SYSTEMATICS AND BIOGEOGRAPHY OF THE REDFIN <u>BARBUS</u> SPECIES (PISCES: CYPRINIDAE) FROM SOUTHERN AFRICA

Dissertation

Submitted in Partial Fulfilment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY
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by

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FRONTISPIECE

A. Pseudobarbus burchelli A. Smith, 1841.
The first redfin species described.

B. Barbus erubescens Skelton, 1974b.
Male from type series in nuptial dress.

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This thesis is dedicated to my parents, Mr and Mrs Harvey Skelton who have given me far more than life and opportunity.

RESUMÉ

This study deals with the systematics and biogeography of a group of minnow-like *Barbus* species which, as adults, are characterized by bright red fins. The species are found in the coastal rivers of the fold belt region of the southern and south-western Cape Province. A closely related species, *Oreodaimon quathlambae*, inhabits certain high altitude streams of the Drakensberg mountains.

Traditional methods were employed to revise the taxonomy of the species. Characters studied included morphometric and meristic measurements, and several qualitative anatomical features, several of which were studied in these species for the first time.

A new species, *Barbus erubescens* Skelton, was described during the course of the study (Appendix 3). The taxonomic status of other species are endorsed or revised (*B.afer* and *B.asper*). Each species is redescribed and figured.

The complete osteology of one redfin species, *B.burchelli*, is described and illustrated. Comparisons are made with all other redfin species and various osteological characters of systematic value are discussed.

The phylogeny of the redfins is studied using Hennigian methods. Comparative data from other southern African *Barbus* species and pertinent literature were used to determine and evaluate synapomorphic characters and character sequences. The redfins *sensu lato* are shown to be diphyletic. *Barbus calidus* Barnard and *B.erubescens* were found to be sister species not closely related to the other redfin species. *Oreodaimon quathlambae* (Barnard) is shown to be monophyletic with the second redfin lineage. *Barbus burgi* Boulenger is placed as the plesiomorph sister species in this lineage and consecutive dichotomies derive *Barbus burchelli* (Smith); *Barbus afer* Peters, and *Barbus asper* Boulenger; *Barbus phlegethon* Barnard; *Barbus tenuis* Barnard and *Oreodaimon quathlambae*.

The classification of the redfins is reviewed in the light of their phylogeny and recommendations for an informal hierarchy are made. The generic status of each lineage is considered and a new genus, *Pseudobarbus*, erected for all the redfin species except *B.calidus* and *B.erubescens*, but including *O.quathlambae*.

The distributions of redfin species are recorded. An hypothesis is given to explain this distribution, based on a comparison of distribution patterns of a number of plant and animal species and a consideration of the geological and geographical history of southern Africa. Vicariance is suggested to be the major factor which influenced redfin distribution. A theory of dispersal explains the distribution of *P.tenuis*. The biogeography suggests the redfins are relatively ancient (possibly Miocene?) southern African fishes.

Suggestions are made on future studies on the redfins. Attention is drawn to possible implications of the redfin study on systematic study of southern African freshwater fishes.

CHAPTER 1

INTRODUCTION

One hundred and seventy years after the settlement of the Dutch colonists in the south-west Cape, the explorer Burchell (1822) provided the first recognised descriptions of freshwater fishes from southern Africa. This was followed nearly twenty years later by A. Smith's (1841) descriptions of freshwater fishes which included a minnow-like cyprinid species *Barbus (Pseudobarbus) burchelli*, named after the previously mentioned explorer. Smith noted that the species was known to the local inhabitants of the region as the "rooye vlerk carper", the Dutch equivalent of red-finned minnow.

In the following hundred years several other redfin species were described, all from the coastal rivers draining the Cape fold mountains. Many of the species were described from small collections sent to overseas scientists. In consequence the descriptions were inadequate by modern day standards. Localities were also poorly pin-pointed and often refer only to the "Cape of Good Hope". This era of sporadic descriptions ended with a revisionary study of the freshwater fishes of the south-west Cape by Barnard (1943) which placed the taxonomy of many of the species on a firm footing. Compared to the earlier describers Barnard's approach was revolutionary and was based on two essentials: familiarity with the living fishes in the field, and the examination of a large series of all sizes of both sexes from as wide a geographic range as possible.

In 1938 Barnard (1938b) described three new redfin species, *Barbus tenuis*, *Barbus phlegethon* and *Barbus calidus*. The latter differed from other known redfin species in two major characters - the form of the dorsal fin unbranched ray and the number of branched rays in the anal fin.
geographical distribution of the species. This distribution was remarkable in that all the species were confined to the rivers of the Cape fold mountain region.

Further work on the redfins by Jubb (1965, 1967) clarified certain details, but left a number of questions unanswered. Surveys carried out by Jubb indicated that the range of several species had been severely reduced in the preceding few decades as a result of increasing human demand on water resources and the introduction of exotic predatory fishes. There were thus two factors involved in the initiation of the present study: a need to complete the taxonomic revision of the group, and to determine the conservation status of the species.

Although cyprinid species continue to be described from Africa the emphasis has changed from an alpha taxonomic level to that of revisionary studies. In Barbus these studies have been directed primarily on a geographic basis (e.g., Groenewald, 1958; Greenwood, 1962; Hopson & Hopson, 1965; Banister, 1973). Most of the works have relied heavily on traditional characters with little specific attention to the interrelationships of the species.

By way of contrast, in North America revisionary studies of cyprinids have concentrated on related groups of species (e.g. Lachner & Jenkins, 1971; Snelson, 1972; Hubbs & Miller, 1977; Barbour & Miller, 1978). A major feature of these studies has been the emphasis placed on thorough character analysis and appreciation, consequently exposing weaknesses in many of the traditionally used characters. Hence there has been a trend towards the reassessment of characters in cyprinid systematics. Often species have been assigned to genera on the basis e.g. of barbel characteristics or the relative length of the intestine and with the new appreciation of the weakness of such characters the generic placement of the species is in a state of flux (Hubbs & Miller, 1977; Gilbert, 1978).

The present study was aimed at the revision of a group of possibly related species and it therefore seemed more appropriate to model the study programme on similar works in North America rather than on any particular African review. The study by Lachner and co-workers on the genus Nocomis (for references see Lachner & Jenkins, 1971) was especially useful, as several striking parallels exist between certain character complexes in Nocomis and the redfins, e.g. the development of strong sexual dimorphism and large tubercles on the head of males.

It is frequently stated that the classification of organisms should be based on the phylogenetic relationships between them (Mayr, 1969; Crowson, 1970; Brundin, 1972; Nelson, 1973). There are two main approaches to the study of phylogenetic relationships, a traditional evolutionary approach which considers relationships on the overall similarity of the organisms, and secondly a cladistic approach (Hennig, 1966) by which the relationships of organisms are inferred on the basis of shared derived characters. Although the traditional approach still enjoys much support Hennigian methodology has considerably influenced ichthyological systematics (Nelson, 1972; Greenwood *et al*., 1973) and has been used in many excellent studies in recent years (e.g. Winterbottom, 1974; Smith-Vaniz, 1976).

The question of the interrelationships of the redfin *Barbus* species has posed a problem ever since Barnard (1938 b) described *B.calidus* and showed that the species were a geographically circumscribed group. One of the main African *Barbus* classificatory characters is the form of the last dorsal fin unbranched ray. In *B.calidus* this ray is bony and serrated whereas in other redfin species it is simple and flexible. Even though Barnard (1943) and Jubb (1965, 1967) considered *B.calidus* to be a redfin it was grouped with other *Barbus* species with a similar unbranched dorsal ray. To solve this paradox it was clearly necessary to establish the true phylogenetic relationships of the species. It was also realised that depending on the outcome this study could be important for *Barbus* classification in general.

It was decided to apply cladistic methods of analysis to provide answers for the interrelationships of the redfins. This requires a prior evaluation of characters in order to determine the primitive and derived states within a sequence of character transformation. Such an analysis had to date not been done for any *Barbus* species (as far as I am aware). This reinforced the need for a new approach to *Barbus* systematics and in this redfin study, for the exploration of new characters and the careful evaluation of traditionally used ones. A field which has not as yet received much attention in African *Barbus* studies but which has been shown to be extremely valuable in many other fish groups is osteology. In order to provide the foundation for use in the present study as well as for future reference it was necessary to provide a complete osteological description of at least one redfin species.

Early in the redfin programme I had the opportunity to examine the enigmatic African cyprinid Oreodaimon quathlambae (Barnard, 1938 a) in its natural habitat and to collect some specimens. The relationships of this species were at the time unknown beyond vague ties with the genus Barbus (Greenwood & Jubb, 1967). The living fishes had red pigment at the base of the fins (Skelton, 1974a) which was strikingly similar to the redfin Barbus species from the southern Cape. Further investigation indicated that there was a close phylogenetic relationship between O.quathlambae and certain redfin species (Skelton, 1976). In consequence the species was included in the redfin programme.

The inclusion of O.quathlambae added a new dimension to redfin distribution. In the absence of any knowledge on the relationships of the redfins, their geographical distribution had not been given adequate explanation. One of the more obvious prerequisites for explaining the distribution of organisms is a knowledge of their relationships. In the light of recent theoretical developments in the sphere of biogeography it has been possible to re-examine the distribution of the redfins and provide an alternative explanation for it.

The major objectives of the study on the redfin Barbus species may thus be summarised as follows:

a) to reconsider the taxonomy of the redfin species with particular emphasis on the evaluation of traditional and new morphological characters,
b) to record and compare the osteology of the species,
c) to assess the phylogeny of the redfins and to relate this to their taxonomy and classification, and
d) to consider the historical biogeography of the redfin species.

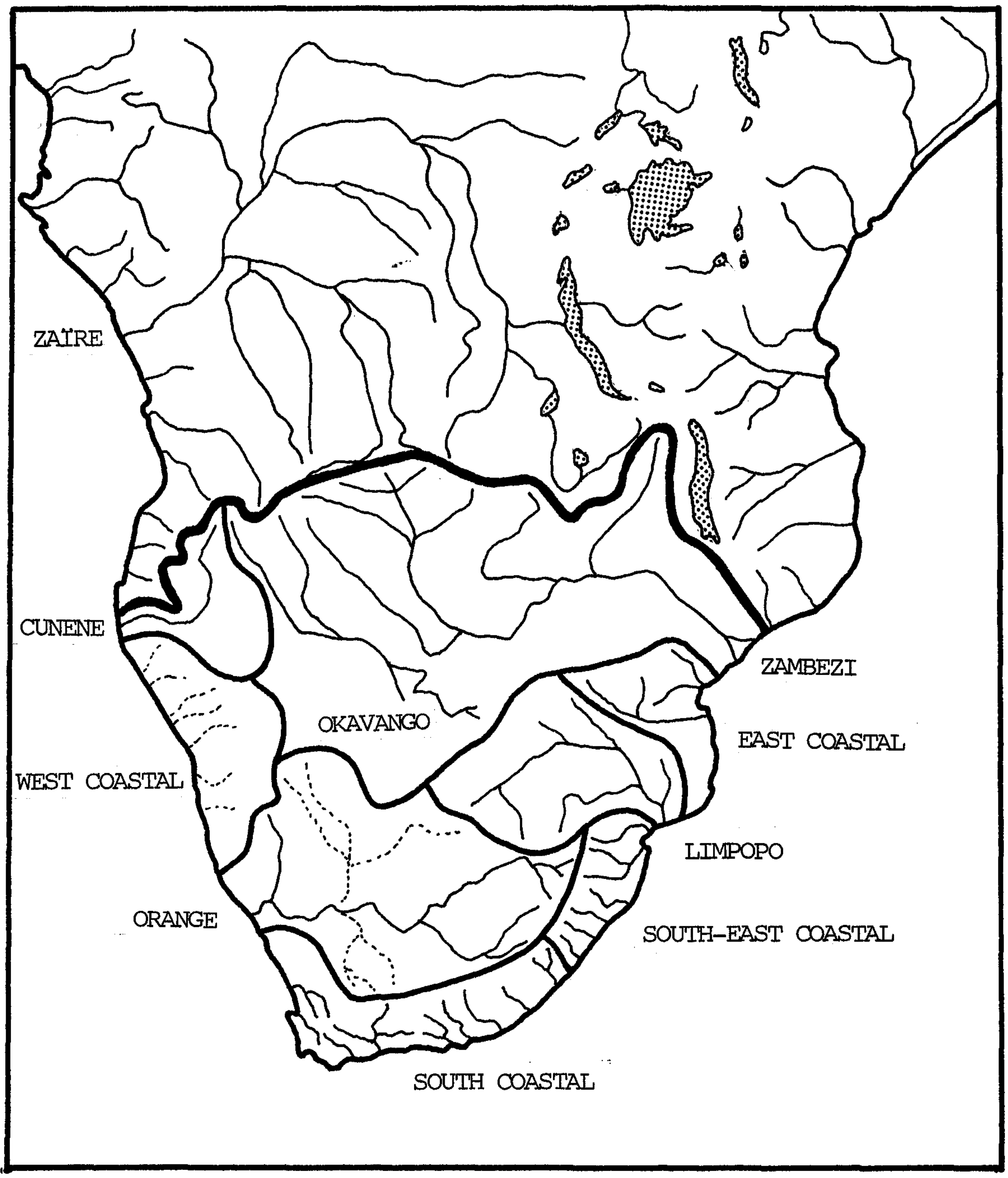


Fig. 2.1 The major drainage basins of southern Africa as defined in this study. The heavy line demarcates southern Africa. Adapted from Jubb (1967).

CHAPTER 2

A GEOGRAPHICAL AND GEOLOGICAL DESCRIPTION OF SOUTHERN AFRICA WITH PARTICULAR REFERENCE TO THE SOUTHERN CAPE

The purpose of this chapter is to provide a brief geographical background to facilitate further discussion on the redfin *Barbus* species in Southern Africa, which is here arbitrarily taken to be Africa south of and including the Cunene - Zambezi watershed (Fig. 2.1). Lake Malawi, technically part of the Zambezi system, is excluded. The redfin *Barbus* are found only in the rivers of the southern coastal drainage and the Orange River System, all within the Cape Ichthyofaunal province of Roberts (1975).

Note on Afrikaans names and duplication of names

The earliest European colonists in South Africa were of Dutch and later French Huguenot origin. By the turn of the nineteenth century when the country came under British administration, the region of the fold mountains in the south of Africa (see below) had been largely explored. The majority of the names given to geographical features such as mountains and rivers are therefore of Dutch origin (Afrikaans). In many cases these names are readily transcribed into English; for the majority, however, local use makes it inappropriate to do so, and the Afrikaans is retained.

The exploration and occupation of the fold belt region of the southern Cape occurred during the 17th and 18th Centuries when communication channels were poor. The names of geographical features are therefore often duplicated and to eliminate possible confusion Table 2.1 gives a schematic listing of the rivers more frequently referred to in this report.

Geography

(i) Relief. Much of southern Africa consists of an elevated plateau in excess of 1000 metres A.S.L.. Altitudes below this are restricted to a narrow coastal strip and a generally broad diagonal zone from the region of the lower Orange River across the Kalahari and dividing

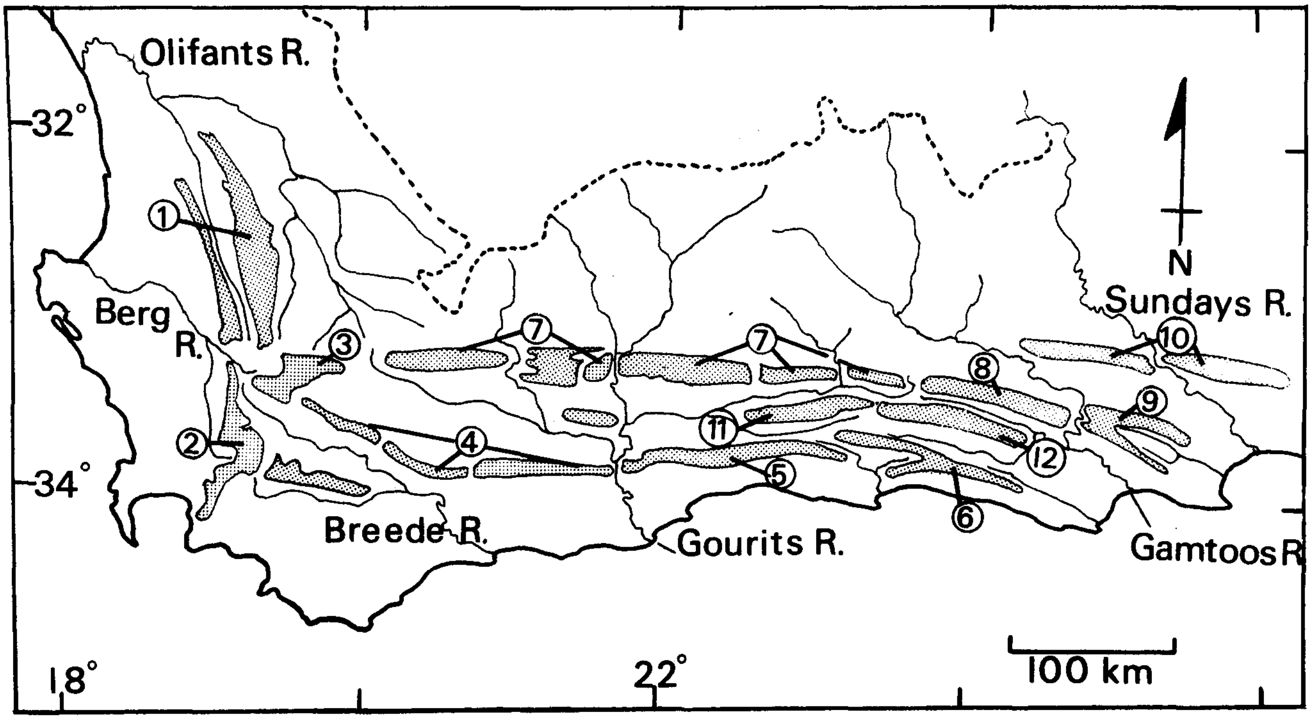


Fig. 2.2 The southern and south-western Cape Province showing the main mountain ranges of the Cape fold belt and the drainage patterns of the major river systems. The mountain ranges are numbered as follows (1) Cedarberg, (2) Hottentots Holland and Great Drakenstein, (3) Hex River Mountains, (4) Langeberg, (5) Outeniqua Mountains, (6) Tsitsikamma Mountains, (7) Swartberg, (8) Baviaanskloof Mountains, (9) Great Winterhoek and Elands River Mountains, (10) Little Winterberg and Suurberg Mountains, (11) Kamanassie Mountains, (12) Kouga Mountains. The dashed line represents the line of the Great Escarpment.

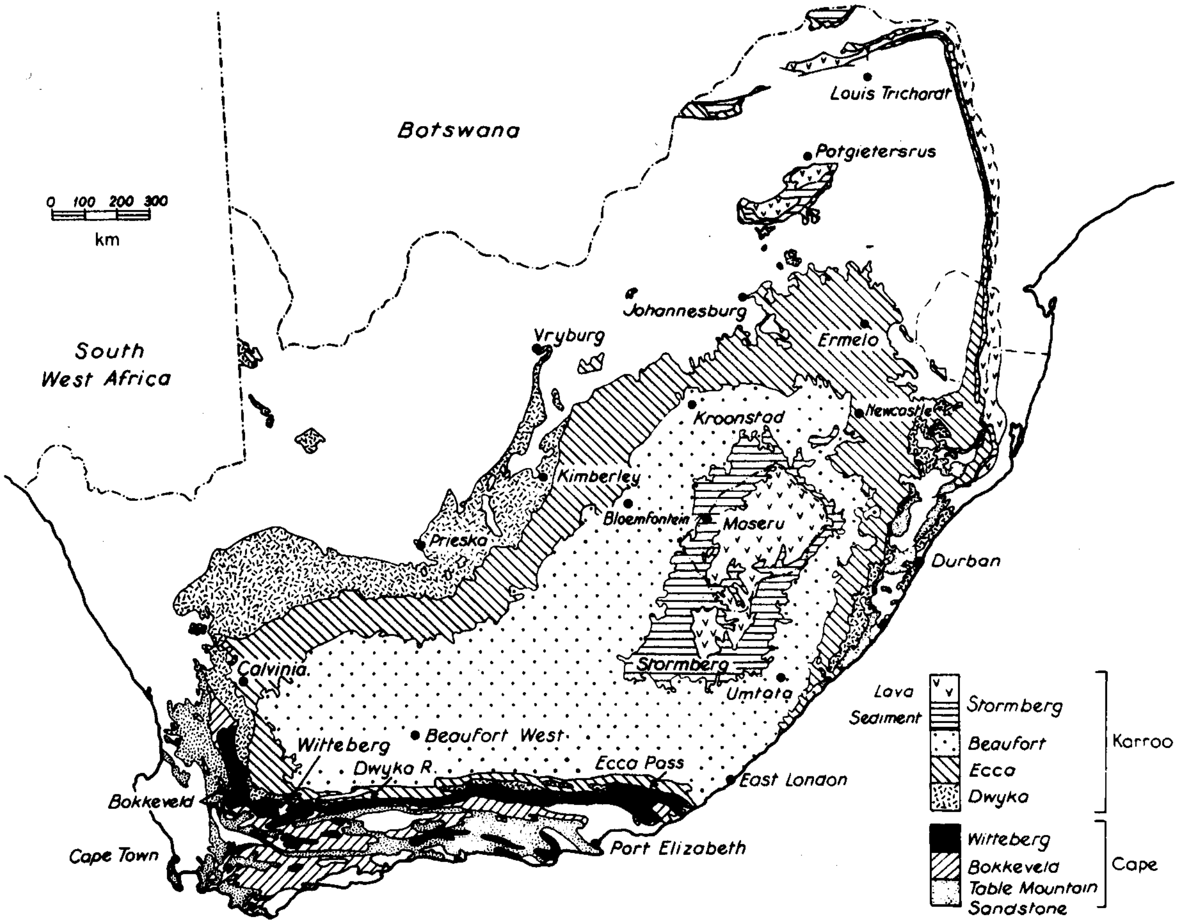


Fig. 2.3. The major geological formations over the distribution range of the redfin species. The Cape and Karroo Systems. After Truswell, 1977.

to reach the wide coastal lowlands of Mozambique via the Zambezi and Limpopo river valleys. To the south-east the plateau rises to above 3000 m in the Drakensberg highlands, which form a steep escarpment on the coastal (east) side. South of the Limpopo the escarpment runs parallel to the coast, receding inland in the south and south-west. Here the ranges of the Cape Fold Mountains lie between it and the coast (Fig. 2.2).

The mountains of the Cape Fold belt (Fig. 2.2), generally considered an ancient feature (De Villiers, 1944), are arranged in two series; the northward trending Cedarberg foldings in the west and the arcuate east-west trending ranges in the south and south-east. These mountains are closely associated with but do not entirely dictate the drainage of the region.

Geology

The region south of the Orange-Pongolo river systems is dominated by two large geological systems referred to as the Cape and Karoo Supergroups (Fig. 2.3) which are of Palaeozoic and Mesozoic age respectively. Quaternary and Tertiary deposits are limited to pockets of marine sediments in coastal areas and the vast Kalahari sands of the central and north-western parts of the subcontinent. To the west and east of these sands there are numerous less extensive outcrops of ancient granites, intrusives and outliers of the Karoo Supergroup.

The Cape Supergroup consists of the Table Mountain, Bokkeveld and Witteberg Groups which have been extensively folded and form the mountains of the southern and south-western Cape. The resistant "Table Mountain" sandstones (Peninsula Formation) form the major relief features while the softer, more easily eroded Bokkeveld Formations are exposed in valleys between the ranges. The rock types involved primarily determine the quality of the water of the rivers which drain this area (Bond, 1946). The Peninsula Formation consists predominantly of well leached, reworked, quartzitic sandstones, which impart little soluble salts to the runoff water. Streams draining such strata are consequently acidic and minerally deficient. The Bokkeveld Formations are primarily marine deposits and yield waters of high salinity. The Witteberg Group form low ranges (e.g. the Suurberg Mountains) and include quartzitic strata which again yield waters low in mineral content.

In Natal there are further outcrops of rocks similar to those of the Table Mountain Group. These have for long been considered equivalent to Peninsula Formation sandstones but Lock (1973) provides fossil evidence which strongly indicates that they are in fact contemporaneous with the Witteberg Group.

The extensive Karoo sediments include the Dwyka tillite deposits, the fossil rich Ecca and Beaufort Formations, and the Stormberg sediments capped by Stormberg volcanics. Groundwater from the Dwyka, Ecca and Beaufort sediments is of a highly mineralised chloride - sulphate character (Bond, 1946). The upper strata of the Drakensberg Mountains are erosional remnants of Stormberg volcanics, and source streams are characteristically acidic (Grobbelaar & Stegmann, 1976). Karoo rocks are usually relatively soft and rivers traversing these sediments are turbid and carry high suspended loads (Forbes & Allanson, 1970; Keulder, 1979).

Climate

Schulze & McGee (1978) provide details of the biologically important climatic parameters of Southern Africa. The climate is influenced to a large extent by the major ocean currents. The warm southward flowing Mozambique current passes the eastern seaboard and the cold northward flowing Benguella Current passes the western seaboard. Consequently Southern Africa is progressively drier in the west which includes the Kalahari and Namib deserts.

The extreme south-west part of the subcontinent receives winter rainfall in the form of anti-cyclonic depressions. The high relief in that region results in great variation in local precipitation. In mountain catchments the annual precipitation can average as much as 1400 mm (Midgeley & Pitman, 1969). As pointed out by Harrison & Elsworth (1958) during a winter season there will be several periods of high rainfall followed by fine weather so that the rivers fluctuate rapidly between flooding and normal flow which is generally low during the summer months.

From the winter rainfall in the south-west Cape the pattern changes to an all seasons rainfall in the southern coastal region (Tyson, 1978).

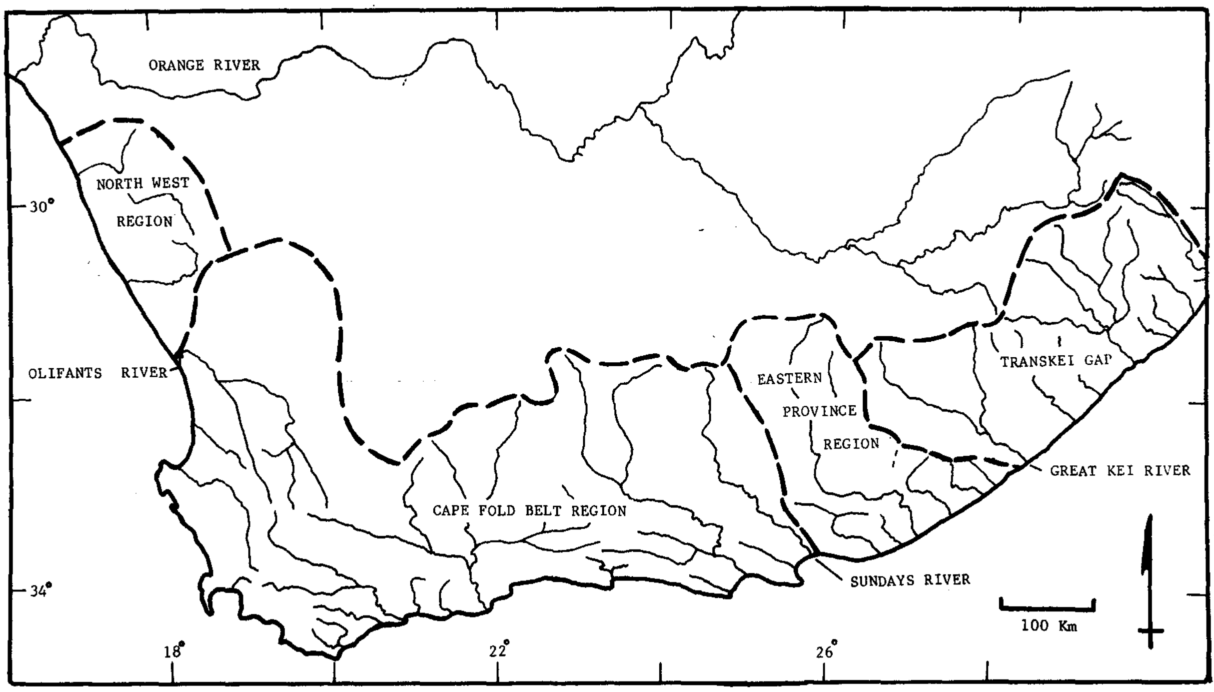


Fig. 2.4 The south coastal drainage basin to show the different regions as referred to in the text.

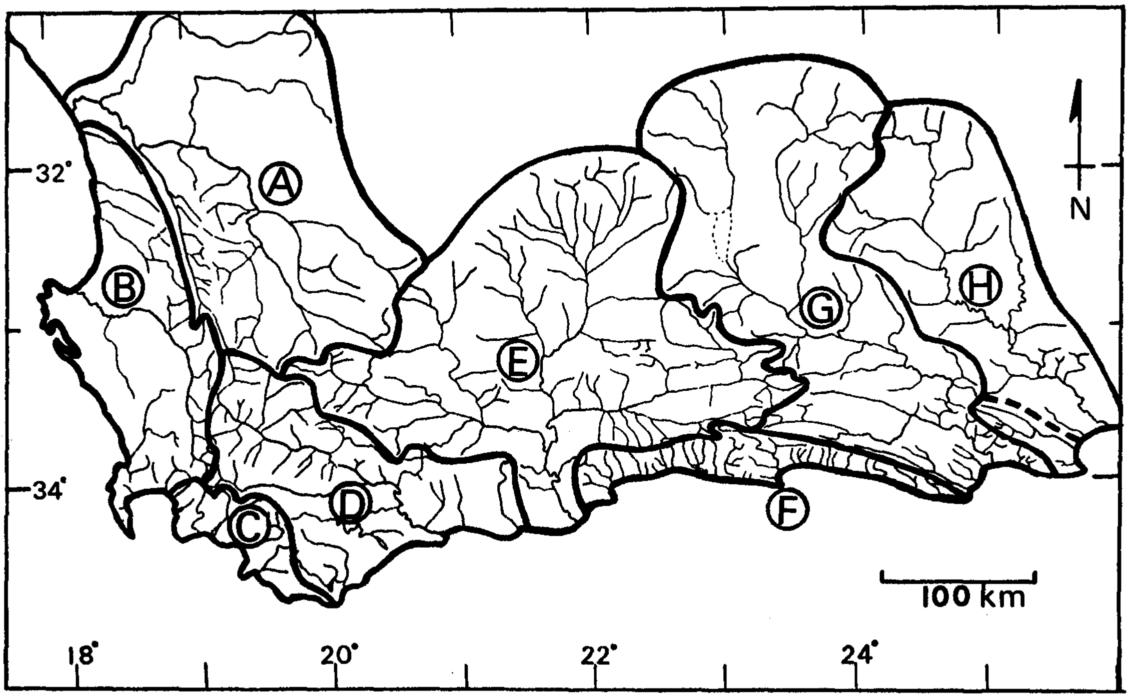


Fig. 2.5 Main catchments within the Cape fold belt region of the south coastal drainage basin. (A) Olifants River system, (B) Great Berg River and adjacent rivers, (C) Western Agulhas rivers, (D) Breede River and adjacent rivers, (E) Gourits River system, (F) South Coastal rivers, (G) Gamtoos River system and adjacent rivers, (H) Swartkops River, Sundays River and adjacent rivers.

The interior and regions to the east of the fold belt receive summer rainfall. Snowfalls occur in the fold mountains and in the Drakensberg but these are spasmodic and usually of short duration. The plateau regions of South Africa also have occasional snowfalls.

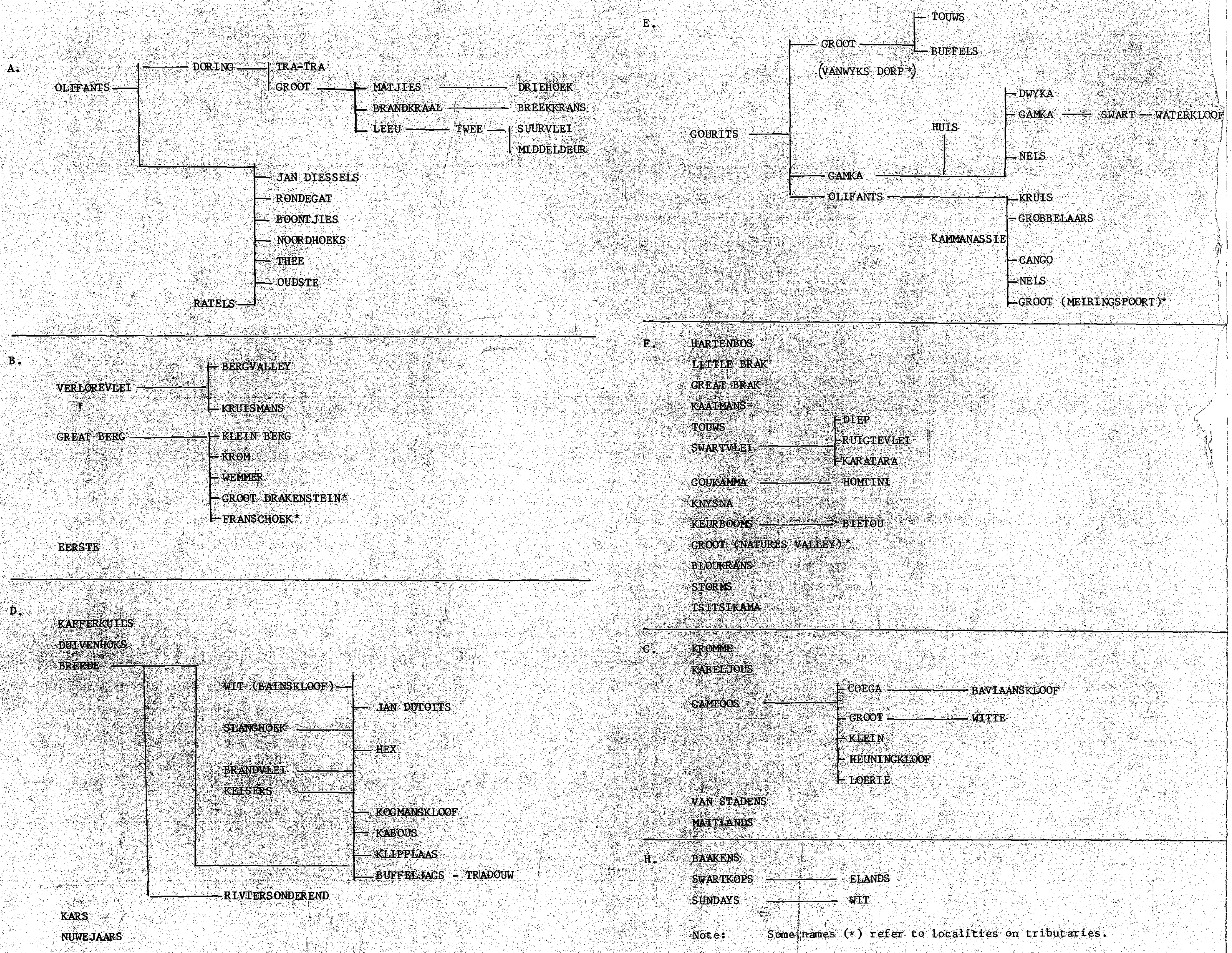
Based on thermal regions (Schulze & McGee, 1978) the climate in Southern Africa may be summarised as follows. Low altitude regions to the north-east have a tropical climate which extends south to northern Natal and up the Zambezi Valley. The climate grades into a narrow sub-tropical band which extends south along the coast into southern Natal. Warm temperate climates occur over much of the more northerly interior of the subcontinent with a narrow south-east coastal strip extending to the southern and south-western Cape. The higher altitude plateaus experience cool-temperate conditions as do the fold mountains of the southern Cape. Sub-alpine conditions exist at high altitudes (above 3000 metres) in the Drakensberg.

<u>Drainage</u> (Fig. 2.1, 2.4 and 2.5)

The Zambezi, Cunene, Limpopo and Orange River System, together drain the major portion of the surface area of southern Africa (Fig. 2.1). Interspersed between these around the perimeter of the subcontinent are the coastal drainage basins, each consisting of a series of relatively minor river systems. The most important of these as far as this study is concerned, is the south coastal drainage (Fig. 2.4), which includes the entire southern extremity of Africa from the Orange River (mouth at 28° 35'S 16° 30'E) in the west to the Umtamvuna in the east (31° 05'S, 30° 12'E), The division of the coastal drainage into southern coastal and south-east coastal has been arbitrarily based on a fish faunal division (Jubb, 1967). The Umtamvuna River marks the natural southernmost distribution of several species including [illegible]
on the basis of fish faunal considerations (Fig. 2.4).

(a) The North-west regions including the rivers between the Clanwilliam, Olifants and the Orange River Systems. These are small intermittent streams in an arid area which as far as is known have not been explored for fishes.

Table 2.1 A schematic listing of the rivers of the Fold belt region where redfins have been collected and are referred to in this study. Divisions of the table are in accordance with the main drainage catchments of the region as given in fig 2.5.



Note: Some names (*) refer to localities on tributaries.

(b) Rivers of the fold belt mountains (from the Olifants in the west to the Sundays in the east). This region is of major interest here and these rivers will be described in greater detail below.

(c) The Eastern Province region, including rivers between the Sundays and the Great Kei. Two distinctive freshwater species are endemic to certain rivers, the anabantid, Sandelia bainsii, and the cyprinid Barbus trevelyani.

(d) The "Transkei gap". This name was first given to the region between the Great Fish and the Umtamvuna rivers by Bowmaker et al. (1978) in reference to the fact that there is a general absence of primary freshwater fishes (with one exception, the minnow Barbus anoplus). On the basis of the distribution of Barbus trevelyani and Sandelia bainsii Cambray (1978) redefined the "gap" as extending from the Great Kei River in the south.

The drainage pattern within the fold belt region (Fig. 2.5) is partly determined by the mountain belts but certain of the larger rivers (the Clanwilliam, Olifants, the Gourits, the Gamtoos and the Sundays) have penetrated beyond the ranges to the Great Escarpment. These larger rivers are notable for having fish species in common with the Orange River system as well as species endemic to the fold region. The drainage can be conveniently divided into eight catchments as in Figure 2.5.

