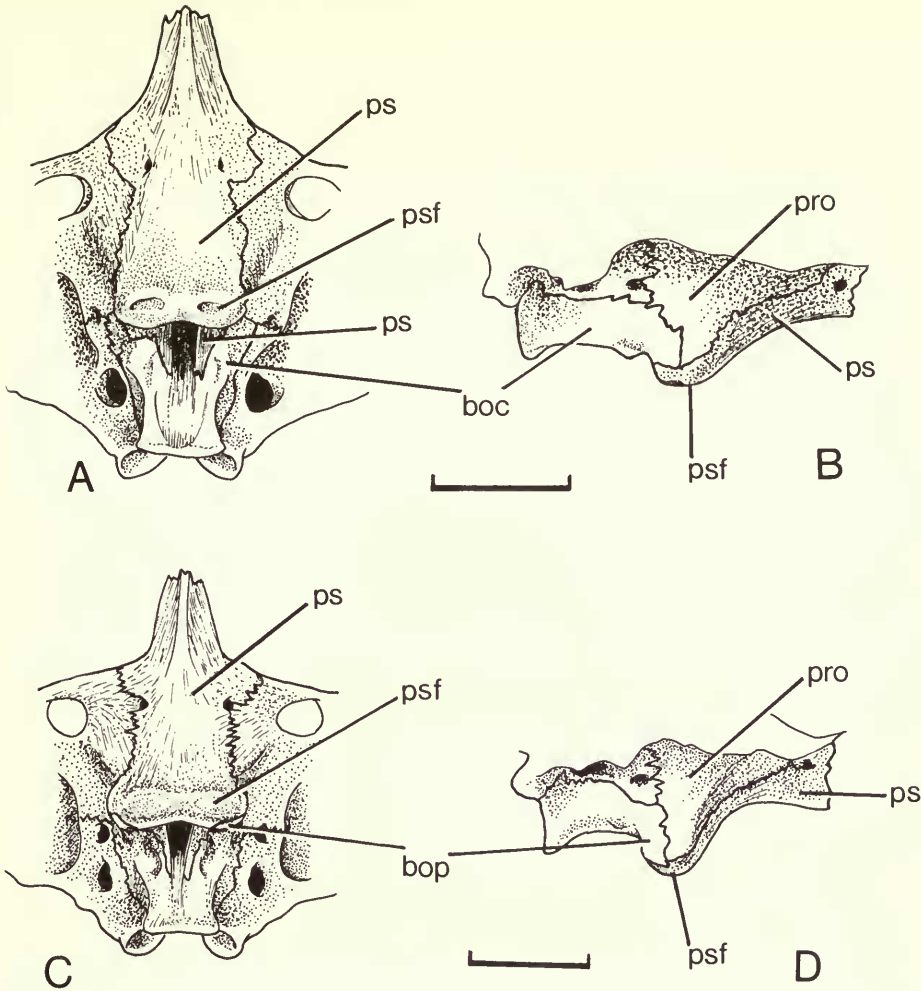


Fig. 7 A and B. *Simochromis dardennii*, apophysis in ventral and right lateral views respectively. C and D. *Simochromis diagramma*, apophysis in ventral and right lateral views respectively. Scale = 5 mm.

### **TROPHEUS** type (p. 302)

Except for those taxa indicated by an asterisk, all the species now placed in this category were previously included by Regan (1920) in his *Tilapia* group. Asterisked species were formerly in the *Haplochromis* group. No annotation after a species indicates that it has a typical *Tropheus* type apophysis (see p. 302).

1 † *Asprotilapia leptura* Blgr.; NcL: 17 mm.

The entire apophysis is greatly inflated, but retains a typical *Tropheus* structure.

2 \*† *Aulanocranus dewindti* (Blgr.); NcL: 21 mm.

Apophysis typical structurally, but inflated.

3 † *Cardiopharynx schoutedeni* Poll; NcL: 27 mm.

4 † *Cunningtonia longiventralis* Blgr.; NcL: 23 mm.

5 a† *Cyathopharynx grandoculis* (Blgr.); NcL: 21 mm.

The basioccipital and the prootic extend ventrally to the level of the parasphenoidal articular surface, but do not contribute to it.

*b* *Cyathopharynx furcifer* (Blgr.); NcL: 29 mm.

The prootic and basioccipital do not quite reach the level of the articular surface, but are not capped by the parasphenoid as in a typical *Tilapia* apophysis (see p. 301).

Poll (1946) synonymized these two species; *C. grandoculis*, the type of the genus, is the junior synonym.

6 \*† *Ectodus descampsii* Blgr.; NcL: 20 mm.

The basioccipital extends ventrally to the level of the parasphenoidal articular surface, but does not contribute to it.

7 \*† *Enantiopus melanogenys* Blgr.; NcL: 22 mm.

Although placed by Regan (1920) in the *Haplochromis* group, the apophysis is of a modal *Tropheus* type. The specimen examined by Regan is poorly prepared and preserved, but nevertheless its *Tropheus*-like apophyseal features are still apparent; a newly prepared specimen confirms this.

Poll (1956) synonymized *Enantiopus* with *Xenotilapia*, which genus has a *Haplochromis* type of apophysis. The other *Enantiopus* species I have examined (*E. boulengeri* (Poll)) does have a *Haplochromis* type of apophysis (see p. 313, under *Xenotilapia*); see also *Stappersia singularis*, page 312, a species now considered to be a junior synonym of *E. ochrogenys* (Poll, 1956).

8 a† *Limnochromis auritus* (Blgr.); NcL: 19 mm.

*b* *L. leptosoma* (Blgr.); NcL: 17 mm.

*c* *L. otostigma* Regan; NcL: 16 mm.

Poll & Thys van den Audenaerde (1974) erected the genus *Triglachromis* for this species.

*d* *L. pfefferi* (Blgr.); NcL: 20 mm.

Poll (1974) placed this species in the genus *Haplochromis* but made no reference to the nature of its pharyngeal apophysis.

9 † *Limnotilapia dardennii* (Blgr.); NcL: 33 mm.

10 a† *Ophthalmotilapia boops* (Blgr.), From a dissection; specimen: 77 mm SL.

*b* *O. ventralis* (Blgr.); NcL: 17 mm.

The apophysis is identical in both species. Poll (1956) erected the genus *Ophthalmochromis* for *Ophthalmotilapia ventralis*.

11 † *Perissodus microlepis* Blgr.; NcL: 20 mm.

See Liem & Stewart (1976).

12 † *Tropheus moorii* Blgr.; NcL: 18, *c.* 21 and 22 mm. Figs 4 & 8.

In two of the three specimens examined, the basioccipital reaches the level of the parasphenoid articular surface on one side but does not contribute to it. It was probably these specimens that led Trewavas to write '... the structure of the pharyngeal apophysis in *Tropheus* was one of Regan's mistakes; it is of the *Haplochromis*-type ...' (quoted *in litt.* by Burchard & Wickler, 1965). In my opinion, however, the entire structure of the apophysis in this specimen is not of the *Haplochromis* type, and the basioccipital tip does not form an articular facet as it would (and bilaterally too) in a true *Haplochromis* apophysis.

The third specimen does not have its basioccipital process extending so far ventrally and its articular surface could not be mistaken for that of a *Haplochromis* type.

13 \*† *Xenochromis hecqui* Blgr.; NcL: 50 mm.

