

**PRELIMINARY OBSERVATIONS ON THE RELATIONSHIPS OF  
*BARBUS* SPECIES FROM CAPE COASTAL RIVERS, SOUTH AFRICA  
(CYPRINIFORMES: CYPRINIDAE)**

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**ABSTRACT**

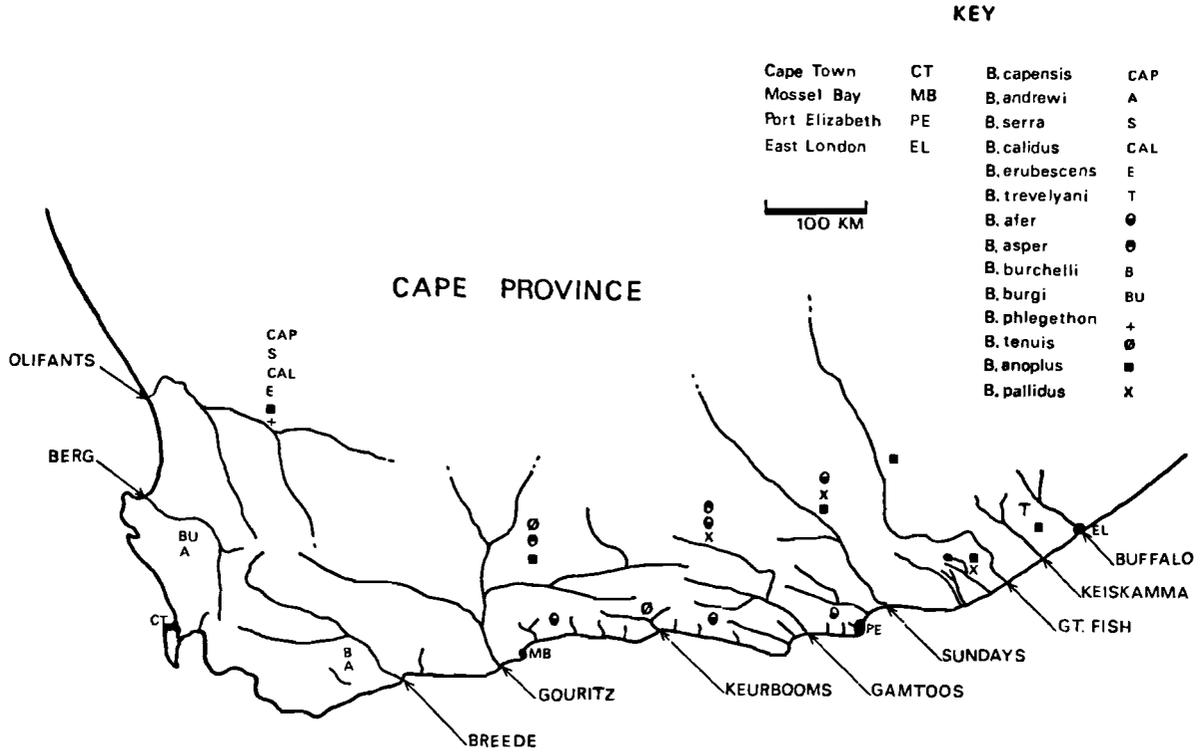
Observations on the phylogenetic relationships of *Barbus* species from the southern Cape Province are made in the light of new data on the post-cranial axial skeleton and other osteological and anatomical features. Particular attention is paid to the relationships of the 'red fin' *Barbus* species, and new evidence on the problematical relationships of the rare African cyprinid species *Oreodaimon quathlambae*, is presented.

**INTRODUCTION**

Species of the cyprinid genus *Barbus* form the major element of the indigenous fish fauna of the southern Cape coastal drainage system. There are, at present, 14 recognized *Barbus* species from the region (Table 1, Figure 1), 12 of which are endemic. Barnard (1943) provided the first thoughts on the presumed relationships of the taxa in this southern Cape freshwater ichthyofauna. Jubb (1964, 1965, 1967, 1968) extended and revised Barnard's taxonomy and has, briefly, provided the most recent considerations on the subject of relationships of the species. Certain zoogeographical aspects have been discussed by both these authors and by Farquharson (1962) and Gaigher & Pott (1973). However, it would appear that many of these 'relationships' are based on overall similarity of form, which as shown by Hennig (1966) does not necessarily reflect true phyletic relationship.

