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THE TAXONOMIC STATUS AND PHYLOGENETIC RELATIONSHIPS OF PSEUDOCRENILABRUS FOWLER (TELEOSTEI, CICHLIDAE)

by

Peter Humphry Greenwood

Various and disparate opinions have been expressed with regard to the phylogenetic affinities of *Pseudocrenilabrus*, a seemingly generalized and primitive haplochromine genus. These views are reconsidered and rejected. Instead, it is suggested that *Pseudocrenilabrus* is a derived and paedomorphic taxon evolved from a generalized haplochromine ancestor such as would be represented amongst extant African cichlids by a species of the genus *Astatotilapia*; for the moment it is not possible to identify a sister group more precisely.

The suggestion that *Pseudocrenilabrus* is a paedomorphic taxon is based on certain osteological and dental features, particularly the reductional trend manifest in the infraorbital bones of its three constituent species.

A new diagnosis and synonomy are provided for the genus, together with notes on its anatomy, osteology and meristic features.
THE TAXONOMIC STATUS AND PHYLOGENETIC RELATIONSHIPS OF PSEUDOCRENILABRUS FOWLER (TELEOSTEI, CICHLIDAE)

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INTRODUCTION

Taken together, the three species constituting the genus Pseudocrenilabrus Fowler (1934) have a broad latitudinal distribution in Africa, from Egypt in the North to the coastal regions of Natal, South Africa, in the South. However, it is only in the southern parts of the range that there is any great longitudinal spread. Here the species P. philander (Weber) extends from coastal Mozambique to the northern parts of the Orange River system in the West. Elsewhere the range of the genus is confined within the limits of 28°-35°E.

The extensive if somewhat disjunct distribution of Pseudocrenilabrus (see Loiselle, 1982a, b) suggests that it might be a lineage of considerable antiquity. Unfortunately that speculation cannot be tested by paleontological evidence since no fossil representatives of the genus have been identified (see Van Couvering, 1982). Indeed, it is very unlikely that any of the diagnostic features of the genus (see p. 4) would be preserved in fossils.

Interestingly, for a cichlid genus, no Pseudocrenilabrus species can be considered truly lacustrine; when populations do occur in any of the major African lakes they are confined to various but usually swampy habitats in or near the lakes' margins (Welcomme, 1969; Greenwood, 1973; Trewavas, 1973; Loiselle, 1982a, b; personal observations). Elsewhere the species occur in the slower flowing parts of rivers, in small lakes and waterbodies, and even in isolated sink-holes (Trewavas, 1936; and references cited above).

As Trewavas (1973) remarked, nowhere has Pseudocrenilabrus given rise to species-flocks. That, perhaps, is not surprising when one considers the essentially nonlacustrine habitats occupied by the three species. More surprising to my mind is the paucity of currently recognized species, especially since the distribution pattern of populations within any one of the two better studied species, P. multicolor (Schoeller) and P. philander, is essentially an allopatric one. However, when these populations are subjected to more detailed studies, particularly those involving a number of morphometric characters and, especially, ethological characteristics, I suspect that several new species will be recognised. In support of that expectation are the observations made in connection with this paper; these seem to indicate that several species are “hidden” under the name philander (Ribbink, pers. comm.), and that the Egyptian, Sudanese and East African samples of P. multicolor were drawn from two, and possibly more species. Similar views have been expressed by Trewavas (1936) and Loiselle (1982a, b).

Further research is also needed on the ecology of the three species, especially on their feeding habits and tolerance ranges for temperature and other abiotic factors. What information we do have on their ecology is admirably summarized by Loiselle (1982a, b).

Aquarium stocks of P. multicolor, possibly descendants of the original wild population imported from Egypt in 1903 (Seegers, pers. comm.), have been the subjects of extensive and detailed ethological research (Reinboth, 1956; Wickler, 1962, 1963, and references therein); some data are also available for the other two species (Ribbink, 1971; Ribbink in Loiselle, 1982b). Indeed, it was an ethologist who first recommended that the species multicolor and philander be removed from Haplochromis (in which genus they were then classified) and recognised as a distinct taxon, which he named Hemihaplochromis (Wickler, 1963).

Wickler’s reasons for recognizing that genus (now treated as a synonym of Pseudocrenilabrus) were based on the breeding behaviour of its species, and the associated colour pattern of the anal fin in males (see p. 3). Those two features led Loiselle (1982b) to add a third species, P. nicholsi (Pellegrin), to the lineage, thus extending its range to include the upper reaches of the Zaire River system.

Currently, four rather disparate views are held on the phylogenetic relationships of Pseudocrenilabrus. Trewavas (1973: 35) referring to P. multicolor and P. philander, P. nicholsi not then being included in the genus, stated that “... In their respective areas they have no close relations ...”, but did not go on to consider what their relationships might be on a broader taxonomic and geographical basis.

Wickler (1963: 91), arguing from the premise that Haplochromis is the “Stammform” of Haplochromis (sensu Regan, 1922; see Greenwood, 1979) believed Pseudocrenilabrus (i.e. his genus Hemihaplochromis) to be the connecting link between those two genera, a phylogenetic relationship not readily described in cladistic terminology.

Van Couvering (1982, Fig. 11) indicated, in a cladogram, that Pseudocrenilabrus is the plesiomorphic sister taxon of Haplochromis (sensu Regan, 1922) and a fossil African taxon Nderechromis (described in her paper). Regretably, nowhere in the text of that paper, nor in the caption to the figure, does Van Couvering give any reasons for this grouping although the derived status accorded to Haplochromis was seemingly based on it having egg-dummies on the anal fin of male fishes (see Wickler, 1963; and below).

Poll (1967: 314), alone amongst the four authors, is at all specific in his choice of the nearest living relative for Pseudocrenilabrus, at least with respect to one of its species, P. philander. In Poll’s view Orthochromis machodi (Poll), then placed in Haplochromis, is “... incontestible voisine et derive de H. philander”.

Unfortunately, none of these authors gives detailed or even broadly comparative arguments for their conclusions, and none apparently took into account more than superficial morphological features (see Greenwood 1984 for a critique of Poll’s conclusions). The present paper is an attempt to remedy those deficiencies and, as a consequence, to reassess both the taxonomic and the phylogenetic status of Pseudocrenilabrus.
MATERIALS AND METHODS

The entire British Museum (Natural History), BMNH, collection of Pseudocrenilabrus was examined, and was supplemented by southern African specimens from the J.L.B Smith Institute of Ichthyology (RUSI) and the Albany Museum (AMG) of Grahamstown, South Africa.

Material used for outgroup comparisons is listed in previous papers (Greenwood, 1979, 1983, 1985, 1987a). Additional material, specially prepared for this paper (i.e. dry skeletons, alizarin and alcian blue transparencies, and specimens dissected to study jaw and branchial muscles) is as follows:

Pseudocrenilabrus philander: Skeletal preparations: Unregistered specimens ex RUSI: 3 from Durban (40, 60 and 80 mm SL); 3 from Bilanhlolo, Natal (50, 52 and 73 mm SL); 5 from Wondergat, Transvaal (60, 81, 85, 92 and 93 mm SL); 4 from Molopo Oog, Transvaal (46, 56, 67 and 73 mm SL); 1 from Augrabies, Orange river, South Africa; 1 from Kuruman, North Western Cape. BMNH: 1 unregistered specimen, collected by G. Bell-Cross, from Mwekera Dam, Kafue river system, Zambia; 1 from 1935.3.20: 12-31, Namibia; 1 from 1966.6.2: 13-22, Durban; 1 from 1937.4.22: 118-127, Upper Zambezi River; 1 from 1984.2.6: 64-79, Kunene River, Namibia.

Alizarin Transparencies: 2 from 1977.6.27: 1424-50, Phongola River; 1 unregistered, from Bell-Cross’ collection ex Mwekera Dam, Kafue River System.

Dissections: 1 from 1906.6.2: 13-22, Durban; 1 from 1935. 3.20: 12-31, Otavifontein, Namibia; 2 unregistered, from RUSI collection, two ex Okavango swamps, Botswana, and the other ex Wondergat, Transvaal.


Astatotilapia burtoni (Günther, 1893): Dissection: BMNH: 1 from 1950.4.1: 2176-2206, Lake Tanganyika.

Unless indicated otherwise in the figure caption, the osteological material illustrated is from unregistered specimens in the RUSI collections. The specimens themselves, however, are marked so as to indicate their use for these illustrations.

The methodology used is that discussed in previous papers (Greenwood, 1979, 1985, 1987a) and in the text below.

It should be borne in mind when reading the section dealing with relationships, that, in previous papers, all authors have used the generic concept of Haplochromis in the sense of Regan (1922), and not in the restricted sense of Greenwood (1979).

Genus Pseudocrenilabrus Fowler

(Only major or revisional papers are included in the following synonymy and list of references.)

Chromis (part) Weber, 1897 (the species C. philander); Schoeller, 1903 (the species C. multicolor).