The Olifants River (Fig. 2.5 A)

To avoid confusion with other rivers of the same name in southern Africa, I shall refer to this as the Clanwilliam Olifants. The system is formed by two major tributaries, the Olifants and the Doring. Although the catchment area of the perennial Olifants tributary is a fraction of that of the annual Doring, it is better watered. This is because the latter lies largely in the rain shadow of the Cedarberg Mountains. The feeder tributaries of the Olifants are rocky streams with steep gradients, and those of the Doring are longer, with more shallow gradients. Within the Cedarberg mountains several of the Doring tributaries arise on marshy intermontane plateaus and descend in a series of steps rather than with an even profile. The Cedarberg mountain tributaries are generally clear streams with rocky or sandy substrates. Water quality is characterised by low pH and low mineral concentrations. There is not much change in the water of the Olifants tributary itself until after the confluence with the Doring. The Doring passes over Bokkeveld and Dwyka formations so that the waters are generally alkaline and highly mineralised.

Great Berg and Adjacent Streams (Fig. 2.5 B)

The Berg River is one of the best studied rivers in Southern Africa from the biological and hydrological points of view (Harrison & Elsworth, 1958; Harrison 1964; Fourie & Steer, 1971; Fourie & Görgens, 1977). This river drains the western slopes of the south-west fold mountains reaching the Atlantic ocean. The fold mountain tributaries are typical of TMS rivers, having rocky or sandy substrates and being low in pH and low in dissolved solids and ions. The character of the mainstream in its middle and lower reaches changes to highly mineralized waters due to the underlying Malmesbury geological series (Fourie & Görgens, 1977).

In the south, also draining the western slopes of the north-south trending fold mountains, the Eerste River flows southwards into False Bay. A profile of the river is given by Seddon (1967). It is similar in character (physical and chemical) to the tributaries of the Berg River, but from the foothill zone to the sea it has been drastically affected by human activity (Harrison, 1958).

Redfins are absent from the small streams draining the mountains of the Cape Peninsula.

To the north of the Great Berg River a few minor independent rivers traverse the coastal plain. The Verlorevlei system is the largest of these and is adjacent to the Berg River. For the main part this is a low gradient, reed-bed river with a muddy or silty substrate.

Western Agulhas Plateau drainage (Fig. 2.5 C)

There is a series of short streams draining the western coastal stretch near Cape Agulhas. Redfins have not yet been reported from them.

Breede and adjacent rivers (Fig. 2.5 D)

The Breede River system is contained entirely within the fold mountains and is therefore well watered and perennial with clear acidic water. The two major tributaries, the Breede and the Riviersonderend, flow south-east in strike valleys. Barnard (1936) has shown that the upper end of the mainstream was probably pirated by the Klein Berg River. In turn it seems that the headwaters of the Breede have captured streams which formerly flowed into the Gourits River.

To the east of the Breede two independent rivers, the Duivenhoks and the Kaffirkuils, each have populations of B.burchelli indicating connection with the Breede during periods of lowered sea levels (Barnard, 1943). To the west of the Breede B.burchelli is only found in those small independent streams which lie eastward of Cape Agulhas, again suggesting former connection with the Breede during periods of lowered sea levels. Off-shore sediment studies (Dingle & Rogers, 1972) show that the extended Breede was directed towards the western slopes of the Agulhas plateau and support Barnard's (1943) conclusions that the Breede and Gourits rivers were not connected during former lowered sea levels.

Gourits River System (Fig. 2.5 E)

The Gourits is a complex system which breaches both the coastal and the northern folded ranges. Three major tributaries drain the southern escarpment, from the west, the Buffels, the Dwyka-Gamka and the Olifants. Each main tributary also receives smaller branches from the northern slopes of the Swartberg Range and breaches this range independently to unite within the large valley between the Swartberg and the coastal fold range (Langeberg-Outeniqua mountains). The Gourits then passes through the Langeberg-Outeniqua ranges to reach the Indian Ocean.

Most of the drainage falls within the rain shadow of the coastal arc of fold mountains and is thus relatively poorly watered. The high relief of the Swartberg and other fold ranges, including the northern slopes of the coastal ranges themselves, ensures that many of the mountain tributaries are perennial. Flow in the major tributaries, at least since European settlement, is erratic and annual. Habitats

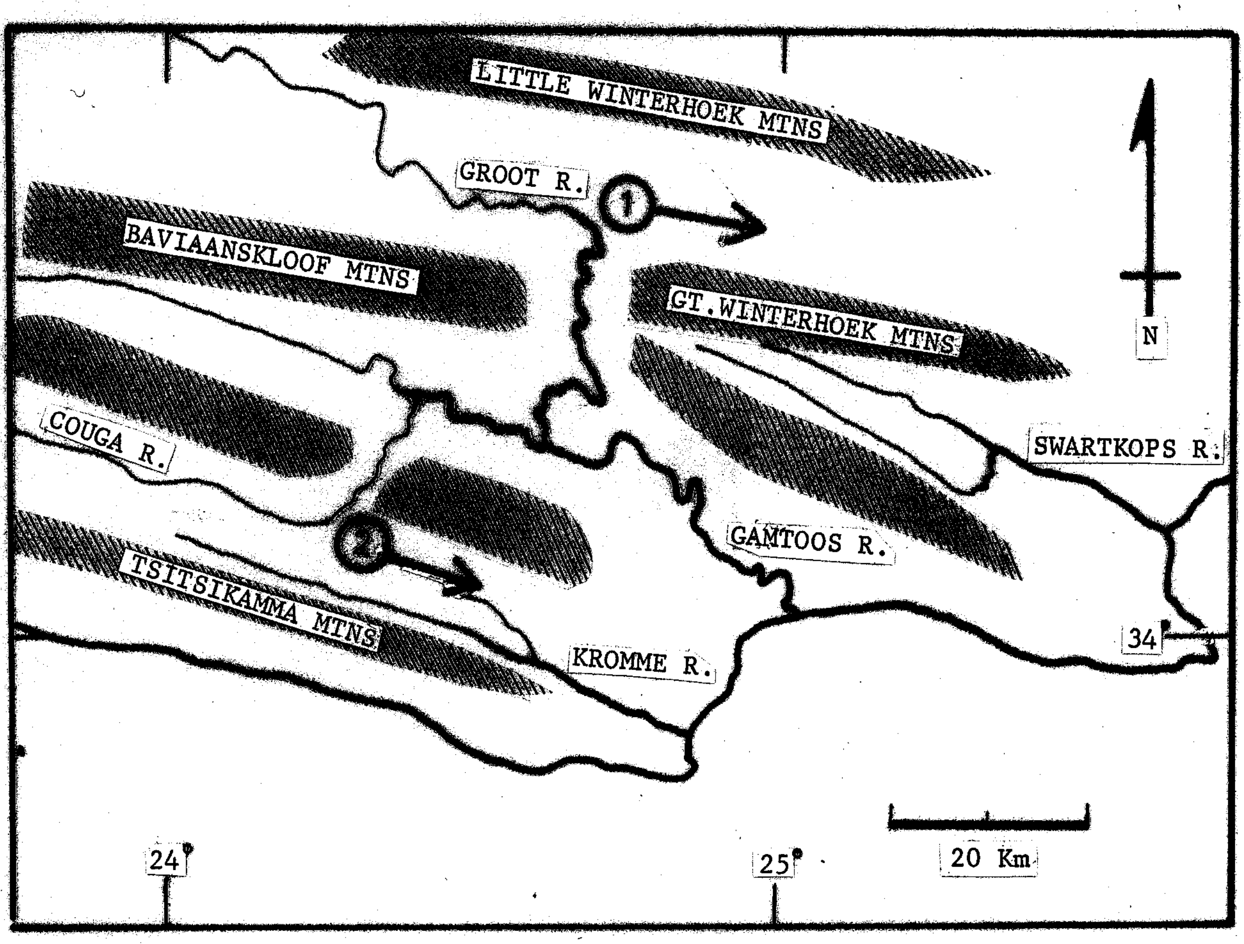


Fig. 2.6 Part of the Cape Fold Belt region to show the drainage of the Gamtoos River system in relation to the fold mountains and adjacent rivers. The numerals and attached arrows indicate sites of drainage capture and direction of former course of captured river.

in the mountain tributaries differ widely from those in these main tributaries. The former, draining Table Mountain formations, are clear and acidic, the latter flow mainly over Bokkeveld and Cretaceous Formations of marine origin, or to the north of the fold belt over Karoo beds, and have turbid, alkaline, mineralised waters.

South Coastal Rivers (Fig. 2.5 F)

The drainage here is determined by the range of fold mountains with peaks up to 1700 m running close to (5-20 km) and parallel with the coast. These mountains are partially divided by the Keurbooms River valley into two ranges, to the west the Outeniqua and to the east the Tsitsikama mountains. A Tertiary marine-cut coastal plain separates the mountains from the coast. The older rivers have gouged deep and narrow gorges across the plain, probably during periods of lowered sea levels (Toerien, 1976).

The mean annual rainfall for the catchments of these coastal streams is high (800-900 mm) (Midgeley & Pitman, 1969) and is distributed throughout the year (Tyson, 1978). Consequently the rivers are all perennial, without a distinct seasonal variation in flow, and since they drain Table Mountain sandstones have water with low pH (4.5-5.5) stained deep brown by organic matter (Bond, 1946; Harrison & Agnew 1962). The waters are invariably clear without particulate matter, and algal growth potential is low (Howard-Williams, pers.comm.).

Gamtoos River and adjacent coastal streams (Fig. 2.5 G)

The Gamtoos River system is complex, its present form evidently derived by a series of river captures (Haughton et al., 1937). Briefly the system may be considered in two parts (Fig. 2.6), the tributaries draining south-east within the strike valleys of the fold mountains, and the Groot River, a major tributary which breaches the Baviaanskloof-Great Winterhoek mountains to drain a large inland area from over the Great Escarpment.

The habitat in the mountain tributaries differs from that in the Groot River due to climatic and geological reasons. The Groot River traverses the relatively soft Beaufort and Ecca Formations of the Karoo Supergroup, the water quality is consequently turbid and silty and falls into the alkaline chloride-sulphate group (Bond, 1946). The mountain tributaries drain Table Mountain sandstones and are clear acidic waters with sandy-rocky substrates. The catchment of the Groot is far larger than that of the mountain tributaries (29169 vs 5258 km^2) but receives an average of half the precipitation (256 vs 522 mm per annum) (Midgeley & Pitman, 1969).

According to Haughton et al. (1937) the Groot River formerly flowed down the strike valley between the Great and Little Winterhoek mountains (arrow no. 1 in Fig. 2.6), its present course being due to capture by a tributary of the Gamtoos, probably by the erosive action of "favourably situated consequent tributaries of the two major rivers". A second capture involves the Couga River (arrow No. 2 in Fig. 2.6), which initially flows south-east down a strike valley but then abruptly cuts northwards across the strike to join the Baviaanskloof River. Formerly the Couga probably reached the sea via the Kromme River.

The Kromme River, as well as the smaller Kabeljous and Seekoei Rivers to the south-west of the Gamtoos system, probably joined the Gamtoos during times of lowered sea level. These streams all flow in strike valleys and generally have acid, peat-stained waters typical of the fold mountain region.

To the east of the Gamtoos there are two small rivers, the Van Stadens and the Maitlands. Although redfins have not been found in the Van Stadens they have in the Maitlands and it seems highly probable that they may have lived in the Van Stadens before the introduction of bass (Micropterus sp.). The Van Stadens is the larger of the two rivers and deeply dissects the coastal plain, flowing in a deep gorge, which testifies to its relatively great age. These streams were probably tributaries of the Gamtoos during lowered sea levels.

Sundays and Swartkops Rivers (Fig. 2.5 H)

The Sundays River rises over the Great Escarpment and penetrates the Klein (little) Winterhoek-Suurberg mountains, eastern outliers of the fold mountain belt. The river has been studied by Forbes & Allanson

(1970) and Scott et al. (1972). In the mainstream, which traverses the soft, easily eroded Beaufort and Ecca Formations, flow is annual and erratic and the water quality mineralised and turbid. One tributary, the Wit River in the Suurberg mountains, is an exception. This stream is perennial and draining Witteberg quartzite has relatively clear, good quality water. Jubb (1965) reports a population of B.afer from this locality.

The Swartkops River flows south-east into Algoa Bay via the strike valleys of the Great Winterhoek and Elands mountains (Fig. 2.6). Rainfall within the catchment is high (650-700 mm per annum) and the streams are mainly perennial. The water of the mainstream, from Table Mountain formations, is usually mildly acidic and clear (Harrison & Agnew, 1962). The large tributary from the Elands mountains runs across an isolated outcrop of Bokkeveld slates and is alkaline. The lower reaches of the river run over the marine beds of the Uitenhage Group which increases the salinity. These lower reaches are also influenced by industrial and urban effluents.

The small Baakens River to the south of the Swartkops also flows into Algoa Bay, has a population of B.afer,and was probably connected to the Swartkops during lowered sea levels.

The Orange River System

This is the largest river south of the Zambezi. It arises in the Drakensberg highlands and high plateau regions on the eastern side of the subcontinent and gathered into two major tributaries, the Vaal in the north and the Orange itself, flows westward to reach the Atlantic Ocean. The middle and lower reaches flow through progressively drier terrain so there is relatively little inflow from these regions.

In the Drakensberg the source tributaries are derived from seepage bogs which provide clear acidic waters when not affected by man-made environmental disturbances (Grobbelaar & Stegmann, 1976). Large waterfalls are common but river gradients are not necessarily steep. The Tsoelikane River where O.quathlambae is found meanders in a broad valley and frequently forms ox-bow cutoffs.

Several large impoundments have been built on the middle reaches of the system. Since dropping from the high altitude regions the source rivers cross Beaufort sediments which contribute large quantities of dissolved and suspended matter (Keulder, 1979) making the system extremely turbid. The Augrabies Falls mark the boundary of the lower Orange. Although there is little autochthonous inflow from the lower reaches at the present time there is evidence that the Molopo and Fish Rivers from the north were formerly extensive tributaries (Wellington, 1958).

CHAPTER 3

TAXONOMY OF REDFIN BARBUS SPECIES

Introduction, the taxonomic history of the redfin Barbus species

The taxonomic history of the redfin Barbus species extends back one hundred and forty odd years. The first redfin species, Barbus (Pseudobarbus) burchelli was formally described by Sir Andrew Smith in 1841. Smith records that the species was well known to the local inhabitants as the "rooye vlerk carper", the Dutch for "redfin minnow". A colour illustration of the fish was provided but no mention was made of any specimens on which the illustration or the description was based. The only reference made by Smith to a collecting locality was "various rivers of the Cape Colony".

In the light of a later discovery that there are two closely similar redfin species in the south-west Cape, the precise identification of Smith's (1841) B.burchelli is open to debate. Three factors suggest that it is unlikely that the problem can be unequivocally solved: there are no type specimens known, the original description is entirely qualitative, and the illustration is clearly inaccurate in those details necessary to provide positive identification. With regard to this latter point Barnard (1943) and Greenwood & Crass (1959) have exposed the inaccuracy of Smith's artists' illustrations of other species in the same work. An examination of the illustration of B.burchelli indicates a lateral line scale count of 46 - many more than is known to occur on any of the redfins with a double pair of barbels.

Castelnau (1861) briefly described a new genus and species, Gnathendalia vulnerata from the Genadendal Mission on the Riviersonderend (Breede R. System). The description was based on two skins originally sent to the Paris Museum but now housed in the British Museum (Natural History). Castelnau (1861) reported of the species "Les habitants lui donnert le nom de Rui-flerke".

Barbus afer was described by Peters (1864) from three specimens collected in the 1820's by Ludwig Krebbs from the "Cape of Good Hope". No further specimens of *B.afer* were identified during the following century until the species was correctly recognised by Jubb (1965). The reason for this failure to recognise the species was probably because Peters (1864) failed to record any coloration and also only recorded a vague locality (Cape of Good Hope). The fact that no colour was recorded is not surprising in view of the 40 years lapse of time between the collection of the specimens and their description.

The next step in redfin taxonomic history was made in the catalogue of Günther (1868). The genus *Gnathendalia* was synonymised with *Barbus* while the species *G.vulnerata* was referred to an earlier species, *Barbus gobionides* Cuvier & Valenciennes (1842). Boulenger (1905b) accepted *B.gobionides* but subsequently he (Boulenger, 1911) reversed the synonymy and re-erected *B.vulneratus*. No reasons for this decision were given. It is however understood (Greenwood pers. comm., 1978) that Boulenger examined the types of *Gnathendalia vulnerata* and therefore probably made the decision in the light of the inadequate description of *B.gobionides*, compounded by the fact that the type skin was missing. In a major review of the fishes from the south-west Cape, Barnard (1943) showed that, in the absence of any type specimens, it was impossible to include any redfin or other species under *B.gobionides*.

Barbus multimaculatus was described and figured by Steindachner (1870). Boulenger (1905b) placed the species in the synonymy of *B.vulneratus* and used Steindachner's figure for a description of *B.vulneratus* in 1911.

The new redfin species were described and figured by Boulenger (1911) from material received from the South African Museum. The first was *Barbus burgi* from three specimens collected in the Berg River near Paarl. The second was *Barbus asper* which was named after the rough tubercles prominently developed on the head of the male holotype. At the time no mention was made of any red fin colouration in either of these two species.

Boulenger (1911) also provided descriptions and illustrations for two other redfins *B.burchelli* and *B.vulneratus*. His description of

B.burchelli was based on three specimens from the Eerste River and four juveniles from Deelfontein. The latter specimens were later shown by Barnard (1943) to be *Barbus anoplus* Weber (1897). The description of *B.vulneratus* was based on two adults from the Riviersonderend and three subadults from the Baakens River near Port Elizabeth. The Baakens River specimens were also shown by Barnard (1943) to be incorrectly assigned and are now referred to as *B.afer*.

In their monograph on Southern African freshwater fishes Gilchrist & Thompson (1917) followed Boulenger's account of the redfin species. Several of the errors made by Boulenger (1911) were therefore carried over and in consequence much new material available to Gilchrist and Thompson was misidentified. Two other errors made by Boulenger (1911) not yet mentioned involve the illustration of *B.anoplus* which was in fact a specimen of *B.afer* (as it is now known), and that the illustration of *B.afer* was of a subadult of *B.burgi*. Gilchrist & Thompson (1917) confused specimens of *B.asper* with *B.anoplus* which they described as a "rooivlerk" or "redfin".

Smith (1936) described a new redfin species, *Barbus senticeps*, from the Kromme River, to the west of the Gamtoos. The species had particularly large scales and a single pair of long barbels and was considered to be close to *B.anoplus* and *B.afer*. These considerations were probably based on the misidentified *B.anoplus* of Gilchrist & Thompson (1917) and the erroneous account of "*B.afer*" in Boulenger (1911).

Two important contributions to redfin taxonomy were made by K.H. Barnard in 1938. In the first Barnard (1938 a) described a new species, *Labeo quathlambae*, from material reported to have been collected in the Umkomazana River and deposited in the Natal Museum. Although described as a *Labeo* the species had definite *Barbus* characteristics. The very small scales were distinctive and Barnard remarked on the traces of orange colour at the bases of the fins.

In a second paper Barnard (1938 b) published his preliminary findings on the *Barbus* species from the Cape Province. In addition to correcting the numerous errors of Weber (1897), Boulenger (1911) and Gilchrist & Thompson (1917) three new redfin species were described:

B.calidus, *B.tenuis* and *B.phlegethon*. Barnard gave type localities only as river systems and provided no reference to type specimens. More detailed descriptions and references to collecting localities as well as tables of growth changes were later provided by Barnard (1943).

The revision of the indigenous freshwater fishes of the south-west Cape (Barnard, 1943) was a major milestone in the history of the redfin *Barbus* species. The species were recognised as a distinct group, the many errors of previous authors had been corrected and certain taxonomic changes made. The geographical distribution of each species was also for the first time reasonably completely plotted. The species of redfins and their distribution as recorded by Barnard (1943) may be summarised as follows:

Barbus calidus - Clanwilliam Olifants River System,
Barbus burchelli - Berg and Eerste River Systems (*B.burgi* is a synonym of this species),
Barbus vulneratus - Breede and adjacent rivers,
Barbus phlegethon - Clanwilliam Olifants River System,
Barbus tenuis - mountain tributaries of the Gourits River System,
Barbus asper - the mainstreams of the Gourits and the Groot River of the Gamtoos System (including a "variant" form in the southern coastal rivers and the mountain tributaries of the Gamtoos River System), and
Barbus senticeps - rivers of the Eastern Province including the Swartkops, Baakens and Kromme River Systems.

In addition *Barbus anoplus* had been definitely shown not to be a redfin.

The success which Barnard had in elucidating redfin taxonomy was partly due to his extensive field experience. This experience was limited in the east and it is largely here with *B.asper* and *B.senticeps* (= *B.afer*) that the taxonomy was not entirely satisfactory. *B.asper* from the Gourits System and from the Groot River (Gamtoos System) agreed with the descriptions given by Boulenger (1911). In the mountain tributaries of the Gamtoos and coastal rivers around Knysna Barnard found "local varieties" which had larger scales than the typical form. The situation was further complicated by the fact that *B.senticeps* was present in rivers to either side of the Gamtoos but not in the Gamtoos itself.

The redfin species were subsequently reviewed by Jubb (1965). Several nomenclatural changes were introduced. *B.afer* was substituted for *B.senticeps*, *B.burgi* was resurrected in place of what Barnard called *B.burchelli*, and *B.burchelli* replaced the name for Barnard's *B.vulneratus*. The substitution of *afer* for *senticeps* was made in the light of a re-examination of the type specimens of *B.afer*. The reasons for the change of nomenclature affecting *B.burgi* and *B.burchelli* were more complex. Barnard (1943) had already stated that it was difficult to decide which species of redfin (i.e. the Berg River form or the Breede River form) Andrew Smith had originally referred to in his description of *B.burchelli*. P.H. Greenwood (BMNH) compared the type skins of *Gnathendalia vulnerata* with Smith's *B.burchelli* description for Jubb and concluded they were synonymous. On this basis Jubb (1965) referred the Breede River species to *B.burchelli*. He then required a name for the Berg River species for which Boulenger's *B.burgi* was available.

In addition to these changes Jubb (1965) made the following useful contributions to knowledge of the species. He provided for the first time full illustrations of *B.calidus*, *B.phlegethon*, *B.tenuis* and *B.afer*, discovered an isolated population of *B.afer* in the Sundays River System, and recorded the polytypic nature of *B.afer*, suggesting that this may be the reason why the species had not previously been recorded from the Gamtoos River System.

The redfins were again dealt with by Jubb (1967) but the accounts were essentially the same as those given in 1965. One notable development concerned *B.calidus*. During surveys of the Clanwilliam Olifants River System a collection had been made of a *B.calidus*-like form which differed from typical *B.calidus* in two essential respects, namely in having a nonserrated dorsal spine and seven branched rays in the anal fin. *B.calidus* has a strongly serrated dorsal spine and six branched rays in the anal fin. At the time Jubb (1967) did not have sufficient material to study the aberrant population further.

Skelton (1974b; appendix 3) studied this population and concluded that it represented a new species, *Barbus erubescens*. There were several differences between it and *B.calidus* other than those which Jubb had noted but the outstanding feature was the number of anal fin branched rays which is greater than in any other *Barbus* species as far as is known.

Another development since Jubb (1967) concerns the species described by Barnard (1938) as *Labeo quathlambae*. Jubb (1966) queried the generic status of the species and Greenwood & Jubb (1967) referred it to a new genus, *Oreodaimon*. Skelton (1976) suggested that *O.quathlambae* is closely related to the redfins, a problem which is examined further in Chapter 5.

The remainder of the present chapter will consider the taxonomy of the redfin species in the light of problems which have not yet been solved or which have arisen subsequently to Jubb (1967). Briefly these may be summarised as follows: (a) The status of *B.burgi* relative to *B.burchelli*. At present the status of the species rests on dubious characters, the delayed appearance of anterior barbels, a slight difference in scale size which is not clear cut and possibly difference in size at maturity.

(b) The status of *B.afer*, *B.asper*, *B.afer* in the Gamtoos River and *B.asper* in the southern coastal rivers. The problem is that typical *B.asper* is clearly differentiated from typical *B.afer* on scale size. However Jubb (1965; 1967) has shown that both species have wide intraspecific variation in this character and there is no clear way at present of positively identifying the populations in the Gamtoos mountain tributaries or those from the southern coastal rivers, which are intermediate in scale size. The populations from the southern coastal rivers will, in this report, be referred to as *B.asper* (variant).

(c) The status of *B.tenuis*. *B.tenuis* was described without reference to type specimens and Jubb (1965) reported that these were lost. According to Barnard (1943) the species has two main diagnostic characters which separate it from *B.asper* and *B.afer*, slender shape and the absence of tubercles on the head of breeding males. However recent collections had shown that there were specimens which appeared to be *B.tenuis* but did have tubercles on the males. The reliability of body shape was open to question as this is known to vary widely in cyprinid species, and therefore the status of *B.tenuis* was open to question.

With the need for a comparative study of the phylogeny of the redfins in mind, the taxonomic status of all the redfin species has been reviewed below.

Materials and Methods

The following taxonomic account of the redfins is divided into three sections:

(a) an inter- and intraspecific comparison of each character in turn;

(b) general conclusions on the status of the species, and

(c) summarized species accounts.

There are several reasons for adopting this approach rather than a detailed species by species account. Firstly it focusses attention on each character which, it is believed, permits a more careful assessment of the taxonomic worth of each character. This was particularly important for those characters which have been studied for the first time in the redfins. Secondly it means that each character is discussed in detail once and not several times. This facilitates the comparison of variation, extent of sexual dimorphism and allometry, all of which have been studied in greater detail than in any previous account of the redfins. Thirdly the redfin programme is intended to form a foundation on which future southern African cyprinid studies can be based. A comparative study of this sort promotes insight into the nature of individual characters at three distinct levels viz., the infra-, interspecific and supraspecific level. It was also realised at the outset that the taxonomic problems of the redfins are basically those of refinement - where sound decisions could only be made in the light of a detailed knowledge of the characters concerned. Finally the taxonomy of the redfins was a preliminary step towards the study of the phylogeny of the species. The methods employed in the phylogenetic study are based on the evaluation of each individual character and not on the general similarity or differences of the species.

Characters: Definitions and Methods

Both quantitative and qualitative characters have been employed in the study. Quantitative characters include both linear measurements and

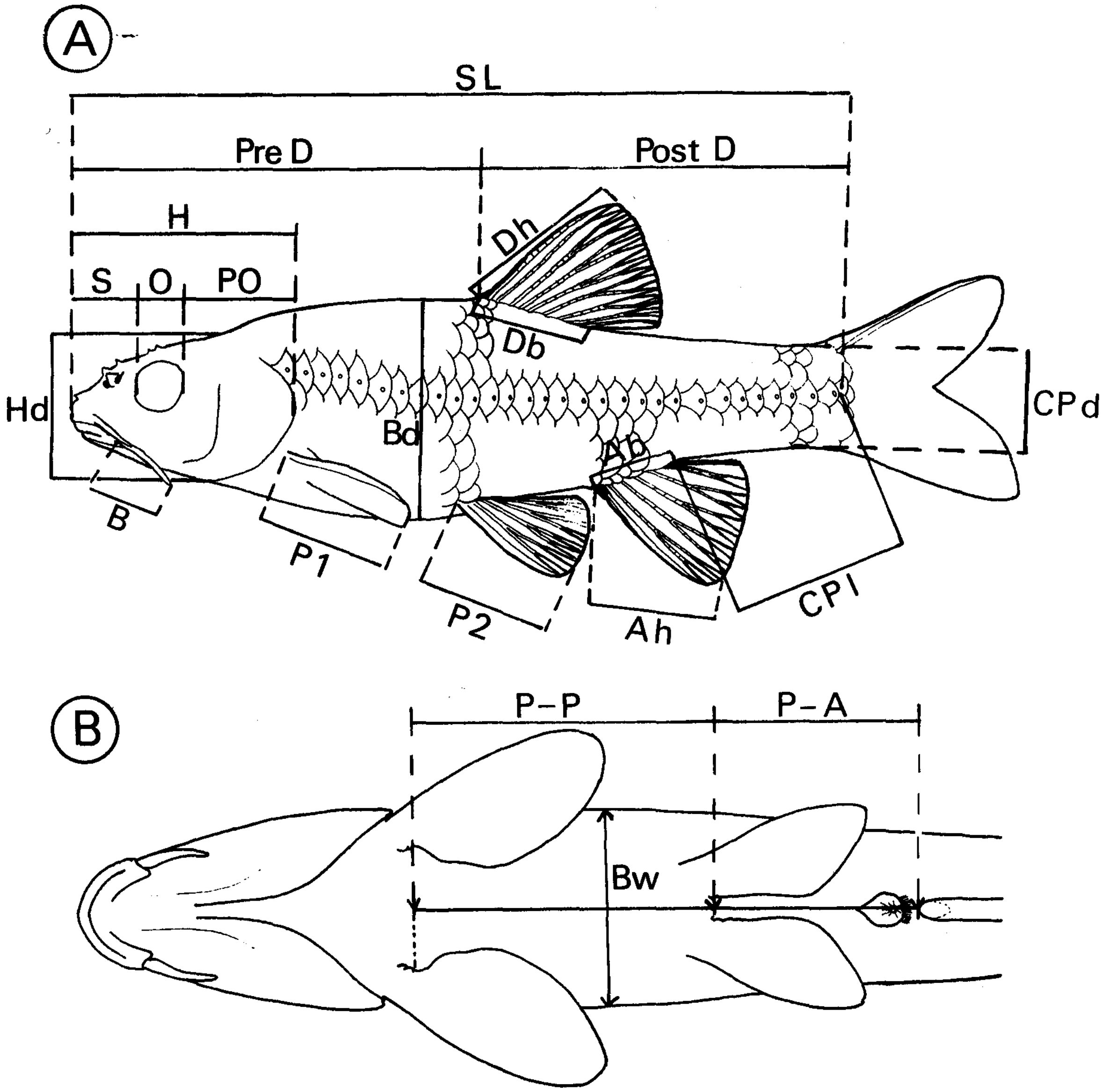


Fig. 3.1 Linear measurements as taken in this study. Abbreviations: Ab - anal fin base; Ah - anal fin height; B - barbel length; Bd - body depth; Bw - body width; CPd - caudal peduncle depth; CPl - caudal peduncle length; Db - dorsal fin base; Dh - dorsal fin height; Hl - head length; Hd - head depth; O - orbit diameter; Pl - pectoral fin length, P2 - pelvic fin length; PO - postorbit length; P-A - pelvic to anal fin length; P-P - pectoral to pelvic fin length; Post D - post dorsal length; Pre D - predorsal length; S - snout length; SL - standard length.

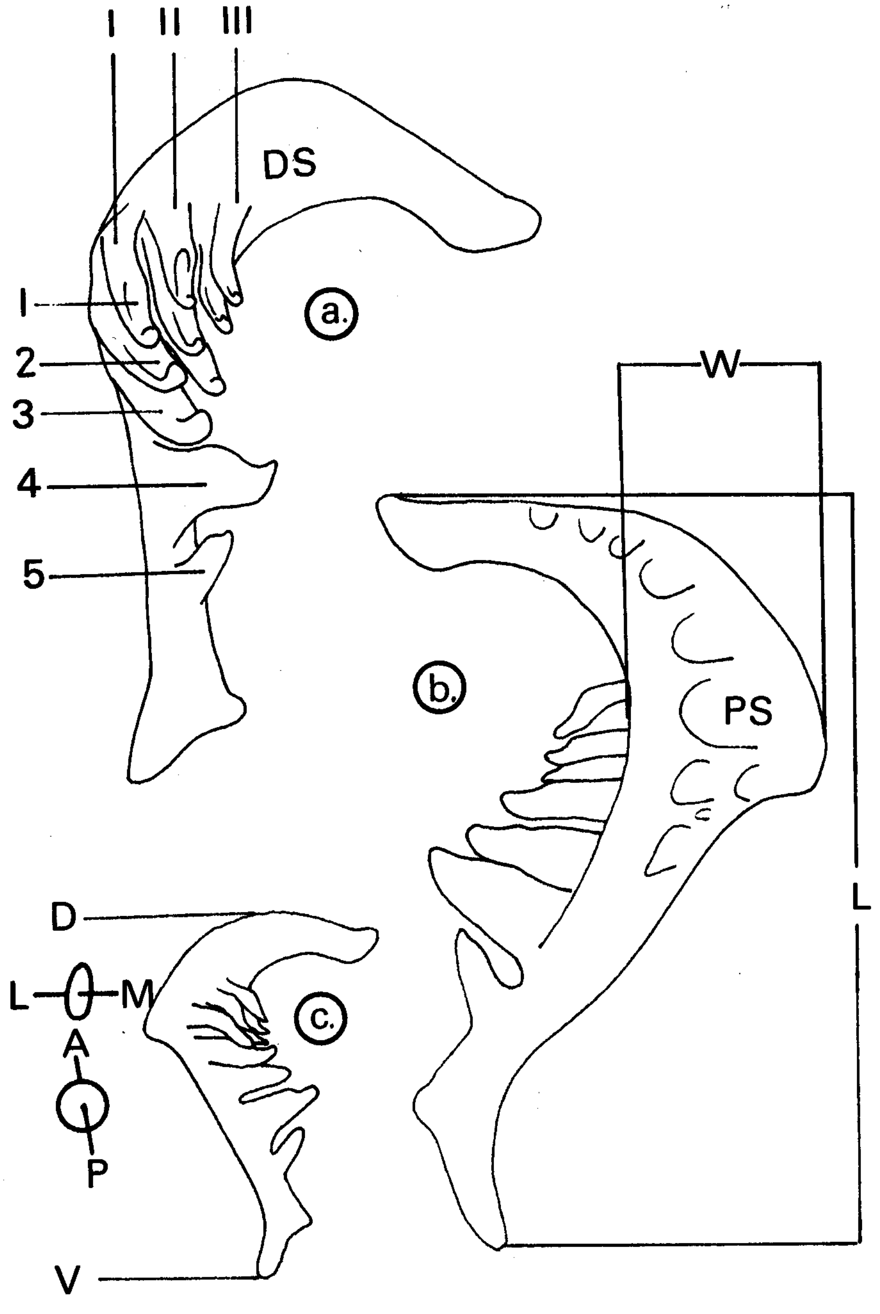


Fig. 3.2 Measurements and orientation of pharyngeal bones and teeth, (a) postero-medial view of the left pharyngeal bone, row I = majrr or inner row, II = middle row, III = minor or outer row. Teeth in major row are numbered, the first being the dorsal tooth on dentigerous or ventral surface; (b) antero-lateral view of left pharyngeal bone, L = length; W = width; ps = dorsal or pitted surface; (c) orientation A = anterior, D = dorsal, V = ventral, L = lateral, M = medial.

proportions, and meristic characters. Measurements were taken with a vernier calipers and recorded to the nearest 0,1 mm. Measurements of the pharyngeal bones were made with a stereo-microscope fitted with a graticule. The results were analysed by "population" (i.e. a statistical sample of about 30 individuals from a single locality) of both sexes combined, and for each sex separately. Specimens were, as far as possible, of adult proportions i.e. larger than 50 mm SL. (Barnard, 1943). This was done to minimise bias due to allometry. Separate samples of as wide a size range as possible were used to assess allometry.

Methods of analysis included the graphical comparison of descriptive statistics (Dice diagrams of Hubbs & Hubbs, 1953); comparison of graphical plots of each species or species sub-group; Students "T"-tests and regression analysis.

Linear measurements (Fig. 3.1 A, B) were taken as in Hubbs & Lagler (1958) with the following exceptions or clarifications.

i) All measurements from the anterior end of the head were taken from the anterior point of the symphysis of the retracted premaxillae.

ii) Measurements on the head (e.g. orbit diameter) were taken from the bony margins of the elements concerned.

iii) Predorsal and postdorsal lengths were taken along the horizontal line to the point of intersection of the vertical through the base of the leading dorsal ray.

iv) Pectoral to pelvic length is the median measurement between the posterior margins of the bases of the pectoral and pelvic fins.

v) Pelvic to anal fin length is the median measurement from the posterior margins of the base of the pelvic fins and the base of the first anal fin element.

vi) Pharyngeal bones (Fig. 3.2 A, B) were measured according to Chu (1935). The pharyngeal bones were dissected out, macerated in trypsin for a few days, and then mechanically defleshed and dried. Orientation of the bones for descriptive purposes is shown in Fig. 3.2 C.

vii) Measurements were taken on the left side except where damaged.

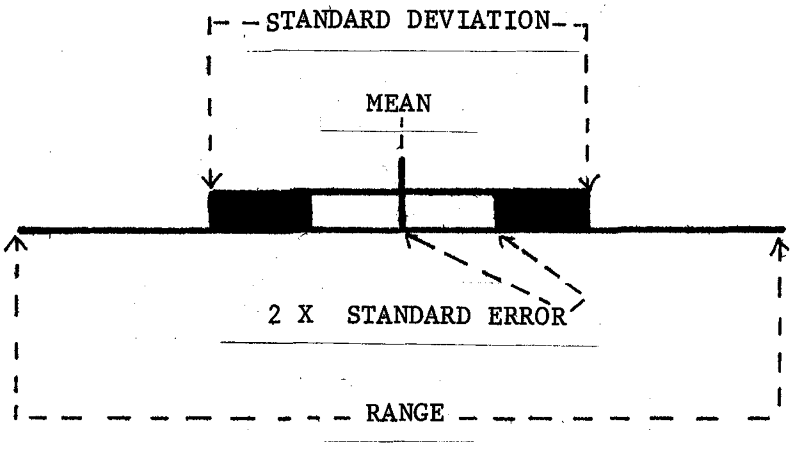


Fig. 3.4 Symbols used in dice diagrams.