Almost all previous attempts to clarify the relationships of various African *Barbus* species are derived from the classificatory keys of Boulenger (1911), which were based primarily on patterns of scale radii, and secondarily on the form of the last unbranched dorsal ray. Recent investigations on species of the genus, e.g. Greenwood (1962, 1970) on certain of the smaller species, and Banister (1973) on certain of the larger species, have indicated that the situation is more complicated than is apparent from Boulenger's work. The lack of osteological and other critically penetrating studies still leaves us at the stage voiced by Greenwood (1962) when he stated 'The taxonomy of *Barbus* has not yet reached the degree of refinement where it is possible to evaluate the phyletic significance of particular taxonomic characters'.

My recent research has been aimed at the clarification of the taxonomy of the small *Barbus* species, known as 'red fins', from the southern Cape coastal drainage. Comparative studies on *Barbus* with regard to the post-cranial axial skeleton have shed some light on possible relationships of some of the species studied.



**FIGURE 1**  
**The southern Cape Province coastal drainage system, showing the occurrence and distribution of *Barbus* species.**

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TABLE 1

*Barbus* species and their distribution in the south Cape coastal drainage

<i>Barbus capensis</i>	Endemic to Clanwilliam Olifants River System
<i>Barbus andrewi</i>	Endemic to Berg and Breede River Systems
<i>Barbus serra</i>	Endemic to Clanwilliam Olifants River System
<i>Barbus calidus</i>	Endemic to Clanwilliam Olifants River System
<i>Barbus erubescens</i>	Endemic to Twee River and tributaries, Clanwilliam Olifants River System
<i>Barbus trevelyani</i>	Endemic to Keiskamma and Buffalo River Systems, Eastern Cape Province
<i>Barbus afer</i>	Endemic to coastal rivers east of Gouritz River System as far as Sundays River System, Eastern Cape Province
<i>Barbus asper</i>	Endemic to Gouritz and Gamtoos River Systems
<i>Barbus burgi</i>	Endemic to Berg River System and adjacent streams
<i>Barbus burchelli</i>	Endemic to Breede River System and adjacent streams.
<i>Barbus phlegethon</i>	Endemic to Clanwilliam Olifants River System
<i>Barbus tenuis</i>	Endemic to Gouritz River System and Keurbooms River System*, South Cape Province
<i>Barbus anoplus</i>	Clanwilliam Olifants, Gouritz, Sundays, Fish River Systems, widespread elsewhere in inland waters of the Republic of South Africa
<i>Barbus pallidus</i>	Gamtoos River System eastwards to the Kowie River System near Grahamstown. Also reported from Natal and Transvaal

\* New distribution record.

#### MATERIALS AND METHODS

Specimens used in this study are preserved and housed in museums as detailed in the appendix on page 410. Radiographs of specimens were made and the following meristic counts on the post-cranial axial skeleton were taken (Figure 2).

1. Total vertebral count. Includes the weberian apparatus as four elements and the ural centrum ( $pu_1 + u_1 + u_2$ ) as one.
2. Precaudal vertebrae. Anteriorly including the weberian vertebrae as four elements, all vertebrae not possessing a closed haemal arch.
3. Caudal vertebrae. All vertebrae posterior to, and including, the first centrum with a closed haemal arch.
4. Dorsal pterygiophore intercept (DPI) count. The vertebral count up to and including that vertebra opposite, or anterior to, the spine of the leading dorsal pterygiophore.
5. Anal pterygiophore intercept (API) count. The vertebral count up to and including that vertebra opposite, or anterior to, the spine of the leading anal pterygiophore.
6. Supraneural bones.

Pharyngeal bones were removed by dissection and defleshed mechanically after soaking in buffered trypsin solution. In addition to the above preliminary osteological observations, traditional morphological characteristics were included in my considerations.

#### RESULTS AND DISCUSSION

Figures 3–6 record diagrammatically a summary of the results of the post-cranial skeletal counts. Studies on vertebral counts in fishes (e.g. Bailey & Gosline 1955; Garside 1966) have shown that environmental parameters such as temperature and salinity can affect the meristic characters. Barlow (1961) concluded that those parameters which retard the rate of embryological development are associated with high numbers of meristic elements and *vice versa*.