Paratilapia (part) Hilgendorf, 1902 (the species P. luebberti, now considered a synonym of Pseudocrenilabrus philander, see Trewavas, 1936, and Greenwood, 1984); Hilgendorf, 1903 (the species P. multicolor); Nichols, 1928 (the species P. ventralis).

Tilapia (part) Pellegrin, 1904 (the species T. philander and T. ovalis; for synonymy of this species, see Regan 1922); Boulenger, 1915 (the species T. ovalis only); Gilchrist & Thompson, 1917 (the species T. ovalis only).

Haplochromis (part): Boulenger, 1915 (the species H. moffati [which included H. philander and H. multicolor as synonyms], H. luebberti, and H. strigigena in part, i.e. all the specimens listed, except the type of H. strigigena, which species is now considered to be a synonym of Astatotilapia bloyeti Sauvage, 1883; see Regan, 1922); Regan, 1922 (the species multicolor and moffati; presumably Regan accepted Boulenger’s [1915] synonymy of philander with moffati since the former is not mentioned in his revision); Barnard, 1948; Jackson, 1961 a & b (the species philander only).

Pseudocrenilabrus Fowler, 1934. Type species Pseudocrenilabrus natalensis Fowler, 1934, by original designation and monotypy, a junior subjective synonym of Chromis philander Weber, 1897 (see Trewavas, 1973); Loiselle, 1982 a & b (P. multicolor, P. philander and P. nicholsi); Banister & Bailey, 1979 (the species P. nicholsi).

Hemihaplochromis Wickler, 1963. Type species Chromis multicolor Schoeller, 1903 by original designation (Wickler also included H. philander in this genus). Jubb, 1967 (the species H. philander).

INCLUDED SPECIES

P. philander (Weber, 1897). See page 4 for comments on the use of this specific name, especially the reason for not considering it a junior synonym of Castelnau’s (1861) Chromys moffati. See Greenwood (1984: 213-4) for comments on the named subspecies. P. philander is widely distributed in central and southern Africa, and in Angola and Namibia. It seems likely that this “species” may represent a complex of closely related taxa each of specific rank.

Pseudocrenilabrus multicolor (Schoeller, 1903). Hilgendorf (1903) is often cited as the authority for the name of this species, but Schoeller’s description of the taxon, and use of the name, predate those of Hilgendorf by several weeks. This “species” occurs in Egypt, Sudan, Uganda, Kenya and Tanzania, and it may also represent a complex of closely related species.

Pseudocrenilabrus nicholsi. This species was originally described by Nichols (1928) as Paratilapia ventralis a junior primary homonym of P. ventralis Blgr., 1898, for which Pellegrin (1928) proposed the replacement
name of nicholsi. It is apparently the only member of the genus occurring in the Zaire system, where it has been recorded from the upper reaches at Ankoro (Nichols, 1928) and from the Upemba Lakes (Banister & Bailey, 1979; see also Loiselle, 1982b).

A fourth Pseudocrenilabrus "species" has appeared, from time to time, in the aquarist literature under the name of Hemihaplochromis (or Haplochromis) kirawira. The trivial name is derived from that of a village in Tanzania near the locality where the first specimens were collected. To the best of my knowledge the species has never been described formally, nor have type specimens been preserved. I have examined nine aquarium specimens (BMNH 1981.3.31: 16-24) obtained by Prof. Hans Peters of Tübingen, and can confirm their identity as Pseudocrenilabrus. Pending a species-level revision of both P. philander and P. multicolor, and without detailed information on the live colours of the "kirawira" specimens, I would hesitate to refer them to either taxon, or to confirm that they represent a distinct species. On the information available, they would seem to be nearest East African populations of P. multicolor.

**DISCUSSION:** Like most species of African cichlids described before the publication of Regan's classic paper in 1922, two of the three Pseudocrenilabrus species were, at various times, assigned to a number of different genera, usually the "catch-all" genus current at a particular time (see synonymy above). After the publication of Regan's paper, both P. multicolor and P. philander were classified as Haplochromis, mainly, it would seem, because of their having a Haplochromis-type neurocranial apophysis for the articulation of the upper pharyngeal bones, and their lacking those features that characterize other genera with a similar type of apophysis. At that time the nature of the anal fin markings in male fishes was not given much attention by taxonomists.

It was Wickler (1963) who first recognised that *Haplochromis multicolor* differed from the other *Haplochromis* species (sensu Regan, 1922) both in its breeding behaviour and in adult males lacking well-defined ocellar egg-dummies on the anal fin. In male *H. multicolor* the egg-dummies are in the form of a single, non-ocellar spot, blotch, or crescentic mark, usually red or orange, situated at the posterior tip of the fin (Fig. 1). The differences in the position, size and appearance of the egg-dummy in *H. multicolor* is also associated with a different behaviour pattern in the males’ use of the fin during spawning. In species with ocellar spots, and in those with either a few or many non-ocellar spots, the fin is spread in front of the female; in *Pseudocrenilabrus*, however, the fin is folded, in that way bringing the spot into prominence (see Wickler, 1962, 1963; Trewavas, 1973). Ultimately, however, this spot, like the ocellar egg-dummies in *Haplochromis*, serves to bring the female close to the male’s genital aperture.

On the basis of their having a single, non-ocellar spot on the anal fin, and because of various ethological features shown by *H. multicolor*, Wickler (1963) erected the genus *Hemihaplochromis* for this species and *H. philander*.

Some ten years later, Trewavas (1973: 33-36) showed that the holotype of *Pseudocrenilabrus natalensis*, the type species of Fowler’s (1934) monotypic genus *Pseudocrenilabrus*, is in fact a specimen of Chromis philander Weber, 1897, and thus that Wickler’s *Hemihaplochromis* is a junior subjective synonym of Fowler’s *Pseudocrenilabrus*.

The third species now included in the genus *Pseudocrenilabrus*, *P. nicholsi* (Pellegrin), was originally described by Nichols (1928) as *Paratilapia ventralis*, despite Regan’s (1922) generic revision, and despite Nichols acknowledging the species’ resemblance to two others which Regan had placed in *Haplochromis*. It
would seem from Nichols’ paper (1928: 3) that he found Regan’s classification less easily followed than the one used by Boulenger (1915) in his Catalogue of African Freshwater Fishes, and also that Boulenger’s “... comprehensive use of Paratilapia is certainly a convenience, and the writer is not prepared to restrict that genus to a single Madagascan species as has been done”.

Be that as it may, and with the right disregard for convenience, Loiselle (1982b), recognising the true relationship of Nichols’ species, placed it in Pseudocrenilabrus.

The original description of Chromys moffati Castelnau, 1861 is quite inadequate for the demands of current cichlid taxonomy, neither a type-specimen nor a figure are available, and the measurements given by Castelnau (140 mm and one twice as large) are greater than those for any known species of Pseudocrenilabrus. For those reasons, Trewavas (1936) treated the taxon as a species dubia, and because of the lengths given by Castelnau, thought it was “probably a Tilapia”. Thus, many subsequent workers (and Trewavas, herself) have identified small adult haplochromine cichlids from Kuruman (the type-locality of ‘moffati’) and other parts of southern Africa as *P. philander* (Weber).

Barnard (1948: 458 & 477), however, disagrees with Trewavas, arguing that the maximum length given by Castelnau (i.e. 140 mm) is only slightly greater than that given by Regan as the maximum length (i.e. 120 mm) of specimens in the *P. philander* material he examined. Furthermore, Barnard pointed out that the rounded caudal fin noted for *P. moffati* by Castelnau serves to distinguish the taxon from the only other cichlid (Tilapia sparrmani) known to occur at Kuruman. Thus, in Barnard’s view, the name for the taxon should be *moffati* and not *philander*.

Barnard’s argument is logical, but nevertheless circumstantial in the absence of a type specimen or figure for Castelnau’s species. For that reason I chose to follow Trewavas’ (1936) decision, at least until a thorough species-level revision of the southern African Pseudocrenilabrus populations has been carried out. When that has been done, there may well be grounds for selecting a neotype for the Kuruman population (as a distinct taxonomic entity) thus “resurrecting” the name *moffati* on a sounder basis than is available currently.

### GENERIC DIAGNOSIS

The questions to be considered here are whether or not the single non-behavioural feature currently used to diagnose *Pseudocrenilabrus*, viz. the anal spot in adult males (Fig. 1), can be interpreted as a synapomorphy uniquely shared by the taxon’s three constituent species (and thus indicative of its monophyly), and whether there are other synapomorphies that have not been recognized previously.

Within the mouth-brooding non-tilapiine and non-pelmatochromine cichlids as a whole (using tilapiine and pelmatochromine in the sense of Trewavas, 1983 and of Greenwood, 1987a, respectively) there appear to be at least four principal kinds of anal fin markings that serve as egg-dummies in adult males (see Wickler, 1962; Greenwood, 1979; and Oliver, 1984). These are:

(i) The ocellar type found in *Haplochromis, Astatotilapia, Astatoreochromis*, in all the haplochromine species of Lakes Victoria, Edward, George and Kivu, in some haplochromines from Lake Malawi, in certain Lake Tanganyika species, and in some if not all *Thoracochromis* species (see Figs. 7 & 8 and discussion in Wickler, 1962; Trewavas, 1973; Greenwood, 1979; and Oliver, 1984).