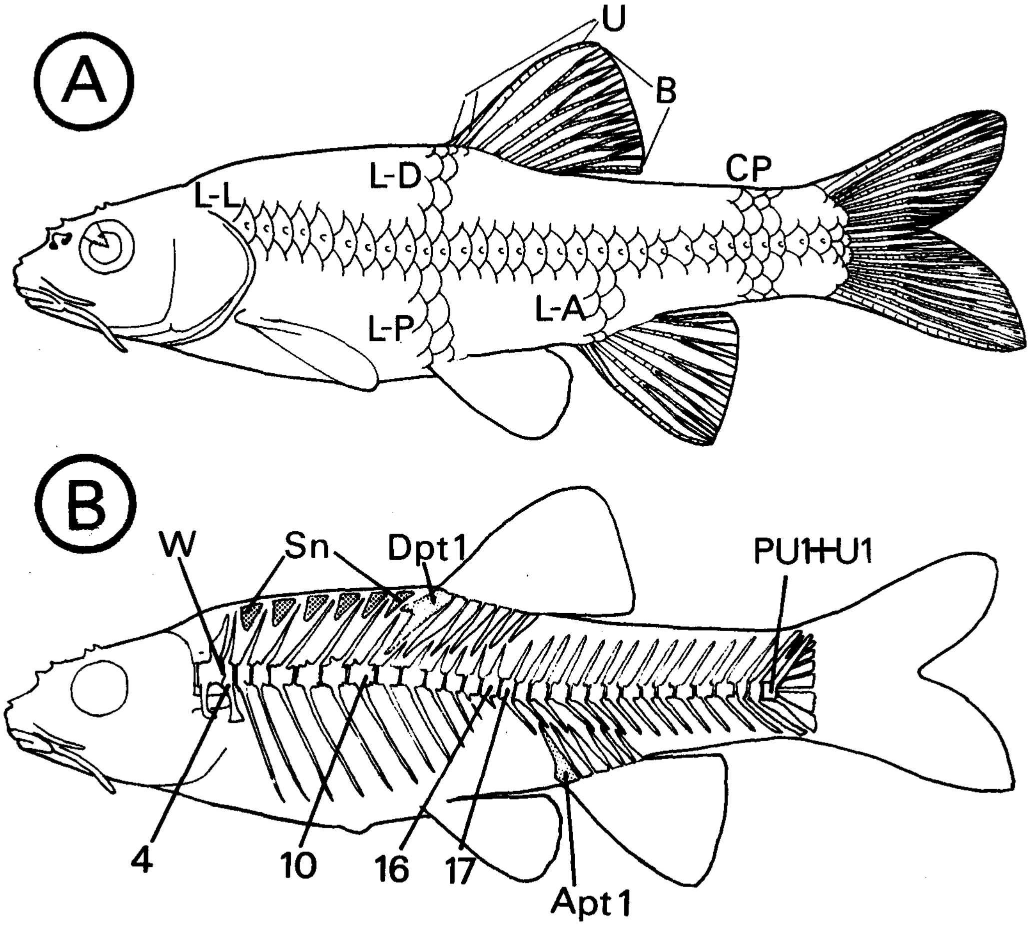


Fig. 3.3 Diagram showing meristic measurements as taken in this study. Abbreviations: A pt. 1 - first anal fin pterygiophore; B - branched rays; CP - caudal peduncle scale rows; Dpt 1 - first dorsal fin pterygiophore; L-A - lateral line to anal fin scale rows; L-D - lateral line to dorsal fin scale rows; L-L - lateral line scales; L-P lateral line to pelvic fin scales; PCR - principle caudal fin rays; PU1 + U1 - compound ural centrum; Sn - supraneural bones; U - unbranched fin rays; W - weberian vertebrae; 4 - 4th vertebrae; 10 - last vertebrae before dorsal fin; 16 - first caudal vertebra; 17 - last vertebra before anal fin.

viii) The length of the intestine was taken according to Snelson (1971). The tract was severed immediately behind the transverse septum of the body cavity and at the anus. Viscera were detached and the tract straightened and pinned onto a board, without stretching. Length was measured to the nearest millimetre with vernier calipers.

Measurements are expressed as % SL with the following exceptions: head depth, snout length, orbit diameter, postorbital length and interorbital length are expressed as % HL; barbels are expressed as % orbit diameter. Results of measurements are expressed in the form of dice diagrams, explained in Fig. 3.4.

Meristic measurements. Meristic values are expressed with the number of individuals in parenthesis. Scale and fin ray counts were made according to Hubbs & Lagler (1958) (Fig. 3.3 A) except for the predorsal scale rows which were taken as in Snelson (1972). This count records oblique scale rows crossing an imaginary line between the anterior base of the dorsal fin and the posterior margin of the head. Single scales interposed between two otherwise regular rows are omitted. This method was used because the predorsal scales of the redfins are often small, without a regular median series.

Branched and unbranched rays are considered separately in the case of the dorsal and anal fins, but all rays are included in a single count in the case of the pectoral and pelvic fins. Caudal fin rays include only the principle caudal rays (branched caudal rays plus one dorsal and one ventral unbranched ray).

Postcranial skeletal meristics (Fig. 3.3 B) were taken using radiographs. Total vertebral counts include the Weberian apparatus as four and the ural centrum (PU1 + U1) as one unit. The first caudal vertebra was taken as the first vertebra with a closed haemal arch. This is detected as a distinct bright exposure point on radiographs. Vertebrae before the dorsal fin and vertebrae before the anal fin include all vertebrae up to and including that which is opposite or immediately ahead of the respective first dorsal or anal pterygiophore. Supraneural bones include all independent units between the neurocranium and the first dorsal pterygiophore.

TABLE 3.1

Redfin samples used in the morphometric and meristic programme. Locality numbers are shown in Fig. 3.5

Species	Museum Reg. No.	Locality (River-System)	Fig. 3.4 A or B Locality No.
B.burchelli	AM/P 1411, 3463	Witte R. (Breede)	23
	AM/P 2079	Klipplaas R. (Breede)	19
	AM/P 2077	Kabous R. (Breede)	20
	AM/P 3472	Duivenhoks R.	18
	AM/P 1368	Hex R. (Breede)	24
	AM/P 1566	Keisers R. (Breede)	21
	SAM 18731	Riviersonderend R. (Breede)	22
B.burgi	AM/P 2076, 1578	Krom R. (Berg)	27
	AM/P 1874, 1875	Verlorenvlei R.	28
	SAM 18747	Berg R. at Groot Drakenstein	26
	SAM 4695, 5090	Eerste R.	25
	BM(NH) 1901-2-11:14-16	Berg R. (ex SAM 4696)	
	SAM 4696	Berg R.	27
B.phlegethon	SAM 22484	Olifants R.	29
	SAM 22749	Olifants R.	29
	SAM 22483	Olifants R.	29
	AM/P 722	Thee R. (Olifants)	30
	AM/P 1394	Keerom, (Olifants)	29
	AM/P 1852	Jan Diessels R. (Olifants)	32
	AM/P 1863	Noordhoeks R. (Olifants)	30
	AM/P 2054	Driehoek R. (Olifants)	35
B.tenuis	AM/P 2081, 1935, 608	(Gourits)	
	AM/P 2666	Waterkloof R. (Gourits)	15
	AM/P 2667	Kruis R. (Gourits)	16
	AM/P 3186	Keurbooms R.	11
B.afer	AM/P 609	Witte R. (Sundays)	1
	AM/P 745, 2524	Elands R. (Swartkops)	2
	AM/P 766	Baakens R.	3
	AM/P 2651	Kromme R.	8
B.afer (Gamtoos)	AM/P 1415	Loerie R. (Gamtoos)	4
	AM/P 1374, 1375	Goega R. (Gamtoos)	5
	AM/P 1921	Wit R. (Gamtoos)	6
	AM/P 2651	Kromme R.	8
B.asper (variant)	AM/P 2652, 2654	Bloukrans R.	9
	AM/P 2656	Groot R. (Natures Valley)	9
	AM/P 2659	Keurbooms R.	10
	AM/P 1790	Knysna R.	11
	AM/P 110, 584	Homtini R. (Goukamma)	11
B.asper	AM/P 1744	Groot R. (Gamtoos)	7
	AM/P 2663	Kammanassie R. (Gourits)	13
	AM/P 1699	Groot R. (Gourits)	17
	AM/P 607	Meiringspoort (Gourits)	14
B.calidus	AM/P 1871	Ratels R. (Olifants)	29
	AM/P 1862	Noordhoeks R. (Olifants)	30
	AM/P 1797, 1371	Rondegat R. (Olifants)	31
	AM/P 1850	Jan Diessels R.(Olifants)	32
	AM/P 1844	Tra-Tra R. (Olifants)	33
	AM/P 1855	Matjies R. (Olifants)	34
	AM/P 1857	Breekkrans R. (Olifants)	34
B.erubescens	AM/P 1867, 2045, 2049	Twee R. (Olifants)	36
	AM/P 1866, 2075	Middeldeur R. (Olifants)	36
	AM/P 2074	Suurvlei R. (Olifants)	36
Oreodaimon quathlambae	AM/P 1540, 1877, 1823, 3473 - 3478	Tsoelikana R. (Orange)	37
	AM/P 3479	Moremoholo R. (Orange)	38
	AM/P 3480	Senqu R. (Orange)	39
	SAM 19018	Umkomazana R. (Umkomaas)	40

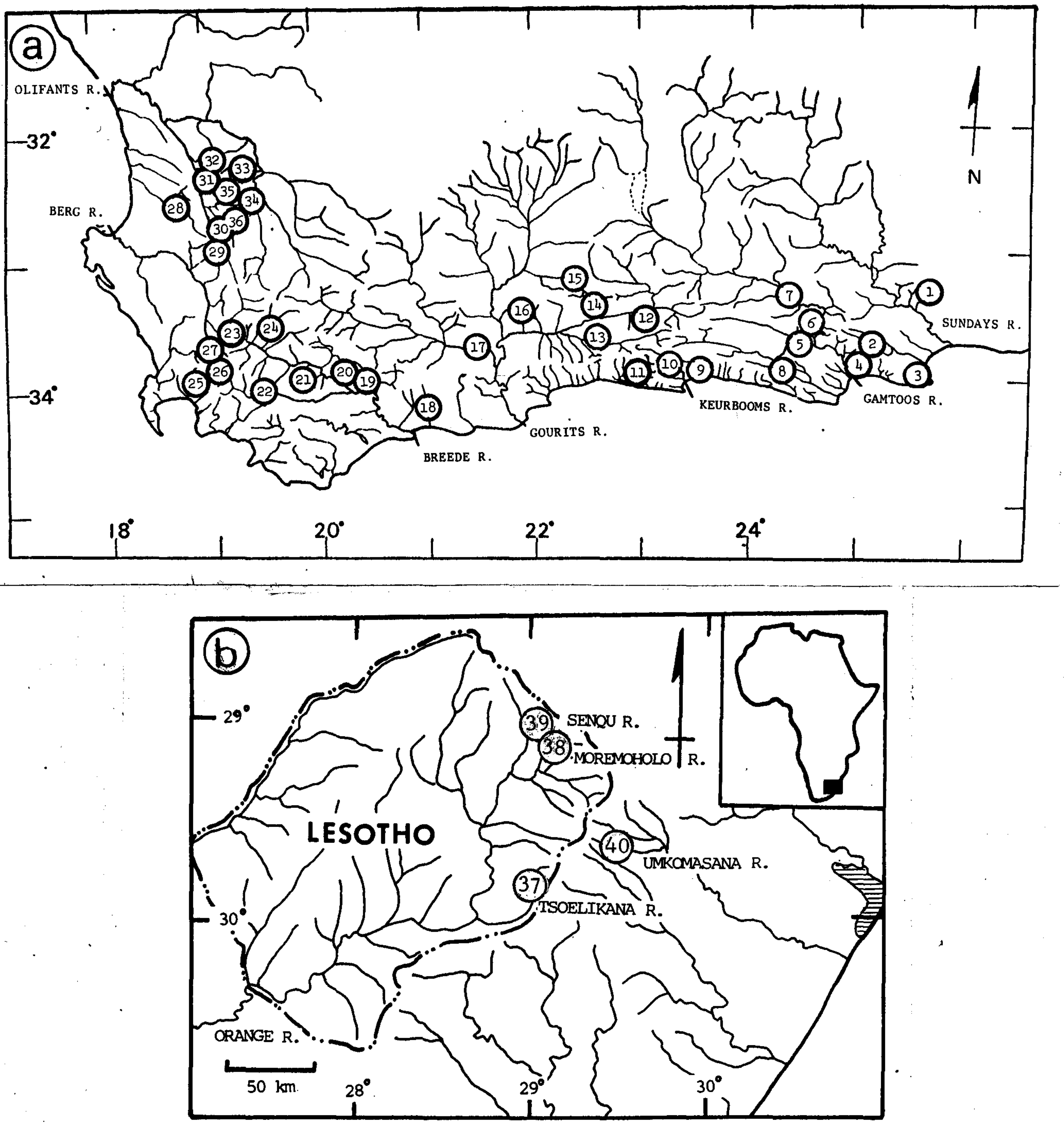


Fig. 3.5 Localities of samples used in the morphometric and meristic study of redfin species, (a) south coastal localities, (b) localities of O.quathlambae samples. Locality numbers of samples are given in Table 3.1.

Scale radii were determined from five scales per specimen taken from the following body regions: anterior to the dorsal fin above and below the lateral line, posterior to the dorsal fin above and below the lateral line, all on the right hand side of the specimen. The scales were stained with alizarin red, defleshed and examined under a stereo microscope. Primary radii were considered as those extending more or less from the focus to the scale margin. Scales with a diffuse focus were excluded. In all the redfin species there are radii on all the fields of the scales.

Material

All redfin material used in this study is recorded in Appendix 1. Those samples used specifically in the morphometric and meristic analysis are given in Table 3.1 and their respective localities are shown in Fig. 3.5. Osteological material used is recorded in Appendix 2.

A recent survey of rivers in the Cape by the Cape Department of Nature and Environmental Conservation has provided many new locality records and sample of redfins. Appendix 1 records most of the available redfin material.

There are relatively few specimens of *Oreodaimon quathlambae* available and most of these are adult specimens. The samples are inadequate for assessing the geographic variation of the species. Some aspects have however, been recently recorded by Gephard (1978).

Presentation and delimitation of taxonomic groups during analysis

The taxonomic grouping referred to during the analysis are those established by Jubb (1967), Greenwood & Jubb (1967) and Skelton (1974 b). There was some doubt as to which species certain populations of redfins should be referred to and these were therefore treated separately and labelled as *B.asper* (variant) and *B.afer* (Gamtoos). *B.asper* (variant) refers to those populations found in the coastal streams between the mouth of the Gourits and the Gamtoos River Systems with the exception of the Kromme River to the west of the Gamtoos. *B.afer* (Gamtoos) refers to those populations of redfins from the mountain tributaries of the Gamtoos River System.

TABLE 3.2

The maximum size of redfin *Barbus* species

Species	Max. size (this study) (SL mm)	Literature (corrected SL)
B.burchelli	136	95 **
B.burgi	109	120 **
B.phlegethon	71	70 **
B.tenuis	80	85 *
B.afer	82	100 **
B.afer (Gamtoos)	80	
B.asper	80	
B.asper (variant)	104	118 **
O.quathlambae	102	130 ***
B.calidus	84	95 **
B.erubescens	95	

*	Barnard (1943)
**	Jubb (1965)
***	Gephard (1978)

As this investigation progressed it was evident that the redfins separated naturally into two groups, the first of *B.calidus* and *B.erubescens*, and the second comprising *B.burchelli*, *B.burgi*, *B.phlegethon*, *B.tenuis*, *B.afer*, *B.asper* and *O.quathlambae*. To facilitate repetitive reference to these species they will be referred to as the "serrated-rayed" and "flexible-rayed" redfins respectively in reference to a character of difference in the last unbranched dorsal fin ray.

The results are presented in a consistently specific order. This order was determined by the *a priori* taxonomic proximity of the species as implied by previous reviewers (viz. Barnard 1943; Jubb 1965, 1967). This is not intended to introduce prejudice but rather to facilitate comparison of the results. The order of presentation is *B.burchelli*, *B.burgi*, *B.phlegethon*, *B.tenuis*, *B.afer*, *B.afer* (Gamtoos), *B.asper*, *B.asper* (variant), *O.quathlambae*, *B.calidus*, and *B.erubescens*.

Results

Size

Barbus species are frequently divided into "large" and "small" categories. Barnard (1943) considered a species which attains a SL greater than 150 mm to be "large". A "small" *Barbus* does not exceed this size. The division is nevertheless arbitrary as Jubb (1967) regarded *B.argenteus* as a "small" species, yet reported that specimens up to 195 mm SL were known. On the division allocated by Barnard (1943) the redfins are all "small" species (Table 3.2). The term is relative and to distinguish these from *Barbus* species which are adults normally less than 50 mm SL a better description of the redfins would probably be that they are "medium" sized species.

The maximum size recorded for a redfin species is 134 mm SL (Table 3.2) for a specimen of *B.burchelli*. Gephard (1978) reports a specimen of *O.quathlambae* of 143 mm total length which would also be in the region of 130 mm SL. Apart from these two exceptions the table of maximum size recorded for redfin species provides a reasonable guide to the maximum size of larger specimens in museum samples. There are no outstanding differences in size attained except in the case of *B.phlegethon*. Large adults in most of the species reach a size of between 80 and 110 mm SL. In *B.phlegethon* equivalent specimens are usually less than 60 mm SL.

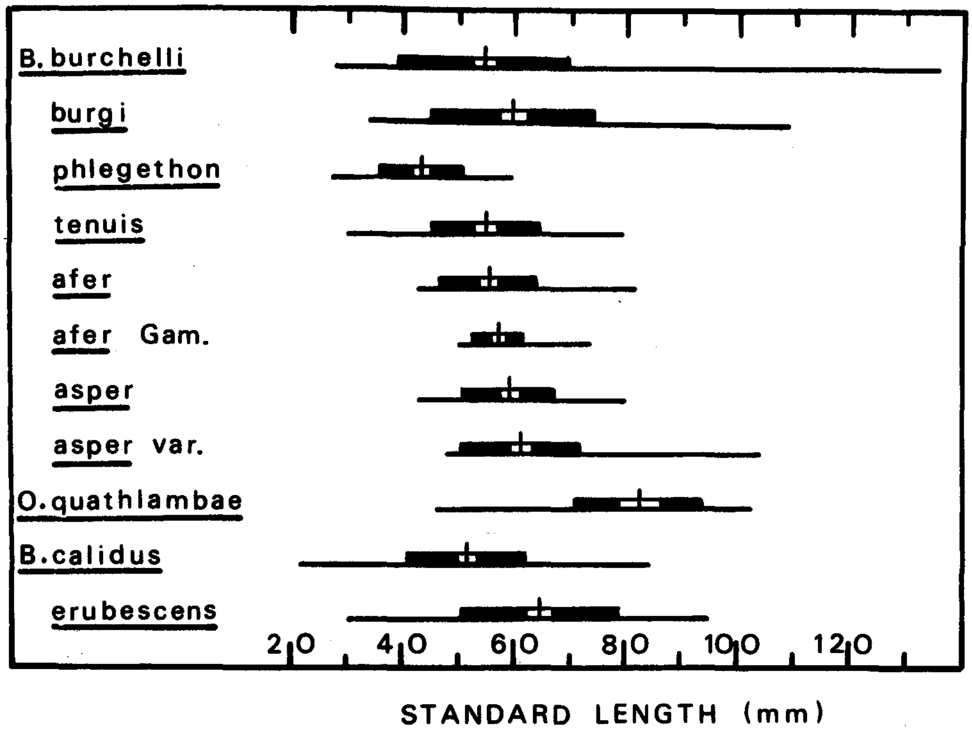


Fig. 3.6 Standard length statistics for samples of redfin *Barbus* species and *O.quathlambae*. Data in Appendix 4, Table 1.

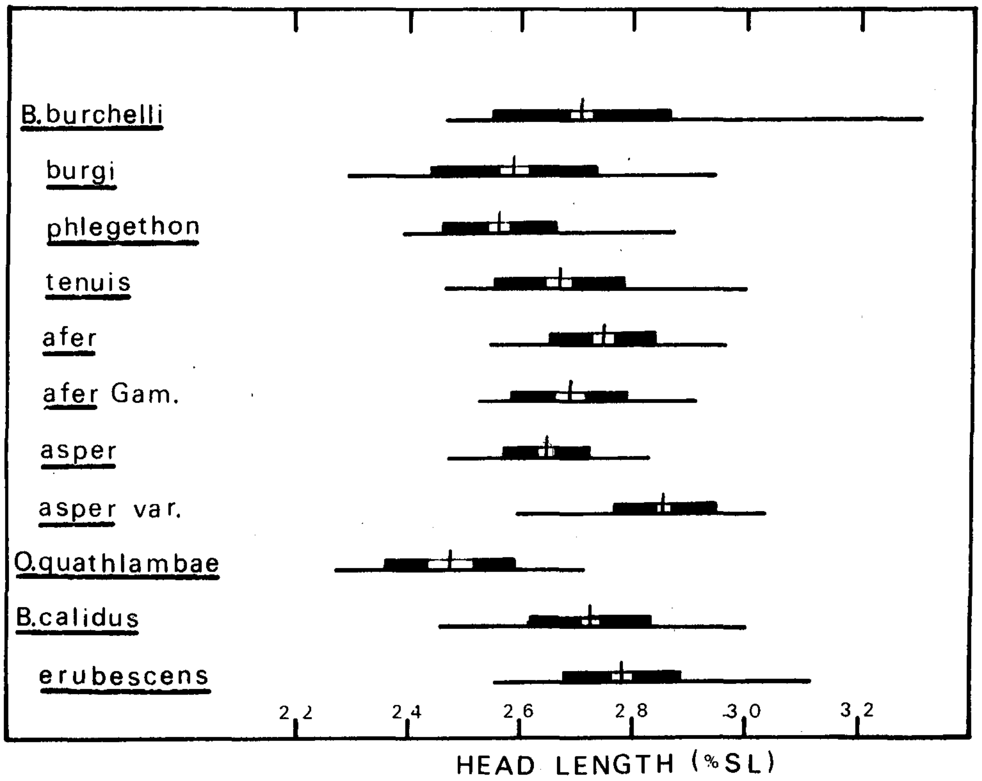


Fig. 3.7 Head length (% SL) of redfin *Barbus* species and *O.quathlambae*. Data in Appendix 4 Table 2.

The mean standard length of the species and species groups samples considered during the morphometric and meristic programme (Fig. 3.6) are within a similar magnitude for all the species except B.phlegethon and O.quathlambae. The low SL of B.phlegethon samples reflects the smaller size of the species but the higher mean for O.quathlambae reflects the available samples which are biased towards larger specimens.

Head length (Fig. 3.7)

Head length is a conservative character in redfin species. The results indicate that the head of O.quathlambae is relatively short. The head length-standard length function for this species is linear so that the result is not ascribed to negative allometry.

The head length of B.asper (variant) is greater than in B.asper or B.afer populations. If the head length ratio of individual populations are plotted in a geographical sequence (Fig. 3.8) an east-west clinal increase is recorded. Similar clines are noted below for other measurements (especially fin lengths) and it seems that a common explanation is possible viz. that the differences are due to environmental differences (see page 52).

Head depth (Fig. 3.9)

The head depth is relatively short in B.tenuis and O.quathlambae and relatively deep in B.burgi and B.phlegethon. The results also indicate a wide intraspecific variation in the head depth:head length ratio in the redfins. Although a significant difference between the head depth in B.burgi and B.burchelli is indicated it has been found that the difference is not consistent between populations and that in both species intraspecific differences are sometimes greater than interspecific differences.

Snout length (Fig. 3.10) and Orbital diameter (Fig. 3.13)

The snout to head length ratio is similar in the redfin species. A more useful relationship is described between the snout length and the orbit diameter (Fig. 3.11) which illustrates an interesting difference between the serrated-rayed and the flexible-rayed species. In B.calidus and B.erubescens the plot of orbit diameter against snout

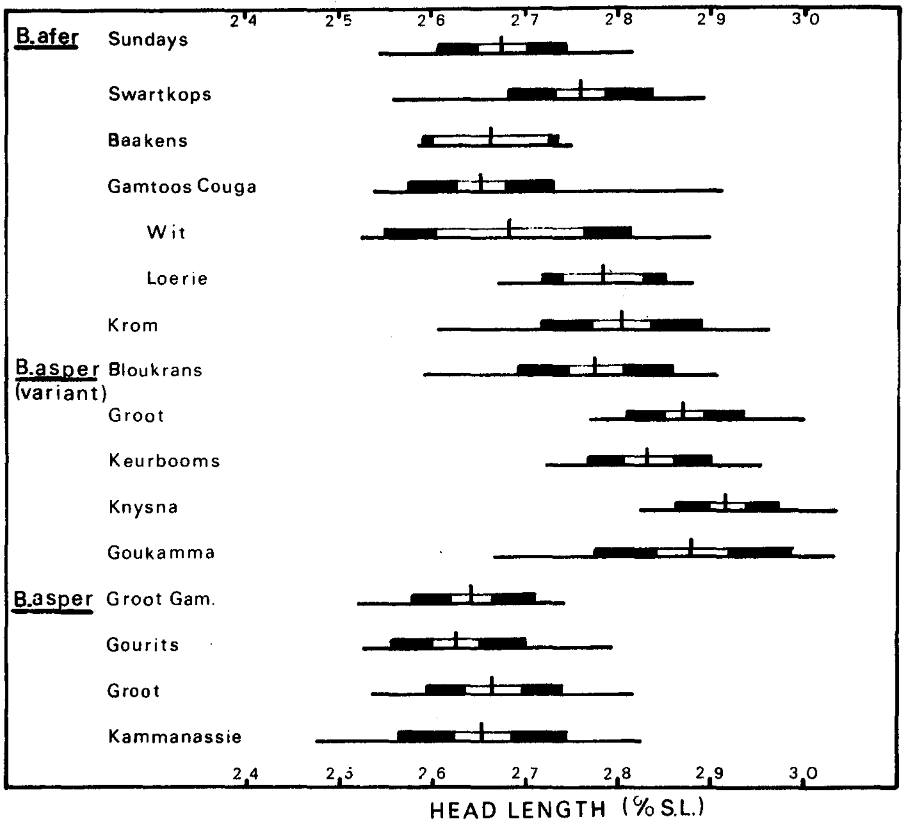


Fig. 3.8 Head length (% SL) of individual samples of <u>B.afer</u>, <u>B.asper</u> (variant) and <u>B.asper</u>. Data recorded in Appendix 4 Table 3.

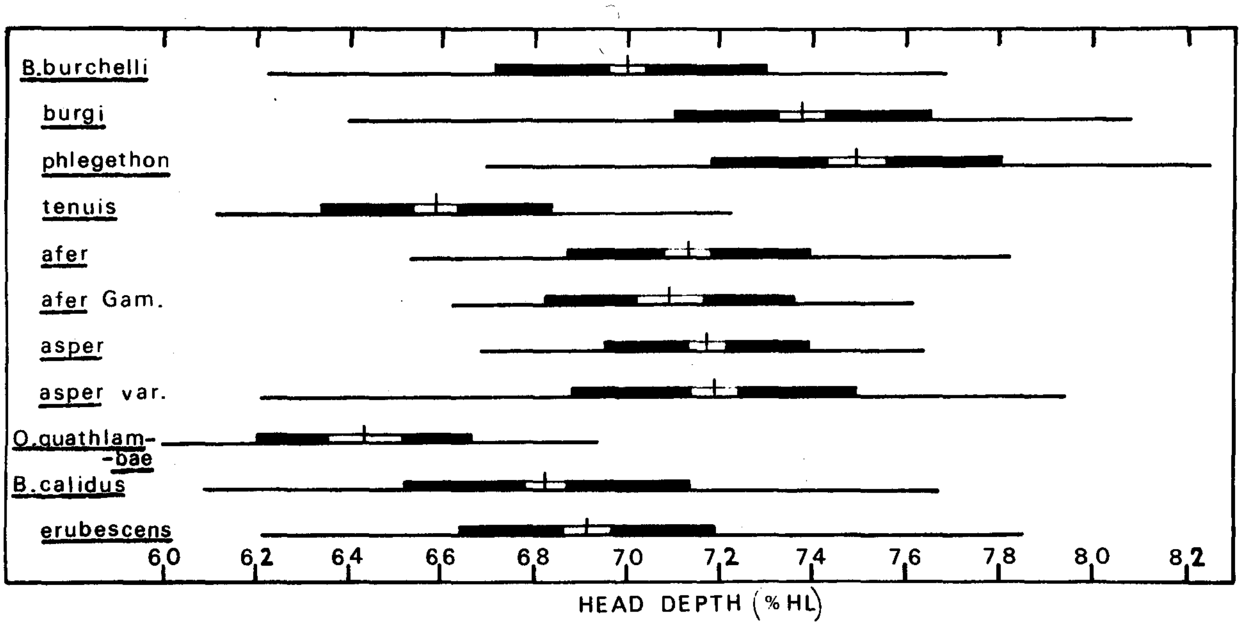


Fig. 3.9 Head depth (% HL of redfin <u>Barbus</u> species and <u>O.quathlambae</u>. Data in Appendix 4 Table 4.

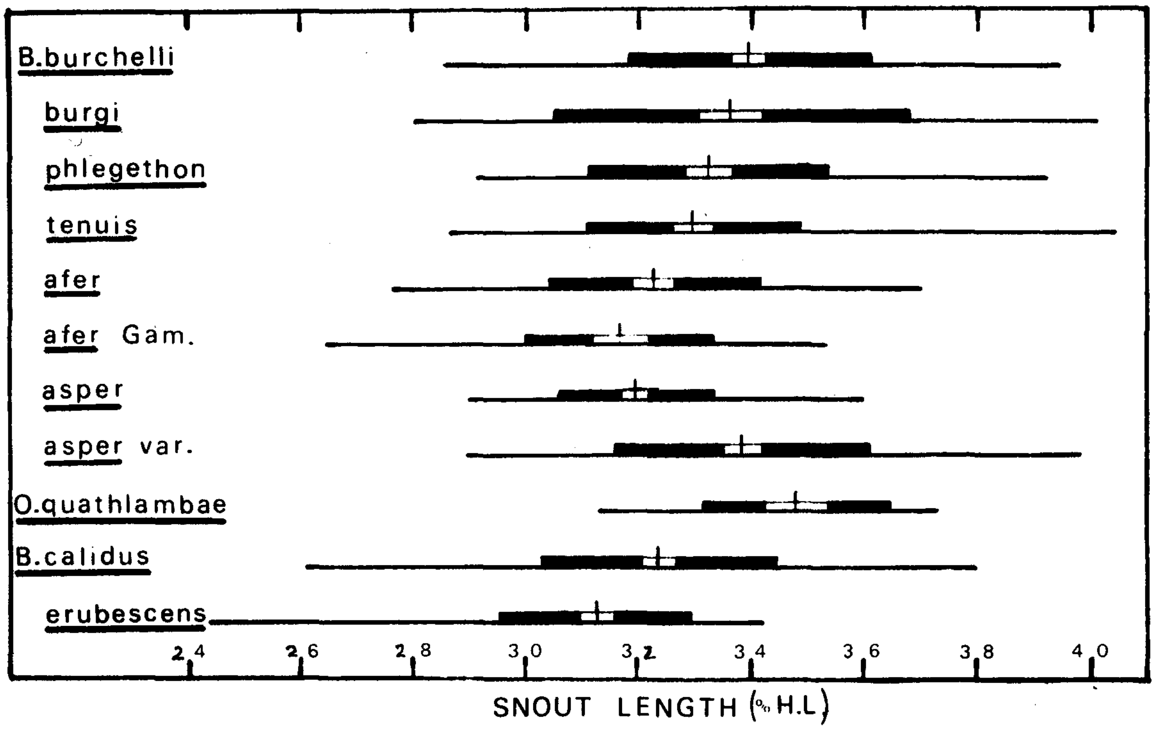


Fig. 3.10 Snout length (%HL) of redfin Barbus species and O.quathlambae. Data in Appendix 4 Table 5.

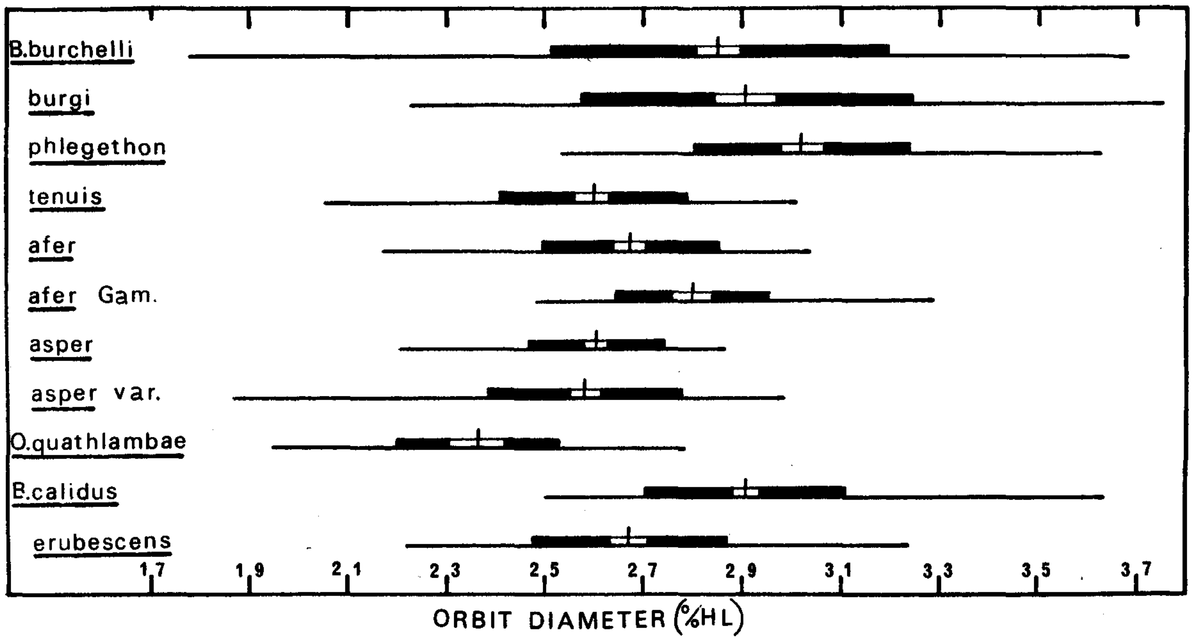


Fig. 3.13 Orbit diameter (% HL) of redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 6.

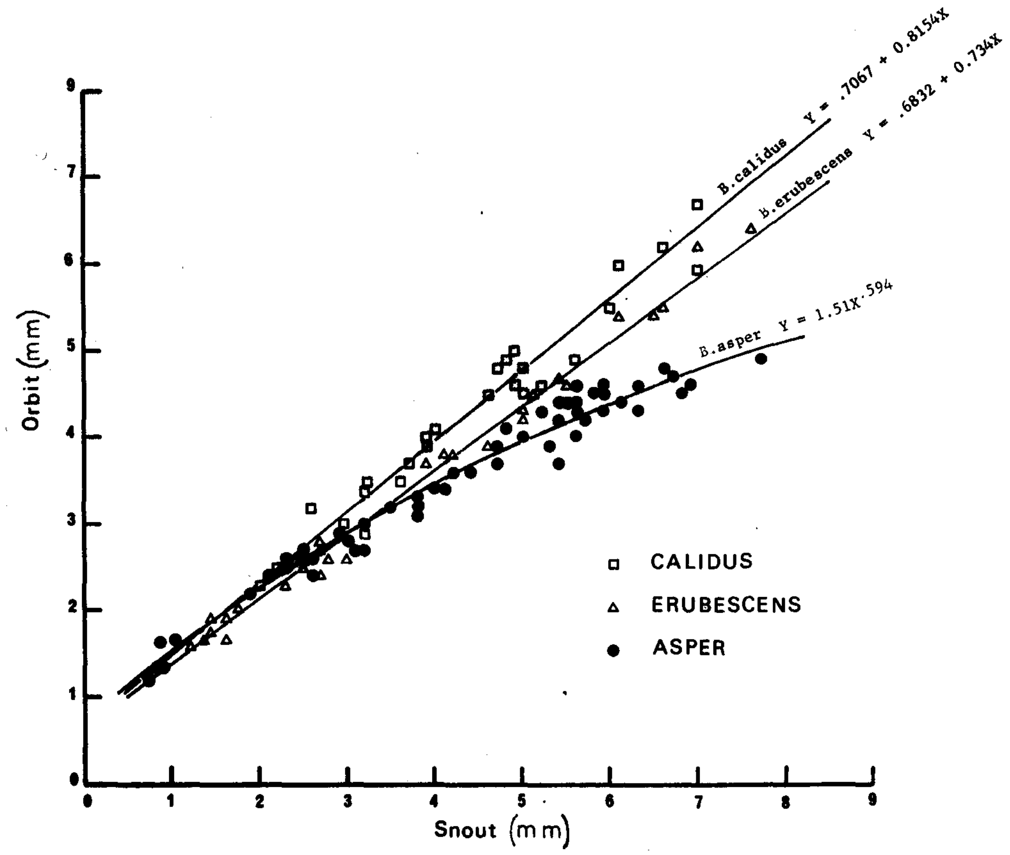


Fig. 3.11 The relationship between the orbit diameter and the length of the snout in B.asper, B.calidus and B.erubescens.

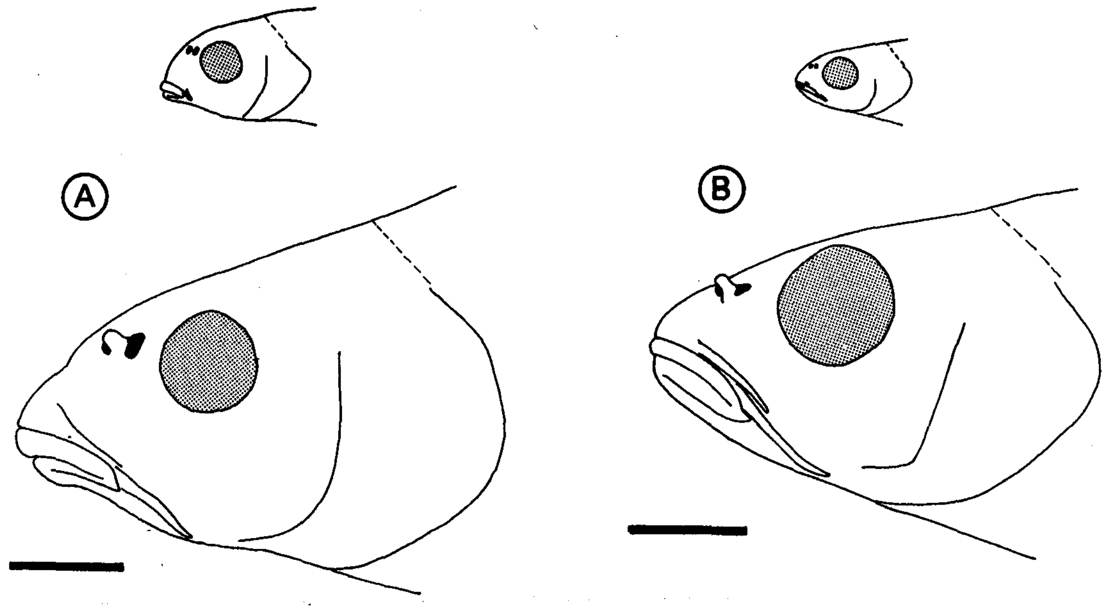


Fig. 3.12 A diagrammatic comparison of relative changes in the size of the orbit in (a) B.asper AM/P 2663, juv.- 20 mm SL, adult 80 mm SL; (b) B.calidus AM/P 1371 juv. 1,7 mm SL, adult 7,6 mm SL. Figure drawn with camera lucida. Scale bar = 5 mm.