Several species (e.g. *B. afer*, *B. asper* and *B. calidus*) are well represented both in numbers of specimens and in geographical range and the values recorded for them probably indicate the range of intra-specific variation likely to be encountered for most *Barbus* species. The variation in vertebral counts for these species is generally from three to five centra, with six being the maximum recorded for any *Barbus* species examined. Thus the ranges for the counts shown in Figures 3–6 may be considered as a reasonably accurate representation of the various species groups from southern Africa.

The data for each species examined was tabulated and summarized in Figures 3–6 within the following broad classification groups after Boulenger (1911):

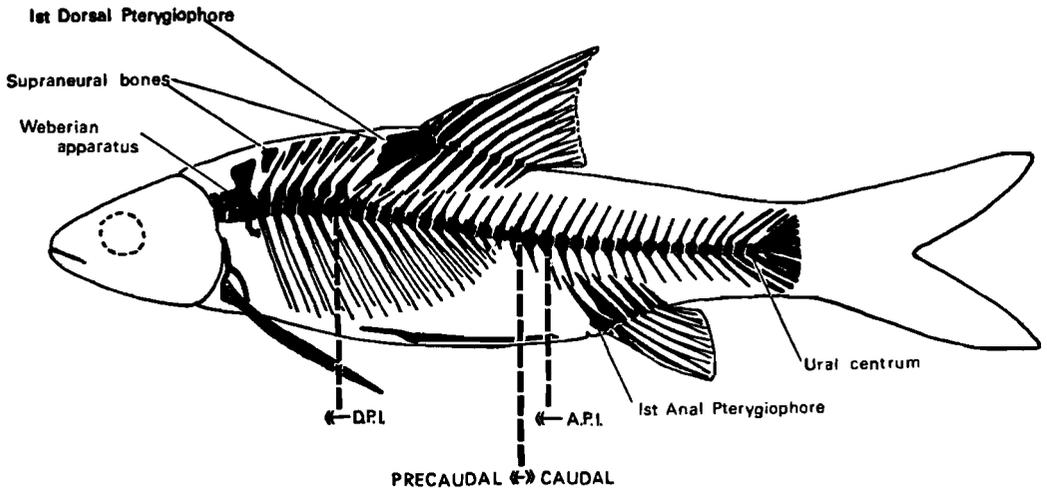


FIGURE 2

Diagram to show the post-cranial axial skeleton of *Barbus* and relevant features in the method of taking meristic counts in this study.

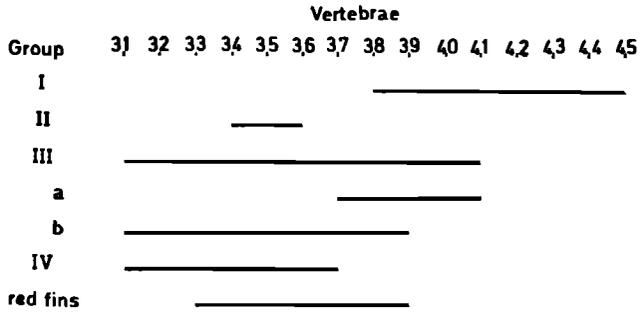


FIGURE 3  
The range of the total number of vertebrae in certain groups of African *Barbus*.  
(In Figures 3-6, see Appendix on p. 410 for definition of groups.)

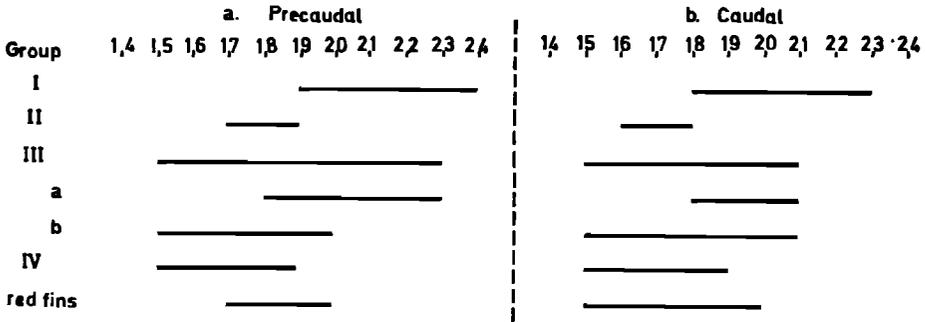


FIGURE 4  
The range of the number of (a) precaudal, and (b) caudal, vertebrae in certain groups of African *Barbus*.