Liem and Stewart (1976) have synonymized this genus with *Perissodus*.

The following species have an apophyseal structure that departs from the modal *Tropheus* type but which could be considered a modification of it.

1 \*† *Haplotaxodon microlepis* Blgr.; NcL: 37 mm.

Regan (1920) was probably misled into placing this genus in his *Haplochromis* group because of the expanded ventral tips to the basioccipital processes. These lie posterolaterally to the parasphenoid articular surface and not within an embayment of the parasphenoid (as do the basioccipital facets in the *Haplochromis* apophyseal type; see p. 304). Furthermore, what appears to be a facet formed on each expanded basioccipital tip actually slopes steeply away from the

parasphenoid articular surface, does not therefore contribute to it, and is not contacted by the upper pharyngeal bone of its side (at least in dried skeletons and preserved whole specimens).

The apophysis in *Bathybates ferox* (here treated as being of the *Haplochromis* type, see p. 310) resembles that in *Haplotaxodon*. But, the extent to which the basioccipital contributes to the lateral and posterolateral walls of the apophysis in *Haplotaxodon* is greater than in *Bathybates*. In this respect it approaches the *Haplochromis* condition more closely than it does *Tropheus* one.

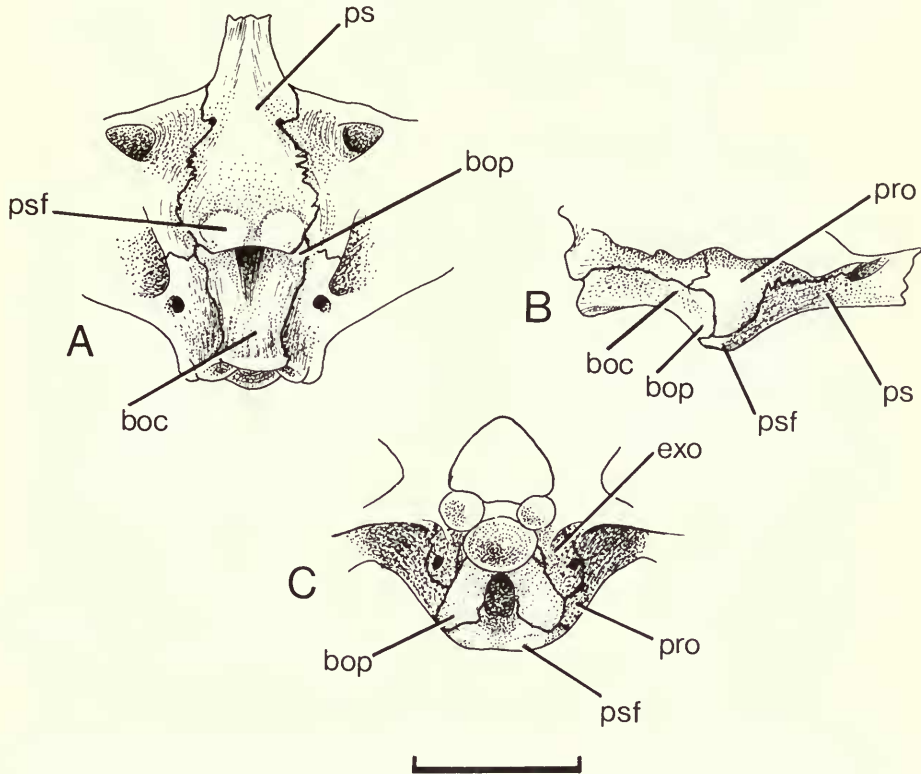


Fig. 8 *Tropheus moorii*. Apophysis in A: Ventral, B: Right lateral and C: Posterior views. Scale = 5 mm.

2 \*† *Hemibates stenosoma* (Blgr.); NcL: 36 mm. Fig. 9.

In this species there is, on each side, a small circular and clearly circumscribed facet developed on the posterolateral part of the basioccipital contribution to the apophyseal wall. The facet abuts on the posterolateral margin of the parasphenoid, which is not, however, indented to receive it (as it would in a typical *Haplochromis* apophysis); its surface is inclined slightly upwards and away from the plane of the parasphenoidal articular surface.

From a dry skull one certainly gets the impression that the upper pharyngeal bones could slide across these basioccipital 'facets'. Their angle and direction might then serve to accentuate any anteroposterior rocking action imparted to the bones as they are moved across the apophysis. However, a dissection reveals that the pharyngeal bones cannot be retracted sufficiently far posteriorly for the 'facet' to serve as such, and also that the paired dorsal aorta of each side actually runs across it. No muscles or ligaments are attached to the 'facet', and so its origin and function remain unknown.

Apophyseal morphology and structure in *Hemibates* are some of the most unusual so far encountered amongst the Lake Tanganyika Cichlidae. I have included *Hemibates* in the modified

*Tropheus* category only because its basic apophyseal structure, in particular the relationship of the parasphenoid and basioccipital, is nearer that of the modal *Tropheus* type than of the modal *Haplochromis* condition. (See also *Haplochromis euchilus*, p. 316.)

3 \*† *Plecodus paradoxus* Blgr.; NcL: 19 and 38 mm.

The apophysis is very like that of *Haplotaxodon*; in the smaller specimen examined, however, there is no facet-like surface developed on the basioccipital. Again, dissections show that the upper pharyngeal bones articulate only with the parasphenoid.

Liem & Stewart (1976) place *Plecodus* in synonymy with *Perissodus*.

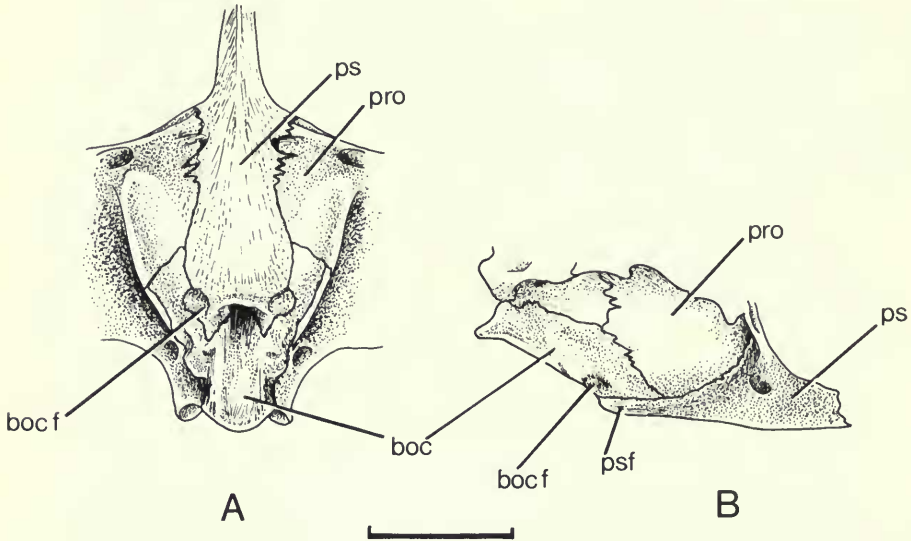


Fig. 9 *Hemibates stenosoma*. Apophysis in A: Ventral and B: Right lateral views. Scale = 5 mm.

4 † *Lobochilotes labiatus* Blgr.; NcL: 21, 32, 57 mm. Fig. 10.