(ii) The one, or a few, simple but well-defined and non-ocellate spots in *Ctenochromis* and numerous Malawi haplochromine species.

(iii) The multi-maculate type characterizing *Serranochromis, Pharyngochromis* and *Chetta* (Greenwood, 1979) in which the spots are small but discrete, cover a large area of the fin, and closely resemble the maculations of the soft dorsal fin.

(iv) The small but distinct spot, blotch or crescentic bar at the tip or posterior margin of the anal fin in *Pseudocrenilabrus* (Fig. 1).

Undoubtedly that classification is over-simplified, despite the very numerous colour photographs now available for a great number of African cichlid species. Photographs can, however, be difficult to interpret, and regrettably few detailed, as opposed to generalized descriptions of anal fin markings have been published.

Assuming, as seems reasonable on the basis of outgroup comparisons within both the Labroidei and the Cichlidae, that the absence of egg-dummies is the pleiomorphic condition, then each of the four listed types represents a derived state, allowing, of course, that apparently similar egg-dummies are homologous and not homoplasic features. The latter problem is seemingly resolved in the case of *Pseudocrenilabrus* by the occurrence in all its species of a congruent apomorphy, namely a reductional trend in the canal bones of the infraorbital series (see pp. 8 – 10). Although reductional trends in the infraorbital series are known from a few other African cichlids (e.g. *Lamprologus, Julidochromis* and *Telmatochromis* [Colombe & Allgayer, 1985], the *Ophthalmotilapia* assemblage [Greenwood, 1983] and *Nanochromis* [Greenwood, 1987a]) those lineages are each characterized by various autapomorphies not found in *Pseudocrenilabrus*, and none has the *Pseudocrenilabrus* type of egg-dummy.

Thus, I would consider the single, non-ocellate and distinctly coloured spot or blotch at the tip of the anal fin in *Pseudocrenilabrus*, together with the reduced infraorbital bone series, to be autapomorphic features diagnostic for the genus and indicative of its monophyly. To these I would add, tentatively, two further features. First, a behavioural one, namely the way in which the male presents the egg-dummy (i.e. the anal fin spot or blotch) to the female. Unlike other cichlids in which markings on that fin are apparently used as egg-dummies, *Pseudocrenilabrus* males fold the anal fin so as to give prominence to the spot, and do not spread the fin as do the other taxa (Wickler, 1963: 91).

The second possible autapomorphy for the genus is the distinctly rounded caudal fin. Judging from extensive outgroup comparisons within the Perciformes, the pleiomorphic condition is that of a truncate, subtruncate or emarginate fin. If, as seems likely, a rounded caudal fin is a derived feature, then it has evolved independently in a few other lineages of African cichlid (e.g. the chiromidotilapiines [Greenwood, 1987a] and the lamprologines [Poll, 1986]). Since *Pseudocrenilabrus* does not seem to share a recent common ancestry with these taxa, (see p. 12 – 13) its occurrence in this genus must represent another independent evolutionary event.
GENERIC DESCRIPTION

This description is based mainly on superficial or readily accessible characters. Other anatomical features, and a more detailed consideration of certain superficial characters, are dealt with in the succeeding section (p.6).

Body-form and general habitus of *Pseudocrenilabrus* are typically of the generalized haplochromine type (Fig. 1), and closely resemble those of *Astatotilapia* (see Greenwood, 1979, 1980); the posterior margin of the caudal fin is distinctly rounded, much more so than in any *Astatotilapia* species.

The neurocranial articulatory apophysis for the upper pharyngeal bones is formed from the parasphenoid medially and the basioccipital on each side; that is, of the *Haplochromis* type (see Greenwood, 1978 & 1987b). The pharyngo-buccal epithelium immediately anterior to the upper pharyngeal bones on each side is developed into a pachydermatous pad, but does not have the visor-like form occurring in chromidotilapiine species (Greenwood, 1987a). The outer-row gill-rakers on the ceratobranchial of the first gill-arch are generally low, stout and cuboidal, but may be somewhat flattened and spade-like; those on the epibranchial are slightly finer, and the lower 1 or 2 on the ceratobranchial are greatly reduced in size. Gill-raker counts on this arch are 6-9+1+1-3. Microbranchiospines are present on the outer face of gill-arches 2-4.

There are from 30-54 teeth in the outer tooth-row of the premaxilla, the number showing a positive correlation with the size of the individual (size range examined 16-95 mm SL), but no obvious interspecific differences were observed. Inner teeth in both jaws are separated from the outer row by a small but usually distinct interspace, and are arranged, sometimes irregularly, in 1 (rarely) or 2 rows anteriorly and anterolaterally, reducing to a single row posterolaterally.

Outer row teeth (Fig. 2), especially in the upper jaw, are an admixture of unequally bicuspid and unicuspied teeth, the former occasionally having the minor cusp reduced to a shoulder rather than a point. There are interspecific differences (usually associated with the maximum size to which individuals of that species grow) in the proportion of uni- and bicuspid teeth, but in all species the posterolateral teeth, either in both jaws or only in the premaxilla, are usually unicuspied and slender. None of the unicuspieds occurring posteriorly in the upper jaw is noticeably stouter or longer than the teeth preceding them; indeed, the posterior teeth are often more slender and needle-like (cf *Astatotilapia*, where the posterior teeth are noticeably longer and stouter; Greenwood, 1979: 282). Inner row teeth are small and slender, and may be tricuspid, bicuspid or unicuspied; sometimes an admixture of all three types occurs. Frequently the bi- and tricuspid teeth are very weakly cuspidate.

The lower pharyngeal bone (Fig. 3) has a triangular dentigerous surface approximately equilateral in outline. The length of the bone’s anterior shaft is contained from 1 1/3 to 2 times in the sagittal length of the dentigerous surface, and from 3 – 4 1/2 times in the total length of...
the bone (measured from the tip of the anterior shaft to a horizontal connecting the two posterior horns of the bone); the shaft is shorter in *P. philander* than in *P. multicolor*.

The pharyngeal teeth are slender and cuspidate, with those forming the two median rows on the lower bone only slightly or not at all coarser than their immediate congener, No "kukri"-shaped lower pharyngeal teeth are present (see Greenwood, 1987a: 196, Fig. 30).

The posterior-facing medial margins of the upper pharyngeal bones on each side are aligned so as to form a broad and shallow "v" whose apex is directed anteriorly (see Reinhoth, 1956: Fig. 9; Greenwood, 1987a: 198; Fig. 4).

The lachrymal (1st infraorbital bone Fig. 6) has 4 or, less frequently, 5 (rarely 3 or 6) openings to its laterosensory tubule, the number of pores on the lachrymal of each side often being different (Table 1). The other bones in the infraorbital series (Fig. 7) show a high degree of variability, both in the number of bones developed and in the extent of fusion between these bones. If the second bone (that normally following the lachrymal) is developed, it never overlaps the posterior margin of the lachrymal and is usually separated from it by a distinct gap; at most it almost abuts against, and is moveably articulated with the lachrymal (see pp. 8 – 10 for a detailed analysis of the entire infraorbital series).

Scales on the body below the upper laterolateral-line series are weakly ctenoid, those situated more dorsally and on the head are cycloid. There is a gradual size gradient between the relatively smaller scales on the chest and those on the belly and ventrolateral flank region. Generally the cheek is completely scaled (with 2 or 3 rows) but in some populations there is a small naked area anterolaterally. In some individuals of at least *P. multicolor* and *P. philander* 1 or 2 scales, continuous with those on the cheek, extend onto the lachrymal, occasionally to between the ultimate and penultimate laterosensory pore tubules of that bone, an unusual feature in African cichlids.

Frequently some scales in both the upper and the lower lateral-line series are without tubules covering the opening to the underlying sensory canal system; the opening then is either absent or reduced to a simple pit. Total counts for scales in both the lateral-line series range from 24 to 30.

No rows of small scales are developed at the base of, and extending onto, the membrane of either the dorsal or the anal fin. The proximal quarter to third (or slightly more) of the caudal fin is covered by small scales.

The pelvic fin has the first ray longest, proportionately more so in adult males than in females; in one species, *P. nicholsi*, the first ray is very greatly produced (at least in sexually active males) and extends beyond the anal fin base almost to the origin of the caudal fin. Dorsal fin with 13-16 spines and 8-11 branched rays, the anal with 3 spines and 6-10 branched rays. The caudal fin has a clearly rounded posterior margin.

Total vertebral counts (excluding the fused PU, and U, centra) are 25 (f 2), 26 (f 19), 27 (f 18) or 28 (f 13), and comprise 12 (f 40) or 13 (f 12) abdominal and 13 (f 6), 14 (f 17), 15 (f 21) or 16 (f 8) caudal elements.

