

A revision and redescription of the monotypic cichlid genus *Pharyngochromis* (Teleostei, Labroidei)

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SYNOPSIS. Since its original description by Boulenger in 1911, *Pelmatochromis darlingi* Blgr (1911), now the type and only species of the genus *Pharyngochromis* Greenwood (1979), has not been fully revised despite the greatly increased amount of material now available from an extensive area of Africa. The type specimen is from the Zambezi river system, but subsequent material has been collected, from several localities, in the upper, lower and middle reaches of the Zambezi as well as from the Okavango and Save-Runde systems, and the Quanza system in Angola.

A wide but intergrading range of intraspecific variability is revealed when material from these areas is examined, and it appears that three other species viz. *Chromis jallae* Blgr (1896), *Pelmatochromis multiocellatus* Blgr (1913) and *Chromis acuticeps* Steindachner (1866), all currently of uncertain generic and specific status, are conspecific with *P. darlingi*. Because *acuticeps* is the oldest available name, the single component species of *Pharyngochromis* must now bear that name.

Consideration is given to the taxonomic and philosophical problems raised when the various allopatric and often physically isolated populations of *P. acuticeps* are viewed in the light of different species' concepts. No formal taxonomic solution, however, can be found.

The phylogenetic interrelationships of *Pharyngochromis*, especially with regard to the genera *Chetia* and *Serranochromis*, are still obscure. In reviewing that problem, questions are raised about the 'reality' of the taxon *Chetia* now that two further species, *C. mola* Balon & Stewart (1983) and *C. welwitschi* (Blgr) 1898, have been included in it and an earlier view that *Chetia brevis* Jubb (1968) may not be a member of that genus is no longer considered tenable.

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INTRODUCTION

The monotypic genus *Pharyngochromis* was erected by Greenwood in 1979 for Boulenger's species *Pelmatochromis darlingi*, at that time referred to the polyphyletic genus *Haplochromis* as delimited by Regan in 1922 (see Greenwood, *op. cit.*). The phylogenetic affinities of *Pharyngochromis* apparently lie with the southern African group of haplochromine genera characterized by simple, non-ocellar and usually numerous spots on the anal fin of males (and often females as well) and by the presence of only cycloid scales or a predominance of such scales on the flanks (Greenwood, 1979: 274–5; 311–12).

Since Boulenger's original description of *P. darlingi*, based on the holotype alone (a fish from the Makabusi river, Zimbabwe), there have been numerous other records of the species from Zimbabwe, and its range has been extended to include Angola and the Okavango system in Botswana (Regan, 1922; Barnard 1948a; Poll, 1967; Jubb, 1967; Jubb & Gaigher, 1971; Skelton *et al.*, 1985; Bell-Cross & Minshull, 1988).

Although both Regan (1922) and Poll (1967) have given either a partial redescription of the species, or published meristic and morphometric data for material from a particular locality, there has been no complete redescription incorporating material from the entire range of the species as presently known. This paper is an attempt to rectify that situation and to consider the relationships of *P. darlingi* with certain similar species from Zimbabwe and Angola whose current status, both specific and generic, is uncertain (see Greenwood, 1979: 312–3; 1984: 233–4). In that context particular attention was paid to *Chromis acuticeps* Steindachner (1866) and *Pelmatochromis multiocellatus* Blgr (1913), both from Angola, and the enigmatic *Chromis jallae* Blgr (1896) from Zimbabwe. All three species were placed in the genus *Haplochromis* by Regan (1922).

Information now available on the intraspecific variability of *P. darlingi* populations from the Zambezi, Save-Runde and Okavango systems indicates that this 'species' is conspecific with at least two syntypes of *Chromis acuticeps* and thus becomes a junior subjective synonym of that taxon. My review also indicates that Boulenger's *Chromis jallae* and his *Pelmatochromis multiocellatus* are additional synonyms of *acuticeps*, the latter union already strongly hinted at by Trewavas (1973: 31).

The reasons which I consider warrant the union of these nominal taxa are as follows: 1. The presence of numerous non-ocellate spots (see Greenwood, 1979: 274–5) on the anal fin of at least adult males, and often on that fin in females and juveniles of both sexes as well. The spots show some degree of individual variability in size, number and orderliness of arrangement, but rarely exceed 18 and usually number between 6 and 10.

It was an earlier ignorance of the variability in spot size, number and arrangement amongst the now extensive collections from Okavango and Zimbabwe that led me to doubt Poll's (1967) identification of certain specimens from Angola as *Haplochromis darlingi* (Greenwood, 1979: 311; 1984: 229–230). It was also partly responsible for my uncertainty about the status of *Pelmatochromis multiocellatus*, as it was my view (Greenwood, 1984: 234) that the anal fin markings in the type-specimen were of a true ocellar type. Further detailed examination of the spots shows that they are

not true ocelli (ie. with a clear surround, see Greenwood, 1979) and that similar spots, at least in preserved material, occur in specimens previously identified as *Pharyngochromis darlingi* from the Zambezi and Okavango systems.

2. The possession of a relatively enlarged and strong lower pharyngeal bone (manifest even in the smallest specimen examined, 27.5 mm standard length; RUSI 21093), usually with a sinuously interlocking median suture (Fig. 7). The anterior keel of the bone is short and deep, its lowermost point lying somewhat below the level of the bone's main body.

3. At least in specimens over 80 mm S.L. the two median rows of lower pharyngeal teeth are noticeably enlarged and coarse. The posterior pair of teeth in this series is distinctly bicuspid (albeit sometimes weakly so) and the posterior half to two-thirds of each row is composed of teeth either with a slightly rounded and molariform crown, or a flat crown with a low nipple-like cusp situated near its centre (ie. a mammilar crown). In the largest fishes there is a relative increase in the number of enlarged and near-molariform or mammilar teeth, and a few similar teeth also occur in the next lateral row.

Individuals less than 80 mm S.L. have fewer enlarged teeth, most of which are mammilar, in the two median rows, but the other teeth in this series are clearly stouter than their lateral congeners. Some enlarged but usually bicuspid teeth do, however, occur in the next lateral rows. Only in the smallest specimens examined (28–35 mm S.L.) are all the median row teeth distinctly bicuspid, but even in these fishes the teeth are relatively coarser and larger.

4. The last 4–8 (usually 5–7) scales in the upper lateral-line series have one large and one small scale separating them from the base of the dorsal fin (*cf.* species of *Chetia* and *Serranochromis* [*sensu* Greenwood, 1979] where the modal number of such lateral-line scales is 2 or 3).

5. There are 14 (mode) or 15, (rarely 13 or 16) abdominal vertebrae, and 14–16 (mode 15) caudal elements (excluding the fused PU₁ and U₁ centra) giving a total count of 28–31 (mode 30) vertebrae.

In effect, these are the principal characters used to define the genus *Pharyngochromis* (see Greenwood, 1979: 310–311; 316), and I can find no others that would trenchantly separate different species within the material examined. This included the type-specimens of *Chromis acuticeps*, *Pelmatochromis multiocellatus*, *Chromis jallae* and *Pelmatochromis darlingi*, large collections of supposedly *Pharyngochromis darlingi* from the Okavango and Zambezi systems and some, but regrettably few, from Angola as well.

None of the features used by Regan (1922) in his key and elsewhere to distinguish between the species *acuticeps*, *multiocellatus*, *jallae* and *darlingi* is effective. When large numbers of specimens are examined, all intergrade and no group shows any modal distinctiveness. Even the obliquely truncate caudal fin margin of *P. darlingi* holotype (Fig. 4), a seemingly diagnostic feature, has not been observed in any further specimens referable to the taxon on other grounds. It is presumably either teratological or the result of *pre-mortem* damage and repair.

As mentioned earlier, this revision is based mainly on characters recorded from preserved specimens, although it has been possible to compare colour notes and descriptions taken from Zambezi, Save-Runde and Okavango populations

(Jubb, 1967: 171, plate 46; Bell-Cross & Minshull, 1988: 248, plate 20 [a reprint of Jubb's plate 46]; Skelton and Greenwood, personal observations). These reveal no apparently significant differences. Regrettably, no data on live colours are available for fishes from other localities. When such information is available and there is more knowledge of other biological characteristics, especially ethological ones, then further division of the now monotypic taxon may be necessary (see Discussion p. 48).

METHODS AND MATERIAL

Method

The systems of counts and measurements are those detailed in Greenwood (1979 and 1984). When making vertebral counts, the last abdominal centrum is identified as that having a pleurapophysis with which a pleural rib articulates (no matter how reduced the rib may be). The urostylar element (the fused PU₁ and U₁ centra) is not included in the count of caudal vertebrae.

Material

Specimen lots that have been radiographed are indicated with a dagger if the plates are in the British Museum (Nat. Hist.) collections, and by an asterisk if held by the J.L.B. Smith Institute of Ichthyology, Grahamstown.

Colour transparencies are held in the J.L.B. Smith Institute, and the original of Hilda Jubb's watercolour painting of a *P. acuticeps* specimen (probably number AMG. P1600 from the Rusawi river, Save-Runde system) is housed in the Albany Museum, Grahamstown.

Institutional abbreviations following Leviton *et al.*, 1985 are: AMG, Albany Museum, Grahamstown; BMNH, British Museum (Nat. Hist.), London; MRAC, Musee Royal de l'Afrique Centrale, Tervuren; MSNTO, Museo Civico di Storia Naturale di Torino; NMW, Naturhistorisches Museum, Vienna; NMZB, National Museum of Natural History Zimbabwe, Bulawayo; RUSI, J.L.B. Smith Institute of Ichthyology, Grahamstown.

Type material examined

Chromis acuticeps[†]. Lectotype, NMW 32-877, 3 paralectotypes, NMW 32-878 (Fig. 1).

Chromis jallae[†]. Holotype, MSNTO P-3192 (Fig. 2).