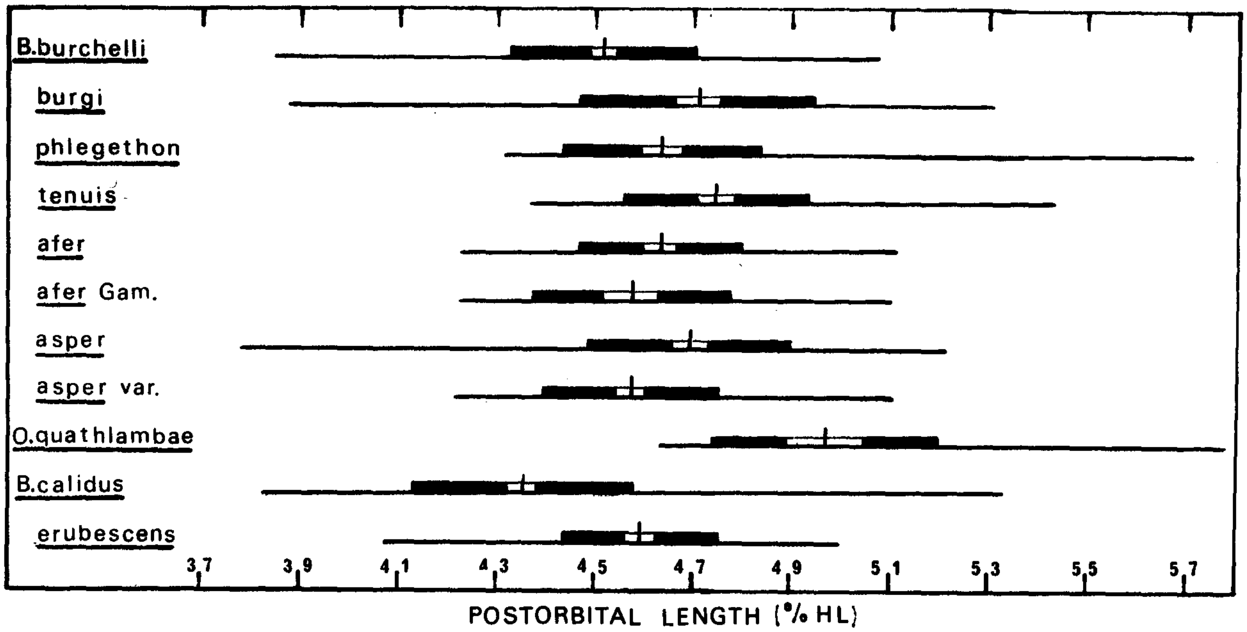


Fig. 3.14 Postorbital length (% HL) of redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 7.

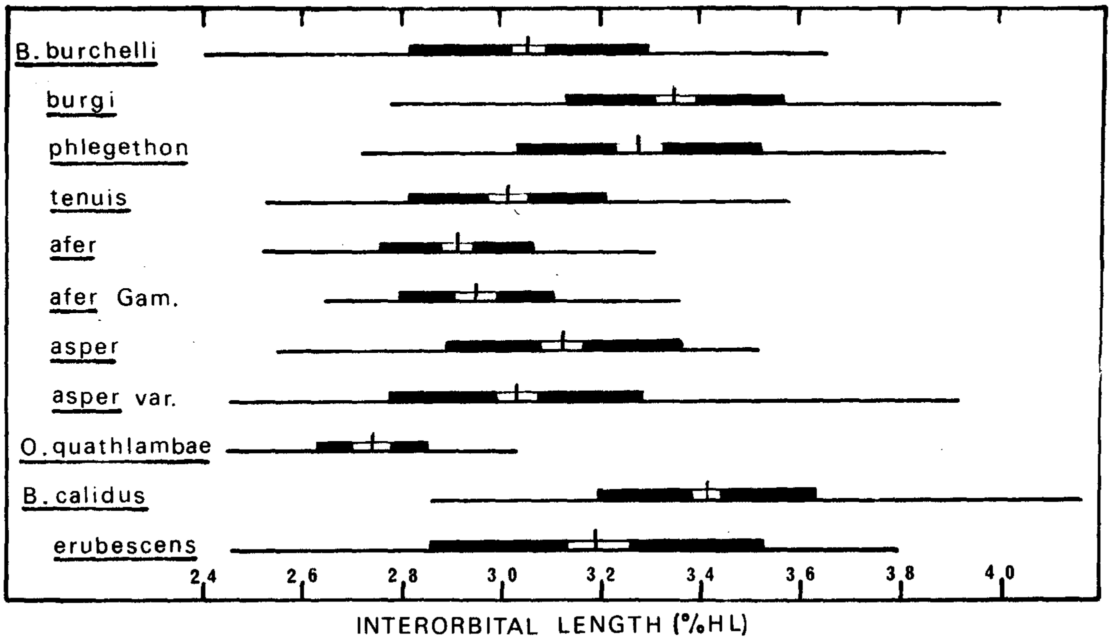


Fig. 3.15 Interorbital length (% HL) of redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 8.

length forms a linear function, suggesting that the relative change in proportion between the characters is small. In the flexible-rayed species on the other hand (e.g. B.asper) a curvilinear function is described indicating a relatively large proportional change between the characters with growth. The difference between the serrated- and flexible-rayed redfins is evident in a comparison of the head of similar sized juvenile and adult specimens (Fig. 3.12). From this it seems that the orbit diameter in the flexible-rayed species does not maintain the same growth tempo that it does in the serrated-rayed species.

This finding has important implications for the interpretation of the results on the orbit diameter (Fig. 3.13). In the flexible-rayed redfins the differences in orbit diameter reflect more or less inversely the differences in the size of the specimens examined e.g. a large orbit in B.phlegethon, a small species, and a small orbit in O.quathlambae of which mainly larger specimens were examined. On the other hand Figure 3.11 suggests that there is a useful taxonomic difference between the orbital diameter of B.calidus and B.erubescens.

Postorbital length (Fig. 3.14)

Apart from O.quathlambae the postorbit shows no outstanding differences between the flexible-rayed redfins. The opercular bone is relatively elongated in O.quathlambae and possibly explains the longer postorbit in the species. The opercular of B.tenuis is also elongated and it is noted that the postorbital ratio is also slightly higher in this species.

The difference between the postorbital ratio of B.calidus and B.erubescens (Fig. 3.14) correlates inversely with the difference between the orbital diameter of the two species which suggests that the two measurements are complementary.

Interorbital length (Fig. 3.15)

Differences between species are evident in the interorbital length, e.g. between B.burgi and B.burchelli or B.calidus and B.erubescens. The interorbit is narrow in O.quathlambae. The interorbit does not

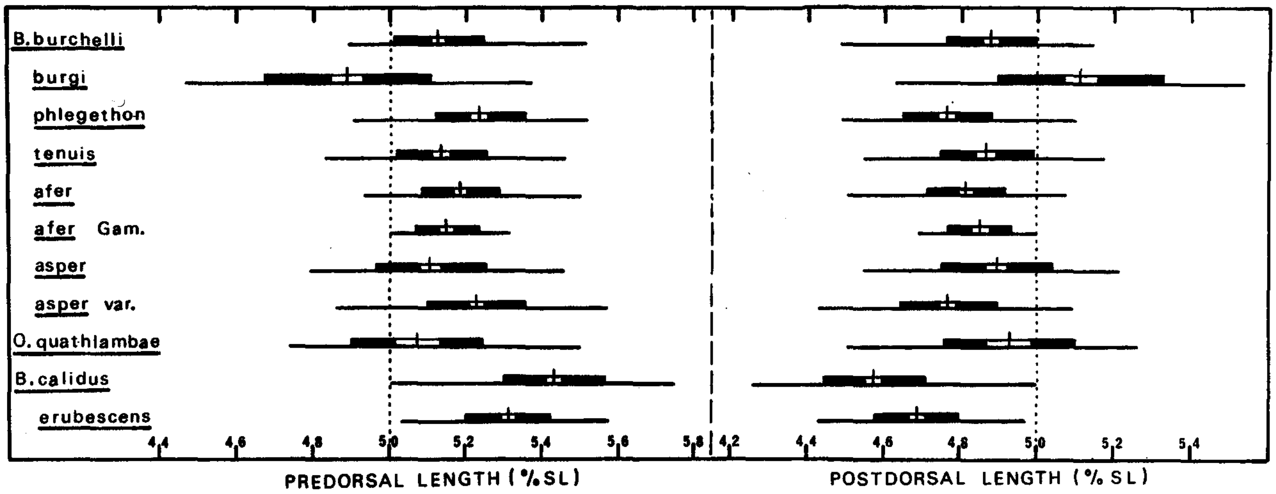


Fig. 3.16 (A) Predorsal length (%SL) and (B) postdorsal length (% SL) of redfin Barbus species and O.quathlambae. Predorsal and postdorsal length are complementary in SL. Data given in Appendix 4 Tables 9 and 10 respectively.

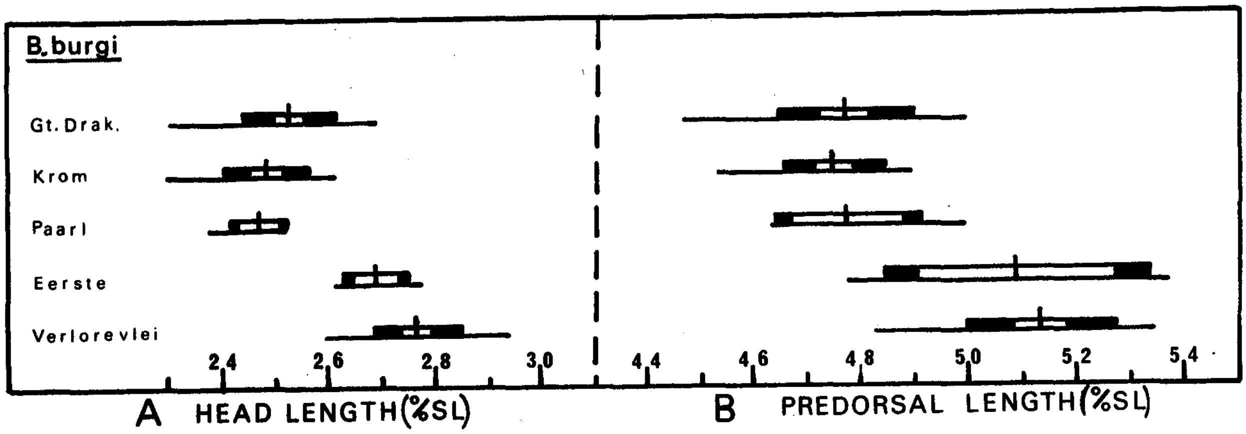


Fig. 3.17 (A) Head length (% SL) and (B) predorsal length (%SL) of samples of B.burgi showing correlation between the two measurements. Data given in Appendix 4 Tables 11 and 12 respectively.

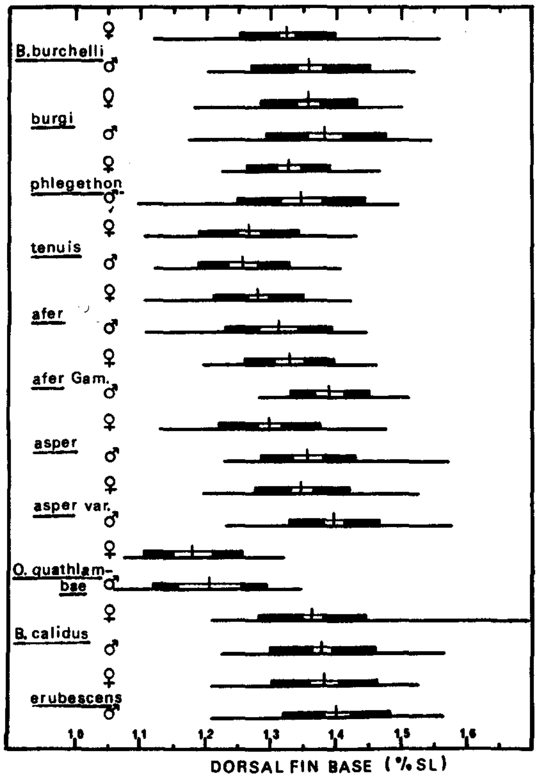
correlate with the width of the neurocranium. *B.tenuis* has a broad neurocranium and *B.phlegethon* a narrow one (Ch. 4), whereas the interorbit of *B.tenuis* is relatively narrower than that of *B.phlegethon*. An alternative suggestion which appears to be more explanatory is that the width of the interorbit depends to a certain extent on the relative placement of the eyes. No quantitative data are available on the placement of the eyes and the differences do not appear to be large. However, the impression gained from handling many specimens of each species is that in those with broader interorbits the eyes are more lateral, and in species with narrower interorbits the eyes are more dorso-lateral.

Predorsal and Postdorsal lengths (Fig. 3.16)

These measurements are complementary (Fig. 3.16) and the results indicate two pertinent taxonomic features (a) *B.burgi* is the only species in which the predorsal length is usually less than the postdorsal length and (b) *B.calidus* and *B.erubescens* have relatively longer predorsal lengths than the other redfin species.

The predorsal length in *B.burgi* is only shorter than the postdorsal length in populations from the Berg River System (Fig. 3.17). A possible explanation for this is that the head length of these specimens is relatively short (Fig. 3.17 b) but it is also noted that *B.burgi* has the lowest modal predorsal fin vertebral count (Table 3.11d) which could be a factor reducing the predorsal length in the species.

B.calidus records the longest precaudal length of the redfins. This species has a high predorsal vertebral count (Table 3.11d) which possibly provides an explanation for the result. The relatively long predorsal lengths of *B.calidus* and *B.erubescens* are evident when the position of the dorsal fin is gauged relative to the origin of the pelvics. The dorsal fin originates behind the pelvics themselves in *B.calidus* and over the posterior base of the pelvics in *B.erubescens*. In other redfin species the dorsal originates over or slightly behind the origin of the pelvics.



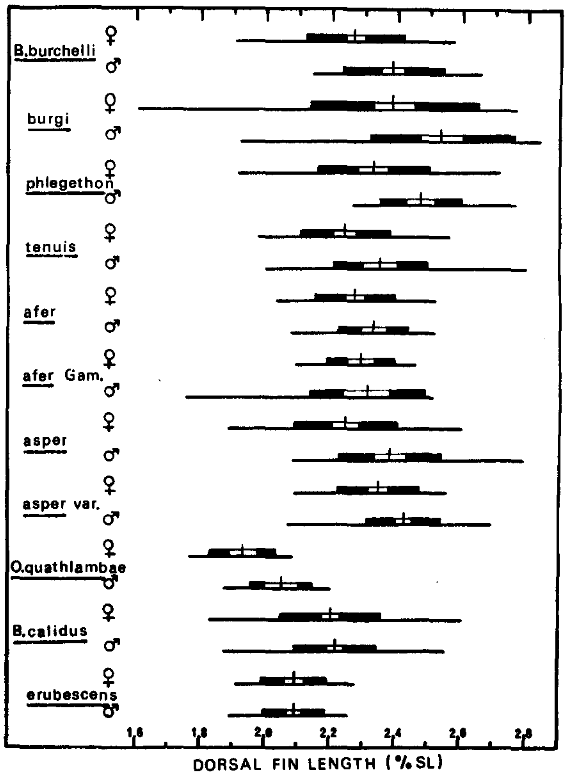


Fig. 3.18 The length of the base of the dorsal fin (% SL) of each sex of the redfin Barbus species and O. quathlambae. Data given in Appendix 4 Table 13.

Left

Fig. 3.19 The length of the dorsal fin (%SL) of each sex of the redfin Barbus species and O. quathlambae. Data given in Appendix 4 Table 14.

Right

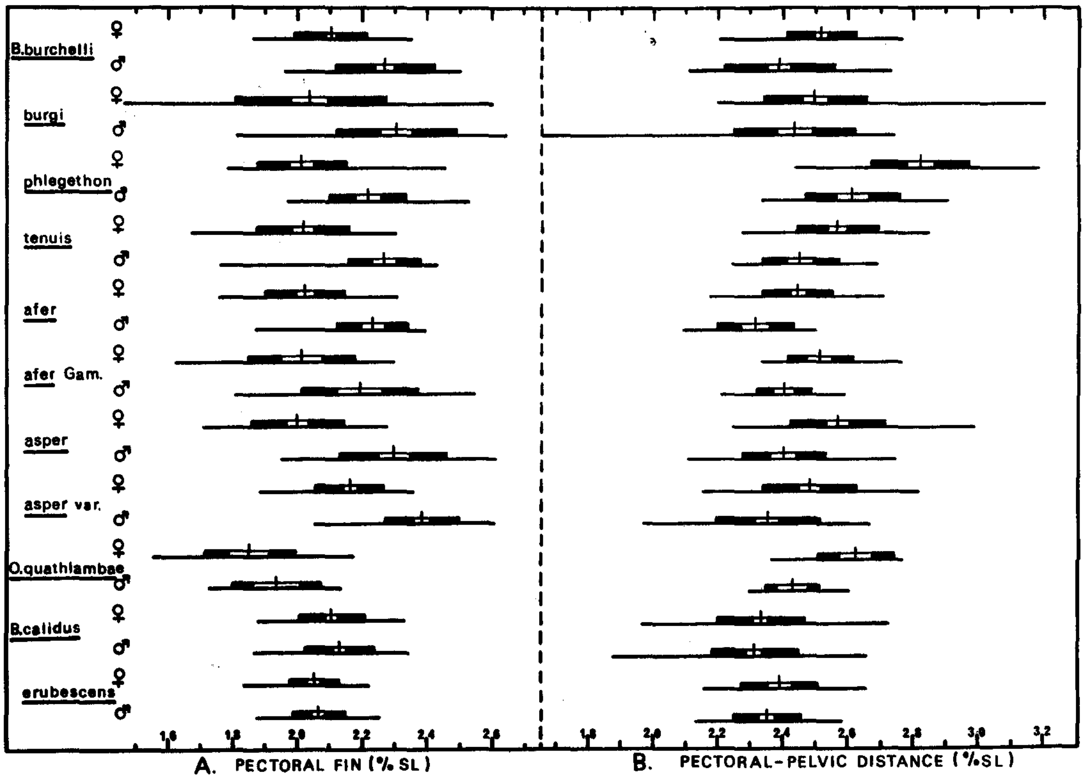


Fig. 3.20 (A) The length of the pectoral fin (%SL) and (B) the distance between the pectoral and pelvic fins of each sex of redfin Barbus species and O. quathlambae. Data given in Appendix 4 Tables 15 and 16 respectively.

Fins

The length and shape of the fins in the cyprinids are labile features which are frequently subjected to the influence of the environment. Fishes which are active swimmers or which are usually exposed to strong currents often have fins which are longer and more falcate than the fins of fishes from quieter environments or who are less active swimmers (Hubbs, 1940; Alexander, 1967). Fin form is also connected with functions other than locomotion and cyprinids frequently show sexual dimorphism in fin proportions (Nikolsky, 1963).

The dorsal fin shows relatively little interspecific variation in the redfins (Figs 4.18, 4.19). The base and length of the fin is shorter in O.quathlambae than the other redfins. In the flexible-rayed species the males have slightly longer proportions in the dorsal fin than the females but this is not a very marked characteristic. Apart from O.quathlambae the serrated-rayed species have slighter shorter dorsal fins than the flexible-rayed species.

The length of the pectoral fin is shown in Figure 3.20 A together with the distance between the pectoral and pelvic fins (Fig. 3.20 B). Boulenger (1911) was the first to refer to sexual dimorphism in the pectoral fin of B.asper. Barnard (1943) established that this is a general trait of the flexible-rayed redfins. He qualified the feature by referring to the length of the fin relative to the base of the pelvic fins. In the males the pectorals reached the base of the pelvics whereas the pectorals in the females fell short of this point. In the juveniles (excepting those of B.phlegethon) the pectorals, like those of male specimens, reached the base of the pelvics.

Figure 3.20 shows that there is sexual dimorphism in both the length of the pectorals and in the distance between the pectoral and pelvic fins of the flexible-rayed species. The males have longer fins and shorter distances between the fins which emphasizes the dimorphism. Non-sexual interspecific differences are not great although the fins of O.quathlambae are shorter than other redfin species. B.calidus and B.erubescens show no sexual dimorphism in these dimensions.

TABLE 3.3

The difference between the length of the pectoral fin and the pectoral to pelvic length of redfin species.

* The pectoral length is greater than the pectoral to pelvic length.

Species	Pectoral to pelvic length less pectoral length (%SL)	
	♂	♀
B.burchelli	1.19	4.11
B.burgi	1.31	4.59
B.phlegethon	3.98	8.13
B.tenuis	1.9	5.48
B.afer	0.8	4.23
B.afer (Gamtoos)	2.12	5.02
B.asper	1.05	5.71
B.asper (variant)	- 0.23*	3.22
O.quathlambae	4.96	7.77
B.calidus	1.83	2.33
B.erubescens	2.88	3.99

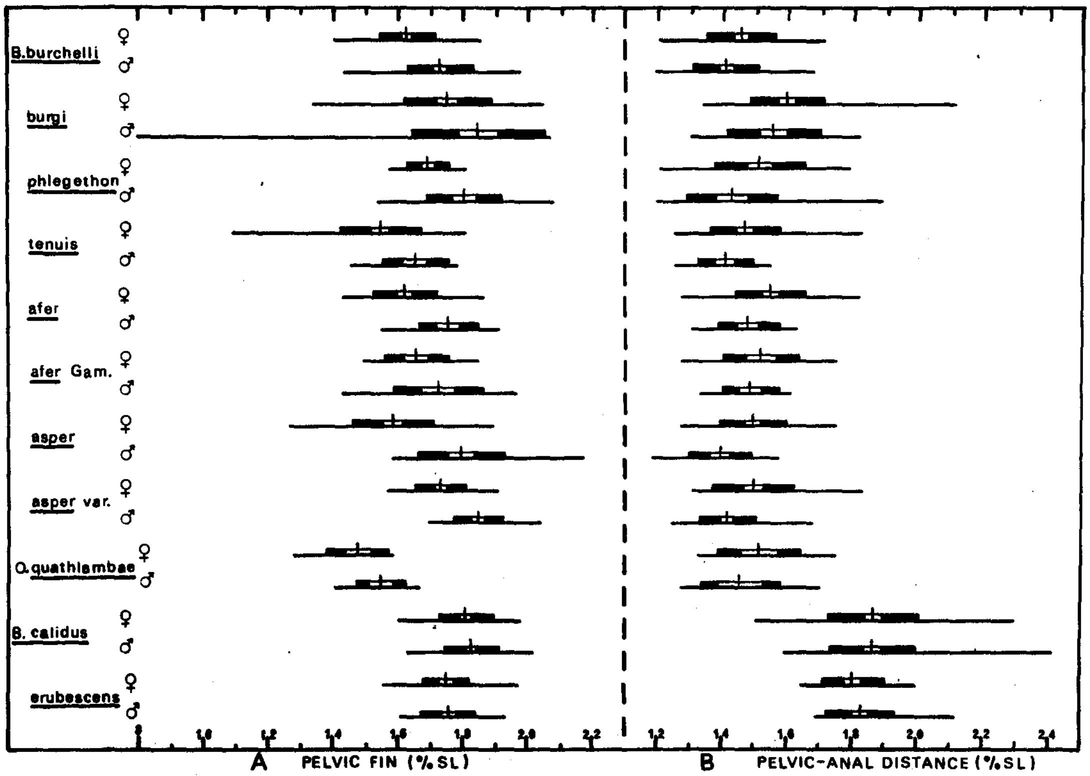


Fig. 3.22

(A) The length of the pelvic fin (%SL) and (B) the distance between the pelvic and anal fins of each sex of redfin Barbus species and O.quathlambae. Data given in Appendix 4 Tables 17 and 18 respectively.

Comparison of the pectoral fin lengths and the distance between the fins (Fig. 3.20) may explain Barnard's observation noted above with respect to the juveniles of *B.phlegethon*. Pectoral fin length in this species is similar to other redfins but the distance between the fins is greater. Thus the difference between the pectoral fin length and the distance between the pectoral and pelvics is greatest in the case of the females of *B.phlegethon* and, except for *O.quathlambae*, also the males (Table 3.3). The effective result is a female-like appearance for both sexes of *B.phlegethon.*

The pectoral fins do not reach the bases of the pelvic fins in *O.quathlambae*. This is a result of the combination of relatively short pectoral fins and a long pectoral to pelvic length (Fig. 3.20; Table 3.3). The pectoral fins are particularly long in the *B.asper* (variant) populations (Fig. 3.20) which register the least difference between pectoral length and pectoral to pelvic length (Table 3.3). The pectorals in both sexes of these populations reach or extend beyond the bases of the pelvics. Usually the pectoral fins of the males reach the pelvic bases in *B.tenuis* and *B.afer* but not in the females. In *B.calidus* and *B.erubescens* the pectorals almost reach the bases of the pelvic fins.

In the redfins the males have more rounded pectorals (Fig. 3.21) than the females. This sexual dimorphism is more evident in the flexible-rayed species. The pectorals of *B.calidus* and *B.phlegethon* are more slender (spatulate) than those of the other species.

Within the species certain populations have, as a rule, shorter or longer fins than other populations. Circumstantial evidence suggests that at least in certain cases this variation is a phenotypic phenomenon. For example the Keurbooms River population of *B.tenuis* has relatively longer fins than conspecifics in the Gourits River System. The catchment of the Keurbooms receives a relatively high rainfall compared to catchments of the Gourits System (Midgeley & Pitman, 1969) and flow is therefore most likely to be relatively stronger in the Keurbooms.

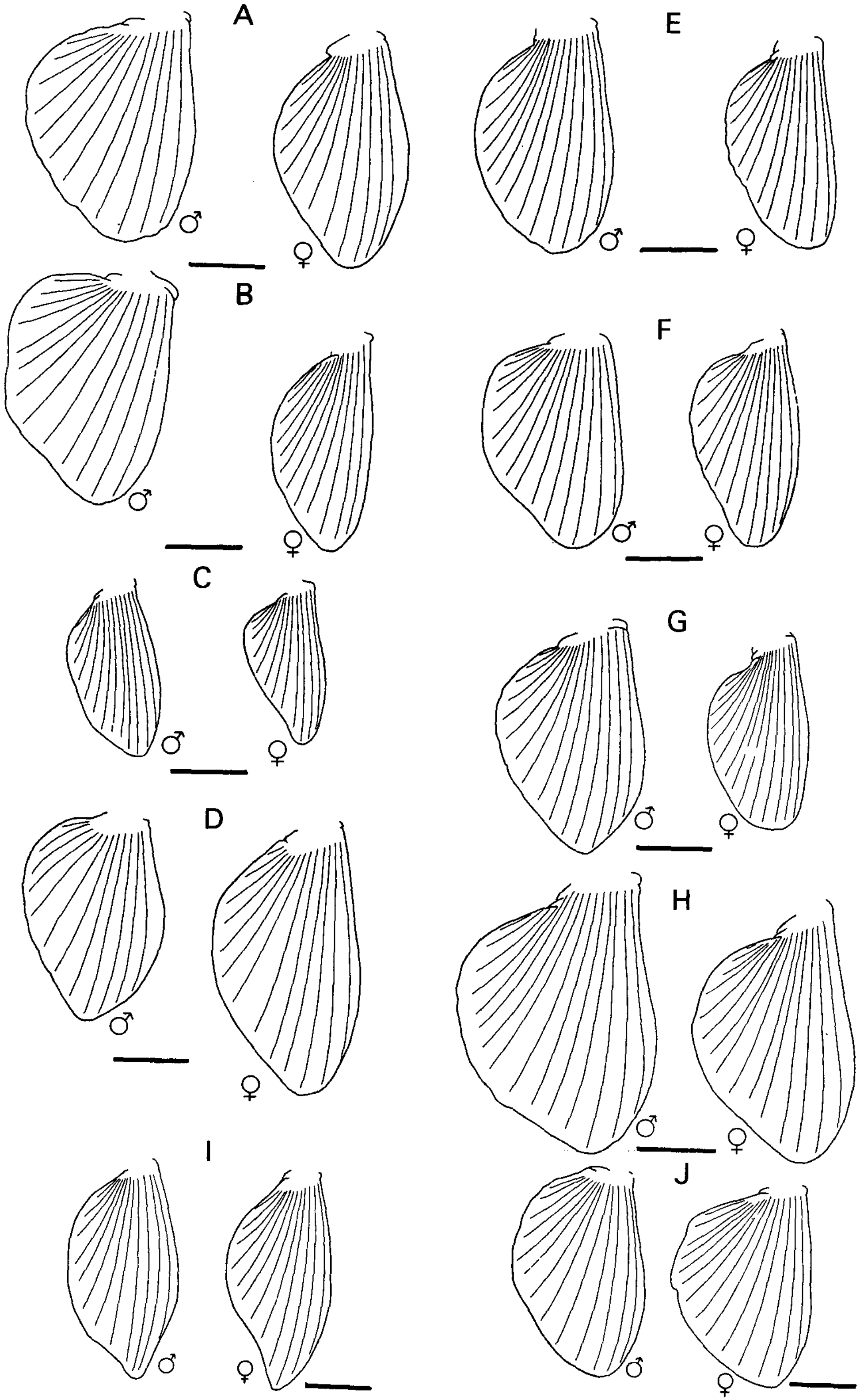
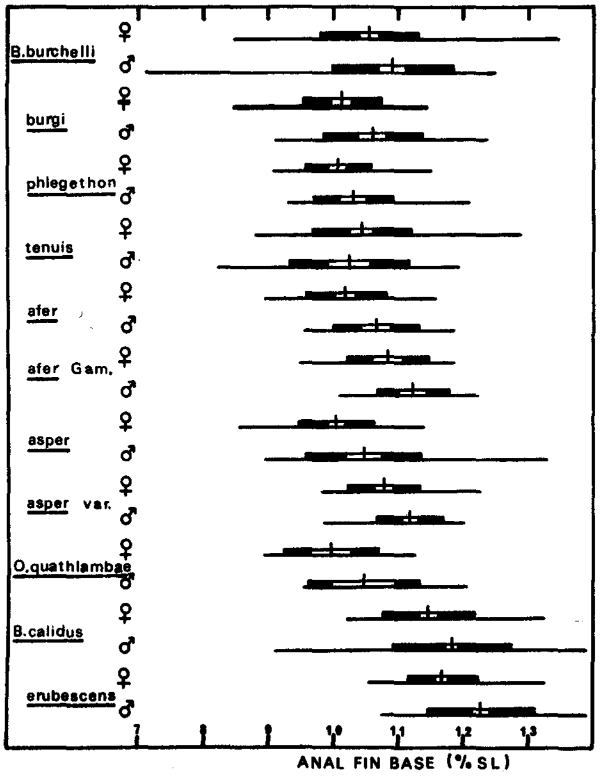


Fig. 3.21 Examples of pectoral fin shapes in redfin species. A - B.burchelli; B - B.burgi; C - B.phlegethon; D - B.tenuis; E - B.afer; F - B.asper; G - B.asper (variant); H - O.quathlambae; I - B.calidus; J - B.erubescens. Dorsal view of right fin. Scale bar = 5 mm.



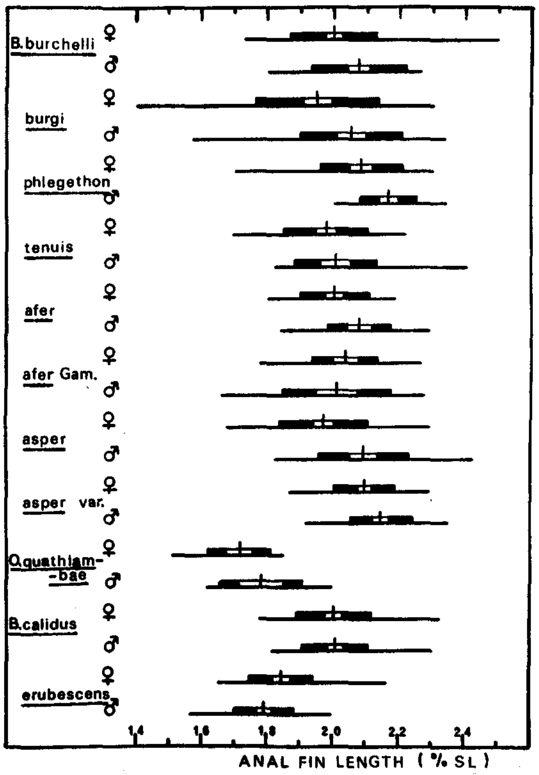
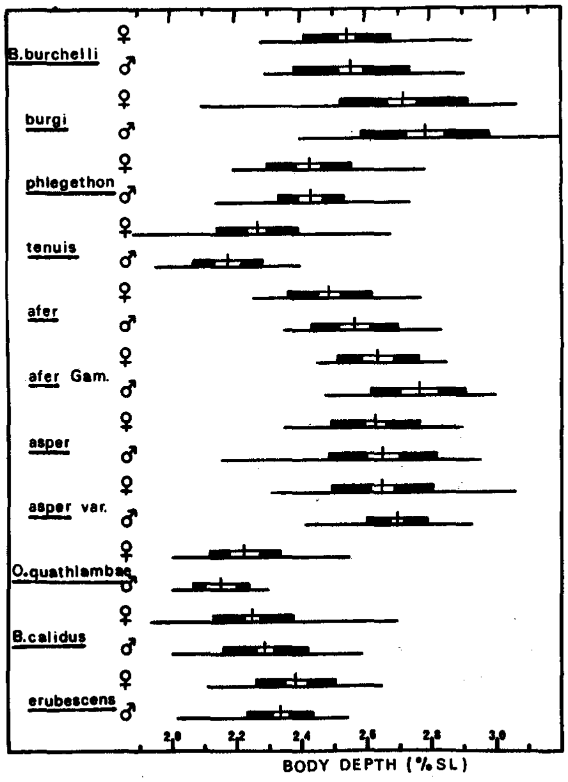


Fig. 3.23 **Left** The length of the base of the anal fin (%SL) of each sex of the redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 19.

Fig. 3.24 **Right** The length of the anal fin (%SL) of each sex of the redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 20.



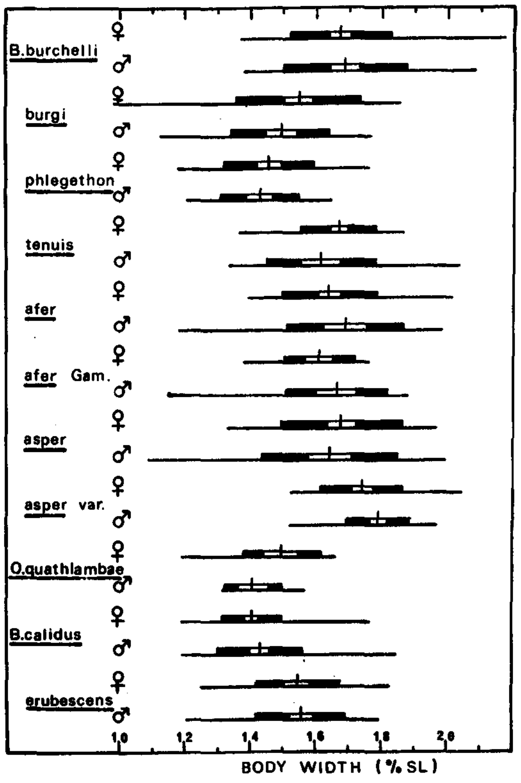


Fig. 3.25 **Left** The depth of the body (%SL) of the redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 21.

Fig. 3.26 **Right** The width of the body (%SL) of each sex of the redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 22.

TABLE 3.4

Mean body depths and gut lengths of three populations of *B. burgi*

Population	N	$\overline{M}$ Body Depth (%SL) (S.E.)	$\overline{M}$ Gut length (%SL) (S.E.)
Gt. Drakenstein	(30)	28.21 (0.24)	291.5 (6.4)
Krom R.	(30)	26.31 (0.26)	152.8 (4.8) (N=21)
Verlorevlei	(30)	28.92 (0.26)	250.8 (7.9)

The length of the pelvic fin (Fig. 3.22 A) also shows sexual dimorphism in the flexible-rayed redfins, the males having longer fins than the females. Again the reach of the pelvic fin is emphasised in males by the fact that the distance between the pelvic and anal fins is shorter than in the females (Fig. 3.22 B). This pelvic to anal length is larger in the serrated-rayed species than in the flexible-rayed redfins. Interspecific differences in the length of the pelvic fins themselves are not large and only the pelvics of O.quathlambae are relatively short.

The proportions of the anal fin are of minor interest in the redfins (Figs 3.23; 3.24). The base of the fin is longer in B.calidus and B.erubescens which is correlated with the increase in anal branched rays in these species (see Table 3.5 D).

Body depth (Fig. 3.25)

Body depth was used by Barnard (1943) to distinguish between B.tenuis and the similar B.asper and B.afer. Body depth is generally an unreliable character in the cyprinids because it may be influenced by extraneous factors such as the presence or absence of food items in the alimentary canal, degree of sexual ripeness, general condition, or the presence of parasites. In the present study, however, it is found to correlate well with the length of the intestine.

The redfins form two groups with regard to body depth (Fig. 3.25); those with a shallow body - B.tenuis, O.quathlambae, B.calidus and B.erubescens and the rest with a relatively deeper body. The species with a shallow body all have a relatively short intestine with a simple flexure (p. 88) and the deeper bodied forms have longer and more involuted intestines. To a certain extent this correlation is extended to populations within a species (e.g. B.burgi populations, Table 3.4).

Body width (Fig. 3.26)

B.phlegethon, O.quathlambae and B.calidus are slightly narrower than the other redfins. The character is of little assistance with regard to the particular problems within the redfin species.