The basioccipital contribution to the apophysis is very like that in *Simochromis diagramma* (see below); the relative size of the facet-like surfaces differs in the three specimens examined, but is always small.

5 a † *Simochromis diagramma* Günth.; NcL: 22 and 30 mm; Fig. 7C & D.

As in several other species with a *Tropheus* type apophysis, the basioccipital in *S. diagramma* reaches the level of the parasphenoidal articular surface posterolaterally. *Simochromis diagramma* differs, however, in having the ventral tip of each basioccipital process somewhat more expanded and thus facet-like. The position and size of each 'facet' suggests that, unlike the other *Tropheus* type species, the facets in *S. diagramma* may form part of the articular surface. In this sense the apophysis is *Haplochromis*-like, but its overall structure is more like that of the modal *Tropheus* type.

b *S. babaulti* Pellegrin; NcL: 15 mm.

The apophysis is nearer the *Tropheus* type than is that of the *S. diagramma* specimens examined; the basioccipital 'facet' is developed unilaterally, and is smaller than in *S. diagramma*.

The entire apophysis in both *S. diagramma* and *S. babaulti* is more inflated than it is in *S. dardennii* (here considered to be of the *Tilapia* type).

#### HAPLOCHROMIS type (p. 303)

1 a † *Bathybates ferox* Blgr.; NcL: 26 and 80 mm; Fig. 11.

In many respects the apophysis of the smaller of the two specimens could be classified in the *Tropheus* group. The basioccipital, which forms about half the lateral wall of the apophysis,



extends ventrally to the level of the parasphenoidal articular surface and lies adjacent to the entire lateral aspect of that surface (which is not indented to receive the basioccipital). That part of the basioccipital adjacent to the parasphenoid is somewhat inflated, and its ventral surface is flattened to form a facet-like region which continues the surface of the parasphenoid articular area posterolaterally. Unlike the typical *Haplochromis* condition, these facet-like areas of the basioccipital are not sharply demarcated from the overlying body of the bone. It is the seemingly continuous articular surface between the parasphenoid medially and the basioccipital laterally that most clearly distinguishes the apophyseal surface in a small *B. ferox* skull from that in a larger (38 mm NcL) skull of *Plecodus paradoxus* (here treated as a modified *Tropheus* type; see p. 310). In other words, the basioccipital in *P. paradoxus* does not contribute to the articular surface, whereas in *B. ferox* it does appear to do so.

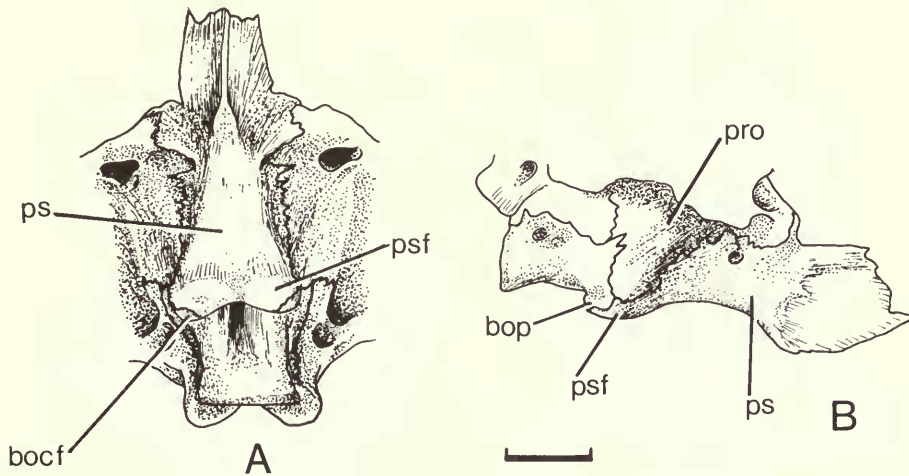


Fig. 10 *Lobochilotes labiatus*. Apophysis in A: Ventral and B: Right lateral views. Scale = 5 mm.

The apophysis in the smaller specimen of *B. ferox*, when compared with that from a larger fish, provides a good example of the rather blurred demarcation between the *Haplochromis* and *Tropheus* apophyseal types. In the larger skull (80 mm NcL) the apophysis is almost typically *Haplochromis*-like, with large and clearly demarcated basioccipital facets formed from the ventral face of each process. The parasphenoid, however, is not indented to receive the facets as is usual in an apophysis of the *Haplochromis* type.

*b B. minor* Blgr.; NcL: 40 mm. Fig. 12.

The basioccipital facets are much more clearly differentiated in this species, are larger, and make the apophysis a typical *Haplochromis* one.

2 † *Callochromis macrops* (Blgr.); NcL: 26 mm.

The basioccipital facets are smaller than is usual in most apophyses of the *Haplochromis* type, but otherwise the apophysis is typical for that group.

3 † *Eretmodus cyanostictus* Blgr.; NcL: 15 mm.

A typical *Haplochromis* apophysis in which the basioccipital facets are large and contribute to slightly more than half the area of the articular surface.

4 † *Grammatotria lemairii* Blgr.; NcL: 44 mm.

A typical *Haplochromis* apophysis, but one with elongate and narrow basioccipital facets (cf. *Stappersia singularis* and *Xenotilapia* spp.).

5 *Haplochromis burtoni* (Günth.); NcL: 14 mm.

6 *Haplochromis horii* (Günth.); NcL: 28 mm.

7 † *Julidochromis ornatus* Blgr.; NcL: 14 mm.

Structurally the apophysis is of the *Haplochromis* type and has large basioccipital facets, but the entire body is flatter and broader than is usual in that group.

8 a † *Lamprologus congolensis* Schilthuis; NcL: 14 mm.

The posterior part of the apophysis is typically *Haplochromis*-like, but the prootic section is greatly inflated. The basioccipital facets are large and clearly demarcated.

b *L. lemairii* Blgr.; NcL: 37 mm.

A typical *Haplochromis* apophysis.

9 † *Leptochromis calliurus* (Blgr.); NcL: 20 mm.

The apophysis is squat and broad, but otherwise is typical.

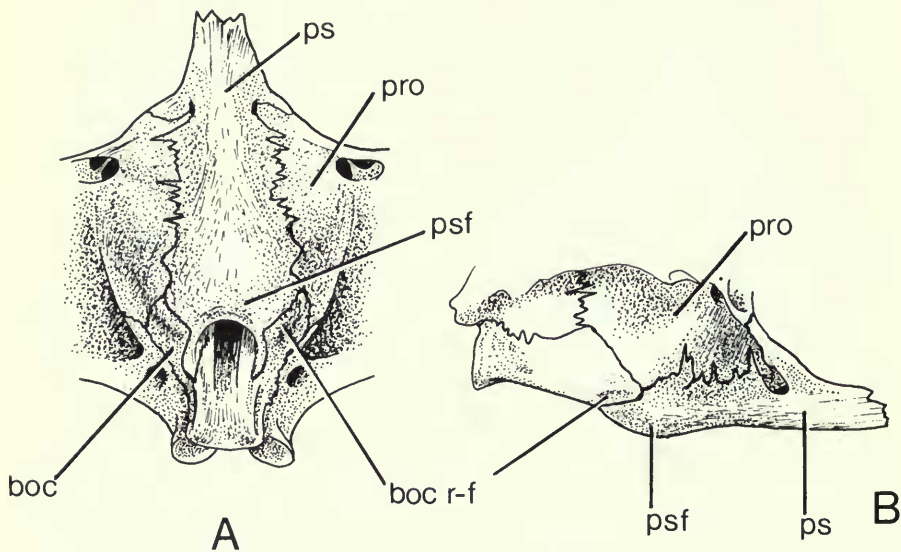


Fig. 11 *Bathybates ferox*. Apophysis in a skull 26 mm long. A: Ventral and B: Right lateral views. Scale = 5 mm.