Pelmatochromis darlingi[†]. Holotype, BMNH 1908.12.11:5 (Fig. 4).

Pelmatochromis multiocellatus[†]. Holotype, BMNH 1911.6.1:167 (Fig. 3).

Other material

Zambezi system

AMG. P128*. Nampini confluence of Zambezi-Chobe systems.

RUSI. 30121. Kazungula, about 1 km above Katamboro rapids, Upper Zambezi.

NMZB. 3360. Lake McIlwaine (Hunyani river, middle Zambezi).

NMZB. 3490. Caprivi strip, between Chobe and Zambezi rivers.

NMZB. 3930. Kafue river, near Kitwe.

BMNH. 1910.3.7.3.[†] Maramba river, an affluent to the Zambezi (see Boulenger, 1915).

BMNH. 1919.5.22:1-4[†]. Sesheke, upper Zambezi.

BMNH. 1937.4.22:99-108[†]. Balovale (upper Zambezi).

BMNH 1970.6.25:48-50[†]. Hunyani river (upper Zambezi).

MRAC. 163981-7[†]. Lake Calundo, Angola (upper Zambezi).

Save-Runde system (Zimbabwe)

AMG. P132*. Macheke river.

AMG. P1600. Rusawi river.

Quanza system (Angola)

BMNH. 1911.6.1:162[†]. Lucala river.

Okavango system

RUSI 20163 and 22107. Popa rapids, Okavango river.

RUSI 21516. Boro river, Buffalo fence.

RUSI 20722*. Boro river, 5 km upstream of Thamalakane confluence.

RUSI 20610. Nxaraga lagoon, Boro river.

RUSI 34974*. Xakanika lagoon, Maunachira river.

RUSI 21317. Maxegana lagoon, Botletle river.

RUSI 21463*, 34973 and 34976*. Chanoga lagoon, Botletle river.

RUSI 21093*. Third bridge, Sekiri river.

RUSI 23748. Thamalakane river, upstream of Okavango River Lodge.

RUSI 20283*. Okavango river, Mkena.

RUSI 34972. Okavango river, Rundu beach.

The majority of Okavango localities are shown in maps provided by Skelton *et al.* (1985).

A REDESCRIPTION

Pharyngochromis acuticeps (Steindachner) 1866.

Figs 1-5

SYNONYMY. Arranged alphabetically under species.

For amplification of entries marked with an asterisk, see notes on pages 40-43.

Chromis acuticeps Steindachner, F., 1866. *Verh. zool.-Bot. Ges. Wien*, **16**: 764, Taf. XV, fig. 2.

Tilapia acuticeps (part): Boulenger, G.A., 1915. *Cat. Afr. Fw. Fish.* **3**: 218-9, fig. 141 (The other specimen, from Kazungula, Upper Zambezi, cannot be located at present).

Haplochromis acuticeps (part): Regan, C.T., 1922. *Ann. Mag. nat. Hist.* (9) **10**: 225 (The type, the specimen from Lucula [see *T. acuticeps* above], and the reference to *Tilapia ramsayi* Gilchrist & Thompson, 1918* [the trivial name *ramsayi* misspelt and the date an error]).

Paratilapia arnoldi Gilchrist, J.D.F. & Thompson, W.W., 1917. *Ann. S. Afr. Mus.*, **11**: 521.

Pelmatochromis darlingi Boulenger, G.A., 1911. *Ann. Mag. nat. Hist.* (8) **7**: 377; *Idem*, 1915. *Cat. Afr. Fw. Fish.* **3**: 410,

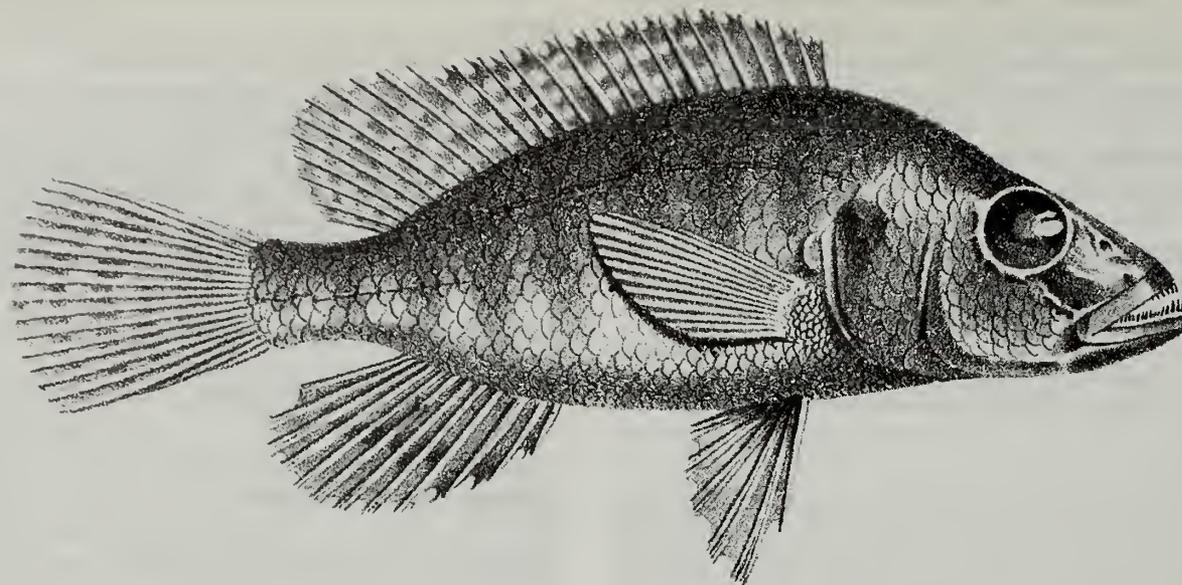


Fig. 1. *Chromis acuticeps* Steindachner. One of the type series; this figure is not positively identifiable with a particular specimen in that series. From Steindachner (186).



Fig. 2. *Chromis jallae* Blgr. The holotype; S.L. 59.0 mm. Photographed by Robin Stobbs.

- fig. 280; Gilchrist, J.D.F. & Thompson, W.W., 1917. *Ann. S. Afr. Mus.* 11: 535.
- Haplochromis darlingi*: Regan, C.T., 1922. *Ann. Mag. nat. Hist.* (9) 10: 256; Barnard, K.H., 1948. *Cape Inland. Fish. Dept., report no. 5: 60*. *Idem*, 1948. *Ann. S. Afr. Mus.* 36: 453.
- Haplochromis darlingi* (part: excluding *Astatotilapia ellenbergeri** Pell.): Jubb, R.A., 1961. *An illustrated guide to the freshwater fishes of the Zambezi river*; *Idem*, 1967. *Freshwater fishes of Southern Africa*: 47; Jubb, R.A. & Gaigher, I.G., 1971. *Arnoldia* 5 (7): 20; Jackson, P.B.N., 1961. *The fishes of Northern Rhodesia*: 112; Poll, M., 1967. *Publicoes cult. Co. Diam. Angola* no. 75: 313 (tentatively excluding Pellegrin's [1936] material identified as *Pelmatochromis welwitschi**).
- Pharyngochromis darlingi*: Greenwood, P.H. 1979. *Bull. Br. Mus. nat. Hist. (Zool.)* 35 (4): 310–11; Skelton, P.H. *et al.*, 1985. *Ichthyol. Bull. J.L.B. Smith Inst. Ichthyol.* no. 50:11.
- Chromis jallae*: Boulenger, G.A., 1896. *Boll. Mus. Torin* 9: 260.
- Tilapia jallae*: Boulenger, G.A., 1915. *Cat. Afr. Fw. Fish.* 3: 213.
- Haplochromis jallae*: Regan, C.T., 1922. *Ann. Mag. nat. Hist.* (9) 10: 255; Barnard, K.H., 1948. *Cape Inland. Fish. Dept., report no. 5:60*; *Idem*, 1948. *Ann. S. Afr. Mus.* 36: 477 & 453.
- Haplochromis lucullae**: Trewavas, E., 1973. *Bull. Brit. Mus. nat. Hist. (Zool.)* 25 (1): 31.
- Haplochromis moffati* (part): Boulenger, G.A., 1915. *Cat. Afr. Fw. Fish.* 3: 300 (the specimen, no. 43, from the Moramba River, affluent of the Zambezi, only).
- Pelmatochromis multiocellatus*: Boulenger, G.A., 1913. *Ann. Mag. nat. Hist.* (8) 12: 484; *Idem*, 1915. *Cat. Afr. Fw. Fish.* 3: 409–410; fig. 279.
- Haplochromis multiocellatus*: Regan, C.T. 1922. *Ann. Mag. nat. Hist.* (9) 10: 256.

NOTES ON SYNONYMY.

1. ?*Tilapia rumsayi* Gilchrist & Thompson, 1917. This species (its entry preceded by an interrogation mark) was first synonymized with *Haplochromis acuticeps* by Regan (1922), who misspelt the trivial name as *ramsayi*. Barnard (1948b) questioned Regan's tentative action on the grounds that the type of *T. rumsayi*, which he, but not Regan, had seen, ' . . .