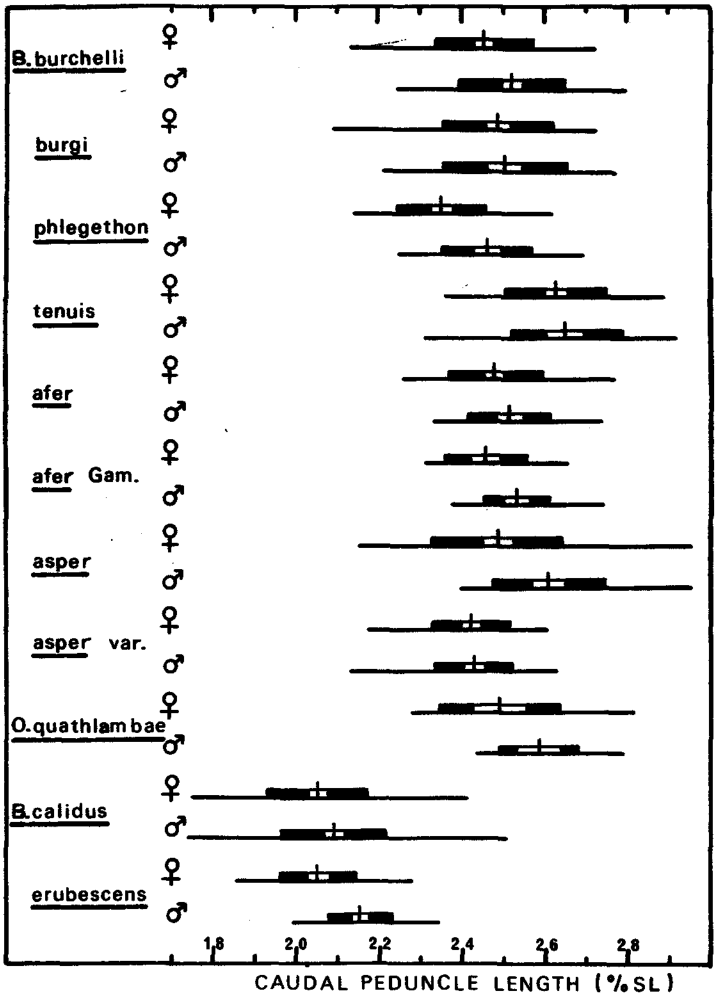


Fig. 3.27 The length of the caudal peduncle (%SL) of each sex of the redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 23.

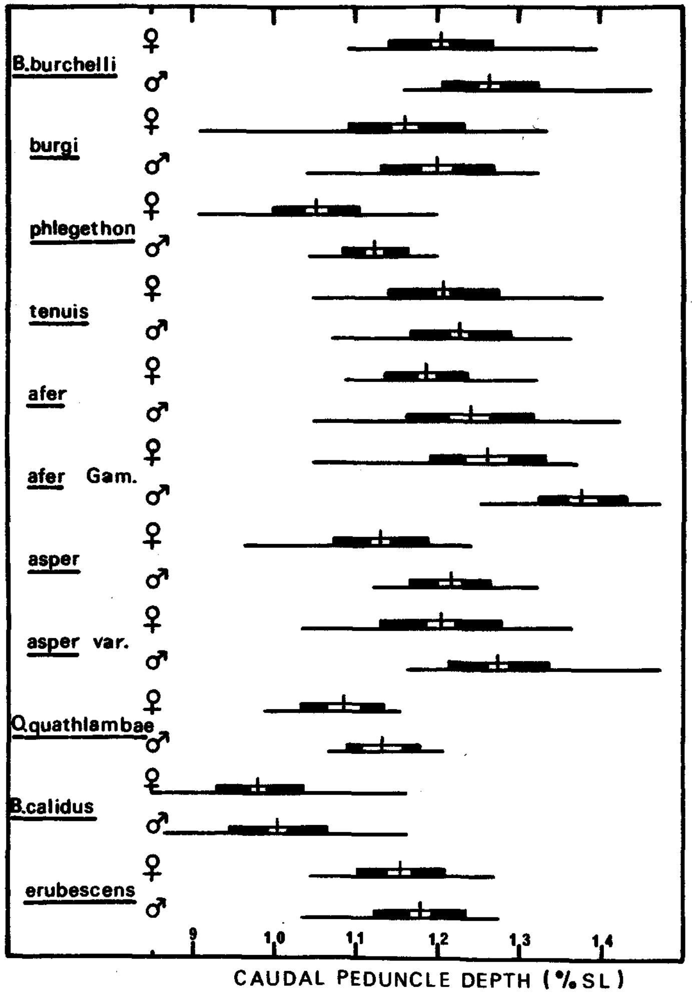


Fig. 3.29 The depth of the caudal peduncle (%SL) of each sex of the redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 25.

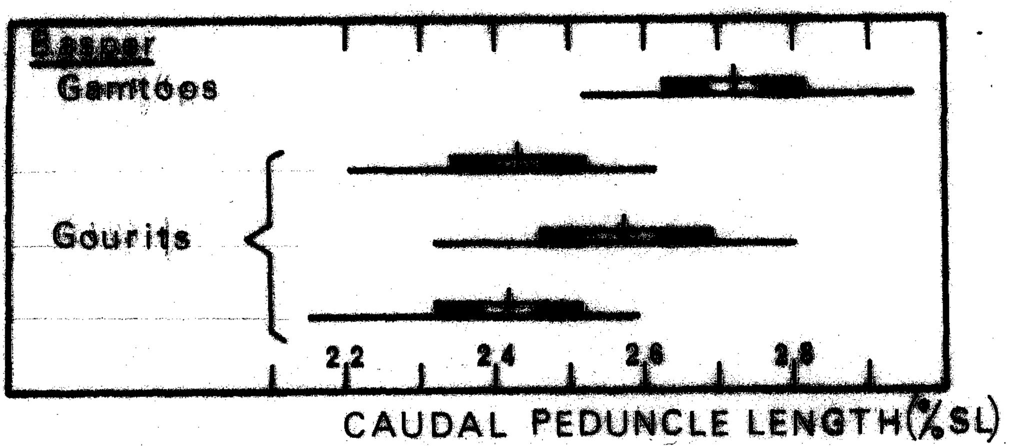


Fig. 3.28 The length of the caudal peduncle (%SL) of samples of B.asper showing the difference between the population in the Groot River (Gamtoos) and Gourits River system populations. Data given in Appendix 4 Table 24.

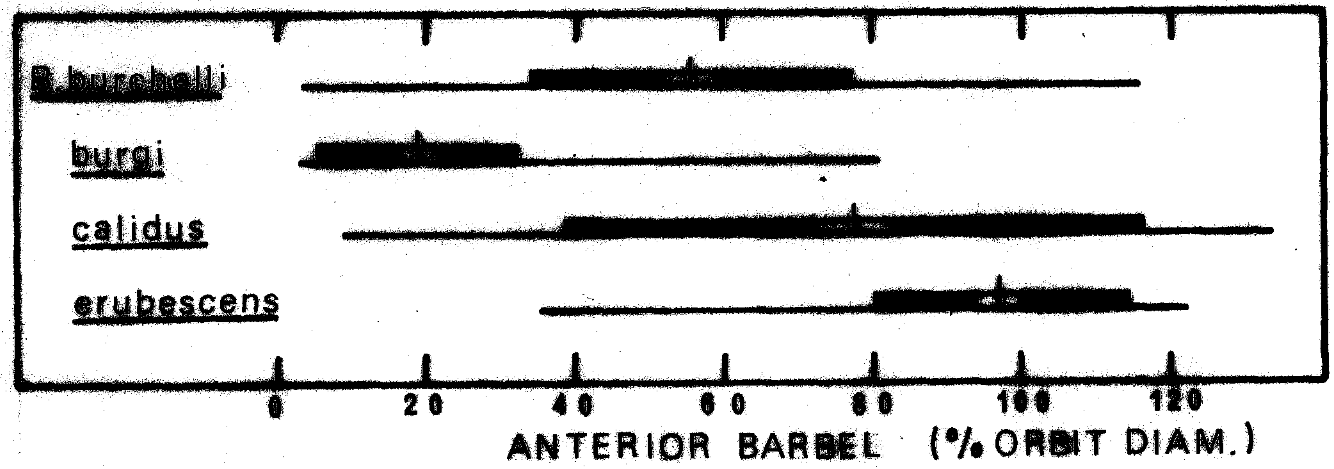


Fig. 3.30 The length of the anterior barbel (% orbit diameter) of certain redfin Barbus species. Data given in Appendix 4 Table 26.

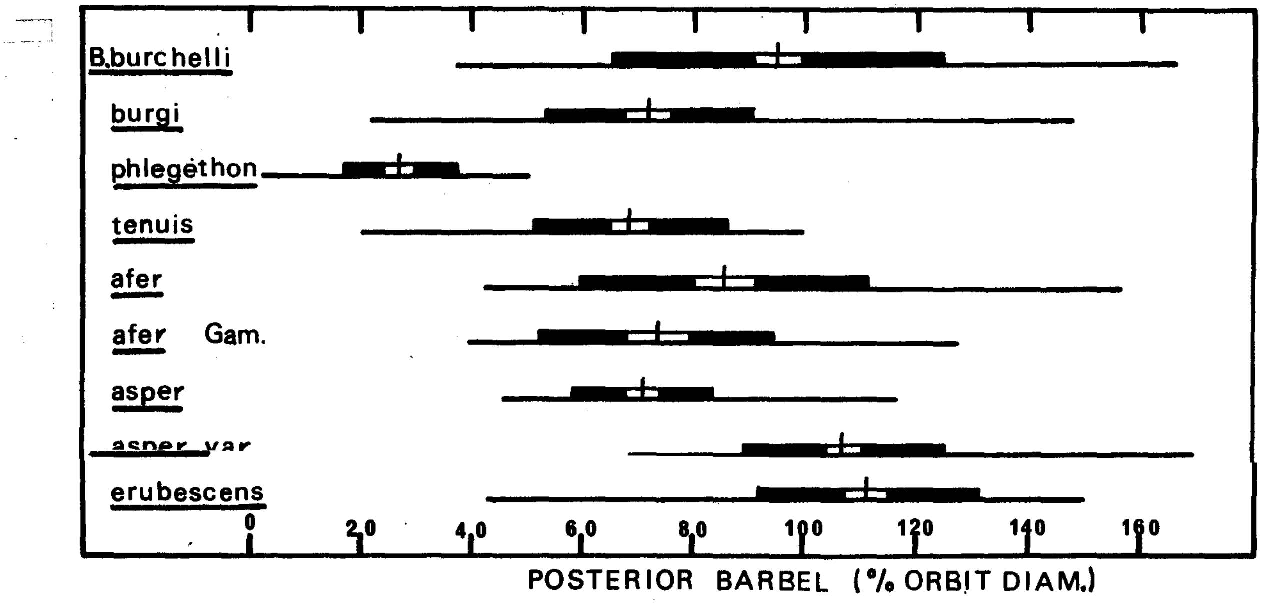


Fig. 3.31 The length of the posterior barbel (% orbit diameter) of the redfin Barbus species and O.quathlambae. Data given in Appendix 4 Table 27.

Caudal peduncle length (Fig. 3.27)

B.calidus and B.erubescens have relatively short caudal peduncles. Intraspecific variation in this character is usually not outstanding but an exception is found in the populations of B.asper from the Groot River (Gamtoos) and the Gourits River System (Fig. 3.28). The Gamtoos B.asper have significantly longer caudal peduncles than those from the Gourits. This correlates with longer fins in the Gamtoos population which suggests the difference is related to hydrological differences between the two systems.

Caudal peduncle depth (Fig. 3.29)

Sexual dimorphism is well marked in the depth of the caudal peduncle of several redfin species, but is slight or absent in B.tenuis, B.calidus and B.erubescens. In species with sexual dimorphism in this character the males have deeper peduncles than the females.

The caudal peduncle depth is notably shorter in B.calidus than in the other redfins.

Barbels (Figs 3.30, 3.31)

Cyprinid barbels are frequently employed as taxonomic characters and although their value is often overestimated (Gilbert & Bailey, 1972) they are nevertheless consistently present or absent in many species and are therefore taxonomically useful for these species. The redfins either have one or two pairs of simple barbels, including a posterior (maxillary) pair which is always present and an anterior pair which is only consistently present in B.burchelli, B.burgi, B.calidus and B.erubescens. Occasionally individuals of other species have an additional one or two anterior barbels. An exceptionally high incidence of additional barbels was recorded in certain B.tenuis populations, e.g. from the Waterkloof River (Gamka-Gourits) 20% of specimens examined (N=30) had additional barbels; 50% of these had a single extra barbel and 50% a pair of extra barbels.

In those species with a regular anterior pair of barbels (Fig. 3.30) it is well developed from an early age in B.burchelli, B.calidus and B.erubescens. In B.burgi the anterior pair is always very short and only develops in individuals above approximately 45 mm SL. This provides a useful character of contrast with B.burchelli.

TABLE 3.5

Number of fin rays in redfin species

Species (Group)	N	A. Unbranched dorsal fin rays		B. Branched dorsal fin rays			C. Unbranched anal fin rays			D. Branched anal fin rays				
		3	4	6	7	8	2	3	4	4	5	6	7	8
B.burchelli	179	74	105	8	166	5		130	49	1	171	7		
B.burgi	107	93	14	3	102	2	1	103	2		104	2		
B.phlegethon	90	63	27	4	85	1		85	5		89	1		
B.tenuis	96	69	27	6	88	2		90	6		93	3		
B.afer	105	37	68	2	103			105			104	1		
B.afer (Gamtoos)	50	14	36		50			48	2		49	1		
B.asper	110	11	99	5	104	1		95	15		109	1		
B.asper (variant)	142	54	88	5	133	4		137	5		142			
O.quathlambae	39	39		1	37	1		39			35	4		
B.calidus	300	10	290	1	287	12		280	20		2	278	20	
B.erubescens	110	33	77		27	83	1	107	2			7	96	7

Species (Group)	N	E. Pectoral fin rays								F. Pelvic fin rays		
		11	12	13	14	15	16	17	18	7	8	9
B.burchelli	179		1	40	90	44	4			7	160	13
B.burgi	107			4	46	42	12	2	1	1	80	26
B.phlegethon	90	1	4	36	42	7				11	78	1
B.tenuis	96		4	30	48	13	1			70	26	
B.afer	105			5	29	41	25	5			98	7
B.afer (Gamtoos)	50				4	29	12	5		2	46	2
B.asper	110				7	48	43	12		4	86	20
B.asper (variant)	142			9	41	68	22	2		8	123	11
O.quathlambae	38					8	21	9		4	31	3
B.calidus	280	1	10	141	116	12				28	237	15
B.erubescens	110	1		5	62	41	1			14	96	

The posterior barbels are short in B.phlegethon and O.quathlambae (Fig. 3.31). In widespread species with isolated populations such as B.afer the length of the posterior barbels shows considerable intraspecific variation. B.afer from the Kromme River as well as B.asper variant populations have long barbels (Fig. 3.32), whereas they are of moderate length in other B.afer and B.asper populations. The posterior barbels are invariably well developed in B.burchelli, B.calidus and B.erubescens becoming much longer than the orbit diameter in adults.

Fin Rays (Table 3.5)

The first and second unbranched rays of the dorsal and anal fins are very small and difficult to count accurately. Four unbranched dorsal rays and three unbranched anal rays appear to predominate in the redfin species (Table 3.5). The form of the last unbranched dorsal ray is of importance. In B.calidus this ray is bony and stout with a flagellate tip and a series of strong serrations along the posterior margin (Fig. 3.33 A). In B.erubescens the last unbranched ray is flexible and more slender in comparison to B.calidus. Serrations are present but much reduced (Fig. 3.33 B). The ray is thin and flexible without serrations in the flexible-rayed redfins (Fig. 3.33 C).

The number of branched dorsal fin rays (Table 3.5 B) is conservative in redfin species. All species usually have seven branched dorsal rays, except B.erubescens which has eight. The degree of intraspecific variation is higher in B.erubescens than in the other redfins which suggests that the character is less stable in this species. Variation in branched dorsal rays, albeit slight (6-8 rays), usually tends to a reduction from the mode with the exception of B.calidus. In the Bloukrantz River population of B.asper (variant) there is a tendency to increase the number of branched dorsal fin rays. Of the specimens examined, 13% had eight branched rays which is notable in view of the fact that in all other B.asper (variant) or B.asper or B.afer populations less than 0,25% had eight branched rays.

All flexible-rayed species have three unbranched and five branched rays in the anal fin (Table 3.4 C, D). B.calidus is one of few African Barbus species with six and B.erubescens is exceptional with a mode of seven branched anal fin rays.

Table 3.6. The frequency distribution of the number of scales or scale rows in redfin species.

		A. Lateral line scales																					B. Lateral line to dorsal fin scale rows										
:oup)	N	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	4	5	6	7	8	9	10	11	12	13	14
l	179					2	4	7	10	18	32	51	33	15	6	1								28	133	18							
	107				2	4	14	17	23	19	14	9	4	1									6	66	35								
on	90					1			7	7	19	40	14	2									33	56	1								
	96								2	8	14	36	30	6									3	86	7								
	105	1	2	3	4	12	14	11	24	11	16	5	1	1									16	70	19								
ntoos)	50										2	11	22	15										6	43	1							
	110											1	10	26	24	17	15	11	2	1	2	1			4	65	37	4					
ariant)	142					2	1	6	12	27	34	38	20	1	1									41	101								
bae*	34																												4	16	13		1
	283										2	13	67	124	69	8								60	220	3							
ns	110											2	6	50	45	6	1							38	72								
		60	61	62	63	64	65	66	67	68	69	70	71	72																			
bae	34	1	2	1	1	4	5	6	5	3	5			1																			

		C. Caudal peduncle scale rows															D. Lateral line to pelvic fin scale rows									
roup)	N	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	3	4	5	6	7	8	9	10	11	12
li	179			92	23	23	17	20	3	1								122	53	4						
	107			98	4	4		1									2	76	29							
hon	90	1	6	65	15	3											24	66								
	96		1	51	19	18	4	3									20	73	3							
		1	10	45	10	16	15	8									15	87	3							
amtoos)	50					1	7	41	1									10	39	1						
	110							7	2	20	25	46	3	7					15	65	26	4				
variant)				2	5	25	33	76		1							1	89	52							
mbae*																						2	7	14	9	2
	283			33	31	78	51	86	4								217	64								
ens	110						26	58	22	3	1						8	100	2							
		30	31	32	33	34	35	36	37	38																
mbae	34	1		8	5	6	4	7	2	1																

		E. Predorsal scale rows															F. Lateral line to anal fin scale rows								
(Group)	N	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	3	4	5	6	7	8	9	10	11
lli	176			2	13	23	49	40	35	7	4	3						105	72	2					
	107	5	18	21	43	12	5	3									3	98	6						
thon	90			1	8	21	34	15	10	1							43	46	1						
	96			1	8	35	15	11	5	13	7	1					6	89	1						
	105		2	27	49	23	4										20	81	4						
Gamtoos)	50			1	5	21	11	5	6									11	39						
	110							1	7	15	26	32	17	10	1	1			18	81	10	1			
(variant)	142		3	14	32	36	19	14	16	6	1	1					1	68	73						
ambae*																							12	18	4
s	283			2	12	64	101	79	18	5	2						16	206	61						
cens	110			1	22	30	39	11	4	2	1						1	91	18						
		28	29	30	31	32	33	34	35	36	37	38	39	40											
ambae	34	1			2	2	4	6	1	8	4	2	1	2											

Pectoral fin rays are more variable, with the more western species tending to have lower modal frequencies (Table 3.5 E). The broad overlap of these counts between species precludes the usefulness of this character.

Pelvic fin rays (Table 3.5 F) show less variation than the pectoral fin rays. Eight rays is the mode for all the redfins except B.tenuis which has seven.

There are invariably 10 + 9 principle caudal fin rays (i.e. 17 branched rays and one dorsal and one ventral unbranched principle ray). This is the usual number in cyprinids (Roberts, 1973). [Note: Howes (1978) questions this generalization on the grounds that he recorded in all the cyprinids, including Barbus species, which he examined, a count of 9 + 9. All the Barbus species I have examined have 10 + 9 principle caudal fin rays. Both Gosline (1961) and Buhan (1972) have found a constant 17 branched caudal fin rays in cyprinids which, if the dorsal and ventral unbranched rays are included, support the generalization made by Roberts (1973)].

Scale counts (Table 3.6)

In the past much importance has been attached to the difference in scale counts and the results here obtained underline several of the taxonomic problems. The only species which is clearly different in all scale counts is O.quathlambae, but B.asper also has relatively smaller scales than other redfins.

The scales of B.burgi are slightly larger than those of B.burchelli This has also been shown by Barnard (1943) and Jubb (1965). The differences recorded between these two species are not so great that they can be considered specifically distinct on scale size alone.

Scale size, as represented by scale count frequencies, is the crux of the B.asper - B.afer problem. The frequency distribution of the lateral line scales of the populations of the B.asper and B.afer groups is given in Table 3.7. A summary of the distribution frequency of the lateral line scales for each "group" is given in Table 3.6 A, and diagrammatically as % frequency in Figure 3.32.

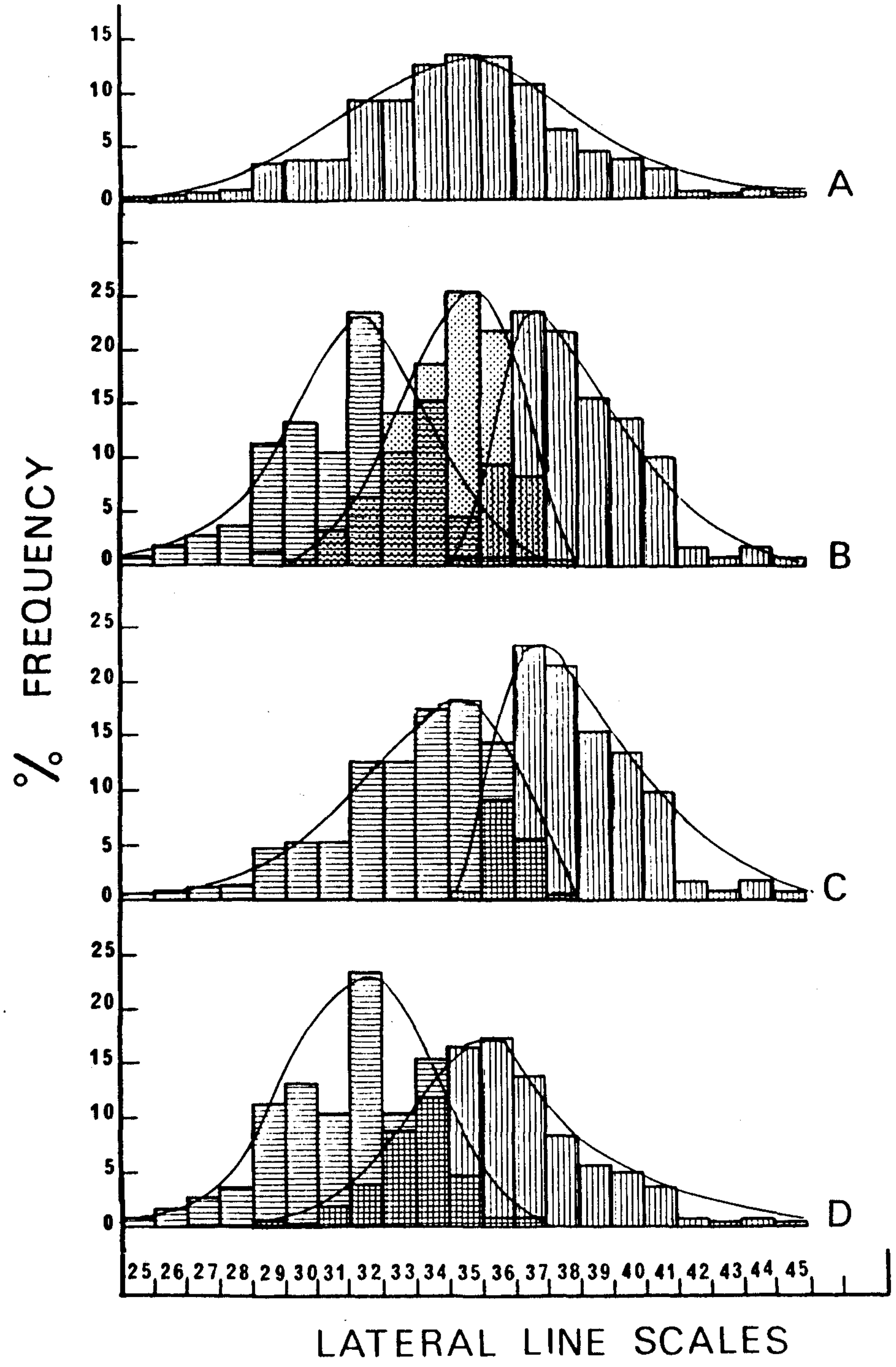


Fig. 3.32. Percentage frequency distribution of lateral line scales of B.asper and B.afer (A) All samples of both species combined;
B) ▤ - B.afer (typical), ░ B.afer (Gamtoos) and B.asper (variant) samples combined, ▥ B.asper (typical)
C) ▤ - B.afer (typical) and B.afer (Gamtoos) and B.asper (variant) combined, ▥ B.asper typical
D) ▤ - B.afer (typical); ▥ B.asper (typical) and B.afer (Gamtoos) and B.asper (variant) combined. Graph curves added by eye to assist interpretation.

TABLE 3.7

Frequency distribution of lateral line scales in *Barbus afer*, *B.afer* (Gamtoos), *Barbus asper*, *B.asper* (variant)

Population	N	Lateral line scales																				
		25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
B.afer																						
Sundays	40					3	4	4	12	8	9											
Swartkops	30						3	4	10	2	5	4	1	1								
Baakens	5						1	2			1	1										
Kromme	30	1	2	3	4	9	6	1	2	1	1											
B.afer (Gamtoos)																						
Couga	30										1	7	13	9								
Wit	10											1	4	5								
Loerie	10										1	3	5	1								
B.asper (variant)																						
Bloukrans	30							2	2	6	7	8	4	1								
Groot (Natures Valley)	30					1	1	1	7	5	8	5	2									
Keurbooms	22									3	6	10	3									
Knysna	30					1		3	3	7	9	4	3									
Goukamma	30									6	4	11	8		1							
B.asper																						
Groot (Gamtoos)	30												5	10	6	5	3	1				
Meiringspoort	30												1	3	7	6	5	4	2	1	1	
Van Wyksdorp	20													1	4	3	5	5			1	1
Kammanassie	30											1	4	12	7	3	2	1				

The range of lateral line scales is wide (25-37) in B.afer with a low mode of 32 scales. The Kromme River population has a wider range (25-34) and lower mode (29) than other B.afer populations. B.afer in the Gamtoos have a range of 34-37 lateral line scales with a mode of 36. B.asper has a wide range (35-45) with a mode at the lower end of the spectrum at 37-38 scales. B.asper (variant) has from 29-37 lateral line scales with a mode at 34-35.

For the purposes of further discussion the results show that B.asper (variant) and B.afer can be combined. Considering then the three groups B.afer, B.asper and the intermediates, four taxonomic solutions can be suggested (Fig. 3.32). Firstly all the populations can be combined into a single polytypic species (Fig. 3.32 A); secondly (Fig. 3.32 B) each of the three groups can be recognised separately (possibly separately within the first solution); thirdly the intermediates can be combined with the B.afer populations [here an overlap of 8% (calculated according to the method of Ginsberg, 1938) is indicated between the combined B.afer group and B.asper which is sufficient separation for each to be considered full species]; fourthly the intermediates can be combined with B.asper (Fig. 3.32 D) which gives a greater degree of overlap (17.35%) compared to the third solution.

The first solution is rejected because this would mean that the species would have a scale size range which is approximately twice that of any other redfin Barbus species (and other southern African Barbus species). There is no single population which approaches this range in the redfins. The second solution is also rejected because the degree of overlap between the intermediates and the two nominal species is too large for practical purposes and there are no other characters which really support the decision. The third solution appears to be the most acceptable from all aspects, and is supported by the fact that there is a general cline in many morphometric characters of the "combined" populations. The fourth alternative offers a less practical solution than the previous one and is not supported by alternative characters.

TABLE 3.8

A comparison of the frequency of caudal peduncle scale rows in *B.calidus* of two different size groups from a single sample (AM/P 1844)

Size Group (mm SL)	N	Caudal peduncle scale rows				
		12	13	14	15	16
30-49	23	6 (26)	8 (35)	8 (35)		1 (4)
50-69	27	10 (37)	5 (18.5)	10 (37)	1 (3.7)	1 (3.7)
Total	50	16 (32	13 (26)	18 (36)	1 (2)	2 (4)

Barnard (1943) reported that the number of scale rows around the caudal peduncle of B.calidus increased with age from 12 in specimens about 30 mm SL to 16 for large adults longer than 60 mm SL. Barnard suggested that similar increases occurred in other redfins and the phenomenon therefore has important implications. In order to test this a series of B.calidus was examined (Table 3.8). These data do not support the findings of Barnard (1943). The percentage of specimens with 12 peduncle scale rows actually increases in the larger size group and there is no increase in percentage of specimens with more scale rows in this larger group.

Squamation

The pattern of squamation provides several taxonomic characters. Barnard (1943) referred to the crowding of the scales on the nape in B.asper and B.tenuis. In the latter species the nape sometimes appears to be naked. The nape scales are not markedly reduced in the other redfins (except O.quatlambae where all the scales are extremely small).

The scales of the breast region (i.e. from the isthmus posterior to between the bases of the pectoral fins) are reduced in size and embedded deeply in all the flexible-rayed species. Consequently the region appears to be naked. In the species with relatively larger scales (e.g. B.burgi and B.afer) the "naked" area is smaller and confined mainly to the isthmus region. In the smaller-scaled species (B.asper and O.quathlambae) the naked area extends behind the pectorals on to the belly region. The breast scales of B.calidus and B.erubescens are not as markedly reduced as in the flexible-rayed species and are not deeply embedded.

A well developed triangular axillary scale which is commonly present in cyprinids is absent in the flexible-rayed redfins. This scale is present (but not prominent) in B.calidus and B.erubescens.

In O.quathlambae there is a scaleless fleshy region at the bases of the dorsal, anal and pelvic fins. This region is pigmented red in life.

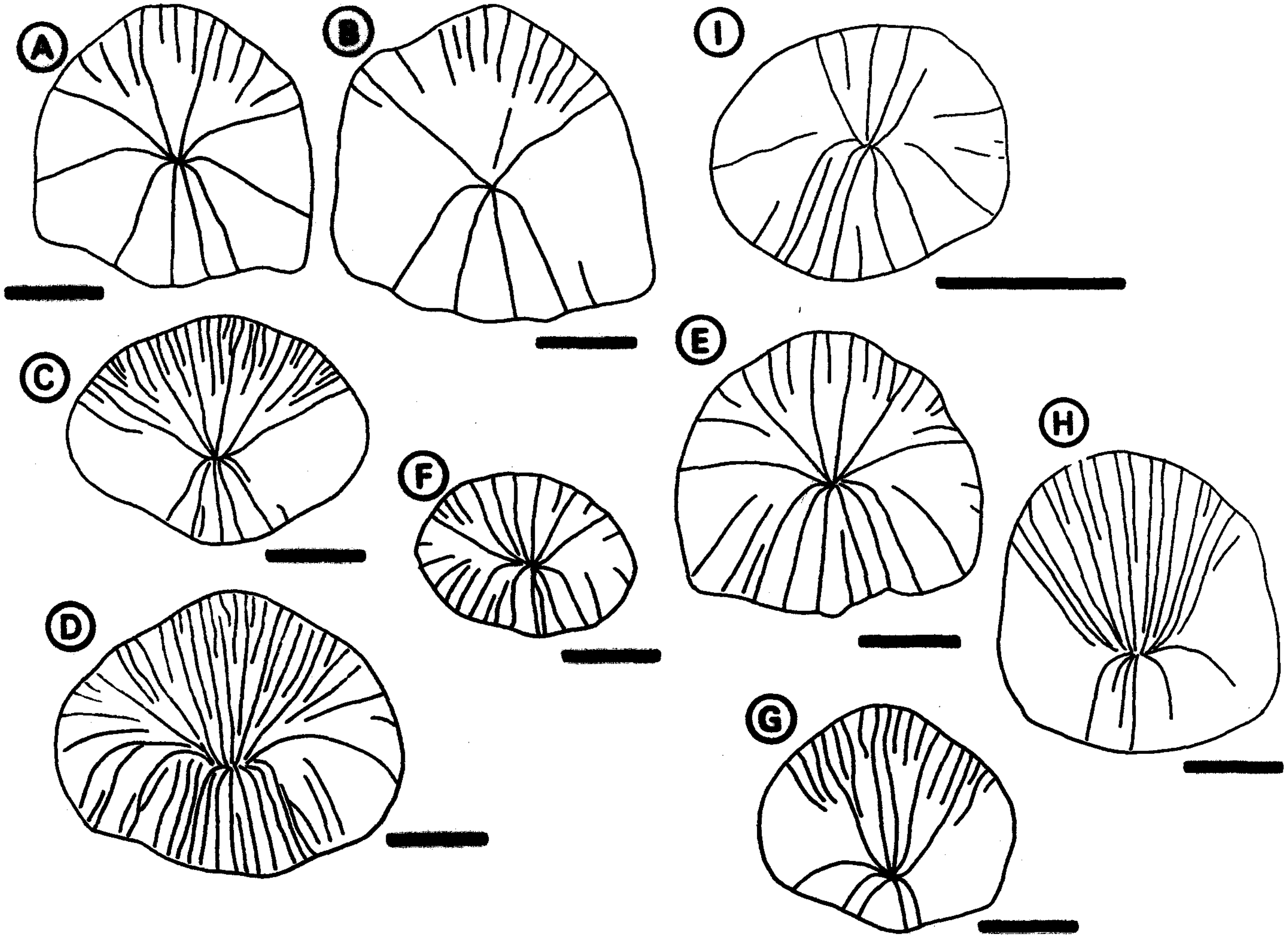


Fig. 3.33 Examples of scales of the redfin Barbus species and O.quathlambae (drawn using camera lucida). A - B.burchelli; B - B.burgi; C - B.phlegethon; D - B.tenuis; E - B.afer; F - B.asper; G - B.calidus; H - B.erubescens; I - O.quathlambae. Scale bar = 1 mm.

TABLE 3.9

A comparison of primary scale radii from specimens of different sizes in four redfin species

Species	N	SL (range)	Mean numbers of radii/scale	order of difference
B.burchelli	13	(31-39)	9	0-1
	17	(40-68)	9.7	
B.phlegethon	29	(27.5-39)	11.9	0-1
	30	(43-57)	12.2	
B.tenuis	10	(30-39)	14.1	2-3
	18	(41.5-66)	16.5	
B.erubescens	7	(30.5-35.6)	13.1	0-1
	30	(62-95)	13.6	

TABLE 3.10

The number of scale radii in adults and juveniles of redfin species as reported by Barnard (1943). (Radii determined as "main striae" on the "exposed portion" of scales only)

Species	Juveniles Number of radii/scale	Adults Number of radii/scale	± difference
B.burchelli (= *B.vulneratus*)	3-4	14-16	12
B.burgi (=*B.burchelli*)	3-4	10	6
B.phlegethon	4-5	7-9	4
B.tenuis	8	24	16
B.afer	4-5	12	7
B.asper	4-5	10-11	6
B.calidus	4-5	12-14	8

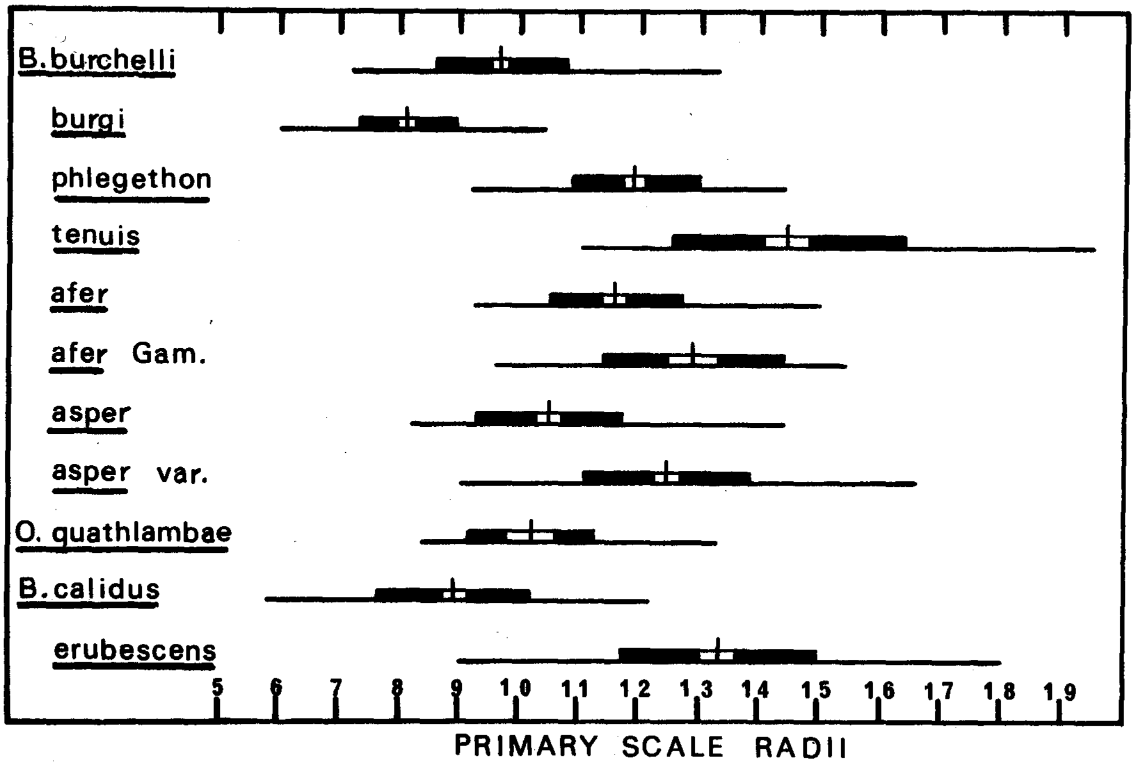


Fig. 3.34 The number of primary scale radii of the redfin *Barbus* species and *O. quathlambae*. Data given in Appendix 4 Table 28.