Adult coloration is sexually dimorphic, males more brightly coloured than females and with darker pelvic fins. The anal fin in adult males has a clearly defined, but sometimes small, orange, red or yellow spot, blotch or crescentic mark at its posterior tip or posterior margin (see Fig. 1, and p. 3 for a comparison with the situation in other African cichlid species).

All three *Pseudocrenilabrus* species are known to be female mouth-brooders, but no information is available for natural populations of *P. nicholsi* (Reinhoth, 1956; Wickler, 1962, 1963; Loiselle, 1982a, b).

### ANATOMICAL FEATURES

The osteological information in this section was derived mainly from specimens of *P. philander* and *P. multicolor*, the specimens being chosen so as to cover several localities within the species’ ranges. Accounts of the soft anatomy stem mostly from dissections of *P. philander*, but also from two specimens of *P. multicolor* (one from the Sudan, the other from Uganda). Vertebral counts are mainly from radiographs.

A shortage of *P. nicholsi* material has confined anatomical observations on that species to superficial features of the head, and to relatively non-destructive dissections.

**NEUROCRANUM** (Fig. 4): In its general form and in its architecture, the skull of *Pseudocrenilabrus* is of the generalized haplochromine type, and is thus closely similar to that in *Astatotilapia* species (Barel et al., 1976; Greenwood, 1979), especially *A. desfontainesi* and members of the *A. blooeti* species complex. The basicranial apophysis for the upper pharyngeal bones, and the nature of the *pars jugularis* are both of the *Haplochromis* type (Greenwood, 1978, 1986 respectively), the latter, as is usual, without a precommissural bridge. The mesethmoid is sutured to the vomer, and the two cranial facets for the hyomandibular condyles are well-separated from each other.

Neurocranial width (measured as the maximum skull breadth across the pterotics) appears to show both inter- and intraspecific variability. Expressed as a percentage

### Table 1. Frequency distribution of the number of specimens of *Pseudocrenilabrus* species with various numbers of cephalic sensory pores in the lachrymal bones. The number of specimens examined from each area is given in parentheses.

<table>
<thead>
<tr>
<th>Number of pores in lachrymal of each side</th>
<th>3/3</th>
<th>3/4</th>
<th>3/5</th>
<th>4/3</th>
<th>4/4</th>
<th>4/5</th>
<th>5/5</th>
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of neurocranial length (i.e., tip of vomer to the rim of the basioccipital condyle), that in *P. multicolor* is from 56-69% (3 specimens) and in *P. philander* 50-58% (n = 25); no correlation with skull length is apparent.

An outstanding feature of the skull in *Pseudocrenilabrus*, and one I have not encountered in other African cichlids, is the marked degree of intraspecific variability in the height and shape of the supraoccipital crest, and hence of its area (Figs 4 & 5). The angle at which the anterior margin of the crest slopes upwards is, of course, related to the height of the crest posteriorly. Generally it is in the taller crests that departures from the usually straight upper margin are encountered. In some specimens the margin is distinctly concave, in others it is convex. Another variant has the anterior part of the crest rising abruptly and almost straight up from the underlying bone before it curves posteriorly and continues upwards and backwards to meet the posterior margin of the crest at an obtuse and rounded angle; often the entire upper margin is gently rounded, thus giving the crest a somewhat cock’s-comb appearance.

Maximum height of the supraoccipital crest (measured from its tip to the supraoccipital bone vertically below the tip) varies from 12.5-23.3 per cent of the neurocranial length.

From the material examined it does not seem that particular supraoccipital shapes are characteristic of particular populations, but larger samples are necessary to confirm this.

Causal factors responsible for these variations in shape and size are unknown. Crest area does not appear to be correlated with relative hyper- or hypotrophy of the epaxial musculature extending onto the skull roof since crest form cannot be anticipated from the external appearance of the fish.

At least in *P. philander*, the species for which most osteological material is available, there is considerable intraspecific variation, sometimes unilaterally manifest, in the shape and extent of the fronto-parietal crests. Usually it is the frontal portion of the crest which is most affected, with, in some specimens, the greater part of the crest reduced to a low but obvious eminence. In most individuals examined the frontal crest extends to a point above the supraorbital lateral-line pore, but in others it does not reach that level, and in some it curves laterally to end a short distance behind the pore. The height of both the parietal and frontal sections of the crest is variable, as is the shape of their distal margins. These vary from almost straight to noticeably wavy.

**Suspensorium and Palatopterygoid Arch:** Neither complex differs from that in *Astatotilapia* (see Barel et al., 1976; Anker, 1978: Fig. 6; personal observations); both can be considered as being of the generalized haplochromine type (Greenwood, 1985: 144 & 166) but with a well-developed calyx formed from the metapterygoid. As in all but a few of the African taxa studied, there is a two-point articulation between the palatine bone and the ethmoid region of the skull (Greenwood, 1985: 132, 166).

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![Figure 4. Pseudocrenilabrus philander. Neurocranium in left lateral view. Neurocranial length 16.0 mm; specimen from Durban.](image-url)

![Figure 5. Individual variability in the outline and area of the supraoccipital crest in Pseudocrenilabrus. A, B and C: P. philander; D: P. multicolor. Geographical localities and neurocranial lengths of the specimens, respectively, are: Durban, 19.5 mm; Molopo Oog, 17.5 mm; Wondergat, 14.0 mm; Lake Nabugabo, Uganda, 13 mm. The broken line is drawn through the fronto-parietal crest a little below its margin and parallel with the parasphenoid bone.](image-url)
**JAWS:** There are no outstanding features in any elements of the jaw skeleton. The ascending process of the premaxilla is as long as, slightly longer, or shorter than the dentigerous arm of the bone. The tip of the articular process lies at a point a little more than halfway along the ascending process (both vertical measurements taken from the dentigerous surface of the premaxilla).

The dentary is not noticeably foreshortened or deep, and its coronoid (ascending) process rises fairly steeply. There is a passage through the anguloarticular for the preopercular-mandibular laterosensory canal.

**BRANCHIAL SKELETON:** Adequate material for alizarin and alcian blue staining was only available for *P. philander*; specimens of *P. multicolor* neither stained or cleared properly. However, dissections made on *P. multicolor* from Uganda indicate that the two species do not differ in any obvious ways.

Basically, the branchial skeleton in *P. philander* does not depart markedly from that of *Astatotilapia* (personal comparisons made with *A. desfontainesi* and *A. bloyeti*, and comparisons made with figure 6 in Stiassny [1981] for *A. calliptera*, and figure 7 in Barel et al. [1976] for *A. elegans*). In its overall proportions, however, the branchial skeleton of *Pseudocrenilabrus* is relatively shorter and broader than in *Astatotilapia*. One slight, but obvious intergeneric difference (at least in *P. philander*) concerns the outline shape of the second basibranchial. In *P. philander* the bone has the shape of an inverted bottle, with the neck directed anteriorly; in *Astatotilapia*, as it is in *Hemichromis* (Greenwood, 1985: fig. 14B), the second basibranchial has a near-hourglass outline.

There is a well-developed spine on the fourth epibranchial, and the expansive quadrangular area of the bone is rectangular rather than square in outline. Epibranchial 2 has a short cartilaginous projection on its anterior face. The two arms of epibranchial 1 form an angle of ca 20°, and the anterior arm is noticeably shorter than the posterior one. No interarcual cartilage is developed. In all these latter features, too, *Pseudocrenilabrus* differs very little from *Astatotilapia* (see Barel et al., 1976).

**INFRANASAL BONES** (Figs 6 & 7). The descriptions and discussions in this section are based on a comparative study between *Pseudocrenilabrus* on the one hand and six haplochromine species on the other (viz. a member of the *A. bloyeti* group, on *A. stappersi*, *A. vellifer* and *A. pallidus* and on *Thoracochromis albertianus* and *Th. buysi*). In addition, the overall nature of the infranarial series was checked in a large number of other African species (see also Oliver, 1984; Greenwood, 1983; Colombe & Allgayer, 1985). Most of the haplochromine specimens used in this survey are over 40 mm SL, but a few smaller fishes were available (see below).

When specimens over ca 40 mm SL in the two groups are compared it will be noticed, in the haplochromine species, the second infraorbital bone overlaps the posterior margin of the lachrymal (the first infraorbital) and is closely adherent to it. In contrast, species of *Pseudocrenilabrus* always have the second infraorbital separated from the lachrymal. The extent of that separation can vary from little more than a hair-line space, with the bones virtually contiguous, to a clear-cut gap visible even without the overlying skin being removed. Gap size is related to the size of the second infraorbital which can be greatly reduced or even, apparently, absent; the latter condition, however, may result from the bone fusing with the third element in the series (see below). Irrespective of gap size, the lachrymal and second infraorbital are joined by a band of dense connective tissue.

In specimens between ca 25 and 40 mm SL, the intergroup difference noted above is sometimes less obvious. This is because the second infraorbital in some individuals of the haplochromine group does not overlap the lachrymal, the two bones either being contiguous or separated by an obvious gap. A gap, usually a very distinct one, is, however, always present in *Pseudocrenilabrus* of this size, whilst in some specimens the second infraorbital and sometimes the third as well are often still undifferentiated.