10 † *Parectodus lestradei* Poll; NcL: 18 mm.

The basioccipital facets are small and, unlike the condition in a typical *Haplochromis* apophysis, are not clearly demarcated from the overlying body of the bone. However, since the parasphenoidal part of the articular surface is indented to receive the basioccipital facets, and because the antero-ventral part of the basioccipital is clearly produced into a pair of ventrally directed processes (whose distal surfaces form the facets) the apophysis must be considered structurally of the *Haplochromis* and not of the *Tropheus* type. The presence of functional basioccipital facets in the articular surface of the apophysis reinforces this conclusion.

Poll (1956) placed the genus *Parectodus* in synonymy with *Xenotilapia* (see p. 313).

11 † *Stappersia singularis* Blgr.; partial dissection of holotype, 76 mm SL.

As far as I can tell from a partial dissection, the apophysis is of a *Haplochromis* type, but has elongate and narrow basioccipital facets.

The apophysis in a similar-sized specimen of *Enantiopus ochrogenys*, the species with which *S. singularis* is now synonymized (see below), is definitely a *Haplochromis* type, with narrow and elongate basioccipital facets.

Poll (1946) synonymized *S. singularis* with *Enantiopus ochrogenys* Blgr., 1914. Later (1956), he considered *Enantiopus* to be a junior synonym of *Xenotilapia*. It will be recalled that the type

species of *Enantiopus*, *E. melanogenys*, has a *Tropheus* apophysis (see p. 308) but in *Xenotilapia* it is of the *Haplochromis* type (see below).

12 † *Telmatochromis temporalis* Blgr.; NcL: 14 mm.

13 a † *Trematocara marginatum* Blgr.; NcL: 30 mm.

b *T. unimaculatum* Blgr.; NcL: ca 28 mm.

Both species have a greatly inflated apophysis; the basioccipital facets form slightly more than half the articular surface.

14 a † *Xenotilapia sima* Blgr.; NcL: 25 mm.

The apophysis is structurally of the *Haplochromis* type, but has long and narrow basioccipital facets.

b *X. ornatipinnis* Blgr.; NcL: 21 mm.

Apophysis as in *X. sima*.

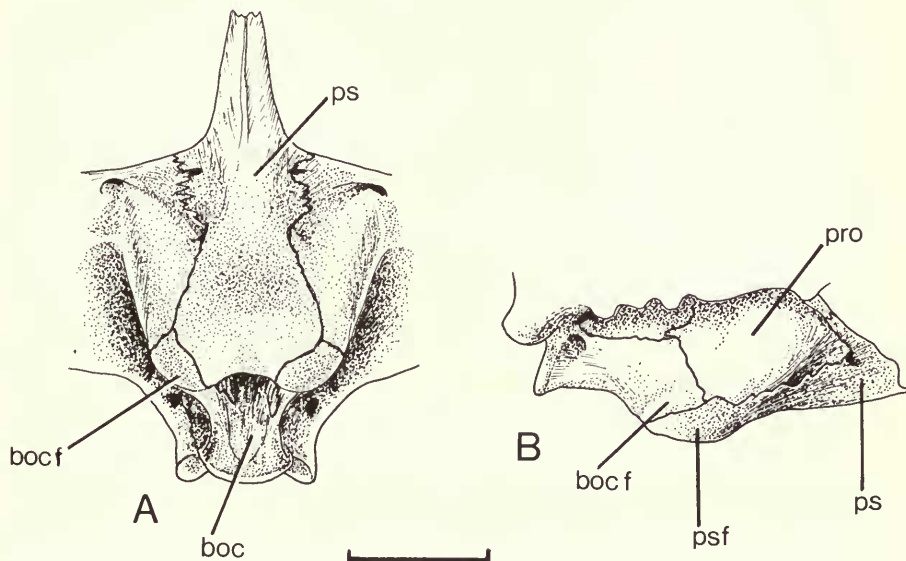


Fig. 12 *Bathybatés minor*. Apophysis in a skull 40 mm long. A: Ventral and B: Right lateral views. Scale = 5 mm.

c *X. boulengeri* (Poll); NcL: 26 mm.

Apophysis as in *X. sima*. Originally this species was placed in the genus *Enantiopus*, a genus which Poll (1956) later synonymized with *Xenotilapia*. The type species of *Enantiopus* has a *Tropheus* type of apophysis (see *E. melanogenys*, p. 308).

The genus *Parectodus* (see p. 312) has also been synonymized with *Xenotilapia* (see Poll, 1956).

## Lake Malawi

Trewavas (1935 : 69) considered all the endemic genera of Lake Malawi to be members of Regan's *Haplochromis* apophyseal group.

In an earlier paper, Regan (1921) had classified *Corematodus* and *Hemitilapia* in his *Tilapia* group, and described the apophysis in *Otopharynx* and *Chilotilapia* as being formed by the parasphenoid and prootic only, an apparently unique apophyseal form otherwise found only in *Chilochromis* from the Congo drainage basin (Regan, 1922; see also p. 320 below). Trewavas (1935) synonymized *Otopharynx* with *Haplochromis* (considering it to have a *Haplochromis* type

apophysis) but retained *Chilotilapia* as a genus because of its characteristic jaw structure and dentition; its apophysis she identified as being of the *Haplochromis* type. Trewavas retained *Corematodus* and *Hemitilapia* as distinct genera, also on the basis of their jaw structure and dentition, and again considered the apophysis to be *Haplochromis*-like.

I have examined the apophysis in all these disputed taxa, as well as in at least one species of the other endemic genera. Regrettably it has not been possible to study skeletal preparations of all the so-called *Haplochromis* species in Lake Malawi. Those that are available will be considered below. Even from this small sample it is clear that not all conform to the modal *Haplochromis* type described on page 303, and that there is, in this respect, greater variation than amongst the *Haplochromis* of Lake Victoria.

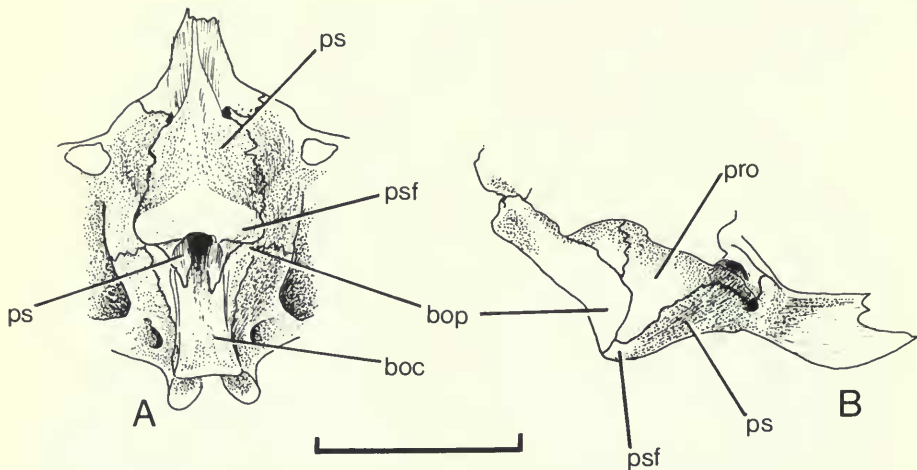


Fig. 13 *Haplochromis triaenodon*. Apophysis in A: Ventral and B: Right lateral views. Scale = 5 mm.