Scale Radii (Fig. 3.33)

The redfins have radiately striated cycloid scales (Fig. 3.33). There are reports that the number of scale radii increase with age in cyprinids (Chu, 1935; Barnard, 1943; Jenkins & Lachner, 1971) which suggests that radii should be used cautiously as a taxonomic character in these fish.

To gauge the extent (if any) of primary radii increase in the redfins a comparison was made between juveniles and adults of four species with different mean radii (Table 3.9). The results show that the tendency to increase these radii is minimal which suggests that the scale radii characteristics of the redfins may be used as a taxonomic character where necessary. These results differ considerably from the figures given by Barnard (1943) for redfin species (Table 3.10). The reason for this discrepancy in results probably depends on the methods of counting and criterion for what are primary radii. Barnard (1943) counted "main striae" on the exposed portion of the scale which suggests that the scales were not removed from the fish for the purpose of the counting. If they were not removed or they were not defleshed it is possible that Barnard's counts include many secondary radii and it is probably these which have increased in number in his figures. The fact that Barnard only counted radii on the exposed portion of the scale makes it almost certain that he included radii which I have interpreted as secondary radii.

The scales of B.tenuis are distinctive with a relative high number of primary radii (Fig. 3.34) supplemented by many secondary radii (Fig. 3.33). The difference in the number of primary radii between B.calidus and B.erubescens (Fig. 3.34) is diagnostic (Skelton, 1974 b). B.burgi and B.burchelli have relatively few radii on the scales (Fig. 3.33 & 3.34).

The focus on the scales of the flexible-rayed species is usually centrally located (Fig. 3.33) whereas it is displaced towards the anterior field in the serrated-rayed redfins.

TABLE 3.11

Frequency distribution of vertebral counts in redfin species

Species	N	A. Total vertebrae 33	34	35	36	37	38	39	40	B. Precaudal vertebrae 17	18	19	20	21	22
B.burchelli	167		1	15	85	59	7			3	60	76	28		
B.burgi	135			6	53	67	8	1		2	36	75	23		
B.phlegethon	146			25	111	10				6	95	45			
P.tenuis	104	1	2	16	46	37	2			14	59	31			
B.afer	95			1	12	63	18	1			22	61	12		
B.afer (Gamtoos)	50				26	24					10	34	6		
B.asper	114			7	68	36	3			2	36	69	7		
B.asper (variant)	138			6	81	46	5			5	56	69	8		
O.quathlambae	31						3	16	12			1	9	16	5
B.calidus	369				27	227	111	4		1	95	265	8		
B.erubescens	151				1	80	67	3			25	122	4		

Species	N	C. Caudal vertebrae 15	16	17	18	19	20	D. Predorsal vertebrae 10	11	12	13	14	15	E. Preanal vertebrae 17	18	19	20	21	22
B.burchelli	167	3	19	50	73	20	2		61	103	3				2	82	67	14	2
B.burgi	136		8	46	60	20	2	7	82	45						29	88	19	
B.phlegethon	146		1	56	85	4			1	83	60	2			1	30	104	11	
B.tenuis	104		3	23	50	28			12	64	28			1	12	69	22		
B.afer	95		1	11	55	28			11	75	9					24	66	5	
B.afer (Gamtoos)	50		3	19	25	3				40	10					14	35	1	
B.asper	114		2	48	58	6			15	89	10				5	62	43	4	
B.asper (variant)	138		8	46	54	25	4		10	113	15				1	98	35	4	
O.quathlambae	31			2	10	14	5				6	22	3				1	24	6
B.calidus	369			12	181	160	15			70	263	36					52	268	49
B.erubescens	151			1	64	80	6		3	123	25						10	129	12

Vertebrae (Table 3.11)

Vertebral counts are recorded in Table 3.11. All species under consideration have a mode of 36 or 37 vertebrae except O.quathlambae which has 39. Variation usually extends over 4 or 5 vertebrae in each species. B.calidus and B.erubescens tend to have more vertebrae than the flexible-rayed species (again except O.quathlambae).

The majority of the species usually have 19 precaudal vertebrae, (Table 3.11 B). B.tenuis and B.phlegethon have 18, O.quathlambae 21. The number of caudal vertebrae (Table 3.11 C) is conservative and usually 17 or 18, although O.quathlambae, B.calidus and B.erubescens have 18 or 19.

The results in Table 3.11 suggest that the overall difference in vertebral counts between O.quathlambae and the other redfins is due to a difference in precaudal vertebrae (1-2 units) and an additional caudal vertebra. The difference in total vertebrae between B.calidus and B.erubescens and the other redfins is that the serrated-rayed species have an additional caudal vertebra.

The number of vertebrae before the dorsal fin (Table 3.11 D) varies intraspecifically from two to three vertebrae and the mode from 11 to 14 depending on the species. B.burgi tends to have fewer predorsal vertebrae than the other redfins and the possible implications of this with respect to the predorsal measurement has already been stated. The majority of redfin species have a mode of 12 predorsal vertebrae but B.calidus has 13 and O.quathlambae 14. It seems that it is largely in these counts that O.quathlambae has increased its vertebral complement relative to other redfin species.

B.calidus, B.erubescens and O.quathlambae have more vertebrae before the anal fin (Table 3.11 E) than the other redfins (mode 21 vs. 20 or 19). B.burgi, B.phlegethon and B.afer have 20 and B.tenuis, B.asper and B.asper (variant) 19 pre-anal fin vertebrae. One exceptional case of intraspecific variation in pre-anal vertebral counts was recorded: the normal count in B.burchelli is 19 or 20, but in a sample of 9 specimens from the Wit River (Bainskloof) 7 had 21 and 2 had 22 pre-anal fin vertebrae.

TABLE 3.13

Frequency of occurrence of teeth in each row on the pharyngeal bones of redfin species.

		Left pharyngeal											Right pharyngeal										
		Outer row teeth			Middle row teeth				Inner row teeth				Inner row teeth				Middle row teeth				Outer row teeth		
Species	N	0	1	2	1	2	3	4	2	3	4	5	2	3	4	5	1	2	3	4	0	1	2
B.burchelli	61		10	51		9	52			1	15	45		2	15	44		7	54			10	%L
B.burgi	30		10	20		4	26			1	9	20		1	6	22		6	22			9	19
B.phlegethon	32	5	24	3	1	5	26			4	13	15		1	8	23	1	6	25		6	24	2
B.tenuis	34	33	1			6	28			1	8	25		1	7	26	1	7	26		33	1	
B.afer	39	1	15	23		1	38			2	7	30		1	10	29		6	34		4	12	24
B.afer (Gamtoos)	30	2	13	15	1	2	27			1	9	20			8	22		5	25		2	12	16
B.asper	40	2	4	34		3	37			4	6	30		4	11	25		2	38			5	35
B.asper (variant)	50	5	14	31		8	41	1		4	18	28		1	14	35		4	46			16	34
O.quathlambae	12	11	1		1	4	7		1		11		1	1	11			6	7		12	1	
B.calidus	58		6	52		4	53	1		3	14	41		2	22	35		9	49	1		5	54
B.erubescens	30		4	26		2	28		1	6	23			7	24			4	27			4	27

TABLE 3.12

Frequency distribution of the supraneural bones in B.calidus and B.erubescens

Species	N	Supraneurals 5	6	7	8	9
B.calidus	258	4	35	137	78	4
B.erubescens	134		50	81	3	

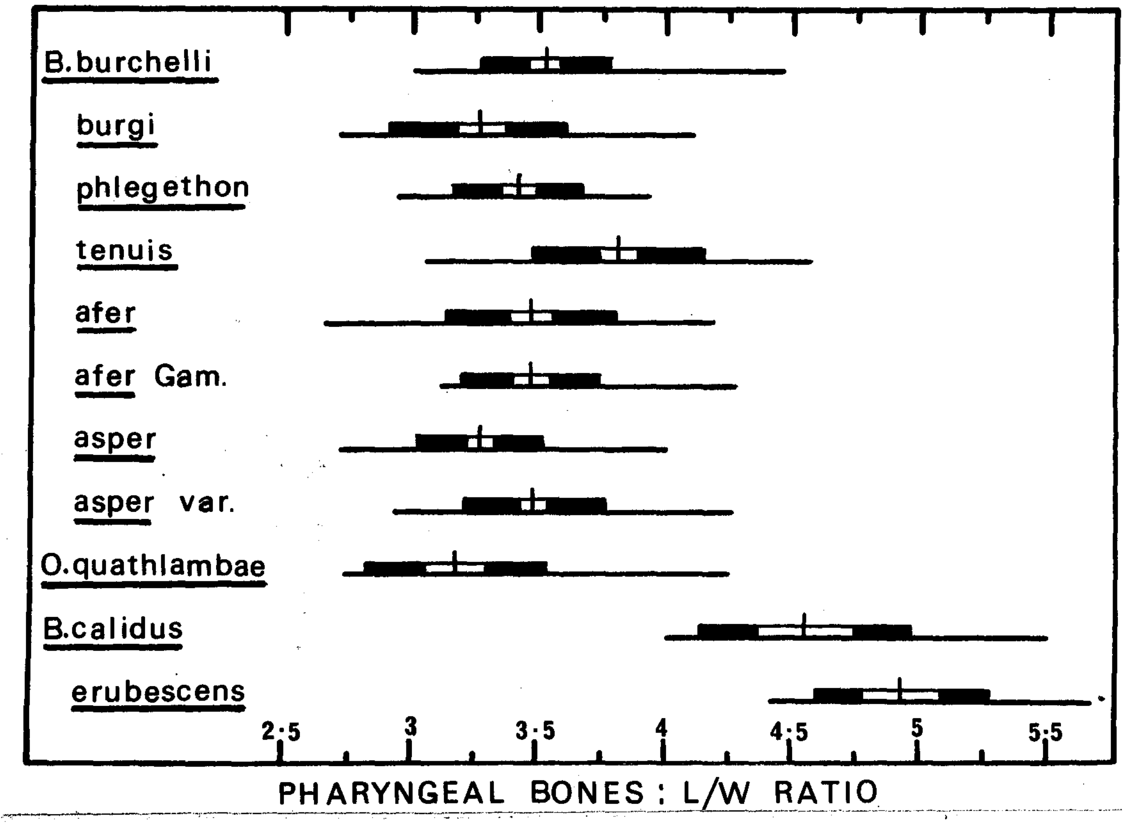


Fig. 3.35 The length to width ratio of the pharyngeal bones of redfin Barbus species and O.quathlambae.

Supraneural bones (Table 3.12)

Only B.calidus and B.erubescens have well developed supraneural bones. B.erubescens has usually 6 or 7 and B.calidus 7 or 8 supraneurals (Table 3.12).

Pharyngeal bones and teeth

The following characters of the pharyngeal bones and teeth were considered (1) the length to width ratio of the bones, (2) the pharyngeal teeth formulae and (3) the shape of the teeth.

Chu (1935) suggested a correlation between the shape of the pharyngeal bones and the feeding habits of cyprinids - the more slender the bones, the greater the tendency toward a carnivorous diet.

The length to width ratio of redfin pharyngeals (Fig. 3.35) shows that there is a similarity within the flexible-rayed species (1:3-4) which are markedly different (broader) to the serrated-rayed species (1:4-5). The degree of consistency in this ratio for the flexible-rayed species is all the more remarkable in view of the considerable differences in tooth shape and formula found amongst them.

The pharyngeals of B.erubescens are slightly more slender than those of B.calidus. This difference is consistent with other differences of feeding structures of the two species (e.g. pharyngeal teeth formula, length of gut). The differences between these two species contrasts with the relatively low differences between the proportions of the pharyngeal bones of the flexible-rayed species.

The frequency distribution of pharyngeal teeth in redfins is recorded in Table 3.13 from which a summary of modal counts had been extracted (Table 3.14). The usual Barbus formula of 2,3,5 - 5,3,2 (Chu, 1935; Matthes, 1963; Banister, 1973) is characteristic of most redfin species. O.quathlambae and B.tenuis have only the two inner rows of teeth. Two other species show regular tooth loss: B.phlegethon which has normally only a single outer row tooth, and B.erubescens which has only four inner row teeth (Skelton, 1974 b). Certain populations of B.afer and B.asper (variant) normally have only a single outer row tooth.

TABLE 3.14

Modal number of pharyngeal teeth in redfin species

Species	Left pharyngeal teeth			Right pharyngeal teeth		
Row:	O	M	I	I	M	O
B.burchelli	2	3	5	5	3	2
B.burgi	2	3	5	5	3	2
B.phlegethon	1	3	5	5	3	1
B.tenuis		3	5	5	3	
B.afer	2(1)*	3	5	5	3	2(1)*
B.afer (Gamtoos)	2(1)*	3	5	5	3	2(1)*
B.asper	2	3	5	5	3	2
B.asper (variant)	2(1)*	3	5	5	3	2(1)*
O.quathlambae		3	4	4	3	
B.calidus	2	3	5	5	3	2
B.erubescens	2	3	4	4	3	2

O - outer (minor) row

M - middle row

I - inner (major) row

* certain populations

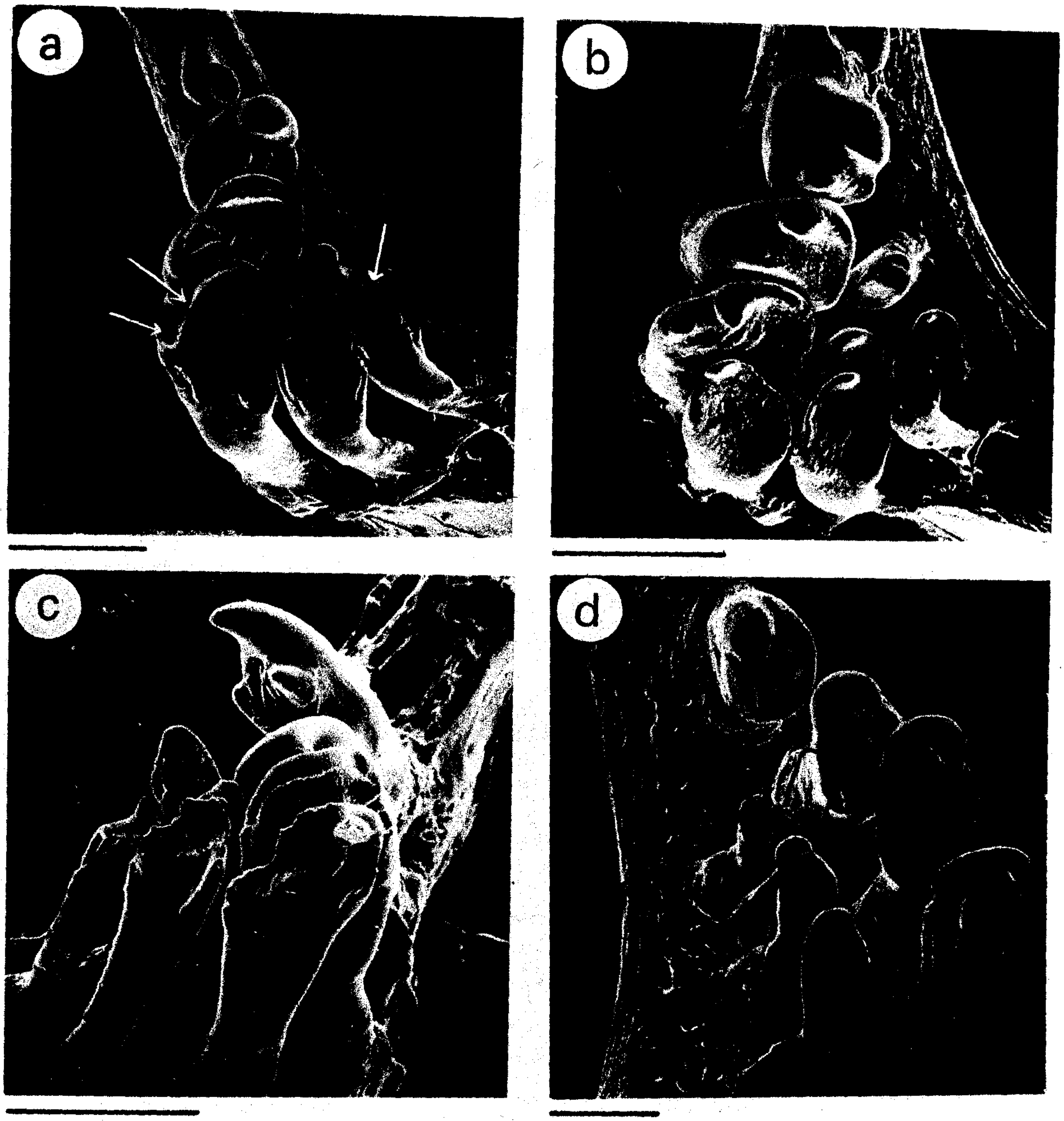


FIGURE 3.36. Occlusal view of pharyngeal teeth of redfin *Barbus* species (Scanning electron micrographs). Scale bar = 0,5 mm.

(a) *B.burchelli*, SL 52,5 mm AM/P 1566, right arch, arrows direct to lateral placement of major cusps.

(b) *B.burgi*, SL 41 mm AM/P 1874, right arch

(c) *B.phlegethon*, SL 46 mm AM/P 722, left arch

(d) *B.tenuis*, SL 66 mm AM/P 1935, left arch

An increase in the number of pharyngeal teeth was rarely encountered (Table 3.13). Of seven such observations five were B.burchelli and four of these from a single sample (Wit River, Bainskloof). This population also showed the longest gut length for the species and the development of the lips in certain specimens was exceptional. It seems likely that these features are interrelated.

A single specimen each of B.tenuis and O.quathlambae were found with a tooth on the outer (minor) row. Several specimens from the same sample of B.tenuis were examined and found to lack outer row teeth. The O.quathlambae specimen was the only one from the Moremoholo River which was examined for this character (only two specimens were available) and the possibility that others from this locality also have an outer row tooth cannot be ruled out.

The shape of the pharyngeal teeth is illustrated in Figures 3.36-3.38. Tooth shape is considered an important character in the redfins and will therefore be described in detail. Two patterns are present with evidence of convergence between certain forms. Both patterns are described, the first with reference to B.burchelli and the second with reference to B.calidus.

The pharyngeal teeth of certain redfin populations are encrusted with a brittle dark brown deposit. The crust appears similar or identical to the deposits of iron oxide on the teeth of Sarotherodon mossambicus reported by Lanzing & Higginbotham (1976), and has also been found on the teeth of several Haplochromis spp. (Greenwood, pers.comm.). The occurrence of the deposit is inconsistent and no systematic importance is attached to it. The pharyngeal teeth of B.erubescens (Fig. 3.38) show these crusts clearly.

The outer row teeth of B.burchelli (Fig. 3.36 a) are relatively small and slender with the stems and crowns compressed. The distal half of the first tooth in the row is bent postero-ventrally. The crown is slightly concave with a thickened rim which is worn to a sharp edge in places. The second tooth is equally small and modelled along similar lines as the first. The crown is less worn and usually features a small semi-terminal cusp situated on the medial side of the tooth (arrowed on Fig. 3.36).

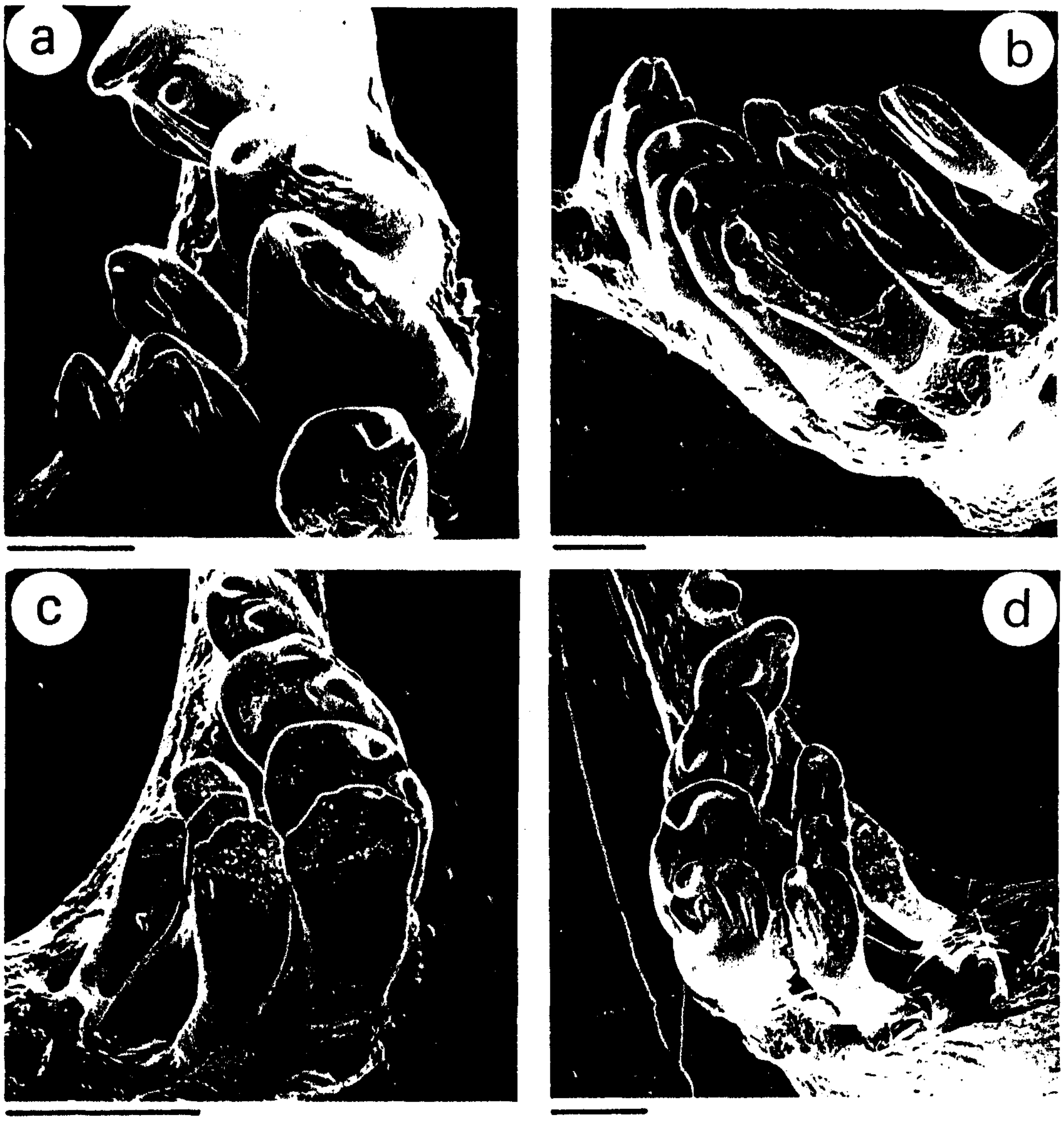


FIGURE 3.37. Occlusal view of pharyngeal teeth of redfin *Barbus* species. (Scanning electron micrographs). Scale bar = 0,5 mm.
(a) *B.afer*, SL 53 mm AM/P 3460, left arch
(b) *B.afer* (Gamtoos), SL 58 mm AM/P 1415, right arch
(c) *B.asper*, SL 47 mm AM/P 1744, left arch
(d) *B.asper* (Variant), SL 56 mm AM/P 2656, right arch.

The first tooth of the middle row has a compressed stem progressing to an expanded spatulate crown, which, like that of the first tooth in the outer row, is bent postero-ventrally. There is a low rim to the crown which is unevenly worn to a thin edge especially on the antero-lateral side. The second and third teeth in the row are less compressed and have a relatively strong cusp on the medial edge of the crown.

Four of the five teeth in the inner or major row are large and well developed, the fifth is small and simple in form. The first tooth in the row is similar to, but larger than, the first teeth in the other two rows. Thus the stem and crown are strongly compressed, the crown bent postero-ventrally, expanded and spatulate, with a rim which is obliquely worked to a sharp edge on the antero-lateral margin. The median rim is thick and developed into a ridge-like cusp separated from a terminal major cusp.

The second tooth of the major row is less compressed than the first but still conforms to the form of the latter. The obliquely worn crown has a prominent median terminal rim which forms a major cusp and a proximal secondary cusp. The thickness of the rim tapers away from the major cusp over the crest of the crown to the antero-lateral edge which is worn to a thin edge. The tooth is less arched (bent) than the first.

The third tooth is comparatively stout and the stem not noticeably compressed. The crown is moderately expanded and has a prominent rim which features two cusps on the medial edge. The distal cusp forms the median head of the crown rim which tapers obliquely to the antero-lateral side.

The fourth tooth is the largest and has a stout, more or less cylindrical stem with a conical tip. There are two smaller cusps on the side of the crown. The median shoulder and cusp is usually slightly larger than the lateral one so that the tooth is not entirely symmetrical in occlusal view (Fig. 3.36 a).

The fifth tooth is variously developed or vestigial but always much reduced in comparison with the other teeth in the row and is usually a simple peg with a conical tip.

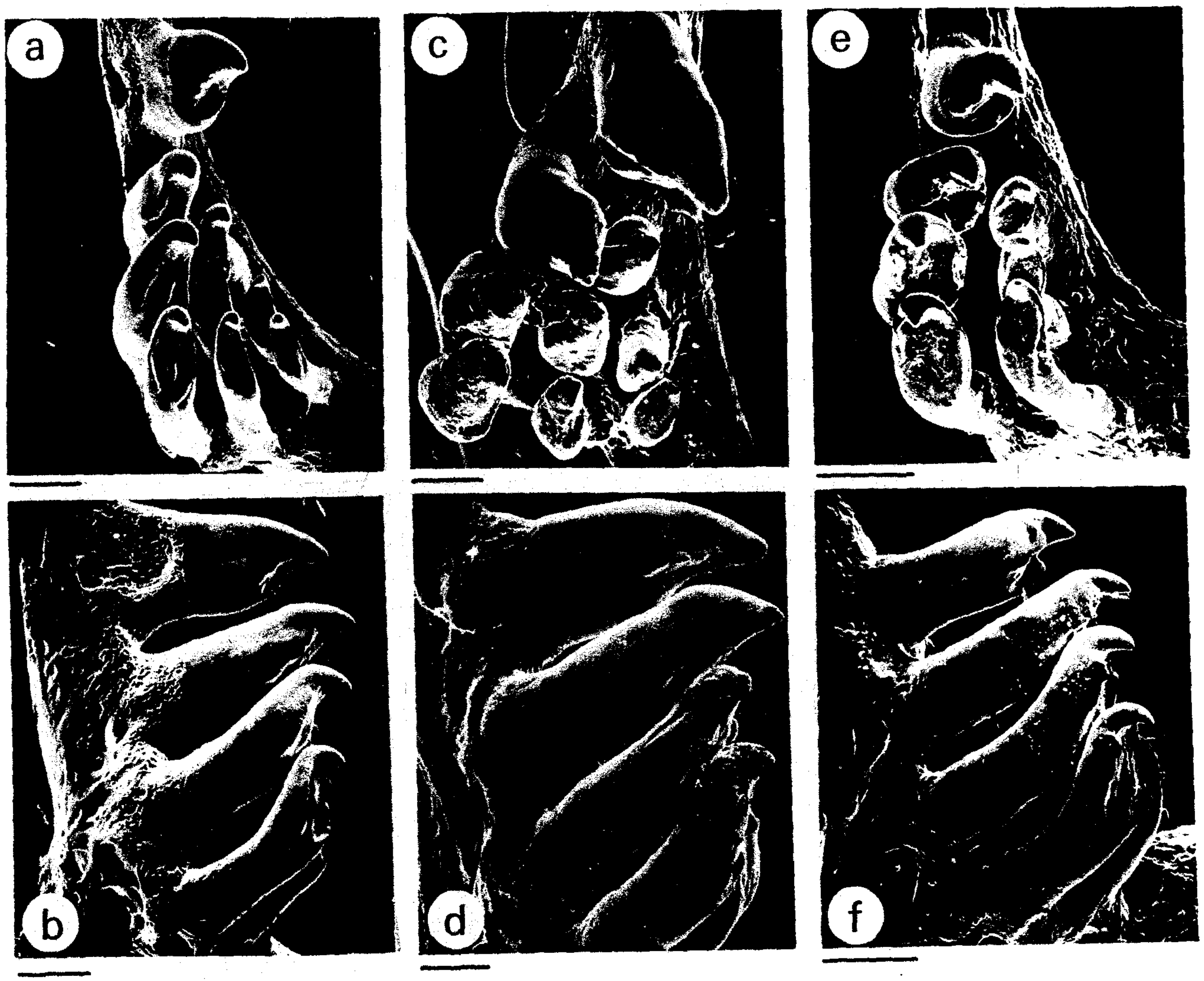


FIGURE 3.38. Occlusal and side (Postero-medial) views of the pharyngeal teeth of redfin *Barbus* species and *O.quathlambae* (scanning electron micrographs). Scale bar = 0,5 mm. a & b) *B.calidus*, SL 65 mm AM/P 1844, right arch ; c & d) *B.erubescens*, SL 65 mm AM/P 1866, right arch ; e & f) *O.quathlambae*, SL 82 mm AM/P 1877, right arch.

Variation in tooth form in this and the other redfin species depends on the age of the tooth and the extent of wear to which the crowns have been subjected. Newly replaced teeth have well defined cusps and crown rims and these become rounded and low with wear.

Key features of the pattern of tooth shape in the flexible-rayed redfins for comparison with other groups are: the compression of the first and second teeth in each row, the distinctly oblique wear on the crown, and the asymetrical placement of the cusps.

The teeth of *B.burgi* (Fig. 3.36 b) are essentially similar to those of *B.burchelli*. There is however more wear on those of *B.burgi* illustrated and consequently the crowns are lower. The pharyngeal teeth of *B.phlegethon* (Fig. 3.36 c) are also similar in shape to those of *B.burchelli*, except for the very high crown of the fourth tooth in the major row. This is a general feature of the species and is still evident in relatively well worn teeth. The single tooth in the outer row is arched postero-ventrally and has a small cusp on the medial edge of the crown. The position of the tooth suggests that this is the second tooth in the row, the first having been lost.

While the teeth of *B.tenuis* (Fig. 3.36 d) differ substantially in shape from those of *B.burchelli*, they still reflect the basic pattern for *B.burchelli*. There are only two tooth rows in *B.tenuis*. The first teeth in each row are slender with compressed stems and expanded, spatulate and postero-ventrally arched crowns. There is a distinct conical cusp on the median edge. A second cusp is present, but is much reduced relative to equivalent cusps of other redfin species. The subsequent teeth in the lateral row are similar to but progressively stouter than the first tooth. The conical cusp is prominent in these teeth as well. The second through fourth teeth in the major row are progressively stouter and the crowns all have prominent, conical cusps on the median side. The fourth tooth is more or less cylindrical and is not arched. The crown of each tooth is relatively remote from its neighbour in the same row.

The pharyngeal teeth of *B.afer*, *B.afer* (Gamtoos) and *B.asper* (variant) (Figs 3.37 a, b, c) show no major differences and are all similar to the shape of those of *B.burchelli*. The teeth of *B.asper* have wide compressed stems and crowns which are moderately expanded but well worn and closely applied to each other. The first tooth in each row is gently arched and lacks prominent cusps, although vestiges of these are present in the major row. Oblique wear and cusps on the medial edge of the crown are again more evident in the fourth tooth of the major row of *B.asper* than in the other species. The fifth tooth is small and vestigial.

The teeth of *O.quathlambae* (Fig. 3.38 e & f) differ in shape but not the pattern to those of *B.burchelli*. They are less compressed, more cylindrical and well arched and have more prominent major cusps than the other redfins already described. In spite of this the micrographs show that the crowns are not symmetrical, and the recurved conical cusp at the tip is displaced medially. All the teeth feature such a cusp. The nearest approach to tooth shape of *O.quathlambae* from the flexible-rayed group is that of *B.tenuis*.

The pharyngeal teeth of *B.calidus* (Fig. 3.38 a & b) show a certain resemblance to those of *O.quathlambae*. The stems are nearly all cylindrical, the crowns are narrow and there is a prominent conical recurved tip to each tooth. There are no definite secondary cusps although low ridges are present on the postero-dorsal surface leading to the base of the cusp. The stem of the fourth tooth in the major row is laterally compressed. The teeth of this species are more-or-less symmetrical.

B.erubescens (Fig. 3.38 c & d) has characteristically strong peg-like teeth. The first tooth in each row has a cylindrical stem and arches postero-ventrally to form a tapered crown with a prominent recurved terminal conical cusp. Subsequent teeth are less bent but otherwise similar to the first of a row. The third and fourth teeth in the major row are larger than the rest and have strong conical crowns with but low ridges on the postero-dorsal surface, breaking the smooth surface of the teeth.

It is possible to suggest the action of the pharyngeal teeth in redfin species from the form and nature of the wear on them. In *B.burchelli* *B.burgi*, *B.phlegethon*, *B.afer* and *B.asper* the shape is probably derived

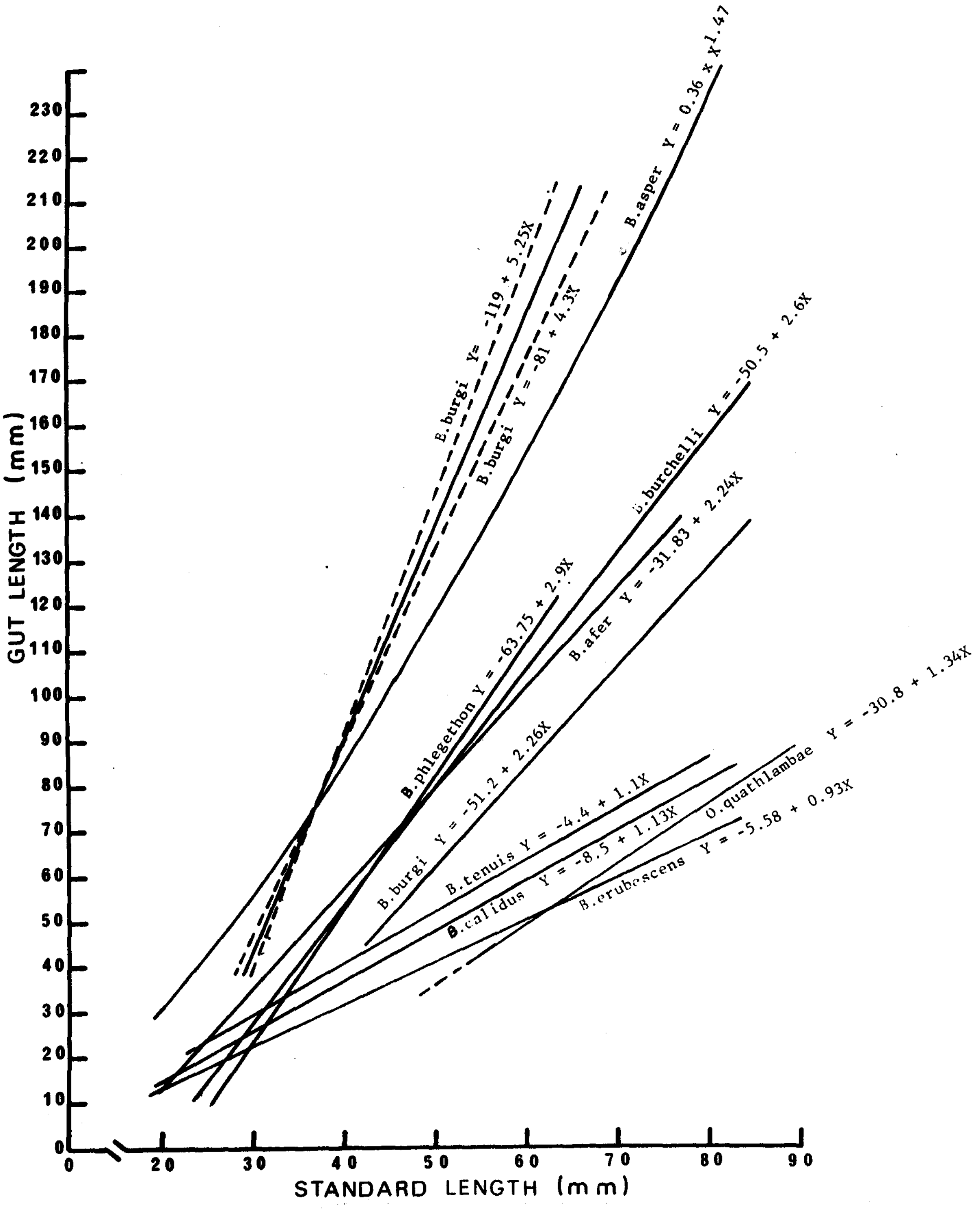


Fig. 3.39 Regression lines of the gut length versus standard length of redfin Barbus species and O.quathlambae. Correlation co-efficient for each species as follows: B.burchelli r^2= ,8651; B.burgi (i) r^2 = ,8414, (ii) r^2 = ,9051; (iii) r^2 = 9263; B.phlegethon r^2 = ,8564; B.tenuis r^2 = ,9026; B.afer r^2 = 9495; B.asper r^2 = ,8901, B.calidus r^2 = ,9528; B.erubescens r^2 = ,9656; O.quathlambae r2 = ,8995.

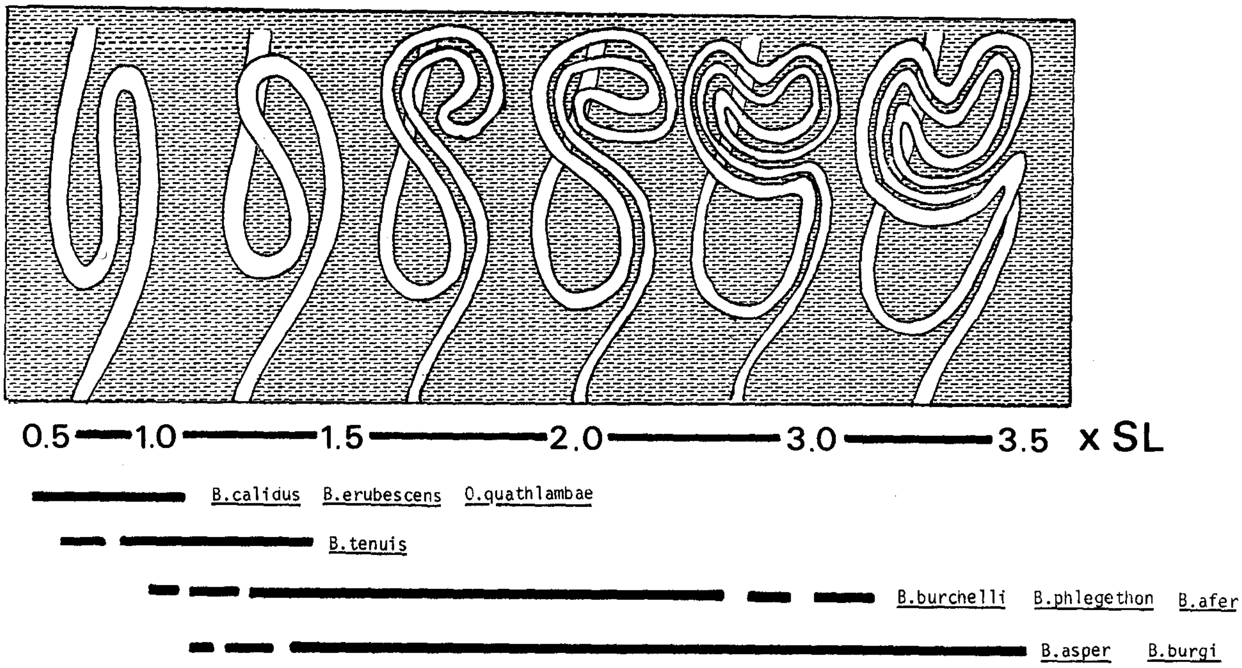


Fig. 3.40 A diagrammatic representation of the pattern of flexure, length of the gut and approximate range of variation of gut length of redfin Barbus species and O.quathlambae.