When specimens between 16 and 25 mm SL (the smallest available) are compared, the intergroup distinction is even less obvious, but again it is always more apparent in *Pseudocrenilabrus*, where the second infraorbital is either very small, poorly ossified and incomplete, or is entirely wanting.

Thus, it appears that in specimens of comparable sizes (ages could not be determined) the condition in *Pseudocrenilabrus* is, in an ontogenetic sense, retarded relative to that in the haplochromines, and that even in sexually mature individuals of the genus the definitive condition is comparable with that in much smaller and juvenile specimens of haplochromine-group species.

The lachrymal itself (Fig. 6) in *Pseudocrenilabrus* shows considerable variability in the number of pores opening into its laterosensory canal; the range for the genus is from 3 to 6, see Table 1. Overall, the modal number is 4, but in *P. philander* there is a significant number of individuals with 5 pores. In both *P. philander* and *P. multicolor* it is not uncommon for there to be a different number of pores on the left and right lachrymals of one individual (see Table 1).

Variation in number, shape, size and disposition is also a characteristic of the other bones in the infraorbital series of *Pseudocrenilabrus*. The basic condition in *P. philander* (especially fishes over 40 mm SL) is for there to be, in addition to the lachrymal, 4 canal-bearing bones (each with 2 [terminal] openings) articulating with
one another. The first (i.e. anterior) and the last bone of the series (the positional equivalent of the dermosphenotic) are the smallest elements, the second is the largest.

Departures from that plan include the suppression of the "dermosphenotic", the apparent fusion of the second and third bones (which then have a ventrally directed opening at about the mid-point of the single element), or the loss of the first bone.

Such reductional trends are carried even further in *P. multicolor*. In many individuals from the Egyptian and Sudanese populations examined, the lachrymal alone is present. Others have only the lachrymal present on one side, but a full complement of bones on the other, always with a very wide gap between the lachrymal and the next bone in the series. It is perhaps significant (see p. 13) that in these populations sexual maturity is reached at a small size (30-35 mm SL), and that the largest specimens in the collections examined are only 47 mm SL.

In the East African populations of *P. multicolor* (Fig. 7B & C) the trend is towards fusion, in various combinations, of the 3 bones posterior to the lachrymal, and either the loss of the "dermosphenotic" or perhaps its fusion with the preceding bones. Thus, a variety of patterns is recorded, viz.

(i) A single bone with 5 openings (i.e. 2 terminal and 3 others), implying a fusion of all 4 bones.
(ii) A discrete first bone (with only its 2 terminal openings) and a suturally united second and third bone (implying the loss of the "dermosphenotic")
(iii) An elongate first element with 3 openings, 2 of which are terminal (implying a fusion of the first and second bones) and an elongate second element also with 3 openings (2 of which are terminal), implying a fusion of the third and "dermosphenotic" bones.
(iv) A single long bone with 4 openings (2 of which are terminal), suggesting that the first bone has been suppressed and the second, third and “dermosphenotic” elements have fused.

In none of these various and often bilaterally asymmetrical patterns is the upper terminal opening of the infraorbital canal system close to the neurocranial opening onto the cephalic canal system; a distinct gap is always present.

The situation in the two *P. nicholsi* specimens examined is unlike that in any *P. philander* or *P. multicolor* studied (Fig. 7A). Only 2 bones (in addition to the lachrymal) are present, namely a short upper bone in the position occupied by the “dermosphenotic” in the other species, and an elongate, slightly curved bone situated about midway between the lachrymal and the small upper bone. In one of the specimens the larger bone has 4 openings (2 of which are terminal), but in the other fish only the terminal pores are present.

**Hyoid Arch Skeleton:** This complex is virtually identical with that in *Astatotilapia* (personal observations, and Barel et al., 1976), except for the absence of a dorsally directed spine situated anteriorly on the urohyal. Stiassny (1981: 98) notes that the presence of a spine on this bone is a plesiomorphic feature for the Cichlidae, but that it has been lost independently in a number of taxa occurring in the African lakes (although not in any of the Lakes Victoria and George species for which skeletal material is available). Its absence in *Pseudocrenilabrus*, however, may be correlated with the absence of a ligamentum urohyale rostrale in that genus (see p.11).

**Axial and Caudal Fin Skeletons:** Little comment is required on the axial skeleton. The low vertebral count (25–28, excluding the fused PU and U. centra), together with the number, and relative numbers, of abdominal and caudal centra (12 or 13, and 13–16 respectively) are plesiomorphic for the family (Greenwood, 1979; Stiassny, 1982), as are the 10 pairs of pleural ribs; the single predorsal bone is usual in African members of the family, and in that context can also be ranked as a plesiomorphy (Greenwood, 1987a: 182).

Although there is a broad overlap in the range of total vertebral counts for *P. multicolor* and *P. philander*, the modal number (26) in the former species is lower than that in the latter (27 or 28).

There is a high level of uniformity amongst cichlids in the anatomy of the caudal fin skeleton (Vandewalle, 1973; Stiassny, 1982; Greenwood, 1984: 154). Apart from some slight and individual variability in the development of the neural arch and spine on PU., the caudal skeleton in *Pseudocrenilabrus* does not depart from the modal cichlid condition, including the presence of a well-developed hypurapophysis on the pyuralaphal. Specimens with fused hypurals 1 and 2, as well as fusion between hypurals 3 and 4, are of common occurrence in both *P. philander* and *P. multicolor*. Personal observations on a large number of cichlid species indicate that such hypural fusion is of common occurrence in the family. Its frequency within any particular taxon is not correlated with caudal fin shape or the relative size of the fin (Greenwood, 1979, 1980, 1983, 1985, 1987a).

**Pectoral Girdle:** The pectoral girdle has no unique features, and is closely similar to that in *Astatotilapia*, as are the bones associated with the girdle, namely the supracleithrum and posttemporal.

**Dentition:** The relatively slender and unequally bicuspid outer teeth (and the shouldered form in which the minor cusp is poorly developed) in both jaws, and those unicuspid which succeed them temporally, are like the teeth found in many African taxa. The resemblance is especially marked when comparisons are made with those haplochromine taxa, such as *Astatotilapia*, which are anatomically and trophically unspecialized (Greenwood, 1979 & 1981). Likewise, the inner row teeth in *Pseudocrenilabrus* are similar to those in the same haplochromine species.

One interesting feature of the dentition in *Pseudocrenilabrus*, however, is the small body size (relative to the haplochromine species) at which bicuspid outer teeth are replaced by caniniform unicuspids. Also interesting is the almost invariably presence of some, and often many, unicuspid teeth in the posterior and posterolateral regions of both jaws in specimens of all sizes, including the smallest examined (a 14 mm SL *P. multicolor*, and a *P. philander* 21 mm SL). In those haplochromines in which a change-over from bi- to unicuspid outer teeth occurs, it does so when the fish reaches a length of about 80-100 mm (a size apparently never reached by *P. multicolor* and rarely attained by *P. philander*).

A study of tooth types in small *P. multicolor* specimens (from Sudan and Egypt) indicates that in fishes less than 16 mm SL all the outer row teeth are slender needle-like unicuspids, similar to, but relatively larger than those found in later buccal and immediately post-buccal young of various haplochromine species I have examined (Greenwood, 1987a: 144; Balon, 1977: 165). In slightly larger individuals of *P. multicolor* the needle-like teeth are replaced anteriorly and anterolaterally in the jaws by bicuspid. Postero laterally and posteriorly, the slender unicuspids persist; some are replaced later by bicuspid but the others are replaced by relatively stout unicuspid. In no specimens I examined were the posterior 1–6 (or more) premaxillary teeth replaced by enlarged, caniniform teeth, as is the case in *Astatotilapia* and some other haplochromine genera.

Unfortunately, the number of small *P. multicolor* at my disposal was limited, and these observations need to be checked on much larger samples.

**Head Muscles:** As with so many other features, the jaw musculature in *Pseudocrenilabrus* is like that in *Astatotilapia* (Anker, 1978; Stiassny, 1982; Greenwood, 1985) and can be taken to represent a plesiomorphic state.

There is a complete series of ligaments associated with the jaw, skull and palatine articulations, and tendon A1b of the adductor mandibulae I muscle fuses completely with the tendon of adductor mandibulae Aω, and has no separate insertion on the anguloarticular bone (see Greenwood, 1985 for a discussion of these features).