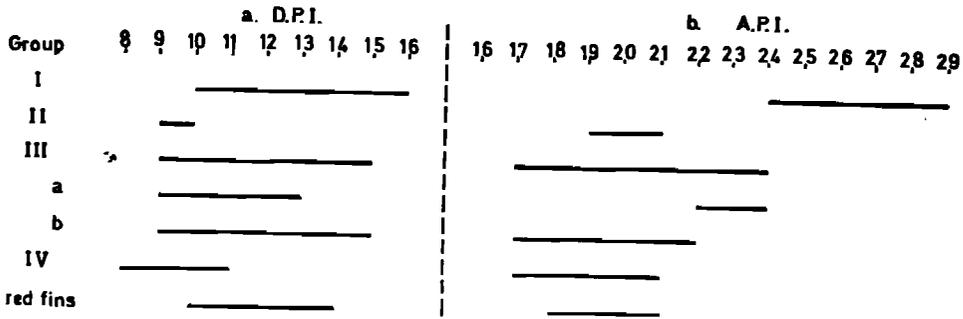


FIGURE 5  
The range of the number of vertebrae (a) before the dorsal fin (D.P.I.) and (b) before the anal fin (A.P.I.), in certain groups of African *Barbus*.

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- I Scales with parallel striae, dorsal unbranched ray bony and smooth.
- II Scales with radiating striae, dorsal unbranched ray bony and smooth.
- III Scales with radiating striae, dorsal unbranched ray bony and serrated. This group is further arbitrarily subdivided into (a) 'large' species with adults exceeding 150 mm standard length and (b) 'small' species with adults of less than 150 mm standard length.
- IV Scales with radiating striae, dorsal unbranched ray soft and not serrated. (The 'red fin' species within this group are separately listed.)

From Figure 3 it is clear that although the total vertebral range for all the *Barbus* species examined is 31–45, the higher counts (38–45) are from species in Group I. The only species of this group from the southern Cape coastal drainage system is *B. capensis*, endemic to the Clanwilliam Olifants River system.

The vertebral data for *B. capensis* and *B. holubi* from the Orange River system support the opinion of Barnard (1943) and Jubb (1964–1968) that they are probably closely related. The samples on hand (Figure 7) show the two species to have similar overall vertebral counts, but differences are noted in the DPI and the supraneural counts. The difference in the position of the dorsal fin of these two species, as recorded by Barnard and Jubb, is strongly correlated with the number of vertebrae and would appear to be a consequence of such differences.

Lack of suitable specimens has precluded my obtaining data for *B. kimberleyensis*, a species from Group I of the Orange River system, also considered closely related to *B. capensis* and *B. holubi* (Jubb personal communication). Petrick (1969) records the number of vertebrae from 'several specimens' of *B. kimberleyensis* as varying from 42 to 44, which agrees closely with that of *B. capensis* and *B. holubi*. The overall vertebral counts for these three species are collectively not only similar to each other, but as shown in Figure 8, are also higher than for other species of Group I from the southern African region examined, viz. *B. marequensis*, *B. natalensis* and *B. polylepis*. Further examination of the vertebral data indicates that this is a reflection of a difference in precaudal vertebrae before the dorsal fin (DPI) (Figure 8), a fact which may be of phyletic significance.

Classification groups II, III and IV are all characterized by radiately striated scales, but differ in the form of the last dorsal unbranched ray. Observations on local populations of several *Barbus* species with serrated dorsal rays show that there is frequently a tendency towards a decrease and often a total loss of such serrations. These groups, therefore, may not be monophyletic, but this can be determined only by a careful study of individual species.

There are no representatives of Group II from the southern Cape coastal drainage system. Group III is represented by both 'larger' species (*B. andrewi* from the Berg and Breede River systems and *B. serra* from the Olifants River system) and 'smaller' species (*B. calidus* and *B. erubescens* from the Olifants River system and *B. trevelyani* from the Buffalo and Keiskamma River systems in the Eastern Cape Province).