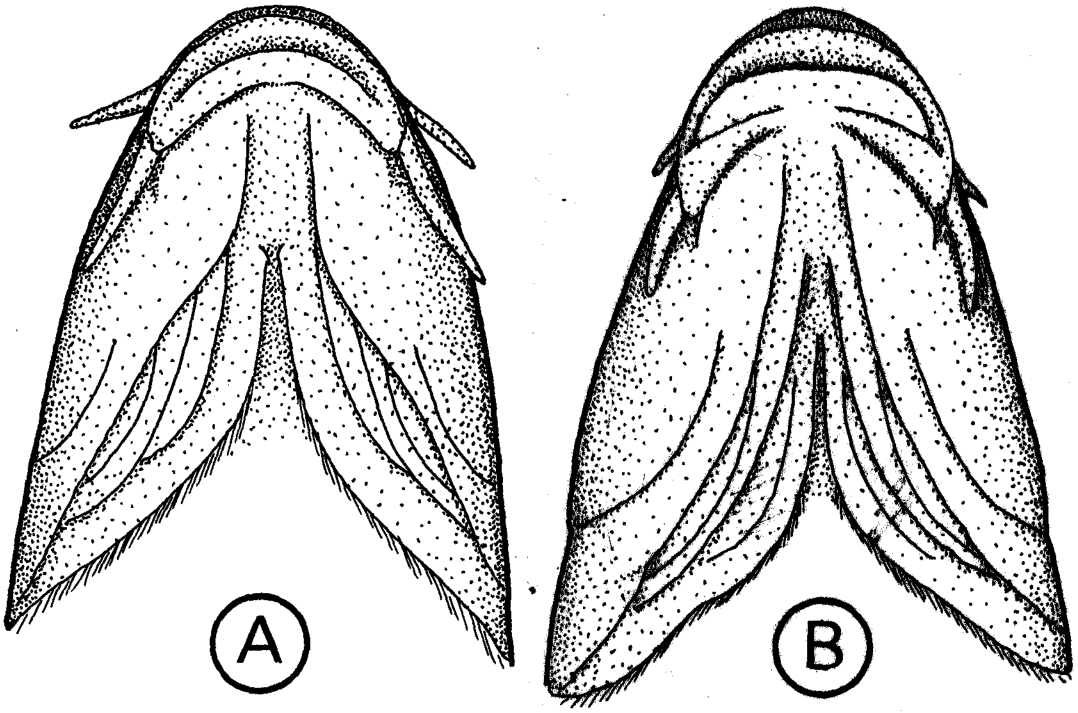


Fig. 3.42 Two examples of different mouth forms in B.burchelli
(A) More common form with well developed lips not retracted from rim of lower mandible (specimen from AM/P 4972)
(B) unusual mouth form with lips retracted from rim of lower mandible (AM/P 1411).

from a scraping action. There is little indication of a crushing or molariform action in their form. The teeth of B.tenuis suggest an increasing tendency for raking rather than scraping. In O.quathlambae and B.calidus the action suggested is definitely a raking one, and in B.erubescens the action appears to be one of raking combined with piercing or stabbing.

Gut length and flexure (Figs 3.39, 3.40)

In fishes as well as other organisms the length of the gut (intestine) usually reflects the diet of the organism (Nikolsky, 1963; Weatherley, 1972). This is particularly true of the Cyprinidae which lack a true stomach. In general the shorter the gut the more carnivorous the feeding habits and the longer the gut the more herbivorous the feeding habits. The length and degree of flexure of the gut have not been fully explored in the redfin species. Smith (1841) referred to the "intestinal canal long and contorted" in Pseudobarbus (which was clearly based on B.burchelli and not B.pallidus the second species in the subgenus but which has a short single flexured intestine). Greenwood & Jubb (1967) found the "gut short, about 0.7 times standard length" in O.quathlambae.

The length of the gut varies both inter- and intraspecifically in the redfins and in certain cases provides a useful taxonomic character. On the length of the gut the redfins may be clustered into three groups (Fig. 3.39). The first group have a short gut more or less equal to the standard length (included are B.tenuis, O.quathlambae, B.calidus and B.erubescens). The second group has a gut length of intermediate proportions about 2-2,5 times the standard length in adults (B.burchelli, B.burgi in part, B.phlegethon, B.afer, B.afer (Gamtoos) and B.asper (variant). The third group has a relatively long gut which exceeds 2,5 times the standard length in adult fishes (B.burgi in part and B.asper).

The increase in gut length is accommodated by the increasing flexure of the organ within the framework of a single coiling pattern (Fig. 3.40). In the first group the gut forms a simple "S"-flexure which is sometimes slightly more involuted in B.tenuis. The flexure involutes progressively

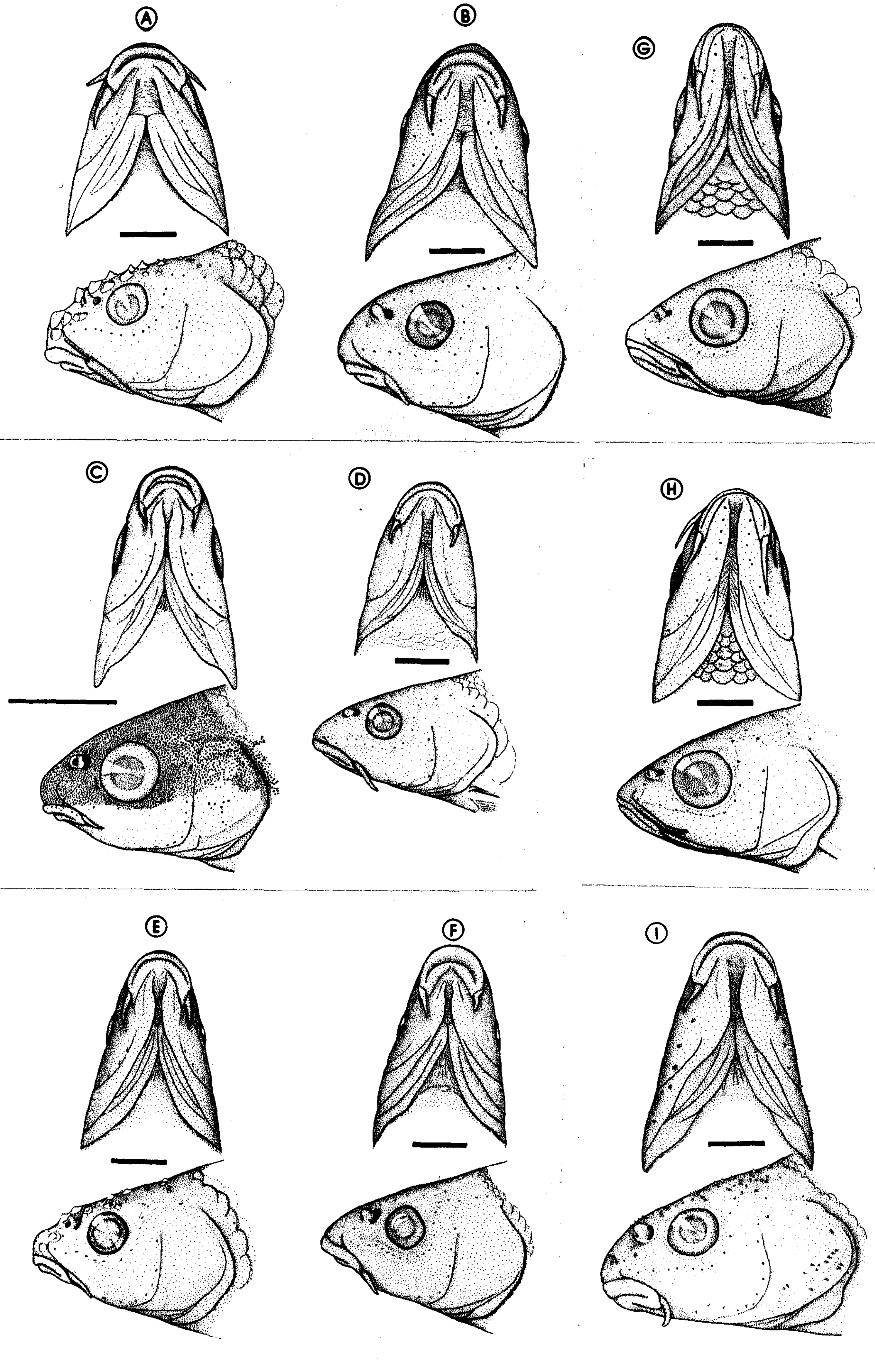


Fig. 3.41 Ventral and lateral views of the head of specimens of redfin *Barbus* species and *O. quathlambae* illustrating the form of the mouth. A - *B. burchelli*; B - *B. burgi*; C - *B. phlegethon*; D - *B. tenuis*; E - *B. afer*; F - *B. asper*; G - *B. calidus*; H - *B. erubescens*; I - *O. quathlambae*.

in the second group and the process is extended to form further involutions during the growth of an individual and the length of the intestine becomes more and more allometric in the forms with higher gut length ratios.

The differences recorded above in the pharyngeal bones and teeth of the redfins correlates extremely well in those forms with a short gut. For example, B.erubescens has a slightly shorter gut than B.calidus (Fig. 3.39) and in correspondence has more slender pharyngeal bones (Fig. 3.35), fewer pharyngeal teeth (Table 3.14) which are more conical (Fig. 3.38). Similarly O.quathlambae has a relatively shorter gut than B.tenuis (Fig. 3.39) which is correlated with fewer pharyngeal teeth and differences in their shape (Table 3.14; Fig. 3.38).

Where gut length exceeds standard length there is a tendency to show an increasing range of variation with longer intestines and greater size. Accordingly the taxonomic weight given to differences between these species (or species groups) is less than that given to those with short intestines. The intraspecific variation in gut length of B.burgi is exceptional (Fig. 3.39). Of three populations examined two (Gt. Drakenstein and Verlorevlei) have an extremely long and greatly involuted intestine. Specimens from the Krom River have a relatively short and less involuted gut more characteristic of B.burchelli populations.

The length of the gut in B.burchelli, B.afer, B.afer (Gamtoos), B.asper (variant) and B.phlegethon (Fig. 3.39) is similar and of moderate proportions within the redfin range. B.asper (Fig. 3.39) has an extremely long and involuted gut similar to that of the Gt. Drakenstein and Verlorevlei populations of B.burgi.

Mouth (Fig. 3.41)

The serrated-rayed redfins have large terminal "U"-shaped mouths. The flexible-rayed species have sickle shaped mouths which are either subterminal or inferior. In these species the lips are usually well developed but variable. An exceptional degree of variation in mouth form has been found in B.burchelli (Fig. 3.42). The usual mouth

TABLE 3.15

A summary of the occurrence, size, form and distribution of tubercles in redfin species.

Species	Occurrence	Max Size (mm)	Type	Head (number on either side of midline on snout)	Body	Fins
B.burchelli	frequent ♂ (♀)	1.5	conical	snout (5-10) dorsum	single row on scale edges; entire body except ventral region	shagreen bands on pectoral (4-6 deep) single rows on other fins
B.burgi	frequent ♂ (♀)	1.5	conical	snout (10) dorsum	single row on scale edges; entire body except ventral region	shagreen bands on pectoral, single rows on other fins
B.phlegethon	rare ♂	1	conical	snout (4) dorsum	?	spaced bands on pectorals (2 deep)
B.tenuis	infrequent ♂	1.5	conical	snout (± 5) dorsum	single row on scale edges; entire body except ventral region	spaced single rows on pectoral and other fins
B.afer	frequent ♂ (♀)	1.5	conical	snout (± 5) dorsum	single row on scale edges; entire body except ventral region	shagreen bands on pectoral (4 deep) single rows on other fins
B.asper	frequent ♂ (♀)	1.5	conical	snout (± 5) dorsum	single row on scale edges; entire body except ventral region	shagreen bands on pectoral (3-4 deep) single rows on other fins
O.quathlambae	frequent ♂ + ♀	0.5	conical	snout (± 5) dorsum & lateral	1-3 per scale - entire body except ventral most region	shagreen bands on pectoral (6 deep) single rows on other fins
B.calidus	ripe only ♂ + ♀	±0.1	erupted	dorsum & lateral	dorsal/scales scattered over scale surface	single spaced rows on pectoral
B.erubescens	ripe only ♂ (♀)	±0.1	erupted	dorsum & lateral	dorsal scales scattered over scale surface	single spaced rows on pectoral

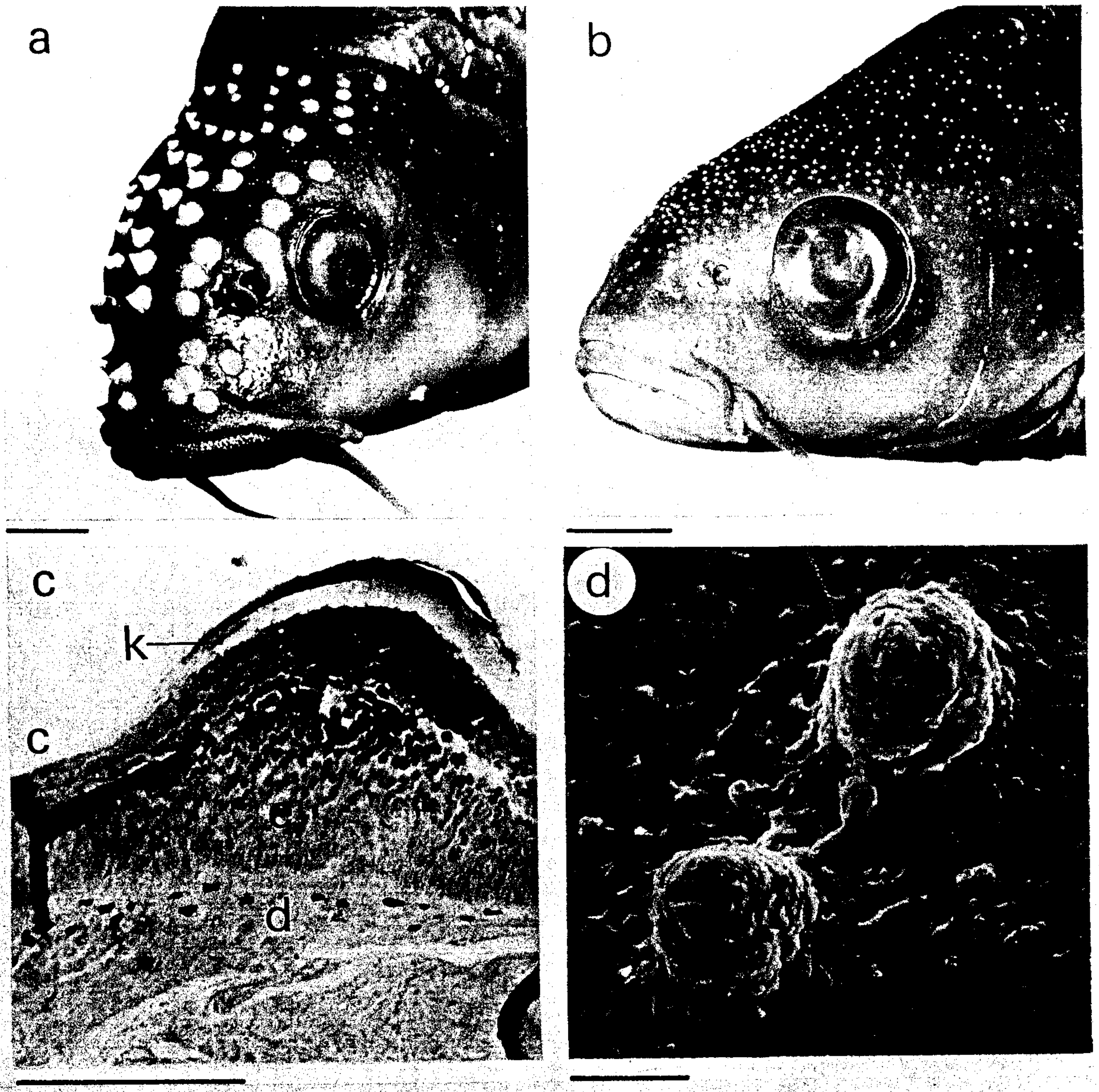


FIGURE 3.43. Aspects of redfin Barbus tubercles.

(a) Antero-dorsal view of head of B.burchelli SL 99 mm AM/P 7223 to show large conical tubercles. Scale bar ± 5 mm.

(b) Lateral view of head of a paratype B.erubescens SL 85 mm AM/P 2074, to show small densely distributed tubercles. Scale bar ± 5 mm.

(c) Transvers section of conical tubercle on head of male B.afer (AM/P 3786) to show keratin cap, hypertrophied epidermal cells and canals of unknown function. Abbreviations: c-canal, d-dermis, e-epidermis, k-keratin cap. Scale bar ± 0.3 mm.

(d) Scanning electron micrograph of head tubercles from a paratype of B.erubescens AM/P 2074. Scale bar ± 0.05mm.

form in this species (Fig. 3.42 A) has fairly well developed lips over the entire rim of the mouth. Specimens from the Witte River (Baineskloof) have the lips retracted from the rim of the lower jaw, which has instead a firm sheath (Fig. 3.42 B). The mouth of B.phlegethon also has a firm rim on the lower jaw but this is not as well developed as in the illustrated specimen of B.burchelli.

Tubercles

Tubercles are valuable systematic characters in cyprinids (Wiley & Collette, 1970; Collette, 1977). Both large tubercles and smaller "pimples" have been recorded in certain redfin species (Barnard, 1943; Jubb, 1965; 1967) but the details of their structure and pattern of distribution have not yet been studied. The development and occurrence of tubercles in redfins is summarized in Table 3.15.

Two kinds of tubercles are present, "conical" and "erupted". Conical tubercles (e.g. Fig. 3.43 a) occur in all the flexible-rayed species and are larger more prominent structures than the tiny erupted tubercles of B.calidus and B.erubescens. The conical tubercles are deciduous, hypertrophied, epidermal structures with a distinct keratin cap (Fig. 3.43 c) which develop on the head, scales and fins of adult male individuals during the breeding season. Large ripe females of flexible-rayed species sometimes develop tubercle buds on the head.

The fact that the tubercles are correlated with sexual maturity and breeding condition strongly suggests that they have one or other function(s) with breeding activity. Wiley & Collette (1970) and Collette (1977) have presented several possible functions which could also apply to the tubercles of the redfins.

Although there are differences in size and degree of development of conical tubercles in the flexible-rayed redfins they do have a common pattern of distribution in the species. For comparative purposes this pattern will be described with reference to B.burchelli (Fig. 3.46).

There are two groups of large tubercles on the snout, one on either side of the midline (no's 1-4). The median tubercles in these groups

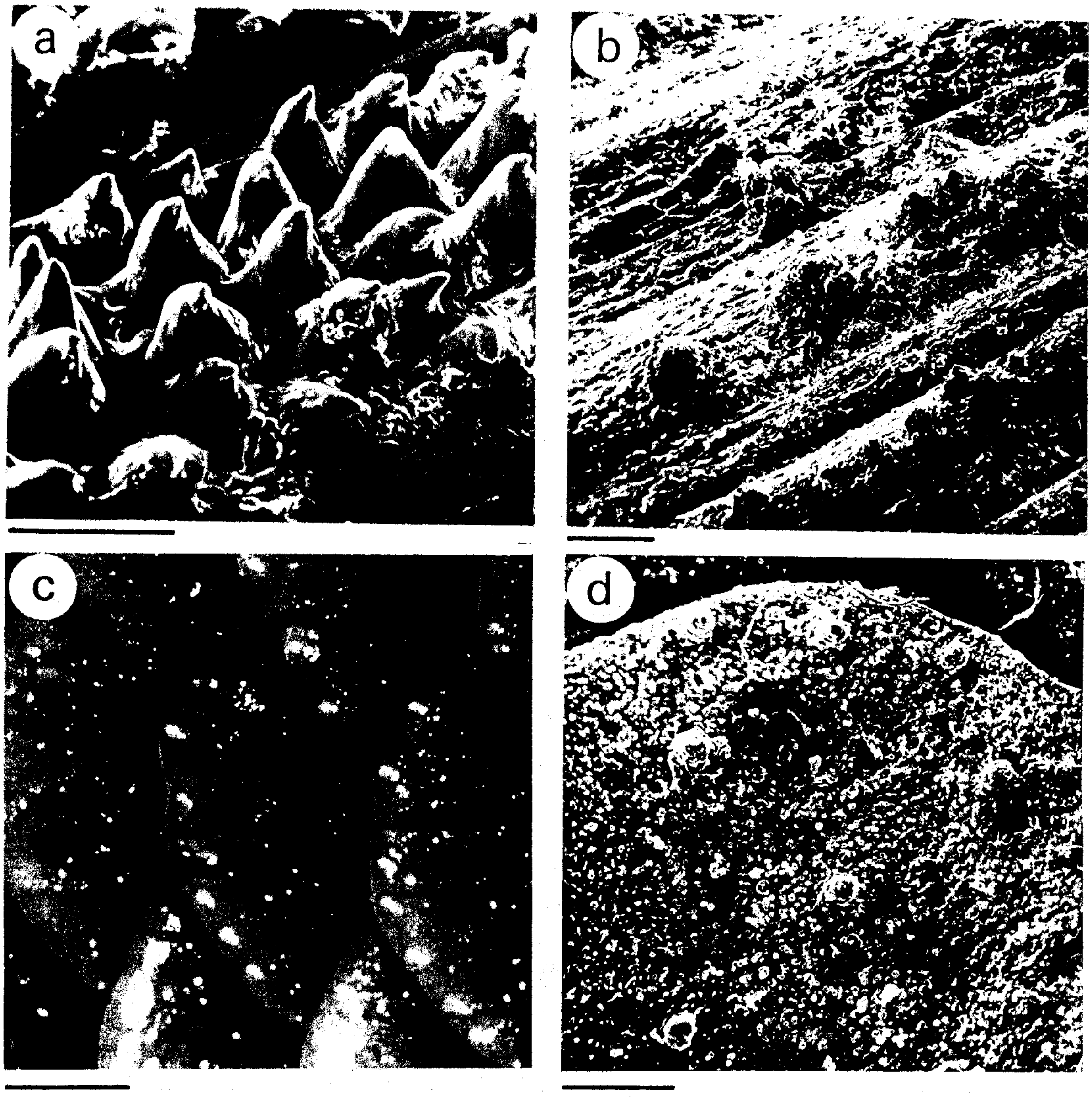


FIGURE 3.44. Tubercles from the pectoral fins and scales of redfin <u>Barbus</u> species.

(a) Scanning electron micrograph of portion of a band of tubercles from pectoral fin of <u>B.burchelli</u> SL 65 mm. AM/P 2077. Scale bar 0.1 mm.

(b) Scanning electron micrograph of portion of upper pectoral fin surface of <u>B.erubescens</u> SL 85 mm AM/P 2074. Scale bar 0.25 mm.

(c) Scales of <u>B.burchelli</u> to show arrangement of tubercles along free edge, SL 67 AM/P 3472. Scale bar ± 1 mm.

(d) Scanning electron micrograph of scale of <u>B.erubescens</u> to show tubercles on upper surface. SL 85 mm AM/P 2074. Scale bar 0.25 mm.

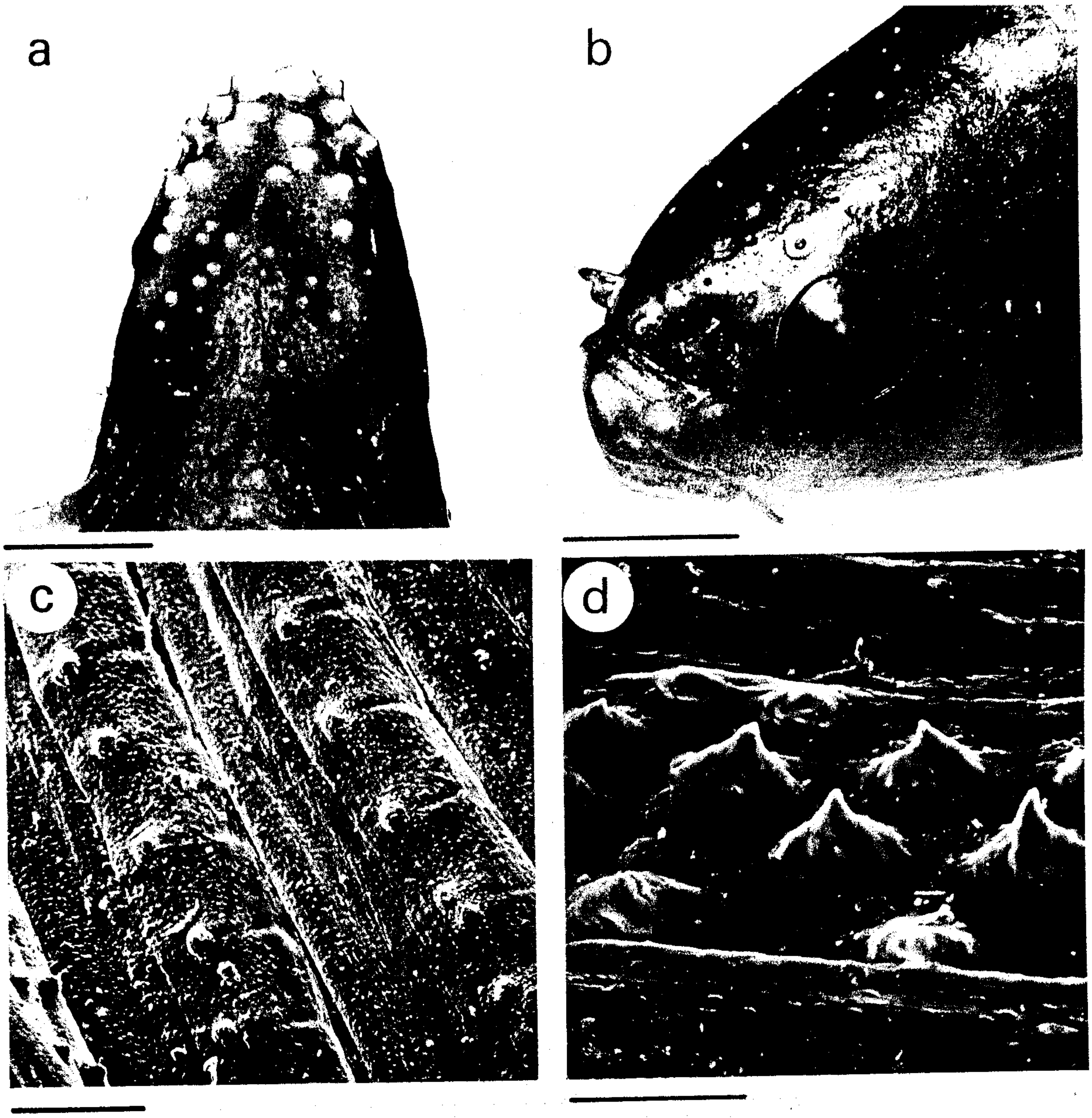


FIGURE 3.45. Aspects of tubercles of *B.tenuis* and *B.phlegethon*.
(a) Dorsal view of tubercled male of *B.tenuis* SL 62 mm. AM/P 3455. Scale bar 5 mm.
(b) Antero-dorsal view of tubercled male of *B.phlegethon* SL 70 mm, AM/P 7366. Scale bar 5 mm.
Scanning electron micrographs (c & d)
(c) Portion of the upper surface of pectoral fin of *B.tenuis* SL 62 mm. AM/P 3455. Scale bar 0.25 mm.
(d) Scanning electron micrograph of portion of band of tubercles on male *B.phlegethon* SL 45.5 mm. AM/P 1399. Scale bar 0.1 mm.

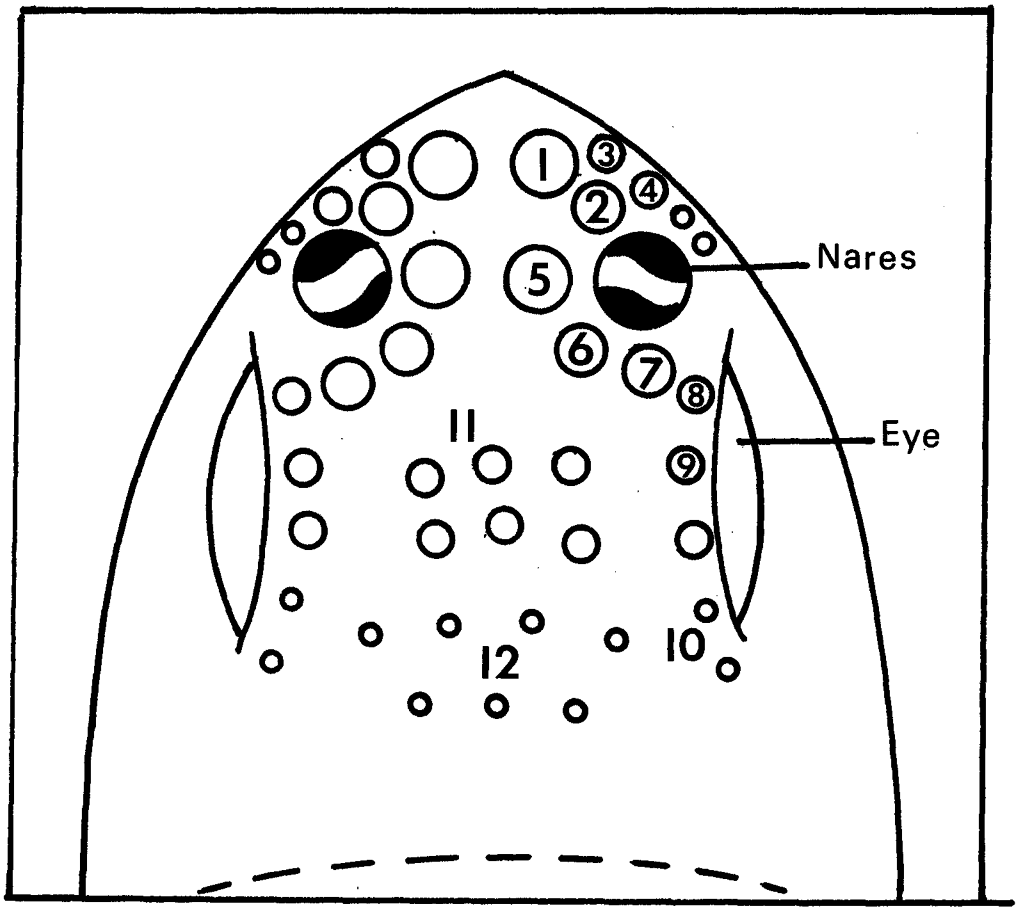


Fig. 3.46 Diagram of the head from above to explain the pattern of tubercles on the head of B.burchelli as described in text.

can measure up to 1,8 mm in diameter and 1,6 mm in height. B.burchelli usually has 5-6 tubercles in each group. A row of tubercles extends in an arc above each nare to the antero-dorsal edge of the orbit (no's 5-7) and continues posteriorly along the dorsal edge of the orbit (8-10). The tubercles decrease in size posteriorly. There are two mid-dorsal groups (no's 11 & 12) in which the tubercles are irregularly scattered. Except for the odd aberrant one there are no tubercles on the cheeks, below the orbit or on the ventral surface of the head.

Small (i.e. approximately 0,08 mm diameter) conical tubercles are arranged in a single linear series along the free edge of each scale (Fig. 3.44c). There are usually from 5 to 10 such tubercles per scale. Only the ventral scales between the pectoral and anal fins lack these tubercles.

Conical tubercles also occur on the fins in B.burchelli, best developed on the pectoral fins where they form distinct bands over the dorsal surface of the larger fin rays (Fig. 3.44 a). Bands do not occur on the leading ray but there are usually a few isolated tubercles along its length. These fin tubercles are very small 0,1-0,2 mm in diameter, the bands a maximum of about 0,6-0,7 mm in width and there are up to five or six tubercles across the bands at maximum width. Single tubercle rows develop over the fin rays of other fins.

The tubercles of B.burgi are similar to but relatively smaller than those of B.burchelli. Well developed tubercles on the snout of a large B.burgi specimen (78 mm SL) measure approximately 0,8 mm in height and base diameter. In each group on the snout there are usually from 10 to 15 tubercles and these extend to beyond the nares, i.e. over the lachrymal bone. Tubercles on the scales and fins are similar to those described for B.burchelli.

B.phlegethon does not have tubercles [illegible]

specimens. Compared to the tubercles of other flexible-rayed redfins they are however vestigial (Fig. 3.45 b). On the head they occur in the same pattern as those of B.burchelli and although small are distinctly conical. There are also weak bands along the pectoral fin rays (Fig. 3.45 b). Tubercles have not yet been observed on the scales of this species.

One of the diagnostic features for *B.tenuis* recorded by Barnard (1943) was the absence of tubercles in males. Prominent tubercles do develop (Fig. 3.43 a) but tubercled specimens are not as frequently encountered in collections of this species as in other flexible-rayed species. The pattern in *B.tenuis* is similar to that in *B.burchelli* but there are fewer tubercles per group on the snout (four or five). There are also similar tubercles in single rows along the free edge of each scale. The pectoral fin tubercles of *B.tenuis* are different to those of *B.burchelli* in that they do not occur in bands (Fig. 3.43 c) but only as single widely spaced rows. Similar single rows occur on the other fins.

Large conical tubercles in the *B.burchelli* pattern are characteristic of *B.afer* males. There are fewer tubercles per snout group (3-5) and the tubercles on top of the head are often more distinctly grouped into anterior and posterior clusters. There are single rows along the free edge of scales except those of the belly region. Bands are present on the pectoral fins up to two or three tubercles in width. Single rows are present over the fin rays of other fins.

There is no notable differences in the tubercle development in *B.afer* (Gamtoos), *B.asper* (variant) or *B.asper* to that described above for *B.afer*. Jubb (1965, 1967) illustrated the head tubercles of two *B.asper* (variant) males from the Homtini River.

The tubercles of *O.quathlambae* were described in detail by Skelton (1974 a). In this species they are more numerous and smaller on the head than in any other flexible-rayed redfin. In spite of their small size they are distinctly conical and the pattern is generally similar to that in *B.burchelli*. There are bi-lateral clusters on the snout, above and between the nares, above the orbits and on top of the head. In addition there are a few tubercles on the operculum and below the orbit. Each scale has a single tubercle (occasionally two or three). There are well developed bands on the pectoral fins in which the tubercles are compressed (vide Skelton 1974 a, Fig. 5). There are single tubercle rows over the rays of other fins.

B.calidus and B.erubescens do not develop large conical tubercles like those of the flexible-rayed redfins. Breeding adults of both sexes of these two species develop tiny (0,1 mm diameter) epidermal excrescences (Fig. 3.43 b & d) described by Barnard (1943) as "pimples". These are distributed over the dorsal surface of the head with clusters on the opercula and cheek regions. They extend onto the dorsal scales where they occur scattered over the exposed surface of the scales (Fig. 3.44 d). Single widely spaced rows are present over the rays of the pectoral, pelvic and unpaired fins (Fig. 3.44 b). The males are usually better endowed with these eruptions than the females.

Colour and Pigmentation

Live specimens of all the redfin species have been observed during the course of this study. Different ecological and physiological situations clearly affect the expression of colour and pigmentation of individuals and the following descriptions are broad generalizations of these characteristics.

Colour illustrations of redfin species have been given by Smith (1841), Jubb (1965, 1967), Smith & Smith (1966) and Skelton (1974 a). The frontispiece records a colour photograph of a live B.burchelli and B.erubescens. Barnard (1943) has provided colour descriptions of several species and Skelton (1974 a & b) has described the live colours of O.quathlambae and B.erubescens respectively.