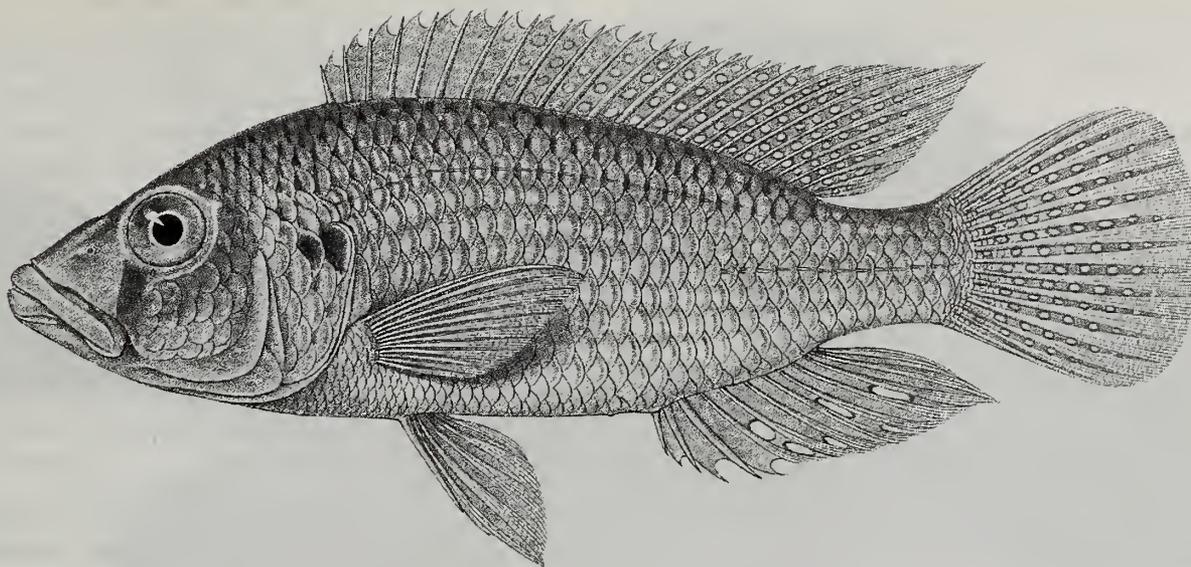


Fig. 3. *Pelmatochromis multiocellatus* Blgr. Holotype; S.L. 97.0 mm. From Boulenger (1915).

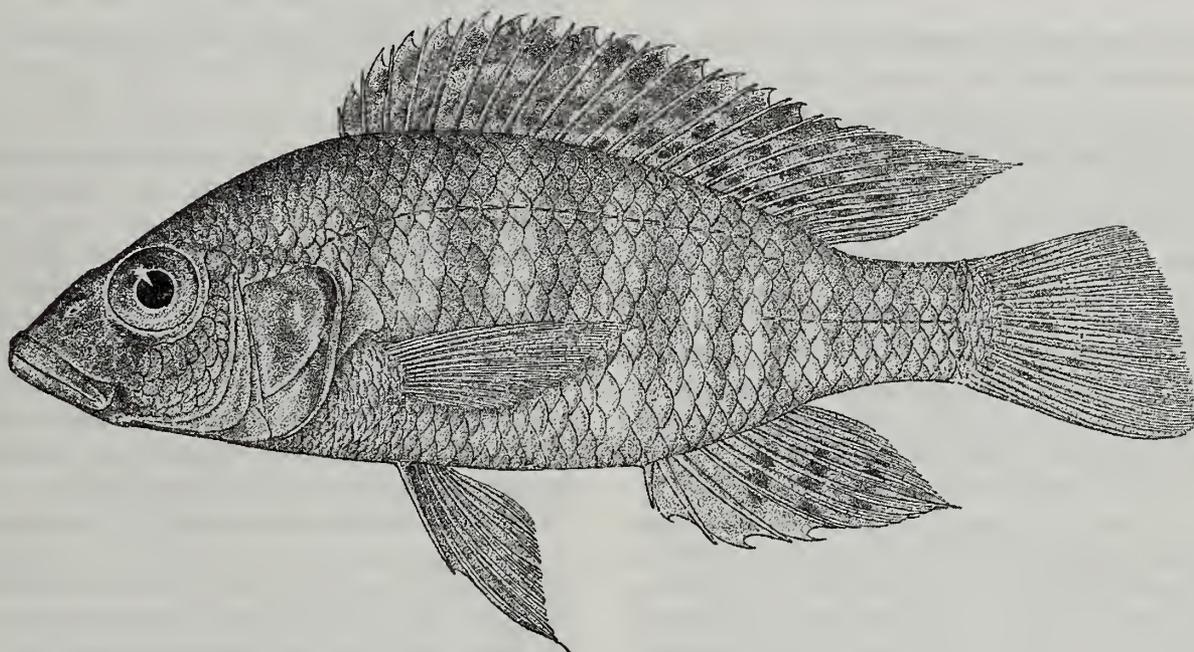


Fig. 4. *Pelmatochromis darlingi* Blgr. Holotype; 84.5 mm. From Boulenger (1915).

has stout and blunt pharyngeal teeth' (cf. small, compressed and hooked according to Regan), and thought that the species should be treated as a synonym of *Haplochromis darlingi*. In the same year Barnard (1948a: 447) repeated his doubts, and listed *T. rumsayi* (again preceded by an interrogation mark) as a synonym of *H. darlingi* in a key to the species of that genus (Barnard *op. cit.*: 453).

I would certainly agree with Barnard's action since I cannot accept Regan's differentiation (or at least partial differentiation) of *H. acuticeps* from *H. darlingi* on the basis of differences in their pharyngeal dentition. The median pharyngeal teeth in the lectotype of *Chromis acuticeps* (from an unknown locality in Angola) are comparable both with those in *Pelmatochromis darlingi* holotype and with most other specimens previously identified as *Haplochromis* or *Pharyngo-chromis darlingi* from the Zambezi and Okavango systems. Furthermore, Regan's other diagnostic criterion for separating *darlingi* from *acuticeps* (the former's greater posterior extension of the maxilla) no longer holds when large samples

are examined, and indeed barely holds when the types of the two taxa are compared.

Barnard's synonymy was accepted by later workers (Jackson, 1961; Jubb, 1967; Jubb & Gaigher, 1971; Skelton *et al.*, 1985).

The reason for my uncertainty about including *T. rumsayi* is the doubts I have about the validity, as Gilchrist & Thompson's holotype, of the specimen thought to have that status; *viz* specimen NMZB. 0711 from the National Museums of Zimbabwe's collection.

This fish is in excellent condition; it is accompanied by a label marked 'Holotype' and bearing the legend '*Haplochromis darlingi*, December 1914, Upper Zambezi River just above the Victoria Falls—Upper Zambezi. Collector F. Rumsay'. Clearly it is not the holotype of *darlingi* (which is in the collections of the British Museum [Nat. Hist.]), and there are reasons to doubt that it is really the type of *Tilapia rumsayi* incorrectly labelled as that of *darlingi* (see below), despite the correct locality and collector's data.

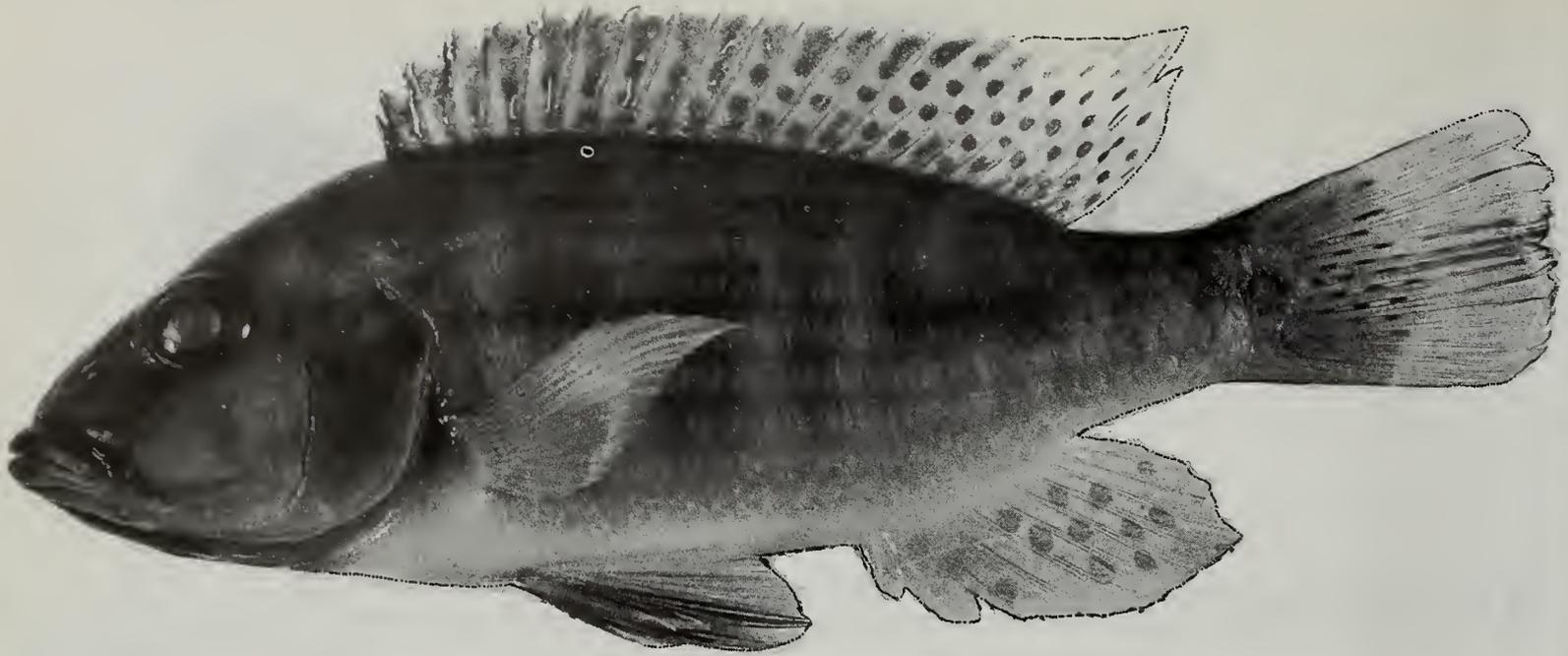


Fig. 5. *Pharyngochromis acuticeps* (Steind.) Adult male; S.L. 98.0 mm. Okavango system (RUSI 34974). Photographed by Paul Skelton.