In overall shape, size and coloration, *B. andrewi* and *B. serra* are similar. They may be distinguished from each other by squamation differences and, of rather rare occurrence within the genus, six branched rays in the anal fin of *B. andrewi* as against the conservative five of *B. serra*. Barnard (1943:113) ventured to suggest that '*serra* and *andrewi* may be closely allied to one another', but perhaps more significantly, placed *B. andrewi* after *B. calidus* in a sequence

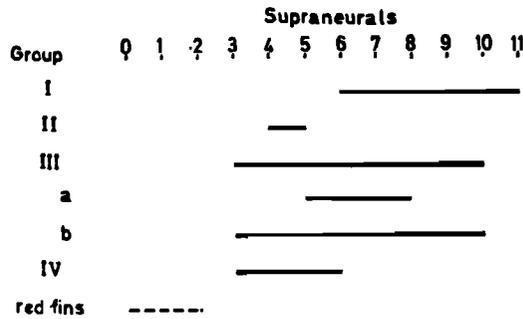


FIGURE 6  
The range of the number of supraneural bones in certain groups of African *Barbus*.

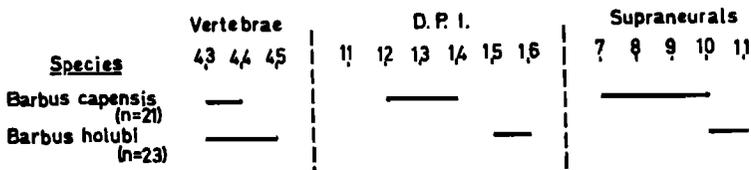


FIGURE 7  
A comparison of the total vertebral range, the number of vertebrae before the dorsal fin (D.P.I.), and the number of supraneural bones in separate samples of *Barbus capensis* and *Barbus holubi*.

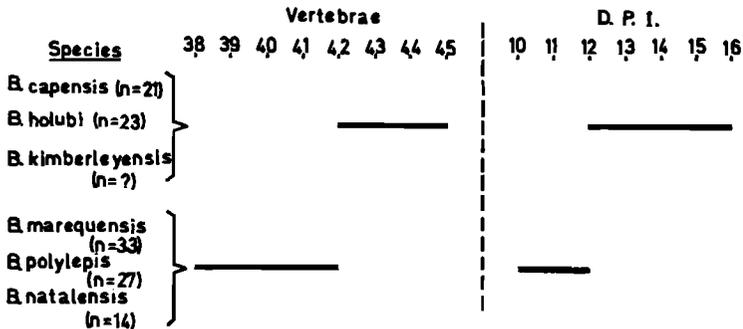


FIGURE 8  
A comparison of the total vertebral range and the number of vertebrae before the dorsal fin (D.P.I.) of two groups of *Barbus*.

apparently determined by common characters.

Jubb (1964–1968) considered *B. andrewi* and *B. serra* broadly related to *B. mattozi* of the Limpopo, Zambezi and certain Angolan rivers. This supposition is based largely on the fact that these are the only *Barbus* species in the southern African region from Group III which reach a large size. As indicated in Figures 3–5 these species show intermediate values of vertebral counts for the genus as a whole. It appears that these vertebral counts are lower than those for Group I mainly because of fewer vertebrae before the anal fin (Figure 5b: API). At the same time specific differences in the mode of vertebral counts between *B. andrewi*, *B. serra* and *B. mattozi* are observed (Figure 9). These specific differences, however, may be linked to differences in the number of vertebrae before the dorsal fin (Figure 9: DPI). Corresponding supraneural count differences between the species are also noted.

*Barbus calidus*, *B. erubescens* and *B. trevelyani* are smaller species of Group III from the southern Cape coastal drainage system. These species, together with *B. hospes* from the Orange River below Aughrabies Falls, show the highest vertebral counts of all the smaller *Barbus* species examined, irrespective of dorsal unbranched ray form. It has been hypothesized by Farquharson (1962) and Gaigher & Pott (1973), on account of the relict nature of distribution of these four species, that historically speaking they are derived from ancestral species of a similar former fauna. Although possibly inferred by these authors on account of present geographical distribution and certain common group characters, a monophyletic ancestry for these species is not to be presumed. Despite the similarities in overall vertebral counts, certain differences within the sub-counts occur, e.g. *B. hospes* is characterized by a high DPI and corresponding supraneural counts; *B. trevelyani* has fewer caudal vertebrae, etc., and the data provide little further information on the relationships of these species.