The gill-arch musculature is also like that in *Astatotilapia* (Anker, 1978; Stiassny, 1982; Greenwood, 1985) and is thus of a plesiomorphic type. Only about one-third (less, or apparently none, in some individuals) of each levator posterior muscle inserts onto the corresponding horn of the lower pharyngeal bone; a few fibres from the levator externus 4 muscles insert onto the fourth epibranchial, the greater part of the muscle inserting on the horn of the lower pharyngeal bone.
Some deviation from the Astatotilapia condition, however, is found in the ventral gill-arch musculature. For example, in two P. philander specimens dissected, there is apparently no B division of the pharyngocleithralis externus muscle (see Stiassny, 1982: 439, Fig. 11). Instead, the aponeurosis, from which the pharyngohyoideus muscle originates in part, arises directly from a single and large muscle occupying the position of what Stiassny designates the A division of the pharyngocleithralis externus. A similar condition is found in the one specimen of P. multicolor examined (a fish from Lake Kijanebalola, Uganda; BMNH, 1933.2.23: 264-73). A third P. philander specimen (from Durban; BMNH 1906.6.2: 13-22) however, has an upper area of the aponeurosis clearly musculose, in that way resembling the condition found in the Neotropical genus Chaetobranchus (see Fig. 11 in Stiassny, 1982).

All four of the specimens mentioned above have a tendon passing to the fourth ceratobranchial from the aponeurotic system linking the pharyngohyoideus, the pharyngocleithralis and the lower pharyngeal bone. This is the usual condition in cichlids (Anker, 1978; Stiassny, 1982; Greenwood, 1985: 162).

One of the four P. philander specimens (a fish from the Okavango swamps; RUSI unregistered) has an uniquely different condition of its transversus ventralis anterior muscle, a bundle of fibres from which passes below the ventral keel of the lower pharyngeal bone. According to Stiassny (1982: 442) this condition is rare in African cichlids but is common in Neotropical, Asian and Madagascan members of the family. Its occurrence in this particular P. philander may be an individual aberration, since the modal African condition occurs in a second Okavango fish dissected.

In none of the Pseudocrenilabrus dissected is a ligamentum urohyale rostrale present (see Anker, 1978: 262; Fig 10). Its absence may be responsible for the absence of a dorsally directed spine on the urohyal since the ligament (see Anker, 1978: 262; BMNH, 1933.2.23: 264-73). A third P. philander specimen has only the P. philander specimens (from Durban; BMNH 1906.6.2: 13-22) however, has an upper area of the aponeurosis clearly musculose, in that way resembling the condition found in the Neotropical genus Chaetobranchus (see Fig. 11 in Stiassny, 1982).

Although there are similarities, there are trenchant differences as well, and these are emphasised when the coloration of other Orthochromis species is taken into account. More important, in a phylogenetic context, it is impossible to show that the few intergeneric similarities in coloration are synapomorphic features, and no other synapomorphies, especially anatomical ones, can be detected (compare anatomical account above with that of Orthochromis anatomy in Greenwood, 1979: 296-297, and 1984: 206-211). It is also impossible to find grounds for suggesting a slightly more distant but particular relationship between Orthochromis and Pseudocrenilabrus since neither genus apparently shares, with a third taxon, any unique synapomorphies.

Poll’s (1967: 314) view that Pseudocrenilabrus is very close to, indeed is the ancestor of Orthochromis machadoi (and thus, by implication, of the genus Orthochromis) has been considered elsewhere and found to be unacceptable (Greenwood, 1984). Essentially, Poll bases his argument on the closely similar preserved coloration of the two species; live colours of O. machadoi are unknown. Although there are similarities, there are trenchant differences as well, and these are emphasised when the coloration of other Orthochromis species is taken into account. More important, in a phylogenetic context, it is impossible to show that the few intergeneric similarities in coloration are synapomorphic features, and no other synapomorphies, especially anatomical ones, can be detected (compare anatomical account above with that of Orthochromis anatomy in Greenwood, 1979: 296-297, and 1984: 206-211). It is also impossible to find grounds for suggesting a slightly more distant but particular relationship between Orthochromis and Pseudocrenilabrus since neither genus apparently shares, with a third taxon, any unique synapomorphies.

Wickler (1963), the first worker to realise that the species multicolor and philander, then classified in Haplochromis, constituted a separate lineage, approached the problem of generic relationship from an essentially ethological point of view. He took only one non-behavioural character into account, namely the nature of the egg-dummies in the two species, and its marked difference from the egg dummies in Haplochromis. According to Wickler (op cit: 91), the spawning behaviour of multicolor and philander is intermediate between that in species of the substrate spawning and guarding genus Hemichromis and the mouthbrooding of the four authors who have commented on the interrelationships of Pseudocrenilabrus, only Van Couvering (1982) employed a cladistic approach to the problem, and then rather vaguely. In what she calls an “hypothetical phylogenetic diagram of cichlid evolution” (op cit: Fig. 11) Van Couvering ranks Pseudocrenilabrus as the plesiomorphic sister taxon of Haplochromis (sensu Regan, 1922) plus a fossil genus, Nderechromis. Van Couvering, (from the lower Miocene of Kenya), the latter being indicated as the sister taxon of Haplochromis itself. That Haplochromis, in Regan’s sense, is undoubtedly a polyphyletic grouping (Greenwood, 1979 & 1980) may be disregarded for the moment, but would in any case invalidate Van Couvering’s hypothesis.

Van Couvering gives no detailed arguments for her phyletic scheme, but from the diagram it would seem that the sole synapomorphy uniting Haplochromis and Nderechromis is their having egg dummies on the anal fin (see Wickler 1962 & 1963 for a full account of these features). Nowhere in her paper, however, does Van Couvering mention that these purely chromatic characters are preserved in the fossils. The synapomorphy uniting Pseudocrenilabrus and the Haplochromis plus Nderechromis lineage is given as the “... development of ancestral Haplochromis feeding apparatus”. Again, nowhere in the text or the diagram does Van Couvering explain what exactly this apparatus is, or involves, and I cannot identify it from my knowledge of haplochromine anatomy. In short, on the evidence given in Van Couvering’s diagram, or elsewhere in her paper, there would seem to be no case for accepting her suggested relationships for Pseudocrenilabrus (see also Greenwood, 1985: 169).

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Haplochromis species (again sensu Regan, and with particular regard to the species *burtoni*). It was this intermediate which led Wickler to coin the name *Hemihaplochromis* for the new genus in which he placed multicolor and philander.

Also according to Wickler (1963: 91), but without any further amplification or justification, *Hemichromis* represents the “Stammform” of *Haplochromis* and its related taxa. Thus, at least by implication, *Pseudocrenilabrus* (i.e. Wickler’s *Hemihaplochromis*) would represent a stage in the evolution of the latter from a *Hemichromis*-like ancestor.

Anatomically, that relationship cannot be substantiated anymore than can the idea of *Hemichromis* being the “Stammform” from which *Haplochromis* was derived. The nature of the ethmopalatine articulation in *Hemichromis* is unique amongst cichlids (Greenwood, 1985), and represents a highly derived condition relative to that in any *Haplochromis* or *Pseudocrenilabrus* species, as does the absence of a passage for the laterosensory canal through the anguloarticular bone. Granted, there are several plesiomorphic features in *Hemichromis*, some of which are represented in *Haplochromis* and *Pseudocrenilabrus* in their derived states (Greenwood, 1985: 164 et seq.). But, the autapomorphies of *Hemichromis*, coupled with the absence of any derived characters shared uniquely with either or both *Pseudocrenilabrus* and/or *Haplochromis*, would preclude a species of *Hemichromis* from being ancestral to either of the other two taxa (see also p. 14).

It is rather more difficult to assess the significance of the ethological features used by Wickler (1962, 1963), especially since comparable information is not available for many haplochromine species, particularly those belonging to the more generalized lineages like *Astatotilapia*. Clearly the spawning and brooding habits of *Pseudocrenilabrus multicolor* represent a more derived condition than those found in substrate spawners and brooders such as *Hemichromis*. On the other hand, the *Pseudocrenilabrus multicolor* pattern, as described by Wickler (1962, 1963) seems to be less derived than those he described for the two *Astatotilapia* species, because in *P. multicolor* some ova are fertilized before being taken into the female’s buccal cavity. However, the significance of that difference, and whether or not it characterises all populations and species of *Pseudocrenilabrus* and *Astatotilapia* remains to be determined in wild as well as in captive populations.

Finally there is Trewavas’s (1973) view that *P. philander* and *P. multicolor* “in their respective areas . . . have no close relations . . .”. At first sight, and especially with regard to the evidence then available, one might well be inclined to agree with that opinion. However, an alternative argument will be developed below.

Essentially, the argument stems from the fact that none of the authors whose opinions are discussed above was aware of the interrupted and often reduced infraorbital series in *Pseudocrenilabrus*, and thus did not involve that generic character in their assessments. Nevertheless, this feature could indicate the manner in which *Pseudocrenilabrus* evolved, and may suggest a possible stem group from which the lineage was derived.

Reduction in the number of infraorbital bones, either by loss or by fusion, and loss of contact between the lachrymal and second infraorbital bones in cichlid fishes can, on the basis of outgroup comparison amongst other perciforms (and within the family itself) be considered a derived feature. On that basis, the situation in a generalization haplochromine such as an *Astatotilapia* species (no reduction; lachrymal and second infraorbital with overlapping contact; see Fig. 8 in Barel et al., 1976) represents a plesiomorphic state. Thus, if one accepts Wickler’s (1963) argument, based essentially on ethological characters, that *Pseudocrenilabrus* is the immediate “Stammform” of *Haplochromis* (= *Astatotilapia*), then the latter would have lost a derived feature and, as it were, reverted to the plesiomorphic condition of that character.