According to Gilchrist & Thompson (1917), their specimen was 61 mm in length (whether total or standard length is not specified); specimen 0711 has a standard length of 74.0 mm, and a total length of 95.5 mm. There are other differences too. The original description gives the dorsal and anal fin formulae as XIV 10 and III 6 respectively; the specimen has counts of XV 11 and III 7. Granted, the difference in anal fin branched ray counts may not be significant because the last ray can give the appearance of being a single, deeply divided ray rather than two separate rays. The difference in dorsal ray counts, however, cannot be so easily dismissed.

Then, if Gilchrist & Thompson's figure is accurate (and their description strongly suggests that it is), then the holotype had a far more acute head profile (in lateral view) than has the presumptive holotype whose profile is steeper and more curved, and whose mouth is almost horizontal and not, as figured, sloping at an angle. Finally, the figured specimen also has 14 (and not 15) dorsal fin spines.

In other meristic and morphometric features there are some slight discrepancies between specimen 0711 and Gilchrist & Thompson's description. These may, however, be attributable to differences in our measuring and counting techniques.

It could be argued that Gilchrist & Thompson's published length measurement is a *lapsus*, or perhaps a typographical error, but that would not account for the other differences. Thus, I have grave doubts about the authenticity of specimen NMZB. 0711 as the holotype of *Tilapia rumsayi*, although it certainly seems to be a specimen of *Pharyngochromis acuticeps*.

Unfortunately, further investigations have not located any specimen which can be identified positively as the holotype of *Tilapia rumsayi*, but the search continues (pers. comm., J. Minshull). Nor has it proved possible to discover how the labelling error came about.

2. The exclusion of *Astatotilapia ellenbergeri* Pellegrin (1920) from the synonymy of *H. darlingi* (see synonymies of the latter species by Jubb [1961; 1967] and Jackson [1961]). As far as I can determine, Jubb and Jackson were the first

authors to identify *A. ellenbergeri* as a definite synonym of *H. darlingi*. The species was overlooked by Regan (1922), but was noted by Barnard (1948a) as a tentative synonym of *H. darlingi*, possibly the reason why both Jubb and Jackson included it in the synonymy of that species although they made no reference to Barnard's uncertainty of the taxon's true status. Interestingly, neither Jubb (1961; 1967), Jackson (1961), Jubb & Gaigher (1971), nor Bell-Cross (1975, see below) comment on Barnard's other view, also expressed in 1948 (a & b), that the species could be a synonym of *Haplochromis giardi* (Pellegrin), now *Serranochromis (Sargochromis) giardi*; see Greenwood (1979).

In 1975, Bell-Cross included *A. ellenbergeri* in his synonymy of *Haplochromis carlottae* (now *Serranochromis [Sargochromis] carlottae*; see Greenwood 1979), basing that decision on an examination of the holotype. He did not, however, mention the previous inclusion of *A. ellenbergeri* in *H. darlingi*, nor Barnard's (1948 a & b) uncertainties about its identity.

I have examined the holotype of *A. ellenbergeri* and agree with Bell-Cross' decision to include it in *S. (Sargochromis) carlottae* (see also Skelton *et al.* 1985).

3. *Haplochromis darlingi* (?in part); Poll, 1967. The indecision implied by the question mark relates to Poll's inclusion of certain Angolan material identified as *Pelmatochromis welwitschi* by Pellegrin (1936). Pellegrin's description of these specimens is quite inadequate, and none is figured. Until Pellegrin's material can be located and re-examined, both his and Poll's identifications should be treated with caution.

4. *Tilapia jallae* Blgr (1896). This species, known only from its holotype (Turin Museum, P. 3192) has received scant attention in previous accounts of the Zambezi system's haplochromine species. Usually it is merely listed without any comment other than it being known only from one specimen (Regan, 1922; Barnard, 1948 a & b; Jubb, 1961 and 1967). Jackson (1961: 131), however, notes that 'This species, described from the upper Zambezi, is probably not valid, but I am uncertain of its exact status'.

The type is now completely bleached and is in very poor conditions (Fig. 2). Its lower pharyngeal bone and dentition are of the *P. acuticeps* kind, and except for its shallow body (seemingly not entirely an artefact of preservation) its morphometric and most of its meristic features do not serve to distinguish it from comparable-sized specimens of *P. acuticeps*. It is, however, unusual in having 16 rather than 15 (the modal number) caudal vertebrae, and in having 6 rather than 4 or 5 rows (the modal numbers) of scales on its cheeks.

Since the holotype of *T. jallae* is not unique in these departures from the mean or modal conditions, and allowing for its poor state of preservation, as well as taking into account its geographical locality (Victoria Falls district, Zambezi River), I would conclude that it is a slightly unusual specimen of *P. acuticeps*.

5. *Haplochromis lucullae*; Trewavas (1973: 31). I do not agree with Trewavas' identification of this specimen as *H. lucullae*, the one B.M.(N.H.) specimen from the Lucala river which Boulenger (1915: 218) placed in the species *Tilapia acuticeps*. In my view, Boulenger's specific identification was correct since the specimen does not show any of the squamation features characterizing the types of *Tilapia lucullae*, a species now included in the genus *Thoracochromis* (Greenwood, 1979: 290; 1984: 190).

LECTOTYPE. A specimen 59.5 mm standard length (NMW 32-877) from Angola.

DESCRIPTION. Most meristic and morphometric data were taken from 100 specimens 27.5–133.0 mm S.L., including the lectotype and one paralectotype of *Chromis acuticeps* (the others are in a poor state of preservation) and the holotypes of *Pelmatochromis darlingi*, *P. multiocellatus* and *Chromis jallae*. For some features, fewer than 100 specimens were used when damage, poor preservation or distortion precluded accurate counts and measurements; vertebral counts are based on 68 specimens; this material covers all known localities for the species.

The principal morphometric and meristic features of the various type specimens included in this description are tabulated in the Appendix, as are those for fishes from the Zambezi and the Okavango systems respectively, as well as the Kazungula population (see Discussion, p. 49, with reference to allopatric populations and speciation). Sample sizes of collections from Angola and the Save-Runde system (Zimbabwe) are too small to justify separate tabulation.

Depth of body 27.6–41.1% of standard length (S.L.), with which it shows slight positive allometry; length of head 30.5–37.7 (mean, m , 33.8)% S.L. In both features, *C. jallae* holotype lies at the lower end of the range for specimens of a comparable size.

Dorsal head profile sloping at an angle of 30°–35° to the horizontal, its outline straight or slightly convex posterior to the orbit, straight or gently concave anterior to the orbit and often with the premaxillary ascending processes projecting a little above the rest of the outline. Mouth horizontal or almost so; dorsal outline of orbit coincident with, or a little below the dorsal head profile.

Preorbital depth 14.3–25.6 (m = 20.2%) of head length, showing slight positive allometry with S.L., least interorbital width 14.3–25.6 (m = 19.6)%. Snout length 25.0–37.2 (m = 32.4)% head length (shows slight positive allometry with standard length) and 0.9–1.2 (mode 1.0) times its breadth.

Eye diameter negatively allometric with standard length; in specimens 71.0–133.0 mm S.L. it is 22.2–31.3 (m = 27.7)% head length, and in those 27.5–70.0 mm S.L. it is 27.3–36.0 (m = 31.5)%.

Depth of cheek shows slight positive allometry with standard length; in fishes < 70 mm S.L. it is 16.0–26.2 (m = 21.6)% of head length, and in larger individuals 20.8–28.2 (m = 25.0)%.

Caudal peduncle 1.2–1.8 times longer than deep (modal range 1.3–1.5), with specimens < 80.0 mm S.L. having the deeper peduncles; its length 15.4–21.8 (m = 17.9)% of standard length.

Jaws equal anteriorly, the lower jaw 34.8–48.9 (m = 40.5)% of head length, and 0.9–1.2 times longer than broad. The posterior tip of the maxilla is variable in its posterior extent, rarely reaching the vertical through the anterior margin of the orbit, but usually extending to a point nearer that vertical than one through the nostril. The variability in this character negates Regan's (1922: 253) primary key character for separating *H. acuticeps* from both *H. multiocellatus* and *H. darlingi*.

Gill-rakers. Seven to 12 in the outer series on the ceratobranchial of the first gill-arch, the modal number nine or 10. The rakers are short, stout and cuboidal, those nearest the angle between the cerato- and epibranchial bones sometimes anvil-shaped.

Microbranchiospines are present on the outer face of the second to fourth gill-arches.

Scales. In most specimens, body scales on the flanks below the upper lateral-line, and on the caudal peduncle, are either cycloid or very weakly ctenoid, the ctenii being confined to a narrow median area on the scale's free margin. Such ctenii are rarely well-developed and, as noted before (Greenwood, 1979: 307; 310), their presence is usually most obvious in small individuals.

Some intraspecific variability exists in the size of the chest scales (ie. on the ventral and ventrolateral region of the body anterior to the insertions of the pectoral and pelvic fins). specimens from fast-flowing water tend to have the smallest scales which, in some individuals, are deeply embedded in the skin. However, even in those specimens there is a gradual size transition between the chest scales and those on the ventrolateral aspects of the flanks and belly (*cf.* the condition in *Ctenochromis* and *Thoracochromis* species where the transition is abrupt; see Greenwood, 1979). In all populations, scales forming the median one to three rows on the chest are noticeably larger than those lateral and dorsal to them.

Lateral-line series with 31 to 36 scales (30 in one individual), the modal range being 32 to 34, and the mode 33. The last 4 (rarely) to 8 scales (usually the last 5 to 7) of the upper lateral-line are separated from the dorsal fin base by one large and one small scale.

The cheek has 4 to 6 (rarely 3) rows of scales, with a small but distinct naked area anteroventrally, and sometimes a narrow naked strip between the lowest horizontal row and the lower limb of the preoperculum.