With the exception of *B. andrewi*, *B. calidus*, *B. erubescens* and a few Moroccan species, the species of *Barbus* in Africa are characterized by having, as a rule, five branched anal rays. In view of the predominance of the five-branched anal ray condition in *Barbus* it appears likely that the presence of six branched anal rays in certain species, including *B. andrewi* and *B. calidus*, represents a derived state. *B. erubescens* with a mode of seven branched anal rays probably shares a common ancestor with *B. calidus* (Skelton 1974b). *B. calidus* has previously been considered, on account of its similar red fin coloration, to be allied to the 'red fin' group of *Barbus* species from the southern Cape coastal drainage. Evidence to be presented below indicates that the species is not phylogenetically a true 'red fin' species. Taking into account the close geographical distribution of *B. calidus* and *B. andrewi* the possibility of relationship between these two species is attractive.

The remaining *Barbus* species from the southern Cape coastal drainage system are characterized by a flexible, non-serrated dorsal unbranched ray. Six of these species are endemic to the region and are characterized by having bright red markings at the bases of their fins, the colour also extending onto the fin membrane. The remaining two species, *B. anophus* and *B. pallidus*, are not endemic to the region, and are not characterized by red markings. *B. anophus* is distributed within the region in the Clanwilliam Olifants, Gouritz and Sundays rivers and from this latter river eastwards to Natal. It also occurs in the Orange and Limpopo River systems, the Kuiseb (South West Africa) and in Natal Rivers. *B. pallidus* occurs in the southern Cape coastal drainage from the Gamtoos eastwards to the Kowie River system near Grahamstown. It is

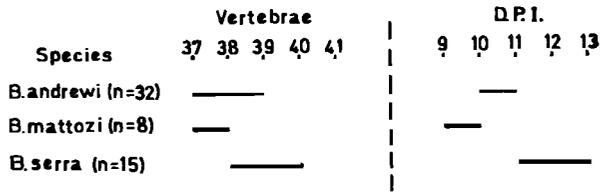


FIGURE 9

A comparison of the total vertebral count and of the number of vertebrae before the dorsal fin (D.P.I.) of three *Barbus* species: *B. andrewi*, *B. mattozi* and *B. serra*.

also reported from Transvaal tributaries of the Vaal and Limpopo Rivers and from the Pongola and Buffalo Rivers (Tugela River system) of Natal. However, the taxonomic status of populations from the Transvaal and Natal requires investigation (Jubb personal communication) and the recorded distribution may be misleading. Vertebral data for these two species are unexceptional within Group IV which, with a range of 31 to 37, generally shows fewer vertebrae than the other groups (Figure 3). With the exception of the 'red fins' to be discussed below, the post-cranial skeletal data for Group IV at present afford no indication of any clear correlations or relationships.

The most striking observation to be made from the post-cranial skeletal data is the absence of predorsal supraneural bones from the 'red fin' *Barbus* species as a group (Figure 6). *B. calidus* and *B. erubescens*, as already mentioned, are also characterized by a red fin-coloration but differ from the rest of the group in having greater anal branched ray counts, in the form of the dorsal unbranched ray and in possessing strong supraneural bones. The occasional appearance of one or two vestigial supraneurals in individuals of one or other 'red fin' species is, relative to the generalized *Barbus* (or even apparently, Cyprinid?) condition, a derived one. These findings lend considerable support to the theory that the 'red fins', with the exception of *B. calidus* and *B. erubescens*, are a monophyletic group.

The significance and function of the red markings on the fins of these fishes is not clear, but in view of the above observations the presence of the markings in two distinct lines probably indicates a convergent state.

In a detailed redescription and osteological account of the unusual and rare cyprinid, *Oreodaimon quathlambae*, from Drakensberg tributaries of Natal rivers, Greenwood & Jubb (1967) discussed the possible relationships of the species. The only definite conclusion reached by these authors with regard to the relationships was that the species was 'nearer to the Barbinae . . . than any other subfamily'. A noteworthy feature of the new genus *Oreodaimon* was that the pharyngeal bones have only two rows of teeth. Three rows of pharyngeal teeth are characteristic of the genus *Barbus*. It was also noted by Greenwood & Jubb that the vertebral number for *O. quathlambae* was higher than the available records for small radiately striated *Barbus* species.