#### **TILAPIA** type (p. 301)

Skeletal preparations are available for only two of the five endemic *Sarotherodon* species (viz. *S. shiranus* (Blgr.) and *S. squamipinnis* (Günth.)). Both have a *Tilapia* type apophysis with, in *S. shiranus* (Fig. 3) the basioccipital contributing from a third to a quarter of the lateral wall, but in *S. squamipinnis* rather less than a quarter.

#### **TROPHEUS** type (p. 302)

The occurrence of this apophyseal type amongst Malawi cichlids has not, of course, been recorded previously (see p. 313 above).

The zoogeographical implications of its presence in Lake Malawi cannot be evaluated until more is known about the phylogenetic history of the *Tropheus* apophysis. If, as seems possible, a *Tropheus* type apophysis is merely a modification of the *Haplochromis* type, then it could have evolved several times over, and from different ancestral stocks within the *Haplochromis* lineage. In that case no great significance can be attached to the presence of a *Tropheus* apophyseal type in both Lakes Malawi and Tanganyika, but not apparently in Lake Victoria (nor from the species of Lakes Rudolf, Edward, George, Kivu and Albert; personal observations based on adequate samples only from Lake Rudolf).

The same restrictions apply to the interpretation of the similar apophyseal morphology in *Haplochromis euchilus* of Lake Malawi and *Hemibates stenosoma* of Lake Tanganyika (see below, p. 316). In this case, the condition found in *Haplochromis euchilus* is nearer the *Haplochromis* type, but the two species could be taken to represent a structural-morphological series linking the modal *Haplochromis* condition with the modal *Tropheus* one.

- 1 † *Cynotilapia afra* (Günth.); NcL: 15 mm (two specimens, one an alizarin preparation). The apophysis is virtually identical with that in *Tropheus moorii* of Lake Tanganyika (see p. 308).
- 2 *Haplochromis triaenodon* Trewavas; NcL: 27 mm. Fig. 13. This species has a non-inflated *Tropheus* type of apophysis in which the basioccipital does not quite extend ventrally to the level of the parasphenoid articular surface. However, it does lie lateral to the parasphenoid so that it is not capped by that bone as it would be in a typical *Tilapia* apophysis.
- 3 *Pseudotropheus macrophthalmus* Ahl; NcL: 18 mm (and a dissection of the apophysis in a specimen 97 mm SL; the skull is from a fish of c. 74 mm SL). See Fig. 14.

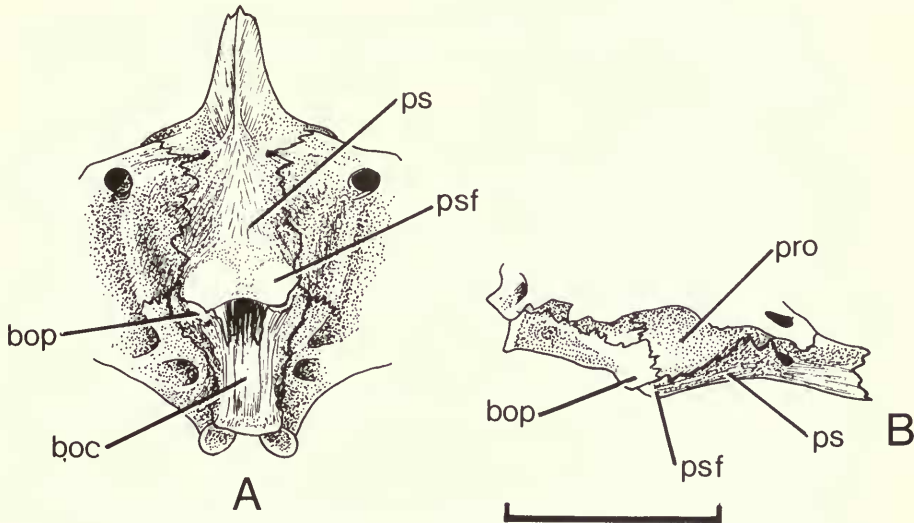


Fig. 14 *Pseudotropheus macrophthalmus*. Apophysis in A: Ventral and B: Right lateral views. Scale = 5 mm.

Both specimens have a somewhat inflated apophysis which closely approximates to that in the *Simochromis babaulti* specimens (*ex* Lake Tanganyika) described on page 310. The basioccipital reaches ventrally to the level of the parasphenoid articular surface, and in one specimen the bone shows what appears to be an ill-defined, facet-like area on one side (see Fig. 14A, right side of apophysis). However, as in *S. babaulti*, the extent to which the facet might contribute to the articular surface, and the general structure of the apophysis, are nearer the *Tropheus* than the *Haplochromis* type.

The other *Pseudotropheus* species examined will be considered below (under *Haplochromis* type).

Three other species should perhaps be reviewed at this point although in some respects their apophyses could be considered as modifications of the *Haplochromis* type.

1 *Haplochromis auromarginatus* (type species of Regan's (1921) genus *Otopharynx*).

The apophysis resembles that in the Tanganyika species *Simochromis diagramma* (see p. 310 and Fig. 7C & D). However, in *H. auromarginatus* (NcL: 42 mm) the basioccipital does not extend quite so far ventrally and the tips of its ventral processes (on either side of the parasphenoid) are more prominent than in *S. diagramma*. Despite the facet-like appearance of these basioccipital tips they clearly cannot serve as such because of their dorsal position relative to the parasphenoid articular surface.

It is difficult to determine whether this apophyseal form should be classified as a modified *Tropheus* type or as a modified *Haplochromis* one. Taken in its entirety, and with especial regard to the position of the basioccipital 'facets' (see above), it would seem to have more affinity with the

*Tropheus* type. I cannot understand how Regan (1921) thought that the articular surface was formed from the prootic and parasphenoid only (see p. 313 above).

The second species included by Regan in *Otopharynx* (*O. selenurus*) has a typical *Haplochromis* type apophysis; together with *O. auromarginatus*, it was transferred to the genus *Haplochromis* by Trewavas (1935).

2 *Haplochromis chrysonotus* (Blgr.); NcL: 21 and 23 mm.

The apophysis is of the inflated *Tropheus* type with the basioccipital reaching the level of the parasphenoidal articular surface. In one specimen (23 mm NcL) the anteroventral tips of the basioccipital are slightly expanded, but neither forms a true facet and the parasphenoid is not indented to receive them.

3 *Haplochromis guentheri* Regan; NcL: 28 mm.

The apophysis is damaged in the only skeleton available. However, its general appearance suggests that the nature of the articular surface is intermediate between that of the two *H. chrysonotus* specimens described above.

### **HAPLOCHROMIS** type (p. 303)

I have examined the apophysis in at least one specimen of all the endemic genera<sup>1</sup> reviewed by Trewavas (1935), except for the monotypic *Christyella* (= *Gephyrochromis*, see Trewavas, 1946) and *Aristochromis*, which are represented by holotypes only.

In general, I would agree with Trewavas' view that these taxa have a *Haplochromis* type of apophysis, although some do deviate from the modal condition.