A reduction in the infraorbital series is not restricted to *Pseudocrenilabrus*. It occurs in at least five genera of African cichlids (all of which are characterised by their own autapomorphic features), and in some Neotropical genera as well (Kullander, 1986). The latter taxa need not be considered further since none has the apomorphic palatinal extension of the *adductor arcus palatini* muscle which is a synapomorphy for African cichlids (Cichoki, 1976; Greenwood, 1985). The possible relationships of *Pseudocrenilabrus* with the other African species must, however, be tested.

Among the African species a reduced or interrupted infraorbital series occurs in *Nanocharis* (Greenwood, 1987a: 186), *Lamprologus* (sensu lato; see Colombe & Allgayer, 1985; Poll, 1986), *Telmatochromis*, *Julidochromis* and in *Chalinochromis* (Poll, op cit). The four latter taxa are brought together as the tribe Lamprologini by Poll (1986), and will be referred to as the lamprologini in the discussion which follows, even though Poll did not establish the group’s monophyly.

*Nanocharis* can be dismissed immediately because various other derived characters clearly demonstrate that it is a member of the chromidotilapiine generic assemblage (Greenwood, 1987a); *Pseudocrenilabrus* shares none of the derived diagnostic features of that group. The nature of the infraorbital series in *Nanocharis* is unique (Greenwood, 1987a: 186; Fig. 27) and since no other chromidotilapiines have these bones reduced, their reduction in *Nanocharis* must be considered an isolated and independent evolutionary event.

The lamprologini, too, share a number of derived features not found in *Pseudocrenilabrus*. These include an increased number of dorsal and anal fin spines, very small nuchal and thoracic scales (sometimes even vestigial or absent), generally a naked cheek, small body scales, 2-8 (rarely more) enlarged and caniniform teeth anteriorly in the outer tooth rows of both jaws, and an increased number of abdominal and caudal vertebrae. Unlike *Pseudocrenilabrus*, the lamprologini have retained a primitive substrate spawning and guarding mode of reproduction, although many species show highly specialized variants of this plesiomorphic trait (Poll, 1986).

Three derived features only are shared by *Pseudocrenilabrus* and the lamprologini. These are the reductional trend in the infraorbitals, the loss of tubules in some scales of the lateral-line series, and a *Haplochromis*-type of neurocranial apophysis for the upper pharyngeal bones. A *Haplochromis*-type of apophysis is of phylogenetically widespread occurrence amongst African cichlids and has apparently evolved independently on several occasions (Greenwood, 1978, 1987a, b). It is thus of no value for
evaluating possible lamprologine-Pseudocrenilabrus relationships. Reductional trends in the organization of the infraorbital bones, and variability in the pattern of that reduction, have also occurred in a number of seemingly different lineages, including Neotropical ones (see above). The loss of tubules in some scales of the lateral-line series, often associated with irregularity in the pattern of loss but generally manifest in the lower lateral-line, is apparently less common. Interestingly, when it occurs consistently in a taxon, or group of taxa, it is usually associated with a reductional trend in the infraorbitals as well. That, for example, is the case in lamprologines, Pseudocrenilabrus and the Neotropical genus Apistogramma. A similar correlation is found in certain members of the Centrarchidae (Eaton, 1953), suggesting that we may be dealing with a single character complex.

None of the points raised above can, in itself, refute or confirm the possibility of Pseudocrenilabrus and the lamprologines sharing a recent common ancestry. But, since none of the characters involved is a derived feature shared uniquely by the two groups, and since no synapomorphies are known only for Pseudocrenilabrus and the lamprologines, the probability of their having a recent common ancestry is certainly weakened.

Once again, we would seem to have returned to Trewavas' (1973) view (see above) that a close relative for Pseudocrenilabrus cannot be recognised, the more so since possible candidates lying outside the area of distribution of Pseudocrenilabrus have also been considered and found wanting. However, I would suggest that this is not so, and would suggest instead that Pseudocrenilabrus could well be a paedomorphic derivative from a haplochromine stem, in particular from a generalized taxon such as is represented today by members of the genus Astatotilapia. That genus alone amongst the fluviatile and lacustrine haplochromines has no derived features that would require reversal, in a phylogenetic and a physical sense, to a generalized or primitive condition if one of its species was to serve as a model for the stem-form of Pseudocrenilabrus; see Greenwood (1979, 1980, 1985) for a discussion of the egg-dummies). For example, if a species of either Thoracochromis or Ctenochromis was chosen, the peculiar and derived squamation patterns on the chest in these fishes would have to be reversed to the plesiomorphic condition found in Pseudocrenilabrus. Even more reversals, involving anatomical and other characters in addition to those of the squamation, would be required if Orthochromis were chosen (see Greenwood, 1979; 1984). Likewise one can eliminate Hemichromis, especially on anatomical grounds (see above) and, going outside the haplochromines, one can discount the tilapiines, the pelmatochromines and chromatotilapiines as well, again on several features (see Trewavas, 1983 and Greenwood, 1987a for the three latter groups).

The absence of detectable autapomorphies characterizing Astatotilapia makes it uncertain if that genus, as currently recognized, is indeed monophyletic (see Greenwood, 1979: 284). Because of that uncertainty, references to Astatotilapia in the discussion which follows should be taken as referring to A. desfontainesi and members of the A. blochii species-group, the taxa on which most of the anatomical comparisons with Pseudocrenilabrus were based.

It will be apparent from the comparative sections of this paper that, anatomically and morphologically, Pseudocrenilabrus differs little from Astatotilapia. Both taxa are, basically, generalized haplochromines. Their differences lie in those derived features characterizing Pseudocrenilabrus, namely the reductional trends in the infraorbital series, the precocious appearance of unicuspide teeth in the oral dentition (precocious, that is, in relation to body length), in the presence of fine unicuspide teeth posteriorly in both jaws of specimens of all sizes, and in having a rounded caudal fin. I would argue that in Pseudocrenilabrus all these features have evolved as the result of heterochronic modifications in the developmental patterns of an Astatotilapia-like ancestral species, with the result that certain juvenile features of Astatotilapia are retained in adult Pseudocrenilabrus, and possibly in the jaw dentition there is a precocious appearance of the adult condition (see p.10).

The reductional trends in the infraorbital bones of Pseudocrenilabrus (p.8 - 12) show some inter- as well as intraspecific variability, the latter being most marked in P. multicolor. When specimens of that species are compared with similar-sized individuals of Astatotilapia species (and, indeed, other haplochromines), the pattern in Pseudocrenilabrus is invariably like that in much smaller Astatotilapia individuals. Even in the largest adult specimens of P. philander (70-90 mm SL), where reduction is least marked and is usually manifest only in the second infraorbital bone being smaller and not contacting or overlapping the lachrymal (first infraorbital), the condition is like that found in much smaller (ca 20-40 mm SL), and juvenile, specimens of Astatotilapia.

In other words, the development of the infraorbital series is retarded in adult Pseudocrenilabrus as compared with juvenile Astatotilapia of the same size. The infraorbital bone most commonly affected in all species of Pseudocrenilabrus is the second in the series, although in some populations of P. multicolor all but the first bone (lachrymal) may be suppressed; the lachrymal, on the other hand, is always present (except in one, presumably teratological, specimen).

Ontogenetically, the second infraorbital in all the small specimens of Astatotilapia examined is the last element of the series to be formed, and remains separated from the lachrymal for some time (as measured by the size of the fish). The lachrymal in these specimens, however, is always fully developed.

Peters (1973) describes a similar developmental sequence in the infraorbital bones of the tilapiine Oreochromis niloticus, and also notes that in the various tilapiines he studied the fourth neuromast associated with the lachrymal is the last to be incorporated into that bone; until this stage in ontogeny is reached, the lachrymal has only 4 openings to its canal system. Although some individuals of all Pseudocrenilabrus species have 5 openings in the lachrymal (p.6), the modal number is 4, and in a few specimens only 3 are developed. In Astatotilapia and other haplochromines there are, almost without exception, 5 openings, the exceptions occurring only as individual variants.

The conclusion I would draw from these observations is that the condition of the infraorbital series in adult Pseudocrenilabrus, as compared with that in Astatotilapia and most other African genera, is a consequence of ontogenetic retardation.

The dental situation in Pseudocrenilabrus is rather more complex, and its interpretation is hampered by in-
adequate samples of individuals less than 20 mm standard length being available for all species.

Bicuspid outer-row jaw teeth are replaced by relatively stout unicuspids in specimens of *Pseudocrenilabrus* of 40 mm SL or less, whereas in *Astatotilapia* the transition takes place at a standard length of between 90 and 100 mm (a length rarely attained in *Pseudocrenilabrus* species). Because it was not possible to age the specimens used, one cannot tell whether or not this apparently precocious dental metamorphosis in *Pseudocrenilabrus* is really the result of ontogenetic acceleration. If in both *Pseudocrenilabrus* and *Astatotilapia* the transition is linked with age and not size then the apparent intergeneric difference may not exist.