Skelton (1974a) described the life colours of *O. quathlambae* and indicated that the species has markings on the bases of its fins somewhat like those in the 'red fins' of the southern Cape coastal drainage. Post-cranial meristic data for the 'red fin' species indicate that as a group

they have slightly higher vertebral counts than other small *Barbus* species with a flexible dorsal ray (Figure 3), another feature suggestive of relationship between the 'red fins' and *O. quathlambae*. However, the most compelling evidence for possible phylogenetic relationship between *O. quathlambae* and the 'red fins' is the observation that supraneural bones are lacking in this species as well, a fact not noted by Greenwood & Jubb (1967).

Further evidence to support the idea of phyletic relationship between *O. quathlambae* and the 'red fins' (and at the same time possibly indicating the former's closest living relative to be the 'red fin' *Barbus tenuis*), is the recent observation that the latter taxon has bi-serial pharyngeal dentition (Figure 10). It is particularly significant from the phylogenetic point of view that the loss of supraneural bones and, in an African context, the presence of bi-serial pharyngeal teeth, probably represent derived character states.

If classification is to reflect phylogeny, as I believe it should, the observations discussed above must necessarily involve taxonomic and nomenclatorial changes. Since further research on this question of phylogenetic relationships is still in progress, and because we lack osteological and other critical data, any taxonomic decision at this stage could well be premature.

Our understanding of interrelationships within the freshwater ichthyofauna of southern Africa is still in its infancy. Such studies are likely to yield not only valuable information on the fauna itself but knowledge in the associated fields of zoogeography, and consequently the palaeohistory, of the sub-continent. It is generally assumed that the southern Cape coastal freshwater ichthyofauna is a relatively ancient one; its importance to science in its wealth of information as yet unearthed demands that every effort be made to ensure and safeguard its continued existence.

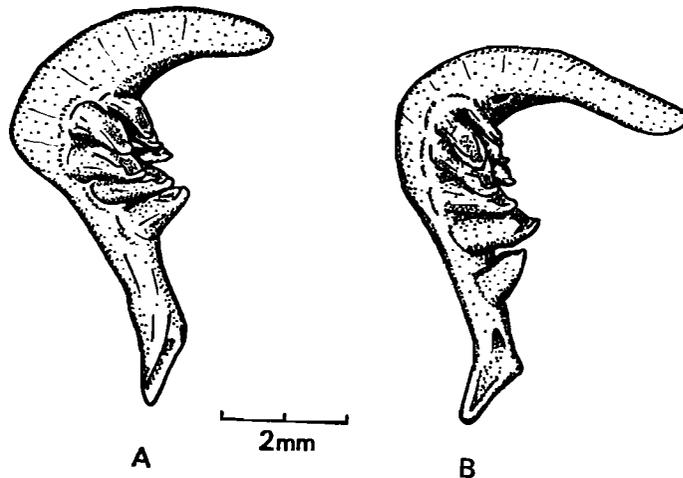


FIGURE 10  
Inner postero-lateral view of the left pharyngeal bone of (A) *Oreodaimon quathlambae* (AM/P 1877, female, S.L. 97 mm) and (B) *Barbus tenuis* (AM/P 2666, female, S.L. 64 mm).

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## APPENDIX

## Material used for post-cranial skeletal meristics

*Abbreviations:*

AM/P: Albany Museum, Grahamstown (fish collection).

BM(NH): British Museum (Natural History).

SAM: South African Museum, Cape Town.

<i>Species</i>	<i>Registered number and locality</i>
<b>Group I.</b>	
<i>Barbus capensis</i>	AM/P 1370 Olifants River System.
<i>Barbus holubi</i>	AM/P 1487 Orange River System
<i>Barbus marequensis</i> (a)	AM/P 2022 Zambezi River System
<i>Barbus marequensis</i> (b)	AM/P 877 Pongola River System
<i>Barbus natalensis</i>	AM/P 988 Umgeni River System
<i>Barbus polylepis</i>	AM/P 284 Limpopo River System
<b>Group II.</b>	
<i>Barbus poechii</i>	AM/P 946 Okavango swamps
<i>Barbus trimaculatus</i>	AM/P 550 Hluhluwe River System
<b>Group III A.</b>	
<i>Barbus andrewi</i>	SAM 18936 Breede River System
<i>Barbus mattozi</i>	AM/P 380 Limpopo River System
<i>Barbus serra</i>	AM/P 1856 and 1361 Olifants River System
<b>Group III B.</b>	
<i>Barbus argenteus</i>	AM/P 904 Incomati River System
<i>Barbus afrohamiltoni</i>	AM/P 47 Sabi-Lundi, Save River System
<i>Barbus calidus</i>	AM/P 728; 1797; 1844; 1850; 1855; 1857; 1862; 1867; 1871; 1881; 1883; 2050; 2052
	SAM 18605; 18756; 19002 Olifants River System
<i>Barbus erubescens</i>	AM/P 2044; 2045; 2046; 2074 Twee River, Olifants River System
<i>Barbus eutaenia</i> (a)	AM/P 1772 Busi River System
<i>Barbus eutania</i> (b)	AM/P 358 Gairezi, Lower Zambezi System
<i>Barbus hospes</i>	AM/P 1834 Below Aughrabies Falls, Orange River System
<i>Barbus manicensis</i>	BM(NH) 1964.9.8.164–1826 Morago River, Ghana