Before discussing these deviant species, mention must be made of the *Pseudotropheus*, other than *P. macrophthalmus* (p. 315; Fig. 14) I have examined, the latter having a *Tropheus* type apophysis.

*Pseudotropheus williamsi* (the type species) has a *Haplochromis* type apophysis, albeit one with rather small basioccipital facets; *Pseudotropheus zebra*, on the other hand, has a typical *Haplochromis* apophysis (see Fig. 15).

Thus, in these three species (*P. macrophthalmus*, *P. williamsi* and *P. zebra*, in that order) the structural-morphological gap between the *Tropheus* and *Haplochromis* apophyseal types is bridged. That the species are members of a monophyletic assemblage seems certain when their shared dental and other cranial specializations are taken into account.

Returning now to those species in which the apophysis is not of the modal *Haplochromis* type. All show certain affinities with the *Tropheus* type but cannot be included in that category if the whole apophyseal structure is considered.

*Haplochromis annectens* (Regan) has very small basioccipital facets which contribute only to the posterolateral angles of the articular surface, and have noticeably domed, rather than flattened or gently rounded articulatory surfaces. Since, however, the anteroventral end of the basioccipital (on which the facets are developed) is clearly produced into a pair of ventrally directed processes of the *Haplochromis* type, and because the facets contribute to the articular surface, the apophysis is essentially a *Haplochromis* one. The two skulls studied have neurocranial lengths of 27 and 33 mm respectively.

*Haplochromis euchilus* Trewavas. (Fig. 16). The apophysis in a skull 23 mm long very closely approaches that in the Tanganyika genus *Hemibates* (see p. 309). The basioccipital reaches the level of the parasphenoid but the ventral tips of its processes, like those in *Hemibates*, are not expanded into flat facets. Instead, each tip is slightly expanded and somewhat rounded. In the skull of *H. euchilus* examined, the left facet is rather more elongate than is the right one, and is somewhat less clearly circumscribed.

As compared with *Hemibates*, the apophysis in *Haplochromis euchilus* is very slightly less inflated, and the basioccipital 'facets' are relatively larger and provide a nearly continuous plane with the parasphenoidal facet. (In *Hemibates* the basioccipital 'facets' slope dorsally away from

<sup>1</sup> i.e. *Petrotilapia*, *Pseudotropheus*, *Labeotropheus*, *Cyathochromis*, *Melanochromis*, *Genyochromis*, *Labidochromis*, *Corematodus*, *Docimodus*, *Lethrinops*, *Chilotilapia*, *Hemitilapia*, *Rhamphochromis*, *Trematocranus*, *Aulonocara*, *Diplotaxodon*, *Gephyrochromis* and *Lichnochromis*.

the plane of the major facet of the parasphenoid.) In this latter feature the apophysis of *H. euchilus* approaches the *Haplochromis* condition more closely than does that of *Hemibates*. However, it is still difficult to classify the *H. euchilus* type more precisely than as 'modified *Haplochromis*'.

Its close resemblance to the apophysis in *Hemibates* from Lake Tanganyika is of particular interest but for the moment it cannot be given any particular phylogenetic significance (see p. 321).

*Corematodus taeniatus* Trewavas, has the anteroventral margin of the basioccipital greatly produced ventrally into a pair of pillar-like processes (at least in a skull 34 mm long). The anterior margin of each 'pillar' reaches the level of the parasphenoid articular surface (which is indented laterally to receive the process), but its entire facet-like ventral surface slopes so steeply upwards and away from the parasphenoid that the 'facet' cannot contribute to the articular surface for the pharyngeal bones.

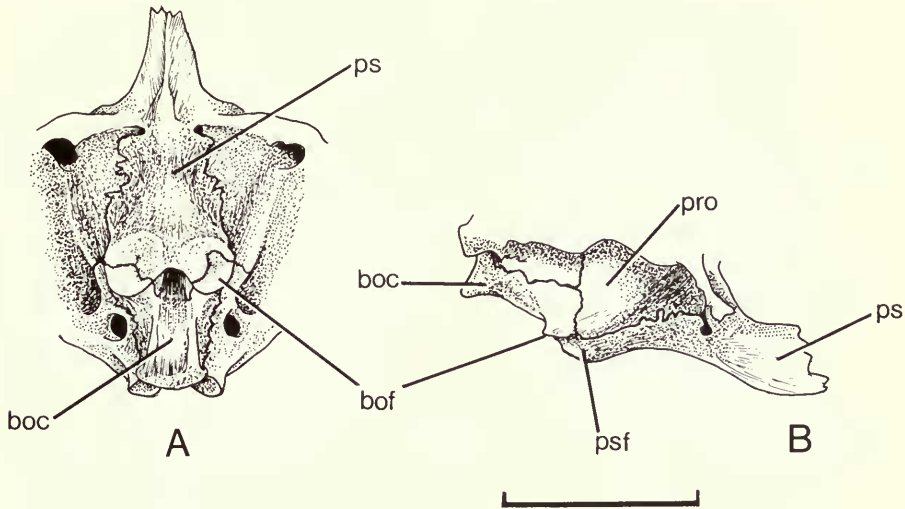


Fig. 15 *Pseudotropheus zebra*. Apophysis in A: Ventral and B: Right lateral views. Scale = 5 mm.

However, the morphology of the basioccipital, and its contribution to the overall structure of the apophysis, is that of a *Haplochromis* and not a *Tropheus* type. The apophysis in the only available skull (NcL: 31 mm) of *C. shiranus* Blgr. (type species of the genus) is very like that of *C. taeniatus* except that the facet-like tips of the basioccipital processes are not so expansive.

*Hemitilapia oxyrhynchus* Blgr., type and only species of the genus, has an apophyseal form (in skull 25 mm NcL) resembling that in *Corematodus*, but it is broader and lower, with the result that the basioccipital processes appear shorter and less pillar-like, and the 'facets' are less well demarcated.

Seemingly these four species should be included in the category of 'modified *Haplochromis* type apophysis', a category to which *H. chrysonotus* and *H. guentheri* (see p. 316) should also perhaps be added. Additional material of the two latter species must be studied to determine their apophyseal relationships more precisely.

Apart from the few *Haplochromis* species discussed above, and those with a *Tropheus* or *Tropheus*-like apophysis (see p. 314), all the other Malawi species of that genus which I have examined<sup>1</sup> do have a typical *Haplochromis* apophysis. There is of course, some variation in its gross morphology, and in the shape and relative size of the basioccipital facets; the latter are relatively larger in species with enlarged pharyngeal bones, a well-known phenomenon in species of that genus and its close relatives (see Trewavas, 1935 : 70; Greenwood, 1965 & 1974 : 75, fig. 44).

<sup>1</sup> *Haplochromis lateristriga*, *H. livingstoni*, *H. macrostoma*, *H. melanotus*, *H. nototaenia*, *H. orthognathus*, *H. placodon*, *H. polystigma*, *H. rhoadesi*, *H. similis*, *H. sphaerodon*, *H. strigatus*, *H. tetraspilus*, *H. venustus*, *H. woodi*.

## Lake Victoria

The two endemic *Sarotherodon* species (*S. variabilis* (Blgr.) and *S. esculentus* (Graham)) have typical *Tilapia*-type apophyses and require no further comment.