There are 15 (mode) or 16 scales around the caudal peduncle, 4 to 5½ between the lateral-line and the dorsal fin origin, and 5–9 (mode 5) between the pectoral and pelvic fin bases; fishes from rapid waters have the highest counts for the latter character.

Squamation on the caudal fin is arranged in a horizontally

aligned and broad-armed 'V', the apex situated at the fin base. Distally, the arms extend to about the mid-point of the fin.

Fins. Dorsal with 14 to 16 (mode 15) spinous and 10 (rarely) or 11 to 13 (rarely 14), modally 12, branched rays. Anal with 3 spinous and 8 or 9 (no distinct mode), rarely 7 or 10, branched rays.

Caudal fin distinctly truncate to almost rounded; the obliquely truncate fin in the holotype of *Pelmatochromis darlingi* (see Fig. 4) has not been encountered in any other specimen, and is probably either teratological or the result of damage and subsequent repair.

The first ray of the pelvic fin is the longest, and is proportionately longer in adult and sexually active males. Pectoral fin length shows some individual variability both as a proportion of head length and its posterior extent relative to the anal fin origin. As a percentage of head length the fin length ranges from 20.2 to 29.8 ($m = 25.2$); relative to the anal fin origin, it may extend to a vertical passing through any point between the anal fin origin and another passing immediately anterior to the anus. In view of this variability, one of Boulenger's (1915) principal key characters for distinguishing between *Pelmatochromis multiocellatus* and *P. darlingi* (*viz.* for the species respectively, pectoral extends to, or does not reach, the anal fin origin) is rendered invalid. From the sample examined, there is an indication of slight positive allometry between pectoral fin length and standard length, but no correlation was found with sex or sexual maturity.

Teeth. The outer row teeth in both jaws of most fishes < 80 mm S.L. are bicuspid, sometimes weakly so as a result of wear. Some unicuspid teeth may occur in larger individuals within this size range, and become the predominant form in fishes over 90 mm S.L. The number of outer row premaxillary teeth shows some correlation with the individual's size; in specimens over 50 mm S.L. the modal range is 40–50, and the range for the whole sample 24–60.

Bicuspid teeth in *Pharyngochromis acuticeps* have a distinctive but by no means unique form. The neck is relatively stout and the slightly recurved cusps are of markedly unequal size (Fig. 6). The small minor cusp often has an obtusely pointed tip and is sharply angled away from the base of the major cusp. When unworn, the latter has an acute tip and, usually, a low flange or ridge on its posterior margin. The flange occupies about half the height of the cusp, extending from the angle between the two cusps towards the tip of the major one.

Unicuspid teeth are caniniform and moderately stout. The crown, especially of teeth situated anteriorly and anterolaterally in the jaws, is slightly recurved.

Irrespective of their form, teeth in the outer row of both jaws are closely spaced but are never contiguous.

In specimens of all sizes the posterior 1–6 (usually 2 or 3) premaxillary teeth are slender unicuspid, generally smaller than the teeth preceding them. Enlarged and stout caniniform teeth, like those occurring in this position in *Astatotilapia* and some other genera (Greenwood, 1979) are never present in *Pharyngochromis*, a characteristic which this genus shares with *Chetia* and both subgenera of *Serranochromis*.

Inner row teeth in fishes less than 80 mm S.L. are generally a mixture of tri- and bicuspid, the latter often with a 'shoulder' rather than a distinct minor cusp. A few unicuspid may also be present, but rarely are all the inner teeth



Fig. 6. *Pharyngochromis acuticeps*. Outer row teeth, situated antero-laterally in the right premaxilla. Scale: 1 mm. Drawn by Elaine Grant.

unicuspid. Larger individuals show a relative increase in the number of unicuspid, and these can be the predominant or even the only form present; however, an admixture of uni- and bicuspid is found in all but the largest fishes (*ie.* specimens between 100.0 and 136.0 mm S.L.).

The number of inner tooth rows anteriorly and anterolaterally in the jaws ranges from 1–3 in the premaxilla, and 1 or 2 in the dentary. Only a single row occurs posteriorly and posterolaterally in both jaws. Often the organization of the rows is very irregular, so that it is difficult to differentiate between single and double rows, or between the latter and a triple row condition. Judging from the material examined it seems that the number of premaxillary rows may increase as the fish grows, since single rows occur most frequently in specimens < 80 mm S.L., and double or triple rows in those over 100 mm S.L. The trend is not, however, a clear one and because the sample is biased towards fishes in the smaller size group it may be artefactual.

Lower pharyngeal bone and dentition. The triangular dentigerous surface of the bone is equilateral, its length 65–70% of the bone's overall length. The keel is short (25–27% of the bone's overall length) and deep, with, in most specimens, a distinctly curved ventral outline whose deepest point lies below the lowest point on the ventral surface of the bone's dentigerous part (Fig. 7). An exceptional population, from a farm dam in Zimbabwe, does not have such a deep keel. In these specimens the keel's ventral outline is almost straight and at no point does it lie below the ventral surface of the dentigerous part; the median row of teeth is less hypertrophied and molar-like than in comparable-sized specimens from other populations, and the body of the bone is also less hypertrophied. Judging from those other populations, however, the shape of the keel is not correlated with either the degree to which the pharyngeal teeth are enlarged, or the extent to which the body of the bone is inflated and strengthened.

Apart from the atypical farm dam population, most other specimens, particularly fishes over 40 mm S.L., have the ventral surface of the bone's dentigerous part somewhat inflated and densely ossified. These features are not always proportionately enhanced in large specimens or in those with coarser and more molar-like teeth in the median tooth rows. However, there is a general trend, with growth, towards a more inflated appearance and denser ossification of the

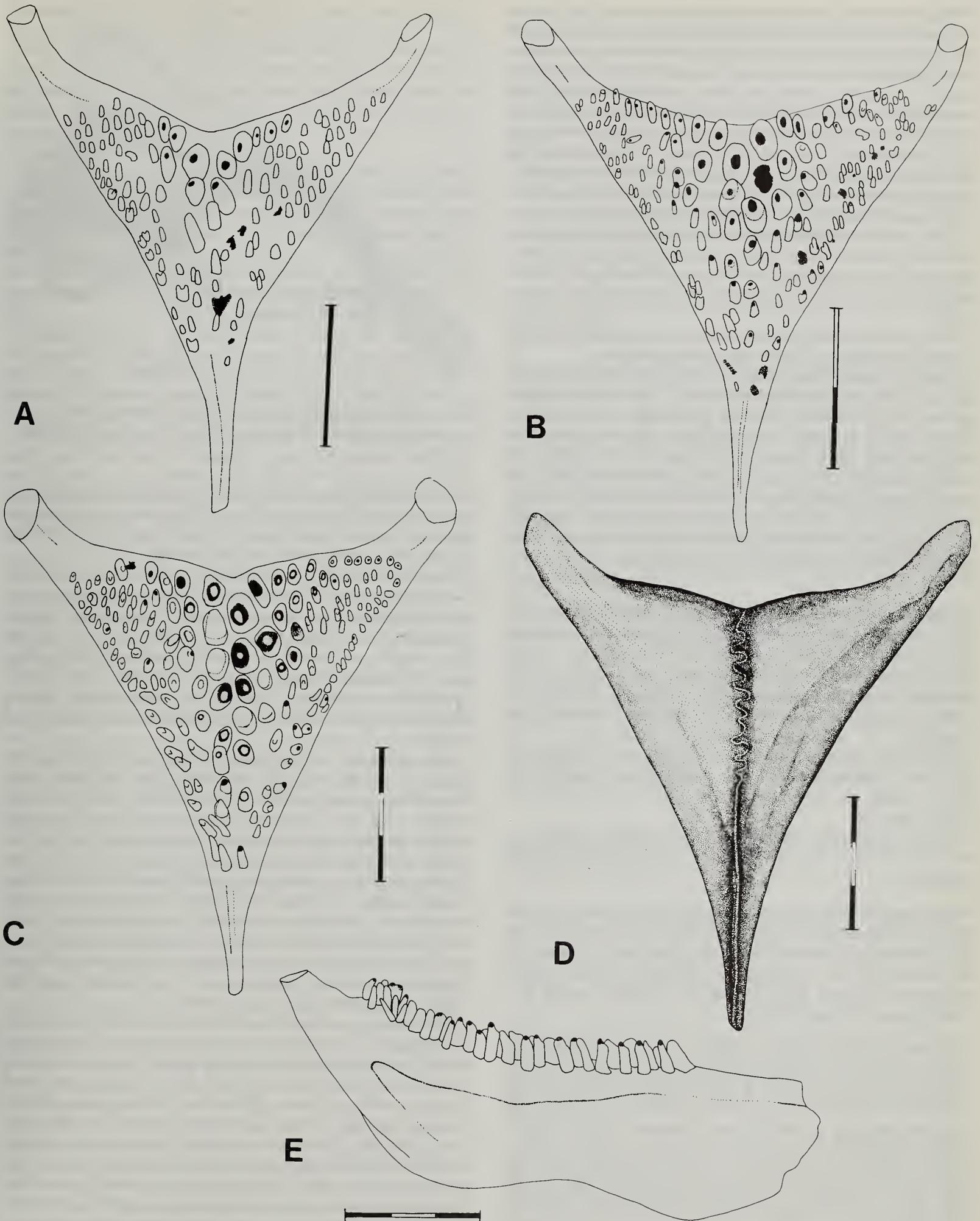


Fig. 7. *Pharyngochromis acuticeps*. Lower pharyngeal bone and dentition from A: a specimen 27.5 mm S.L., B: a specimen 46.0 mm S.L. (both *ex* RUSI 21093), and C: a specimen 102.0 mm S.L. (*ex* RUSI 21317), all in occlusal view; D & E: ventral and lateral views respectively of bone C above. Scale in millimetres. Drawn by Elaine Grant.

dentigerous body. In fishes less than 40 mm S.L. this part of the bone is not noticeably enlarged but above that size, and when compared with, for example, specimens of *Astatotilapia*, *Chetia* and *Serranochromis* (*Serranochromis*) species the bone is distinctly coarser and more massive. Indeed, that comparison can be extended to include certain species of *Serranochromis* (*Sargochromis*) such as *S.(S) gracilis* and *S.(S.) greenwoodi*. In a few individuals of *Pharyngochromis acuticeps* over 75.0 mm S.L., the enlargement can approach or slightly exceed that in comparable sized or even larger *S.(S.) coulteri* (see figs in Greenwood, 1979 and 1984).