<i>Barbus multilineatus</i>	AM/P 2696 Upper Zambezi River System
<i>Barbus paludinosus</i> (a)	AM/P 2067 Below Aughrabies Falls, Orange River System
<i>Barbus paludinosus</i> (b)	AM/P 458 Lundi, Save River System
<i>Barbus paludinosus</i> (c)	AM/P 944 Okavango swamps
<i>Barbus trevelyani</i>	AM/P 11 Buffalo River System

## Group IV.

<i>Barbus annectens</i> (a)	AM/P 1310 Lake Bengwelu
<i>Barbus annectens</i> (b)	AM/P 1295 Incomati River System
<i>Barbus anoplus</i> (a)	AM/P 2061 Olifants River System
<i>Barbus anoplus</i> (b)	ZM/P 901 Limpopo River System
<i>Barbus radiatus aurantiacus</i>	AM/P 943 Okavango swamps
<i>Barbus barnardi</i> (a)	AM/P 1055-1071; 1313; 2095; 2262 Upper Zambezi River System
<i>Barbus barnardi</i> (b)	AM/P 1500 Okavango swamps
<i>Barbus gurneyi</i>	AM/P 847 Natal
<i>Barbus motebensis</i>	AM/P 859 Limpopo River System
<i>Barbus macrotaenia</i>	AM/P 2161; 2138 Lower Zambezi River System
<i>Barbus neefi</i>	AM/P 1605 Limpopo River System
<i>Barbus pallidus</i> (a)	AM/P 1262 Limpopo River System
<i>Barbus pallidus</i> (b)	AM/P 1404 Gamtoos River System
<i>Barbus puellus</i>	AM/P 1195 Upper Zambezi River System
<i>Barbus tangandensis</i>	AM/P 438 Sabi, Save River System
<i>Barbus thamalakanensis</i> (a)	AM/P 1377 Okavango swamps
<i>Barbus thamalakanensis</i> (b)	AM/P 1320 Congo River System
<i>Barbus toppini</i>	AM/P 766 Incomati River System
<i>Barbus treurenensis</i>	AM/P 1536; 1231 Limpopo River System
<i>Barbus unitaeniatus</i> (a)	AM/P 1898 Limpopo River System
<i>Barbus unitaeniatus</i> (b)	AM/P 2010 Kariba, Zambezi River System
<i>Barbus viviparus</i>	AM/P 1615; 1646 Incomati River System

## Group IV (Red fins).

<i>Barbus afer</i>	AM/P 609; 745; 776; 584; 1415; 1374; 1375; 1741; 1790; 1810; 1921; 2524; 2651; 2652; 2654; 2656; Coastal Rivers from Sundays to Goukamma (Cape)
<i>Barbus asper</i>	AM/P 607; 1744; 1699; 2663 Gouritz and Gamtoos River Systems
<i>Barbus burchelli</i>	AM/P 1566; 1368; 2077; 2079 Breede River System
<i>Barbus burgii</i>	AM/P 1875; 1598; 2076; Berg and Verloren-Vallei River Systems
<i>Barbus phlegethon</i>	AM/P 1863; SAM 22484 Olifants River System
<i>Barbus tenuis</i>	AM/P 608; 1569; 1935; 2081; 2659; 2666; 2667 Gouritz and Keurbooms River Systems

## Also considered.

<i>Oreodaimon quathlambae</i>	AM/P 1823; 1877; 1540 Tsoelikana River, Orange River System
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