Far more noteworthy is the fact that none of the currently described *Haplochromis* species (Fig. 17), nor the related monotypic genera (see Greenwood, 1974), has an apophyseal structure or form that departs significantly from the modal *Haplochromis* type (a generalization which perforce excludes the 19 species (out of a total of 105) for which no skeletal material is available, and the large number of known species still awaiting description).

As in the Lake Malawi *Haplochromis* there is some variation in apophyseal shape, and in the relative contribution of the basioccipital facets to the total articular surface (see Greenwood, 1974 : 75).

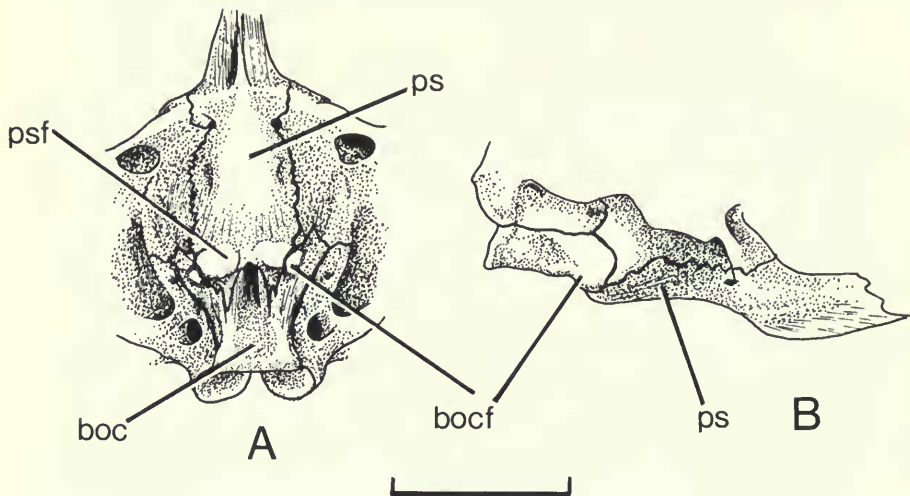


Fig. 16 *Haplochromis euchilus*. Apophysis in A: Ventral and B: Right lateral views. Scale = 5 mm.

## Riverine genera

Although I have examined the apophysis in several fluviatile species of *Haplochromis* and *Serranochromis* (all of which have typical *Haplochromis* type apophyses), detailed comments will be confined to representative species of six genera which have not been discussed so far, viz. *Hemichromis*, *Pelmatochromis* (*sensu lato*, see Thys van den Audenaerde, 1968), *Pseudocrenilabrus*, *Chilotilapia*, *Steatocranus* and *Teleogramma*.

### HEMICHROMIS

I have examined the type species, *H. fasciatus* (Peters), and find, as did Regan (1922), that the apophysis is essentially of the *Haplochromis* type. In a skull 29 mm long, the basioccipital facets are large, the basioccipital itself contributes to almost half the lateral wall of the apophysis, and the anterolateral part of the wall is formed from the prootic. The parasphenoid only contributes to a small anteroventral part of the apophyseal body (and, of course, to the articular surface as well).

In the specimen of *Hemichromis bimaculatus* (Gill) examined (NcL: 17 mm), the pharyngeal bones are slightly enlarged, and many of the pharyngeal teeth, both upper and lower, are coarse and molariform to submolariform. The apophysis, which is a typical *Haplochromis* one, reflects these features in its relatively large basioccipital facets (see Greenwood, 1974 : 75, fig. 44).

### PELMATOCHROMIS

The taxonomic status of this nominal genus is most confused (see Thys van den Audenaerde,



1968, and Trewavas, 1973a). For that reason the species listed below are not grouped in the 'generic' categories proposed by Thys van den Audenaerde (1968).

1 *Pelmatochromis buettikoferi* Steindachner; NcL: 22 mm.

In this, the type species of the genus, the apophysis is somewhat inflated and has a *Tilapia* type structure resembling that in *Cyphotilapia* and *Boulengerochromis* (see p. 306) more closely than the modal type found in *Tilapia* and *Sarotherodon* species.

2 *P. kingsleyae* (Blgr.); NcL: 20, 22 and 29 mm.

The apophysis is relatively tall and has a basic *Tilapia*-type structure except that the articular area of the parasphenoid is relatively thinner, and the basioccipital contributes somewhat more extensively to the lateral walls.

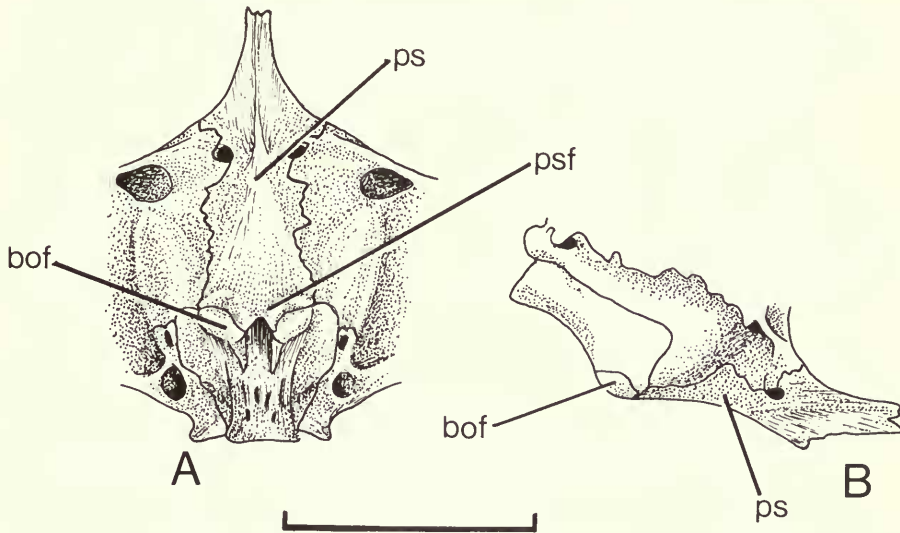


Fig. 17 *Haplochromis obliquidens*. Apophysis in A: Ventral and B: Right lateral views. Scale = 5 mm.

3 *P. batesii* Blgr.; NcL: ca. 20 mm.

Although essentially like that in *P. kingsleyae*, the apophysis in this species differs in having the articular surface of the parasphenoid extending posteriorly beyond the level of its basioccipital buttress, which it thus overlaps slightly.

4 *P. pulcher* Blgr.; NcL: ca 15 mm.

Apart from being a little more inflated and squatter, the apophysis in this species is otherwise like that in *P. kingsleyae*.

5 *P. kribensis* Blgr.; NcL: ca 13 mm.

The apophysis is like that of *P. pulcher*.

6 *P. subocellatus* (Günth.); NcL: ca 15 mm.

The somewhat inflated apophysis is essentially a *Haplochromis*-type structure and thus unlike those in the other species examined. It differs from the modal *Haplochromis* condition in having small basioccipital facets, and a parasphenoidal articular surface that is not indented laterally to receive them.

### **PSEUDOCRENILABRUS**

The status and nomenclature of this genus are discussed by Trewavas (1973b), and its behaviour patterns by Wickler (1963). It was on the basis of its behaviour and certain secondary sexual

features that Wickler (1963) suggested the taxon should be removed from the genus *Haplochromis* in which it was then placed.

1 *Pseudocrenilabrus multicolor* (Schoeller); NcL: 16 mm; skull from a specimen ex Lake Nabugabo, Uganda.