The articular horns of the lower pharyngeal bone are generally short and stout, but as with the body of the bone (and usually correlated with the degree of hypertrophy in that region) there is some intraspecific variability in their stoutness.

The suture joining the two halves of the bone can be straight and simple, or more often, deeply sinuous.

The lower pharyngeal teeth and changes in their form and size have already been described (see p. 38). It only remains to note that even within one size group, and within a single locality, there is some variability both in the number of enlarged teeth in the median rows and in the degree of molarization shown by these teeth. Greatly enlarged, and much flattened molariform teeth such as occur in many species of *Serranochromis* (*Sargochromis*), are not found in *P. acuticeps*, and only rarely are all the teeth in the row next to each median row enlarged with mammilar crowns (see p. 38).

Vertebral column. Counts were obtained from radiographs of 68 specimens, including the lectotype and one paralectotype of the species, and the holotypes of *Chromis jallae*, *Pelmatochromis multiocellatus* and *Pelmatochromis darlingi*. The geographical range of these various specimens includes the Okavango region, the Zambezi and Save-Runde systems, and Angola.

The total count (excluding the fused PU_1 and U_1 centra) is 28–31 with a distinct mode at 30; it comprises 13 (rare) to 16 (rare), mode 14, abdominal centra and 14–16 (mode 15) caudal elements.

From this sample it was not possible to indicate whether or not any correlation exists between locality and vertebral number.

Neurocranium. There is no intraspecific variability in skull form, which is similar to the neurocranium in *Serranochromis* (*Sargochromis*) species except that, unlike most members of the subgenus, the neurocranial apophysis for the upper pharyngeal bones is not enlarged in *Pharyngochromis* (see Greenwood, 1979, and Fig. 8).

Coloration. Information is available on live coloration only for specimens from the Okavango swamps (personal observations) and certain localities in the Zambezi and Save-Runde systems (*qv.* Jackson, 1961; Jubb, 1967: 171 and plate 46 [original painting in the Albany Museum]; Bell-Cross & Minshull, 1988: 248 and plate 15, a darkened reprint of Jubb's plate). Since there is apparently no obvious difference in the live colours of fishes from the Zambezi, Save-Runde and the Okavango systems, the description which follows is based on those sources.

The ground colour on the flanks and caudal peduncle in adults and juveniles of both sexes ranges from silvery-grey (darkest dorsally) to pearly blue-grey, with an overlying

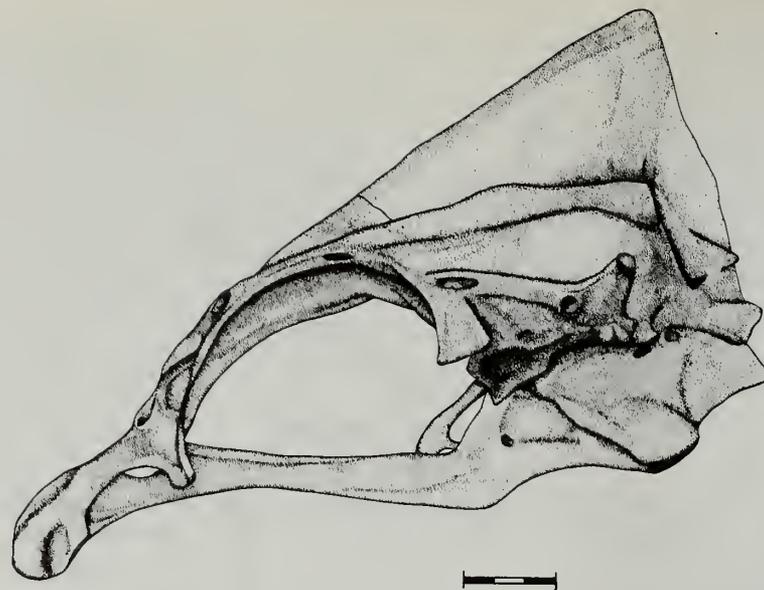


Fig. 8. *Pharyngochromis acuticeps*. Outline drawing of the neurocranium in left lateral view. Scale: 3 mm. Drawn by Elaine Grant.

greenish-golden sheen, and shades dorsally to a darker blue-grey, ventrally to a pearly silver. The cheeks are greenish-golden, and in females and juveniles the branchiostegal membrane is pearly silver, the lips greyish.

In adult males the scale centres on the flanks and upper two-thirds or more of the caudal peduncle are deep maroon; in breeding livery this colour extends to the scale edge, giving a purplish sheen to the upper part of the body. Such fishes have brightly iridescent blue-green (almost turquoise) lips and the branchiostegal membrane is dusky. Jubb (1967), presumably describing Zambezi or Save-Runde fishes, records that the forehead in breeding males assumes a claret colour.

Depending on the emotional state of the individual, the body and caudal peduncle are crossed, at least over their dorsal three-quarters or half, by 8 to 10 dusky bars, often with the upper halves of one or two bars approaching and virtually fusing with one another ventrally. In this way the otherwise well-spaced and regular barred pattern is broken by near V-shaped marks. An interrupted and horizontal dusky stripe is often present, running mid-laterally along the body from immediately behind the operculum to the caudal fin origin where it expands slightly to form a rounded terminal spot. A dark lachrymal stripe passing through the eye and onto the dorsum is sometimes present, and is continued ventrally behind the posterior tip of the maxilla.

The dorsal fin membrane is light greenish-grey, the lappets and margin of the soft fin are bright orange. Immediately below the orange there is a thin white band, particularly noticeable on the spinous part of the fin. Below this band there is a wider and more diffuse band of dark green-grey to charcoal pigment which is also most intense over the spiny part of the fin. The entire or greater part of the dorsal fin membrane carries rust-red to brownish-orange spots. These are most clearly defined and numerous on the soft part of the fin, whereas on the spinous part the spots generally coalesce into streaks or blotches. These markings are most intense in sexually active males.

The pelvic fins are hyaline to very pale lemon-yellow, but with the membrane between the spine and the first two

branched rays dusky in adult males; in sexually active males the whole fin is black or dusky.

The caudal fin is hyaline to pale yellow, often with a slightly dusky margin, especially posteriorly, and with numerous very dark orange or red, near rusty spots over its proximal half. These spots, like those on the dorsal fin, intensify in breeding males.

The pectoral fins are hyaline.

The anal fin is hyaline with a rosy-pink margin in adult males. Both sexes have orange spotted anal fins, but the spots are brighter, larger and more numerous in adult males. There is extensive intraspecific variability in the number and size of the spots, especially in males, but none is ever a true ocellus; that is, the central coloured area is not surrounded by a concentric and transparent band (see Greenwood, 1979: 275).

Judging from the live and recently preserved material I have examined, the coloured centre of each spot, at least in adult males, is usually circumscribed by a very narrow, dark margin. It also seems likely that the margin is only present in adult males, but this observation requires confirmation.

As noted previously, the number and arrangement of anal spots in *P. acuticeps* is variable, with the number ranging from as many as eighteen small spots irregularly dispersed over the entire fin, to as few as three or four large spots in a roughly triangular configuration (*cf.* plate 46 in Jubb, 1967, with fig. 151 in Poll, 1967). Other combinations are not uncommon; for example, amongst Okavango fishes there can be up to ten spots arranged in two approximately horizontal and parallel rows, a similar number of spots aligned in three roughly parallel and posteroventrally sloping rows, or a basically neat and linear pattern but with some randomly distributed spots as well.

From the fresh and preserved material examined, it was not possible to establish any clear-cut correlation between geographical locality and the type or pattern of spots present. Few, that is two or three, and large spots were not found amongst fishes from the Okavango region, and numerous, small irregularly arranged spots were not recorded from the small sample of Angolan fishes available (see p. 48, Discussion).

There is some indication that, in the Okavango and several Zambezi populations, the number of spots may increase with the size of the individual, and that the spots are less obvious in small fishes. However, in the three males from Lake Calundo, Angola, which I examined, there are only three spots in individuals of a size (57.0–71.0 mm S.L.) at which there would be many more in specimens from the Okavango system. But, the spots in the Lake Calundo fishes were much larger than those seen in any Okavango specimens, and thus, in terms of their value as signals to the female, may be of equivalent effectiveness to the more numerous markings in the Okavango fishes (see Hert, 1989, for a discussion on the function of anal markings in mouth-brooding cichlids).

The coloration of preserved material. The ground colour of the body shades from greyish-brown dorsally to fawn ventrally, and is darkest on the dorsum of the head. The darkly pigmented scale centres are obvious as, in most specimens, are the vertical and horizontal markings on the flanks and caudal peduncle (see p. 46), and the lachrymal stripe with its narrow posterior continuation running behind the posterior tip of the maxilla.

Fin maculations (including the anal fin spots) are dark

brown, the narrow black margin to the anal spots usually visible under low magnification. In long-preserved specimens, especially those fixed and kept in alcohol, the anal fin markings are difficult to detect, as are the maculations on the other unpaired fins.

In adult males the pelvic fins are dusky, the extent of the pigmentation depending on the fish's level of sexual activity (see above).

The lappets of the spinous dorsal fin, and the margin of its soft part are colourless and thus become continuous in preserved specimens with the area of the underlying white band visible only in live or fresh specimens.