The presence of needle-like unicuspids (as opposed to relatively stouter and thus caniform teeth) laterally and posteriorly in both jaws of most *Pseudocrenilabrus* specimens at a size when similar teeth have been replaced by unequivocally bicuspid teeth in *Astatotilapia*, does, however, suggest that some “juvenile” teeth are retained in the former genus. That, in *Pseudocrenilabrus*, unlike *Astatotilapia*, the last 1-6 (or more) unicuspid teeth in the premaxilla are never enlarged and stouter than the teeth preceding them, also suggests the retention of a juvenile state in adults of that genus. Enlarged posterior caniniform premaxillary teeth are present in specimens of *Astatotilapia* considerably smaller than the largest *Pseudocrenilabrus* specimen examined.

Finally, attention must be given to the egg-dummy in *Pseudocrenilabrus* as being a possible paedomorphic character. The nature of this feature in *Pseudocrenilabrus* is unique amongst African cichlids, and nothing like it has been described for any Neotropical species.

As an egg-dummy per se, the single, non-occipital coloured spot or blotch at the tip of the male’s anal fin must be considered a derived feature. The problem is to define its polarity with respect to the egg-dummies in *Astatotilapia* and several other haplochromine taxa (see p.3). In these, each egg-spot has a clearly ocellar nature, with the coloured centre (generally yellow) narrowly margined in black and situated in a well-defined hyaline area of the fin membrane (see Wickler, 1962: 145-9; 1963). Usually there are from 3 to 5 ocelli, arranged in a single, or sometimes a double row along the middle of the soft part of the fin. In marked contrast, the single egg-dummy in *Pseudocrenilabrus* is a well-defined but non-occipital spot, blotch or crescentic band at the posterior or tip of the anal fin. It is an altogether simpler arrangement of chromatophores, but nevertheless is quite unlike the typical and numerous maculae on the median fins of *Serranochromis*, *Cheilia* and *Pharyngochromis* (Wickler, 1962: 135-9; Greenwood, 1979).

On the basis of its developing in the growth zone of the anal fin where the precursors of the ocelli first appear in *Astatotilapia*, Wickler (1963: 91) interpreted the anal mark in *Pseudocrenilabrus* as an early stage in the evolution of an *Astatotilapia*-type ocellus. Indeed, it was for this reason that Wickler (op cit) used the *Pseudocrenilabrus* egg-dummy as part of his argument for the phylogenetic intermediary of the genus between *Hemichromis* (a substrate spawner without egg-dummies) on the one hand, and *Haplochromis*, a mouth-brooder with egg-dummies, on the other. However, using the same ontogenetic argument the *Pseudocrenilabrus* condition could represent an arrested early stage in the development of the *Astatotilapia*-type ocellar spot. For the moment it is impossible to develop either argument further from the direct evidence available.

There is very little published information on the ontogeny of cichlid fishes (see Richards & Leis, 1984: 542), and in those few studies which have been made, scant attention was paid to caudal fin shape. I have examined post-hatching intrabuccal young of the Lake Victoria haplochromine *Pyctochrom* xenognathus* (Greenwood) and find that in specimens 8.3-8.5 mm total length (the earliest stages available) the fin is distinctly rounded and like that in adult *Pseudocrenilabrus*. In young *Pyctochromis* of 12.8 mm total length, however, the fin is clearly truncate and like that in the adult. Fisher (1966: 585) illustrates the caudal fin of a larval *Sarotherodon melanotheron* Rüppell in the total length range 8.4-8.7 mm. It too has a distinctly rounded caudal fin, whereas in the adult the fin is slightly emarginate.

These form changes would suggest that a rounded caudal is an early juvenile feature, and that a rounded fin in adults can be interpreted as a paedomorphic feature. Interestingly, several other perciform taxa (and indeed those from other groups) also show an ontogenetic transformation from a rounded caudal fin in larvae to a truncate, emarginate or even forked fin in later stages of ontogeny (see various articles in Moser, 1984).

If *Pseudocrenilabrus* did evolve paedomorphically from an *Astatotilapia*-like stem, then, because of the relative juvenescence manifest in its infrabasal series and its dentition, *P. multicolor* is the most derived species in the genus. *Pseudocrenilabrus philander*, judged on the same criteria, would be the least derived member, with *P. nicholsi* possibly occupying an intermediate position in what seems to be a cline of polarity both morphologically and geographically speaking.

The extreme reduction in the infrabasalts of *P. multicolor* (see p.9) and the tendency in that species for there to be fewer lateral-line scales with tubules and even pores, might appear to be correlated with the very small adult size attained by these fishes; females are mature at 32 mm SL, and I have seen no specimens larger than 65 mm SL. Delayed or suppressed development of either or both features is seen in other cichlids with a small adult size, for example *Apistogramma*, ca 65 mm SL (Kullander, 1986: 155) and *Nanochromis*, ca 40-55 mm SL (Roberts & Stewart, 1976; Greenwood, 1987a). A similar phenomenon is recorded in the pigmy Sunfishes *Elasoma zonatum* Jordan and *E. evergladei* Jordan of the family Centrarchidae (Eaton, 1953; see also Johnson, 1984).

However, since adults of several *Astatotilapia* species do not reach a length of more than 80 mm, a size attained in *Pseudocrenilabrus philander*, the paedomorphic characteristics of *Pseudocrenilabrus* cannot be attributed to small adult size alone. The same can be said for those lamprologine species (p.12) that attain adult lengths of more than 125 mm, yet show extreme reduction in the infrabasal series (Colombe & Allgayer, 1985; Poll, 1986).

Research into many aspects of *P. philander*, including its ontogeny and ethology, is being undertaken at the J.L.B. Smith Institute of Ichthyology in South Africa. This work could well serve to test the hypothesis that *Pseudocrenilabrus* is a paedomorphic derivative from an *Astatotilapia*-like stem. It should also throw light on the seemingly plesiomorphic ethological features which apparently distinguish the genus from *Astatotilapia* (or at
least A. burtoni; see Wickler, 1962, 1963; also p.12 above). Since these differences are concerned with reproductive behaviour they hardly can be considered paedomorphic characteristics. It would seem more likely that if Pseudocrenilabrus shares a common ancestor with the Astosatotilapia lineage, then it has retained the reproductive pattern of their ancestral species, whereas at least some species of Astosatotilapia have evolved a more derived pattern (Wickler, 1962, 1963). Further information is required about the ethology of Pseudocrenilabrus species and of the supposedly generalized haplochromines (especially Astosatotilapia) before the significance of these differences can be evaluated.

SUMMARY AND CONCLUSIONS

In all but a few morphological characters, members of the genus Pseudocrenilabrus are generalized haplochromine fishes (sensu Greenwood, 1979). Apart from the autapomorphies defining the genus, its other derived features, such as the Haplochromis-type pharyngeal apophysys and its female mouth-brooding habits, are of widespread occurrence amongst the haplochromines.

Trochopically, too, Pseudocrenilabrus is a generalized taxon utilizing a wide spectrum of food sources (Greenwood, 1965: 349; Loiselle, 1982a, b). Ecologically its preferred habitats are mostly in slow-flowing rivers, in streams and their backwaters, in lagoons, and in the swampy marginal areas of lakes (including such large water-bodies as Lakes Victoria and Edward). Apparently it never occupies truly lacustrine environments (Greenwood, 1965, 1973; Trewavas, 1973; Loiselle, 1982a, b). Some populations of P. philander do occupy what seem to be more specialized habitats, namely sinkholes and similar places in both Namibia and South Africa. Little is known about the biotic and abiotic parameters affecting the distribution of the Pseudocrenilabrus species.

Certain derived features of Pseudocrenilabrus, namely a reductional trend in the infraorbital bone series, peculiarities in the oral dentition, a rounded caudal fin and the nature of the egg-dummy on the anal fin of adult males, have the appearance of paedomorphic characters. Although one of these features, the reductional trend in the infraorbital bone, occurs in several other lineages of African cichlids (and in some Neotropical species as well), it is not apparent that Pseudocrenilabrus is closely related to any one of those taxa. Likewise, but on different grounds, there is no obvious relationship of Pseudocrenilabrus with any one of the various taxa proposed by other authors, or any synapomorphic features that clearly indicate Pseudocrenilabrus as the pleisiomorphic sister group of any lineage within the haplochromines (sensu Regan, 1922).

Seemingly, a parsimonious solution to the relationship of Pseudocrenilabrus is to hypothesize its paedomorphic descent from an Astosatotilapia-like stem. Since Pseudocrenilabrus shares no known apomorphic feature uniquely with Astosatotilapia or with any other generalized haplochromine group, one cannot indicate precisely the particular haplochromine lineage with which it shares a common ancestor.

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