In all respects the apophysis is a typical *Haplochromis* one; it has relatively large basioccipital facets.

2 *P. philander* (Weber); NcL: 23 mm; skull from a specimen ex Umfuluzi river, Kwa-Zulu.

The apophysis is identical with that in *P. multicolor*.

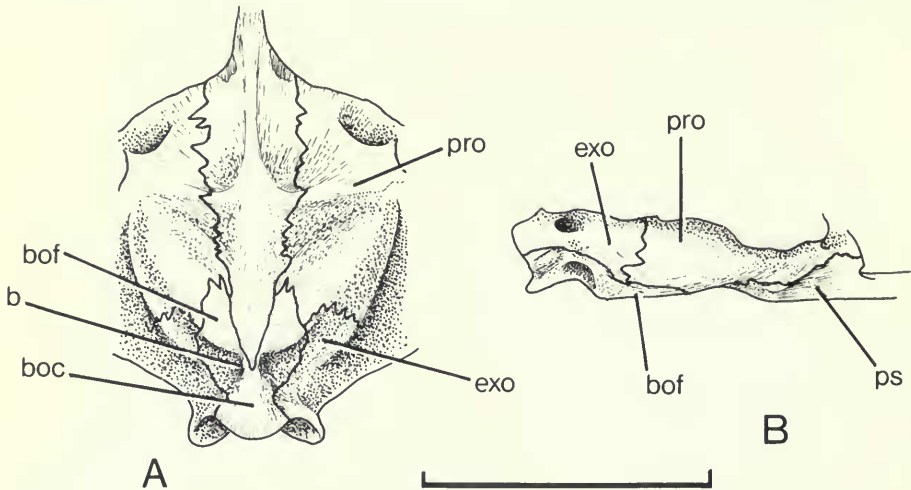


Fig. 18 *Teleogramma gracile*. Apophysis and otic skull region in A: Ventral and B: Right lateral views. Scale = 5 mm.

### CHILOCHROMIS

The apophysis in *Chilochromis duponti* Blgr., the sole representative of the genus, was described as apparently having '... the same structure as in *Otopharynx*' (Regan, 1922). The apophysis in *Otopharynx* Regan, an endemic Lake Malawi taxon, was described as being formed from the parasphenoid and prootic alone, an unusual combination of bones. Trewavas (1935), however, considered that both *Otopharynx auromarginatus*, the type species, and *O. selenurus*, the other species referred to the genus, had apophyses of the *Haplochromis* type (see p. 313).

In my opinion the apophysis of *O. auromarginatus* (see p. 315) is not a typical *Haplochromis* one as Trewavas (1935) thought, but is more like the *Tropheus* type. Thus it was of particular interest to check on the apophyseal structure of *Chilochromis duponti*, a somewhat difficult task since only one specimen, an entire fish, was available for study; the skeleton which Regan (1922) apparently studied cannot be located.

As far as I can tell from a unilateral and partial dissection of the pharyngeal region of this fish, the articular surface of the apophysis is, as Regan (1922) described it, formed from the parasphenoid in the middle and from large prootic facets laterally. The basioccipital seems only to serve as a posterior buttress to the parasphenoid.

If this arrangement of the bones is confirmed in other specimens, then *Chilochromis* has a unique type of apophyseal structure, and one which could be derived from either a *Tylochromis* or a *Tilapia* type (see p. 299 & p. 301).

### STEATOCRANUS

Regan (1922) placed this genus in his *Haplochromis* group, but Roberts & Stewart (1976: 292) note 'Pharyngeal apophysis formed exclusively by parasphenoid bone' (presumably referring, as

did Regan, to the articular surface and not the entire structure); these authors do not indicate which species they examined.

Unfortunately I cannot locate, with certainty, the specimen of *S. gibbiceps* Blgr., that Regan studied; however, there is one fish (1899.6.28:26) in which the gill arches have been removed, and which might be that used by him. The apophysis in this fish (60 mm SL) is basically of the *Tilapia* type and resembles that in *Simochromis dardennii* (see p. 306; Fig. 7A & B).

A specimen of *S. casuarius* Poll (NcL: 15 mm) also has an apophysis of the same type.

### TELEOGRAMMA

Regan (1922) did not include this genus in his review of taxa not restricted to the Great Lakes, nor, as far as I am aware, has its pharyngeal apophysis been described elsewhere.

*Teleogramma gracile* Blgr. (type species of the genus); NcL: 12 mm.

The extraordinarily depressed skull, and greatly inflated otic region, has, as might be expected, led to an equally unusual pharyngeal apophysis (Fig. 18). It is broad and laterally expansive, with the articular surface formed mainly from the enlarged basioccipital facets; the parasphenoidal contribution is reduced to a narrow medial tongue of bone. Thus, the apophysis is essentially of the *Haplochromis* type, albeit the most modified form encountered in this survey.

### Discussion and conclusions

If the structure of the entire pharyngeal apophysis and not just that of its articular surface is taken into account, then Regan's (1920) division of the African genera into *Tilapia* and *Haplochromis* types breaks down. Instead four modal apophyseal types have to be recognized, namely: *Tylochromis*, *Tilapia*, *Tropheus* and *Haplochromis* (see pp. 299–302); a fifth type, *Chilochromis*, may also exist (see p. 320).

Morphologically, the dividing line between the *Tylochromis* and the *Tilapia* types is quite clear cut, despite their structural simplicity. The difference between the *Tilapia* and *Haplochromis* types is even more trenchant because in the latter the basioccipital contributes to the articular surface for the upper pharyngeal bones as well as to the support of that surface (see p. 304).

Problems arise with the *Tropheus* apophyseal type, for although it has a distinctive form in most of the species possessing it, it is structurally intermediate between the *Tilapia* and *Haplochromis* types. Consequently, there are some taxa where the apophysis could be classified as a modified *Tilapia* type or, more frequently, as a modified *Haplochromis* type in which the basioccipital facets are not fully developed.

Apophyseal structure and form in three species of the Lake Tanganyika genus *Simochromis* illustrate this particular difficulty. *Simochromis diagramma* seems almost to have a *Haplochromis* type apophysis (see p. 310), but in *S. babaulti* the apophysis approaches the modal *Tropheus* type (p. 310), whilst in *S. dardennii* it closely approximates to the true *Tilapia* type save for some features (the extent of the basioccipital contribution to the side walls, for example) which are *Tropheus*-like (see p. 306). Thus, on apophyseal structure alone it is impossible to tell whether *Simochromis* evolved from an ancestral species with a *Tilapia*-type apophysis or one with a *Haplochromis* type.

This example, and the one that follows, are particularly instructive because in each the species involved share specialized dental and osteological characters indicative of their respective monophyletic origins. In other words, there can be a considerable range of apophyseal structure within a single phyletic lineage.

In the Lake Malawi genus *Pseudotropheus*, at least one species (*P. macrophthalmus*) has a *Tropheus* type apophysis, while two others have definite *Haplochromis* types (*P. williamsi* and *P. zebra*); see pages 315–316. Here again it is impossible to determine the direction of evolution in apophyseal structure.

It might be stressed that in neither example can any evidence be found to suggest that the 'generic' characters are the results of convergent evolutionary trends.

The structural intermediacy of the *Tropheus* type apophysis poses particular difficulties when attempting to demonstrate the interrelationships of the Lake Tanganyika cichlid flocks. Here,