BIOLOGY

Apart from detailed papers by Balon & Muyanga (1974) and Hustler & Marshall (1990) on respectively age and growth, and population dynamics of *P. acuticeps* in Lake Kariba only generalized accounts of the species' biology are available, and then mainly for fishes also from the Zambezi system (Jackson, 1961; Kenmuir, 1983; Bell-Cross & Minshull, 1988). These accounts, supplemented by personal observations on fishes in the Okavango system, indicate that *P. acuticeps* is a highly eurytopic species, inhabiting fast and slow flowing waters as well as open lagoons, small dams and other artificial impoundments, including the rocky shore-line of Lake Kariba.

Trophically *P. acuticeps* is an omnivorous carnivore which includes small fishes as well as insects and crustaceans in its diet.

Little is on record about the species' reproductive biology except that it is a female mouth-brooder and that the male makes a small sandscrape nest in shallow water (Jubb, 1952; Bell-Cross & Minshull, 1988). Judging from the Okavango material examined, females are sexually mature at a standard length of about 60 mm, and males at about 65 mm.

DISTRIBUTION

Pharyngochromis acuticeps, in its various synonymic guises, has been recorded from the Zambezi system in Zambia and Zimbabwe; the Save-Runde system, the Okavango river and its delta swamp system; Lake Calundo, a waterbody associated with an Angolan tributary (Luena river) of the upper Zambezi; from an unknown locality in Angola (the types of the species) and, also in Angola, from the Lucala river, a northern tributary of the Quanza river (Boulenger, 1915; Barnard, 1948a; Jackson, 1961; Poll, 1967; Jubb, 1967; Jubb & Gaigher, 1971; Skelton *et al.*, 1955; Bell-Cross & Minshull, 1988).

Jubb's (12967: 47 & 171) record of the species (as *Haplochromis darlingi*) from the Limpopo river, repeated by Greenwood (1979: 311), is probably a *lapsus*. I have been unable to locate material from that source in any of the museums with which Jubb was associated, and neither has any material been collected from the Limpopo system in recent years. Doubt is also cast on Jubb's Limpopo record by Bell-Cross & Minshull (1988), who note that the presence of

the species '... south of the Zambezi on the East Coast needs confirmation'.

Pharyngochromis acuticeps has been recorded (as *Pelmatochromis welwitschi*) from the Kuso river, Cunene drainage, Angola, by Pellegrin (1936). Poll (1967: 313), who considered Pellegrin's material to be misidentified *Haplochromis darlingi*, accepted this record. However, there is no indication that he examined Pellegrin's specimens, and I have been unable to locate them. Since no further material of *Pharyngochromis acuticeps* has been collected from the Cunene river (Greenwood, 1984; Bell-Cross & Minshull, 1988), and until it is possible to examine Pellegrin's fishes, the presence of the species in that system should be considered as uncertain but not improbable (see Bowmaker *et al.*, 1978: 1194–9, and fig. 8).

REVISED GENERIC DIAGNOSIS FOR *PHARYNGOCHROMIS*

Information derived from the large number of specimens now available, and the consequent knowledge of intrageneric variability, requires some modification to the original diagnosis and description (Greenwood, 1979: 310–311; 316), *viz.*:

Body depth: variable, from 27 to 41% of standard length.

Cheek: with 4–6 (rarely 3) horizontal rows of scales.

Squamation: Lateral-line with 31–36 scales (modal range 32–34), the last 5–7 (rarely 4 or 8) pored scales of the upper lateral-line separated from the dorsal fin base by one large and one small scale; 15, rarely 16 scales around the caudal peduncle.

Dorsal fin: with 14–16 (mode 15) spinous and 11–13 (mode 12), rarely 10 or 14, branched rays. Anal fin with 3 spinous and 8 or 9 (no distinct mode) branched rays.

Anal fin spots: variable in number (from 3 or 4 large to 18 small spots) and in arrangement (from regular and linear to irregularly scattered). Vertebrae (excluding the urostylel centrum): 28–31, comprising 13 (rare) to 16 (rare), modally 14, abdominal and 14–16 (mode 15) caudal elements.

Other features in the original description of the genus remain unaltered.

DISCUSSION

The discussion includes comments on the generic placement of *Chetia brevis* Jubb, 1968, and the status of that genus.

On an intracontinental scale, *Pharyngochromis acuticeps*, as here construed, has a wide and disjunct distribution, essentially one involving the Okavango, Zambezi and Quanza river systems. Even within one of those extensive systems, the Zambezi, there is a major barrier to dispersion, the Victoria Falls, and there could well be other unrecognised physical or biotic barriers in each system.

As with many other allopatrically distributed cichlid species, the *P. acuticeps* pattern raises questions concerning the conspecific status of the various geographically circumscribed elements involved. In past geological periods the major river systems, or their forerunners, in which *P. acuticeps* occurs have been interconnected (Bowmaker *et al.*, 1978), and their contemporary fish faunas seem to share a number of species

(Poll, 1967; Jubb, 1967; Jubb & Gaigher, 1971; Bowmaker *et al.*, 1978; Greenwood, 1984; Skelton *et al.*, 1985). Those shared elements, which in effect are morpho-species, are assumed to be conspecific, but they could also be aggregates of vicariant sibling sister-species whose status has not been recognised. In part, this problem stems from a lack of biological information (especially ethological data), in part from the particular species concept employed by the workers concerned, and partly from a reticence to burden the literature with specific names for taxa supposedly, and perhaps even truly indistinguishable on morphological grounds. It is against that background that I would consider the seemingly monotypic status of *Pharyngochromis*.

If one takes into account the present physical separation, and thus effective extrinsic reproductive isolation between populations (*sensu lato*) of *P. acuticeps* living above and below the Victoria Falls, and the physical separation of the populations (again *sensu lato*) inhabiting the Zambezi, Okavango and Quanza systems, then these could well meet the requirements of the evolutionary species concept. That is, a lineage of ancestor-descendent populations reproductively isolated from other such lineages, and with its own evolutionary tendencies and historical fate (see various discussions of this concept in Otte and Endler, 1989).

The evolutionary species concept could also be applied at a lower level of geographical isolation if, for example, different populations within a single river system were reproductively isolated from one another by some ecological or abiotic factor.

For the moment, however, there are insufficient data available for *P. acuticeps* to establish, on the grounds of extrinsic reproductive isolation, whether or not the evolutionary species concept is applicable either to the populations occupying the three major areas of its distribution (see above) or to populations within a single river system.

Likewise, there are insufficient data to test the applicability of the phylogenetic species concept, *viz.* that a species is '... an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent' (Cracraft, 1989).

Despite the extent of 'intraspecific' variability manifest by the *P. acuticeps* specimens described above, it has not proved possible to diagnose into irreducible clusters any particular group of specimens. The very unequal sizes of the samples from different localities is one difficulty here, as is the absence of detailed information on the coloration of sexually active males from the various localities. Since male coloration in mouth-brooding haplochromine cichlids is likely to be an important component of a species specific mate recognition system, *sensu* Paterson, 1985 (see Greenwood, 1974; 1981; 1991), that omission is a serious one. So, too, is the lack of detailed information on possible population or geographical differences in the size, pattern and colours of anal fin spots in males, or possibly even in both sexes (see p. 47). In addition to their use for defining a phylogenetic species, such data would be essential if the 'Recognition' species concept of Paterson (1985) were to be utilized, *viz.* a species is the most inclusive population of individual organisms with a common fertilization system.

At one point in this study it seemed possible that the pattern and size of anal spots (see p. 47) could have some geographical correlation, but the range of variation in samples from the Okavango swamps, even within a single locality, seriously weakens that possibility. Nevertheless, the

combination of few and large spots seen in males from the small sample of Lake Calundo fishes (p. 47) is apparently unique, but the sample is too small to warrant its recognition, and naming, as a phylogenetic species on that basis alone.

Other seemingly diagnosable assemblages are provided by the samples from Kazungula, near the Victoria Falls (Zambezi system), and from the Popa rapids on the Okavango river. When compared with others from elsewhere in either river system, specimens from these localities have very small and sometimes deeply embedded scales laterally on the thoracic region. However, in both localities the water is fast-flowing and turbulent, and the substratum is composed mainly of large stones and rocks. Reduced and embedded thoracic scales are often (Trewavas, 1983), but not invariably (Greenwood, 1979) associated with such habitats. Thus, the thoracic squamation in these *P. acuticeps* populations may well be an ecophenotypic response to a rocky and turbulent habitat. Even if the character is genetically fixed, it could be an example of intraspecific parallelism in response to similar environments, and not an indication of the two populations being conspecific and distinct from other *P. acuticeps*. To establish the latter case would require the recognition of congruent synapomorphies uniquely shared by the two rapid-water populations. But, as with all other and physically isolated populations of *P. acuticeps*, none was detected.

Clearly a lot more information, both morphological and ethological, is needed before the present morpho-species *P. acuticeps* can be seen in its true biological perspective.

Perhaps the most realistic phylogenetic interpretation of this situation is to consider the current morpho-species an aggregate of at least five evolutionary species, namely the populations living above and below the Victoria falls in the Zambezi system, populations in the Quanza river (Angola) and those in the Save-Runde and in the Okavango systems. Unfortunately there is no satisfactory way to express that conclusion within the existing system and rules of formal taxonomic nomenclature. To use the category of subspecies is to contradict the evolutionary species concept, and at present it is impossible to provide diagnostic features for the five groups, other than their geographical circumscription, and thus formally establish them as phylogenetic species.

The phyletic interrelationships of *P. acuticeps*, be it a monotypic or a polytypic genus, have not been established more firmly by the additional data now available. The situation remains essentially the unsatisfactory one discussed in my earlier paper (Greenwood, 1979: 312), where interrelationships within the supposed lineage *Pharyngochromis*, *Chetia* and *Serranochromis* were considered.

Within that lineage, and as compared with *Serranochromis*, both *Chetia* and *Pharyngochromis* share the plesiomorphic condition of lower numbers of abdominal vertebrae, but *Pharyngochromis*, unlike *Chetia* and *Serranochromis*, has the apparently apomorphic condition of more than the last two or three pored scales of the upper lateral-line being separated from the dorsal fin base by only one large and one small scale (Greenwood, 1979: 271).

The genus *Chetia* has, since my 1979 paper, been enlarged by the addition of two species, *C. mola* of Balon & Stewart (1983) from the Zaire system, and the referral to it (Greenwood, 1984) of *Pelmatochromis welwitschi* Blgr (1898) from Angola. Also, I would now revise my earlier view (Greenwood, 1979: 307) that *Chetia brevis* Jubb (1968) should be excluded from the genus. That earlier opinion was based partly on Jubb's description of the anal markings in *C. brevis*

as a few large, ocellate spots, and in part on the fact that bicuspid outer jaw teeth are present in specimens of 86–89 mm standard length, a size at which only unicuspid teeth are present in the type specimens of the type species, *C. flaviventris* Trewavas (1961).

Recently I examined the holotype and additional specimens of *C. brevis* (housed in the Albany Museum) as well as colour transparencies of live fishes, and find that the anal spots are not ocellate, and are quite unlike the true ocelli in many haplochromine species (Greenwood, 1979: 274–5). Granted, the spots in *C. brevis* are larger, and fewer, than those in *C. flaviventris*, but judging from the situation in *Pharyngochromis acuticeps* (see p. 47) such variability can occur intragenerically and, if the latter taxon is truly monotypic, intraspecifically as well.

With regard to the dental morphology of *C. brevis*, further material of *C. flaviventris*, from the Limpopo system, shows that, unlike the situation represented in the type series, bicuspid teeth can persist in fishes up to a standard length of 80 mm.

Thus, there are no reasons for excluding *C. brevis* from *Chetia*, or, when its various anatomical and morphological characters are taken into account (see Jubb, 1968), for considering it conspecific with *C. flaviventris*.

Chetia welwitschi, known only from its holotype and two other specimens, all from Angola, appears to be more similar to *C. ventralis* than to *C. brevis*, and is readily distinguishable from *C. mola* whose massive pharyngeal jaws and dentition are unique within the genus (Balon & Stewart, 1983; Greenwood, 1984). Indeed, in its hypertrophied pharyngeal jaws *C. mola* approaches the conditions seen in several *Serranochromis* (*Sargochromis*) species and exceeds those in others such as *S. (S.) greenwoodi* and *S. (S.) gracilis*. However, there is seemingly no reason for placing the taxon in that genus and subgenus (Balon & Stewart 1983), and in the present state of our knowledge about the fluviatile haplochromines, its place would seem to be in the genus *Chetia*.

The existence in *Chetia* of anatomical and dental specializations associated with mollusc eating (*C. mola*) and piscivory (*C. flaviventris* and possibly *C. welwitschi*), and similar specializations occurring in each subgenus of *Serranochromis*, raises interesting, but for the moment untestable speculations about the phyletic relationships of the three taxa.

The problem is complicated by the fact that both subgenera of *Serranochromis* share the apomorphy of increased numbers of abdominal vertebrae (Greenwood, 1979), but there is no currently identified synapomorphy uniquely shared by *Chetia* and *Serranochromis*.

Indeed, as presently construed, there is no autapomorphic feature characterizing *Chetia*. Previously, when that taxon was monotypic, the supposedly early appearance of an entirely unicuspid jaw dentition, and possibly the reduced number of inner tooth rows in both jaws, were considered as generic autapomorphies (Greenwood, 1979). With the inclusion of at least *C. brevis*, the early appearance of a unicuspid dentition can no longer retain its status as a generic apomorphy, a loss which, anyway, would follow from the discovery of the relatively delayed appearance of such teeth in other populations of *C. flaviventris* (pers. obs. on Limpopo specimens in the RUSI and AMG collections). Since only large specimens of *C. mola* and *C. welwitschi* are known (Greenwood, 1984) growth related changes in their oral dentition cannot be checked. All four *Chetia* species do, however, show a reduction in the number of inner tooth rows in both

jaws, but the polarity of that character is difficult to ascertain.

In other words, in a phylogenetic context it seems that *Chetia* could be a catch-all category for those fluvatile haplochromines with non-ocellate and multimaculate (or sparsely spotted) anal fins, but which do not have the apomorphies characterizing *Serranochromis* (increased number of abdominal vertebrae) or *Pharyngochromis* (the increased number of posterior upper lateral-line scales separated from the dorsal fin base by one large and one small scale).

The reality of *Pharyngochromis* as a distinct and monophyletic lineage within the supposed *Serranochromis*—*Chetia* phyletic assemblage (Greenwood, 1979) rests for the moment on the lateral-line scale character combined with the absence of other derived features shared uniquely with either *Serranochromis* or any species of *Chetia*. An unsatisfying and unsatisfactory situation, but one frequently encountered within the Cichlidae. In my view, the situation would not be improved by placing *Pharyngochromis* in the currently indefinable genus *Chetia*, with one of whose species (*C. brevis*) *P. acuticeps* bears a superficial resemblance (Jubb, 1968), but does not share the lateral-line/dorsal fin base scale character.

Interestingly, but at present inexplicably, no *Chetia* species coexists with *Pharyngochromis acuticeps* or, indeed, even occurs within the same drainage system. In contrast, there is complete distributional overlap, except in the Save-Runde system, between the *Serranochromis* subgenera and *Chetia*, as well as an overlap between *Serranochromis* and *Pharyngochromis acuticeps* (Bell-Cross & Minshull, 1989); only *P. acuticeps*, however, occurs in the Save-Runde system.

Appendix

The principal morphometric and meristic features of material from the Zambezi and Okavango systems, the somewhat

atypical Zambezi population (see p. 49) from Kazungula near the Victoria Falls, (Table 1), and of the type specimens examined (Table 2).

Abbreviations and symbols used in these tables are:

+	Expressed as a percentage of standard length
*	Expressed as a percentage of head length
A:	Anal fin formula
Cp:	Caudal peduncle length
Cp l/d:	Length-depth ratio of caudal peduncle
D:	Dorsal fin formula
Gr:	Outer gill-rakers on the first ceratobranchial
Interorb:	Least interorbital width
Preorb:	Depth of preorbital (ie. lachrymal bone)
Ll. scales:	Scales in the lateral series

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Table 1

	Zambezi system Excluding Kazungula specimens n = 28 Size range 32.5–133.0mm SL		Okavango system n = 58 Size range 27.5–102.0mm SL		Kazungula (Zambezi system) n = 5 Size range 53.0–75.0mm SL	
		M		M		M
Depth ⁺	27.6–35.7	34.3	30.8–40.6	35.5	30.2–35.7	32.4
Head ⁺	30.7–36.9	33.7	31.0–37.7	33.8	34.7–36.7	35.9
Preorb.*	14.7–25.6	19.6	14.3–24.2	20.5	15.8–20.8	18.5
Interorb.*	15.0–25.6	19.5	14.3–22.9	19.9	15.4–20.8	17.7
Snout*	28.0–37.2	32.2	25.0–36.7	32.2	31.6–35.6	33.5
Eye*						
<80.0 mm S.L. (n=20)	27.3–36.0	30.9	<70.0 mm S.L. (n=31)	31.8	29.2–31.6	29.6
>80.0 mm (n=8)	22.2–29.3	25.6	>70.0 mm S.L. (n=27)	28.3		
Check*	16.0–31.4	23.9	17.6–27.0	24.7	20.5–22.9	21.5
Lower jaw*	34.8–48.9	41.2	35.7–43.6	39.7	37.5–40.0	38.4
Cp.†	15.9–21.0	17.9	15.4–21.8	17.6	16.9–19.5	18.1
Cp.l/d	1.2–1.7	Mode 1.5–1.6	1.2–1.8	Mode 1.5–1.7	1.4–1.8	
D.	XIV or XV (Mode XV)		XIV–XVI (Mode XV)		XIV or XV	
	10–12 (Modes 11 & 13)		11–14 (Mode 12)		11 or 12	
A.	III 8 or 9 (Mode 8)		III 7–10 (Mode 8)		III 8	
Ll.sc.	30–34 (Modes 32 & 33)		31–35 (Mode 33)		32–34	
Cheek scales	4–6 (Modes 4 & 5)		4–5 (Mode 4)		3 or 4	
Gr.	7–10 (Mode 9)		7–12 (Mode 10)		8 or 9	

Table 2

	<i>Chromis jallae</i> Holotype, 59.0mm SL	<i>Pelmatochromis darlingi</i> Holotype, 84.5mm SL	<i>Pelmatochromis multiocellatus</i> Holotype, 97.0mm SL	<i>Chromis acuticeps</i> Lectotype, 59.5mm SL Paralectotype, 68.0mm SL
Depth ⁺	28.8	34.3	34.0	32.0
Head ⁺	30.5	34.3	35.9	37.0
Preorb.*	22.2	20.7	18.6	15.9
Interorb.*	16.6	20.7	20.1	20.5
Snout*	33.3	33.7	33.1	29.5
Eye*	27.8	29.3	25.9	27.3
Cheek*	25.0	27.5	24.4	22.7
Lower Jaw*	36.1	41.4	43.1	40.9
Cp. ⁺	21.8	17.5	15.5	18.5
Cp. l/d	1.8	1.4	1.2	1.6
D.	XV, 10	XV, 11	XVI, 10	XV, 11
A.	III, 8	III, 8	III, 9	III, 9
Ll.sc.	32	ca.30	32	31
Ck.sc.	6	5	5	4
Gr.	8	10	9	10

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