Predominant background colours are browns and greens which vary from a light yellow to a deep olive. Ventral portions are white or silvery-gold, and the opercula are invariably metallic silvery-gold. The iris of the eye is golden. The proximal portion of the fins, initially orange in juveniles, becomes scarlet in adults of all the species. This is most intense in nuptial males. The caudal fin is least affected by the scarlet pigment and usually only reflects a pink or salmon tinge in the central portion of each lobe. With the exception of O.quathlambae the red colour does not impinge on the body to any great

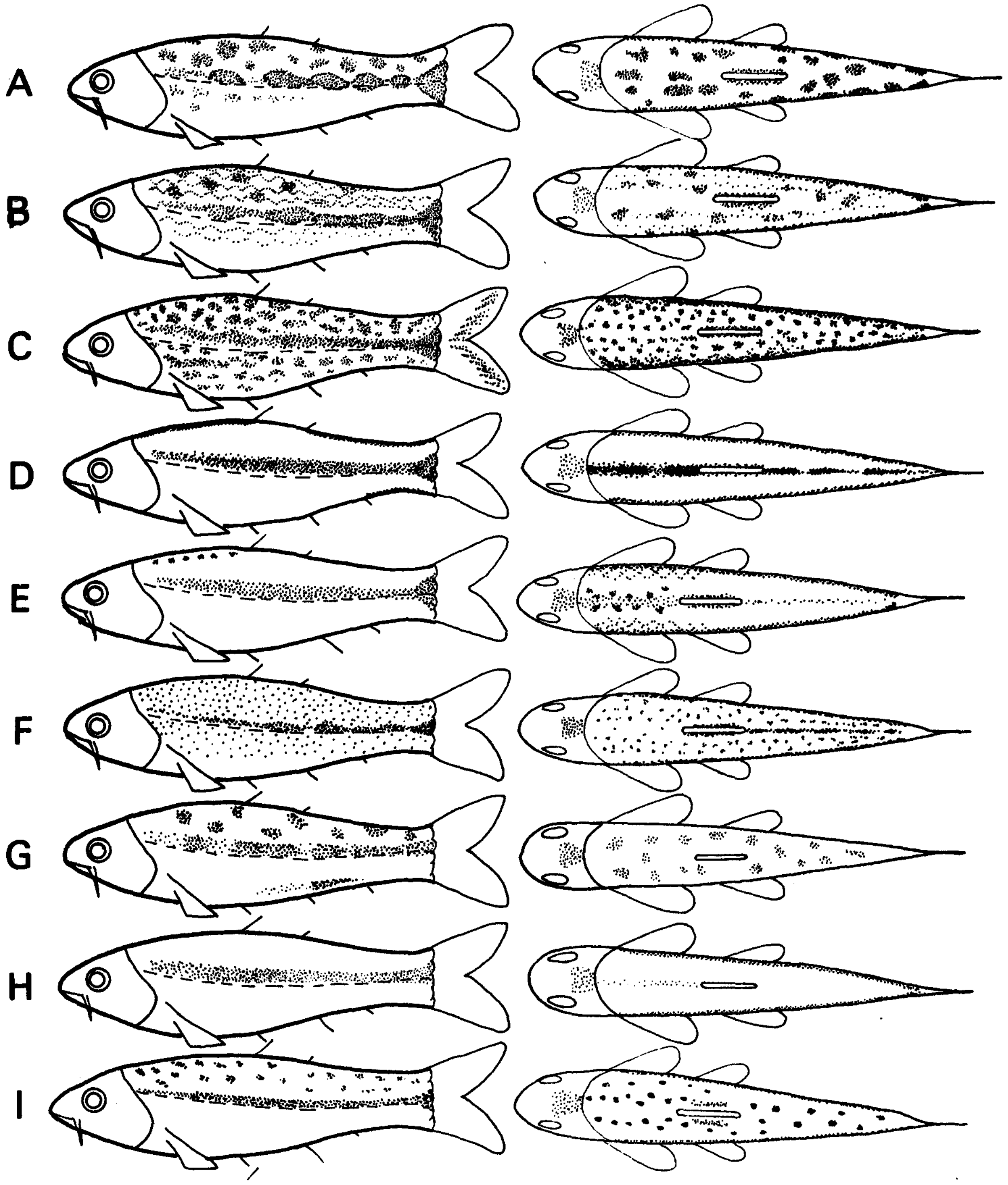


Fig. 3.47

Diagrammatic representation of the pattern of melanophore pigment frequently present in formalin fixed specimens of redfin *Barbus* species and *O.quathlambae*. (Note, actual specimens not represented.) A - *B.burchelli*; B - *B.burgi*; C - *B.phlegethon*; D - *B.tenuis*; E - *B.afer*; F - *B.asper*; G - *B.calidus*; H - *B.erubescens*; I - *O.quathlambae*.

extent. In nuptial males of B.erubescens the whole body is suffused with red. Once attained the red fin patches are persistent although the intensity pales during the non-breeding season.

Markings which are accentuated in preserved specimens are evident to a greater or lesser extent in the live fishes. The following brief descriptions of pigment patterns are based on preserved specimens. A diagrammatic representation of pigment patterns of each species or species group is given in Fig. 3.47.

B.burchelli has a number of large spots or blotches over the dorsal and lateral surfaces. A linear series of irregular spots extends from behind the head to the posterior end of the caudal peduncle and ends with a large sub-triangular mark. Juveniles are more prominently marked than adults where the pattern becomes obscured by dark overall nuptial pigmentation.

B.burgi also tends to form a spotted pattern similar to B.burchelli but this is not as distinct nor as regular as in the latter species. Juveniles are unspotted and have a continuous dark lateral band on the body, which expands into a subtriangular mark on the end of the caudal peduncle. In adults the band is irregular, forming a connected series of spots. Pigment concentrates on the scale margins to form a series of parallel, vague wavy bands above and below the mid-lateral band.

The adults of B.phlegethon are most distinctive being heavily blotched with dark irregularly shaped patches over the lateral and dorsal surfaces. Juveniles unlike the adults lack the dark patches but have a prominent thin mid-lateral band.

B.tenuis has a single mid-lateral band from behind the head to the end of the caudal peduncle. A mid-dorsal stripe is also characteristic of this species although it may be interrupted to form a series of dashes.

B.afer is variable in pigment pattern. Most populations have a single thin lateral stripe with a triangular expansion at the end of the caudal peduncle. A series of small round spots are arranged in more or less two lines on either side of the predorsal midline. In certain

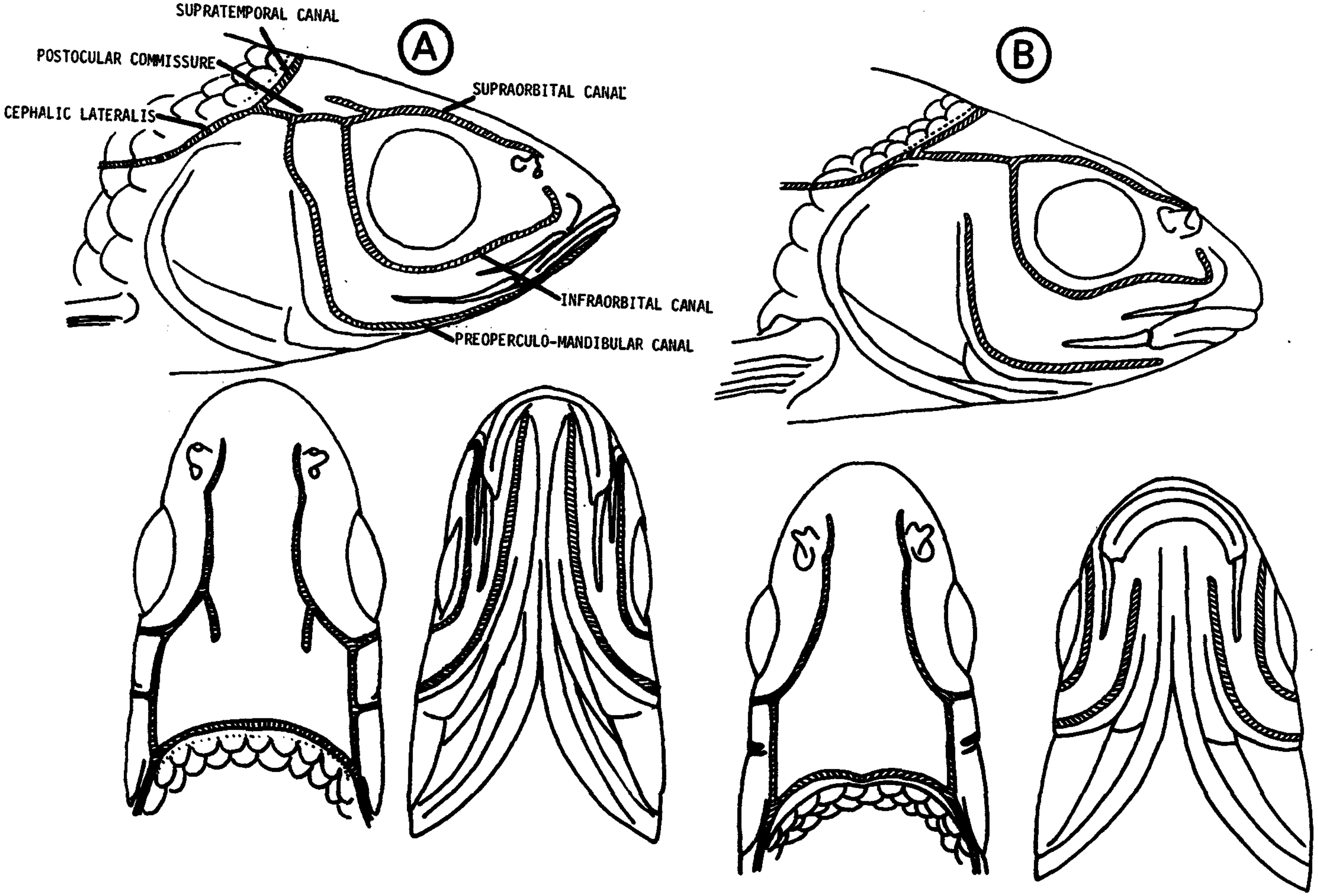


Fig. 3.48 Diagrammatic representation of the cephalic lateral line system of (A) the serrated-rayed redfin *Barbus* and (B) the flexible-rayed redfin *Barbus* species. Lateral, dorsal and ventral views of head given. Canal nomenclature follows Reno (1969).

populations these spots are absent and there is a single mid-predorsal stripe.

B.asper (variant) occurs in deeply stained, acid waters and are often uniformly dark except for the ventral surface. Careful examination shows that there is an underlying pattern similar to that of B.afer viz. a dark lateral band and a series of small dark spots bi-laterally before the dorsal fin.

B.asper was described by Barnard (1943) like a "speckled hen" in appearance. There is usually a conspicuous irregular and interrupted dark lateral band. A small concentration of pigment in the middle of the exposed portion of each scale gives the "speckled" appearance. Juveniles have a thin lateral band.

The pigmentation of O.quathlambae (Skelton, 1974 a) features a dark lateral band and a series of defined smallish dorsal spots. Gephard (1978) has made further observations on the pigmentation of this species and shows that the dorsal markings are variable from being absent or are large clear spots which may coalesce to form a series of dark vermiculations (vide Gephard, 1978: Fig.2).

B.calidus has a broad but more or less broken lateral band and large irregular spots scattered over the dorsal surface. There is also a band of pigment on either side of the base of the anal fin and often a midventral stripe on the caudal peduncle. Juveniles have a single prominent lateral band, and are spotted like the adults.

The colours of B.erubescens are described by Skelton (1974 b). Pigmentation is simple with a prominent unbroken lateral band being the only feature of any note. A light predorsal stripe may also develop. Juveniles are similar to adults.

Cephalic lateral line canals (Fig. 3.48)

The cephalic lateral line canals are interconnected to form a single system in B.calidus and B.erubescens (Fig. 3.48 A). There are three points of comparison between the cephalic lateral line of these species and the flexible-rayed redfins. The short median branch off the supraorbital canal is absent in all flexible-rayed species. Secondly

TABLE 3.16

A summary of the main osteological differences between B.calidus and B.erubescens

Character	B.calidus	B.erubescens
Vomer	Extends beyond posterior region of lateral ethmoid.	Does not extend beyond posterior or margin of lateral ethmoid.
Symplectic-Quadrate	Extends into relatively short groove. Symplectic shorter	Extends into relatively long groove. Symplectic longer
Opercle	less prominent dorsal process for dilatator operculi Postero-lateral corner sharp.	More prominent dorsal process for dilatator operculi. Postero-lateral corner rounded.
Pelvic bone	Processes are short and broad.	Processes are more slender and elongate.

the preoperculo-mandibular canal is disjunct from the post-ocular commissure and there is no suprapreopercular "tube" on the opercular bone. Finally the mandibular canal is reduced or absent in all the flexible-rayed species.

Differences in the cephalic lateral line system of the flexible-rayed species consist of the extent of reduction of the mandibular canal. The canal is reduced to a short segment on the dentary in *B.burchelli*. This is connected to the preopercular by a tube on the angulo-articular. In *B.burgi* there is a short dentary segment but the angulo-articular connection is frequently absent. The other species all lack a mandibular canal.

Osteological characters

The osteology of the redfins is given full treatment in Chapter 4. There are a number of differences which distinguish the flexible-rayed species from the serrated-rayed species which need not be presented here as they do not clarify any of the taxonomic problems under consideration at this stage. A summary of osteological differences between *B.calidus* and *B.erubescens* is given in Table 3.16. Diagnostic characters of individual flexible-rayed species are outlined below.

1) Neurocranium. The shape of the neurocranium differs from species to species. In *B.phlegethon* it is particularly narrow and deep, in *B.tenuis* shallow and broad. It is deep but not particularly narrow in *B.burgi* and shallow but not particularly broad in *O.quathlambae*. In the remaining species or species groups the proportions are moderate and generally similar. Bones in the anterior region of the neurocranium are incompletely ossified in B.tenuis and O.quathlambae.
B.afer these are frequently reduced or vestigial.

3) Infraorbitals. The dermosphenotic is absent (or possibly fused with infraorbital five) in *O.quathlambae*. The dermosphenotic is particularly well developed with wide flanges in *B.burgi*. In the other species it is a small triangular unit.

4) Suspensorium. The hyomandibular is long and narrow with a short antero-dorsal process in B.phlegethon. In B.tenuis and O.quathlambae the hyomandibular is short and broad. The metapterygoid of these two species has a relatively deep cleft on the dorsal side.

5) Lower jaw. The dentary of B.phlegethon is short and in B.tenuis it is long with a tall coronoid process. There is a short canal on the postero-ventral side in B.burchelli and B.burgi which is absent in the other flexible-rayed species. B.burchelli is the only flexible-rayed species with a canal regularly developed on the angulo-articular.

Discussion and conclusions

The above review of the morphological characters of the redfin species provides adequate data to establish the taxonomic status of the species. The majority of the species have several distinctive characteristics separating them from others. Two pairs of similar species, viz., B.burchelli - B.burgi and B.afer - B.asper require further consideration before their status can be settled. Before paying further attention to these particular problems general comments on all the species are in order.

O.quathlambae

From the available material little can be said on the geographic variation of this species. Gephard (1978) has however made a useful contribution in this regard, showing that there are a number of phenotypic differences between the known extant populations. Of five characters considered (dorsal fin rays, anal fin rays, lateral line scales, anal fin pigmentation and dorsal body pigmentation) Gephard found body pigmentation to be the most divergent character between populations. Adopting Ginsberg's (1938) criteria,the three populations showed more than 90% divergence in this character. In spite of this, the difference was not considered worthy of specific significance. Gephard rather used scale size as the evaluating criterion from which the status of the three populations was regarded as "varieties".

Both Greenwood & Jubb (1967) and Gephard (1978) pointed out that O.quathlambae is highly adapted to its high altitude mountain stream environment. Thus the extremely small scales and high vertebral counts suggest adaptations to cool temperatures, swift currents and probably also to the crevice spawning habits of the species (Gephard, 1978). These adaptations enhance flexibility required for manoeuvering in confined spaces. Cooler temperatures are generally conducive to meristic characters with higher counts in fishes (Barlow, 1961; Fowler, 1970) and this factor may have had a large influence on the development of the vertebral and squamation characteristics of O.quathlambae.

The reduction in pharyngeal teeth in O.quathlambae and B.tenuis is an extremely unusual development for an African Barbus or Barbus-like species. This suggests that there has probably been strong selection pressure on these structures. In the general absence of competing species such pressure is likely to have come from the available food source itself. In mountain streams phytogenous organic matter is usually limited (Allen, 1969) and it appears that O.quathlambae is adapted to exploiting the benthic aquatic insect fauna (Pike & Tedder, 1973; Gephard, 1978).

B.tenuis

Barnard's (1943) diagnostic characters for B.tenuis included the following; body depth less than the length of the head, an absence of tubercles on the head of the males, scales with numerous striae, a more or less bare patch on the nape. Of these the tubercle character has fallen away and the development of a bare patch on the nape is inconsistent (Barnard, 1943) and is not a reliable character. However in spite of initial doubts B.tenuis proves to be one of the most firmly established species. The slender profile and the scales with a large number of radii are reasonably consistent characters. Coupled with this is the extremely rare barbine condition of only two rows of pharyngeal teeth. The distinctive osteology establishes the validity of the species beyond doubt. In the field B.tenuis may be recognised by a river bank observer by its distinctive pigment pattern relative to cohabiting redfin species (pers.obs.).

Personal field observations and a host of recent collecting records (appendix 1) indicate that B.tenuis is partial to smaller tributaries which are generally mountain streams in the Gourits System. Relative little syntopy with B.asper has been observed and which, when present,

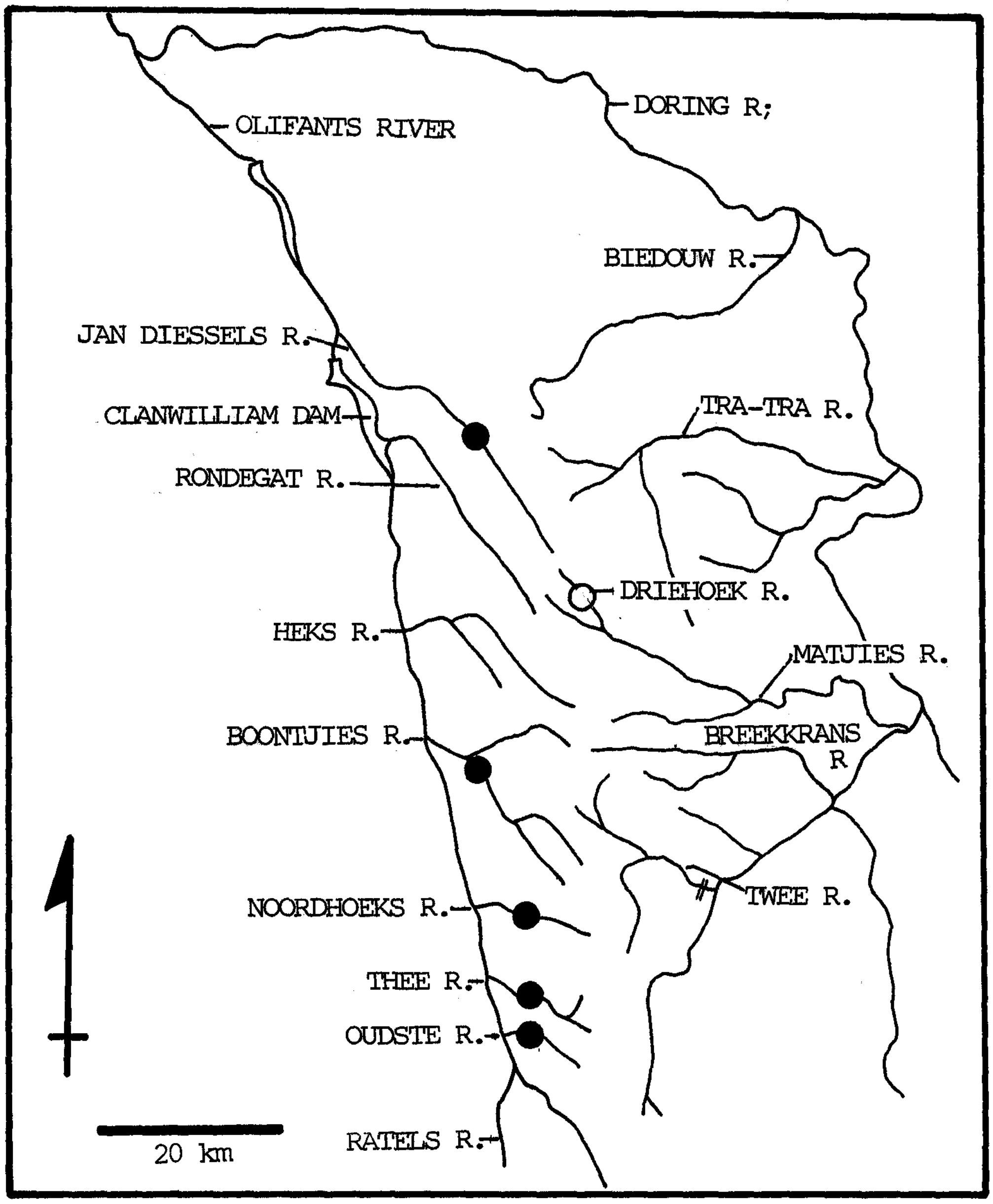


Fig. 3.49 The distribution of B.phlegethon in the Olifants River System. Only one population is known from Doring River tributaries (open circle).

can often be attributed to habitat restriction due to human exploitation of the aquatic resources.

Intraspecific variation in B.tenuis is recorded for the Keurbooms population. Variation is restricted to certain morphometric characters (e.g. fin lengths, caudal peduncle proportions) which could be a reflection of differences in the environment (Barlow, 1961). The Keurbooms catchment has on average a mean annual precipitation of 750 to 900 mm (Midgeley & Pitman, 1969) whereas any comparable stream catchment in the Gourits system has a mean annual precipitation of slightly more than half of this (400 to 500 mm). The pertinent point of such rainfall differences being that the current strength in the Keurbooms is likely to be greater than in Gourits catchments. The characters showing variation are those which are known in many cyprinids to respond in similar fashion to similar situations (Hubbs, 1940; Barlow, 1961; Stewart, 1977).

B.phlegethon

There is no question on the status of B.phlegethon. The main facies of the species may be summarized by the following combination of features. It is smaller than other redfin species with a distinctive adult pigmentation, has a deep and relatively narrow body, a small mouth and short barbels and weakly developed secondary male sexual characters. The claim by Barnard (1938b; 1943) that tubercles are not developed in the males is shown to be not strictly true. Yet the relative development of these structures is still weak and does constitute a valid diagnostic character for the species.

The present distribution of B.phlegethon is restricted to a few tributaries of the Olifants River in the Clanwilliam Valley. Barnard collected the species in the mainstream of the river but there is no evidence that it is still found there. The only record of B.phlegethon from the eastern tributaries of the Cedarberg Mountains is a small isolated population in the Driehoek River (Fig. 3.49). There are differences in certain meristic characters between specimens from the Driehoek population and those from the Clanwilliam Valley tributaries. The normal mode of dorsal fin branched rays is seven in most redfin species including B.phlegethon. Six of ten Driehoek specimens

TABLE 3.17

Summary of certain character differences between *B.calidus* and *B.erubescens*

Character	*B.calidus* $\bar{M}$	*B.erubescens* $\bar{M}$
Orbit diameter (% HL) ($\bar{M}$)	29.1 (25-36)	26.75 (22-32)
Postorbit length (%HL) ($\bar{M}$)	43.6	46.
Interorbit (% HL) ($\bar{M}$)	34.1	31.9
Caudal peduncle L.	19.5	21.1
Dorsal branched rays (mode)	7	8
Anal branched rays (mode)	6	7
Scale radii ($\bar{M}$)	9	13
Predorsal vertebrae (mode)	13	12
Pharyngeal bones L/W (±)	4.6	4.9
Pharyngeal teeth (mode)	2,3,5-5,3,2	2,3,4,-4,3,2
Dorsal unbranched ray	strongly serrated	weak or no serrations
Pigmentation	broken lateral band, spotted dorsal surface	lateral stripe and plain dorsal surface
symplectic bones	short injunction with quadrate, shallow	long injunction with quadrate, deep
opercle	postero-ventral corner angular	postero-ventral corner rounded
pelvic fin bones	ischial process broad, lateral prong short	ischial process slender, lateral prong long

had six branched dorsal fin rays. The Driehoek specimens also have a higher number of pectoral fin rays (mode 15 vs usual 13-14) and lateral line scales (range of 36-39 with a mode of 37-38 vs range 29-37 and mode of 35). The Driehoek sample included several larger than average specimens, one a male with the best developed tubercles yet seen in B.phlegethon (Fig. 3.45b).

Some of these differences are probably environmentally determined as there were notable gross differences between the Driehoek stream and Clanwilliam Valley tributaries of the Olifants. Altitude is one factor, (Driehoek, 900-1200 metres A.S.L., Clanwilliam Valley tributaries where B.phlegethon occurs, 200-400 metres A.S.L.) so that temperatures are likely to be lower at Driehoek. Physically Driehoek is a small (two - three metres wide at most), low gradient, sandy floored stream generally less than half a metre deep (the odd pool up to one or two metres) and with much marginal vegetation. In contrast the Clanwilliam Valley tributaries are rapidly descending mountain rivers which in the foothill zone where B.phlegethon occurs are several metres wide and the bed consists of runs and large pools floored with abundant rocks, stones and quartzitic sand and limited amounts of marginal vegetation.

B.calidus and B.erubescens

A summary of taxonomic characters between B.calidus and B.erubescens (Table 3.17) clearly illustrates the distinction between them. It is the combination of characters considered against the overall variation of B.calidus that confirms the status of B.erubescens. Particular significance may be attached to the fact that B.erubescens has seven branched anal rays, a feature which is unique in African Barbus species as far as is known. This latter point is given further attention in Chapter 5.

The significance of the loss of the serrations on the unbranched dorsal ray was given brief discussion by Skelton (1974 b). The general conclusion was that the development or otherwise of serrations on the unbranched dorsal ray cannot be regarded as a reliable taxonomic character for particular Barbus species. These conclusions have been subsequently supported by Poll (1976) who reported a marked case of intraspecific variation in the serrations of Barbus miolepis miolepis. Individuals of this species from the same locality are found to have well serrated, feebly serrated or non-serrated unbranched dorsal rays.

There is no definitive reason known why these serrations should vary or differ between such closely allied species. Dorsal spines are often developed as defensive structures (Alexander, 1967; Gosline, 1971) and it is possible that the strength of the unbranched ray and its serrations in B.erubescens is reduced in response to the absence of cohabiting predatory species. Other suggestions can also be put forward. The shape of the pectoral fins, the placement of the dorsal fin and the proportions of the caudal peduncle suggest that B.calidus is relatively the more active swimmer of the two species. The function of the unbranched dorsal ray is probably also related to the functioning of the dorsal fin as a keel (Alexander, 1967; Gosline, 1971) and a more active swimmer might need a firmer anterior support for the fin, which is provided by the stouter build and stronger serrations of the unbranched ray in B.calidus. Suggestions that the water chemistry may affect the development of the ray while being possible in other cases is not supported in this case (Skelton, 1974 b).

The weight given to the form of the unbranched dorsal ray in Barbus requires reconsideration. The fact that it is known to undergo reduction in many species suggests that it should not be used as a major character in classification. The potentiality for developing serrations is possibly a better criterion to adopt but this itself can only be ascertained by consideration of other characters of the fishes concerned.

In addition to characters in Table 3.17 there tend to be higher scale counts in B.erubescens and there are fewer supraneural bones. The reduction in pharyngeal teeth is correlated with the more slender pharyngeal bones and the shorter gut in B.erubescens. The reduction in pharyngeal teeth is also correlated with a difference in the shape of the pharyngeal teeth of the species,and it is felt there is sufficient consistency to justify the taxonomic use of the trophic differences. There is support for this conclusion in the study of intraspecific variation in the pharyngeal teeth and bones of forty two cyprinid species by Eastman & Underhill (1973). These authors concluded that although pharyngeal tooth formulae are not by themselves taxonomically reliable,the pharyngeal arches and tooth morphology are uniform within the species, and are generally important taxonomic characters.

TABLE 3.18

Diagnosis of *B.burgi* and *B.burchelli* according to Barnard (1943) and Jubb (1965;1967).

Character	*B.burgi*	*B.burchelli*
Scales. Lateral line	29-36 (tubules complete)	33-36 (tubules complete or incomplete)
Caudal Peduncle	12	14
L.1 to dorsal	4	5
L.1 to pelvic	3	3-4
predorsal	13-15	17-18
Scale radii	4-16	4-10
Head length (into SL)	3.5-3.8	3.25-3.75
Barbels (anterior pr.)	short develop + 50mm SL	long, develop + 20mm
Origin of pelvic fin	below dorsal	anterior to dorsal
Size at first maturity	+ 60mm SL	55-60mm SL

B.burchelli and B.burgi

The features which Barnard (1943) and Jubb (1965; 1967) used to distinguish B.burgi and B.burchelli are summarised in Table 3.18. Of these features Barnard (1943) considered the differences in the development of the anterior barbels as indicating "the real validity of the species". However the emphasis which Barnard gave to this character must be viewed with skepticism as barbels are frequently variable within a species. It is noted at the same time that Barnard based his judgement in the light of the consistency of the difference between the two forms. The present study supports Barnard's findings regarding the consistency of difference in barbel development in these species. There are at least two other consistent character differences and several more divergent characters and it is in the light of these that the status of the species should be viewed.

In the redfins the dermosphenotic bone is usually small and without prominent flanges on either side of the tube for the lateral line canal. This suggests that a certain amount of genetic reorganisation must have occurred in B.burgi for wide flanges to develop consistently. A particular feature of this character is that the condition in B.burgi probably represents a positive development of the bone from a relatively reduced state, and not vice versa. The dermosphenotic is not a common character of distinction in cyprinids but in at least two cases similar emphasis has been placed on it - Miller (1963) uses the enlarged state of the dermosphenotic in Gila crassicauda as a diagnostic character of that species, and Barbour & Miller (1978) consider a broad dermosphenotic as a derived character in the context of North American Cyprinidae.

Tubercles are, generally speaking, not well developed in Barbus species. They therefore do not feature as prominent taxonomic characters in the genus. Considerably more attention is paid to them as systematic characters in the North American cyprinids and guidelines as to their taxonomic value are taken largely from North American sources. Wiley & Collette (1970) and Collette (1977) suggest that these structures probably originally evolved to enable spawning individuals to maintain contact in the fluviatile environments. Subsequently a number of other functions may have evolved, and it is not unlikely that tubercles in different body regions serve different functions. The precise function or functions of the tubercles of redfin species is not yet established but as they only develop prominently in sexually mature males it may be assumed that this function is associated with reproductive biology. Differences in the development of these tubercles therefore most probably reflect differences in one or other aspect of reproductive biology.

The significance attached to differences varies from case to case, depending primarily it seems on whether the pattern itself has changed or whether the tubercle development within a pattern has changed. Distinctive tubercle patterns common to several species have been used as major characters in recognising genera or sub-genera, e.g. one of the major characters of *Nocomis* is the distinctive development of large cephalic tubercles (Jenkins & Lachner, 1971). Snelson (1968) recognised distinctive groups of species within the subgenus *Notropis* (genus *Notropis*) on the basis of differences in pectoral fin tubercles. On the other hand distinctive differences between tubercle development is often only accorded sub-specific significance. Lachner & Wiley (1971) used this as a sub-specific character in *Nocomis leptocephalus*. Similarly Snelson (1973) and Snelson & Pflieger (1975) described several subspecies of *Notropis* species using primarily tubercle data. The major diagnostic character between *Barbus motebensis* and *Barbus anoplus* is that the former develops tubercles on the head and the latter generally does not (Jubb, 1967; 1968). Gaigher (1976) found that the tubercles do develop on the head of individuals in certain *B.anoplus* populations and accordingly suggested the two species should be synonymised.

The above examples suggest that the tubercle differences between *B.burgi* and *B.burchelli* alone are not sufficient to recognise them as distinct species. However in concert with the dermosphenotic bone and the differences in the barbel development as well as the several other distinct tendencies of *B.burgi* (e.g. the short predorsal length) I consider that there is sufficient justification to uphold the status of the species.

In the light of this conclusion the considerable variation in gut length of the different populations of *B.burgi* is of minor significance. Although the length and degree of involution of the gut has been discredited as a generic character in cyprinids in recent years (Snelson, 1971; Hubbs & Miller, 1977; Gilbert, 1978) there are few examples of as large an intraspecific variation as in *B.burgi* in the literature. One notably similar example is given by Lachner & Wiley (1971), *Nocomis leptocephalus* usually has a relatively long "whorled" intestine but in certain populations the specimens have a short "S" flexed intestine. As with *B.burgi* these authors attached no taxonomic significance to this variation.

B.afer - *B.asper*

Scale size is the major character separating *B.afer* from *B.asper*. The question of scale size in the taxonomy of these forms has been discussed earlier. The conclusions reached were that the most acceptable taxonomic decision on the basis of this character would be to include *B.afer*, *B.afer* (Gamtoos) and *B.asper* (variant) populations within a single taxon, separate from *B.asper*. Although these two species are closely similar in a majority of morphological characters,other characters which would support this decision are the pigment patterns and the length of the intestine.

Neither the pigment pattern nor the length of the gut can be considered convincing taxonomic characters when considered independently. The clinal variation of several morphometric characters support the marriage of *B.asper* (variant) and *B.afer*. It is in the light of this marriage, together with the scale size distinction and the situation in the Gamtoos River, which will be explained below, that the status of the two species are upheld.

The presence and distribution of these two species in the Gamtoos River System has always been a problem. Barnard (1943) considered that only *B.asper* was present in the Gamtoos but recognised that the form in the mountain tributaries differed from the typical form in the Groot River tributary. Jubb (1965) found that specimens from certain "coastal tributaries" of the system were "closer to *B.afer* than *B.asper*".

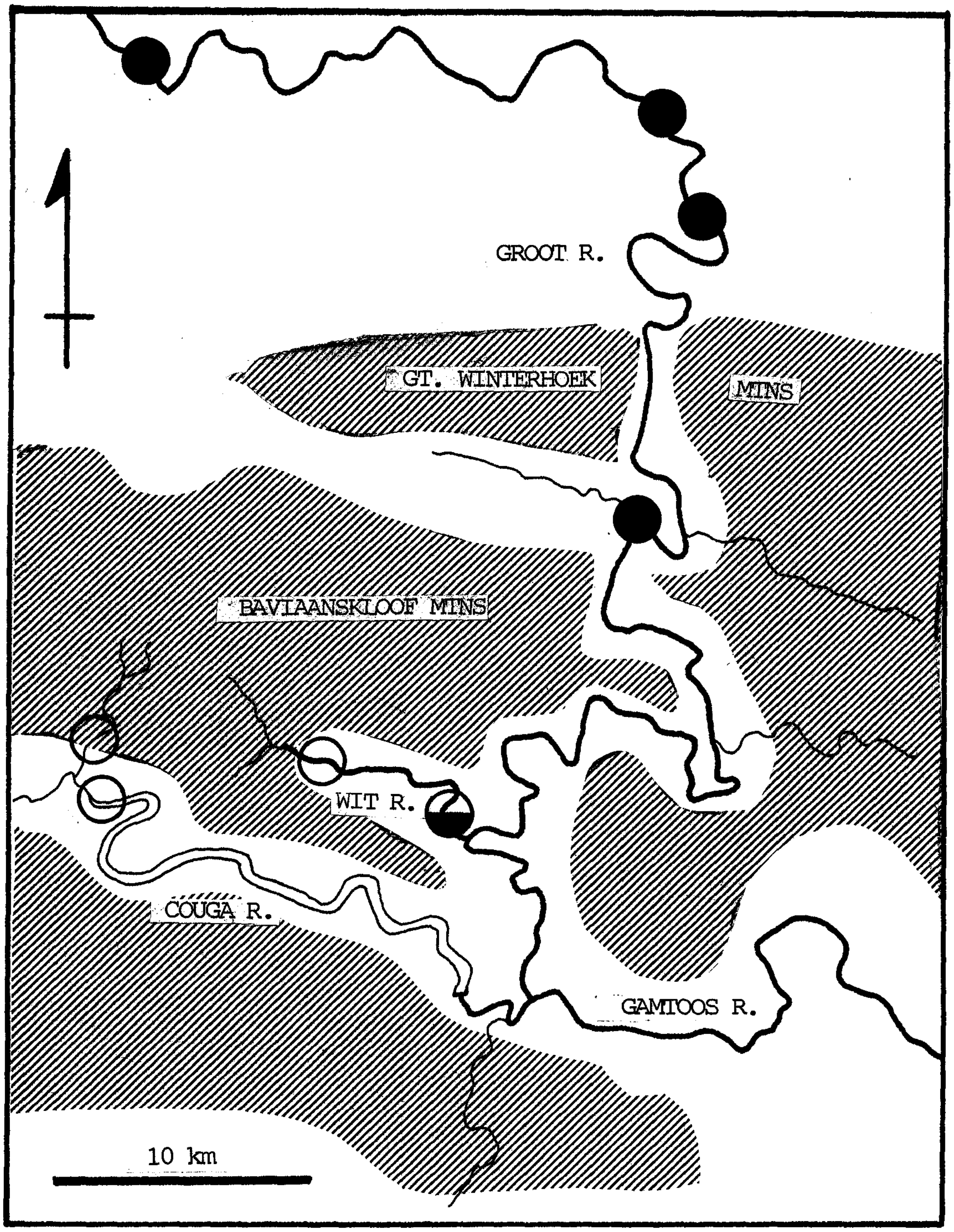


Fig. 3.50 Part of the Gamtoos River System in the fold belt region showing the distribution of B. asper (solid symbols) and B. afer (open symbols). Both species have been collected together in the lower reaches of the Wit River (semi-solid symbol).

At the time there was no way of clearly identifying which were B.afer and which B.asper and museum samples were consequently frequently confused.

The Groot River tributary has its source well beyond the fold mountain belt in the Great Karoo. It eventually joins the rest of the Gamtoos River System after abruptly turning at right angles from its course and penetrating through the Baviaanskloof - Gt. Winterhoek Mountains in a narrow gorge (Fig. 3.50). B.asper is found in the Groot River to within the gorge in the mountain belt whereas B.afer is found in tributaries within the mountains themselves. The caudal peduncle scale counts in Table 3.19 illustrate the distinction of the species on this character in the Gamtoos System. In the Wit River,a tributary of the Groot within the gorge,both species were collected together. The habitat at this site can be considered an ideal compromise between the habitat offered by the Groot River and the mountain tributaries (extremely close to the confluence and yet not far removed from the mountain stream habitat found higher up Wit Valley). There is no evidence of integration of the species at this site.

The distribution of the two species therefore appears to reflect closely their rather different habitat preferences. The Groot River differs considerably in both runoff regime and in the water quality from the mountain streams of the system. It is today an intermittent river draining Karoo system rocks which impart characteristically high total dissolved solids and are known as the highly mineralized chloride-sulphate waters (Bond,1946). The waters of the remainder of the system are derived from the Table Mountain Sandstones of the mountain belts. The waters of these perennial streams are characteristically pure but acidic in nature. Hofmeyr (1966) found that B.asper was more tolerant to chlorides than B.afer, which is clearly a factor in agreement with the pattern of distribution of the two species in the Gamtoos System.

The Groot River appears to have been incorporated into the Gamtoos System by river capture (Haughton et al., 1937). If so, then B.asper was probably present in the Groot before the event and appears to have been prevented from dispersing beyond the confines of the parent river. Possibly both ecophysiological and competitive factors have been involved in maintaining this restriction.

The general conclusions reached from the situation in the Gamtoos System is that there are two distinct forms present and a taxonomic separation of them is justified at present. These two species are nevertheless morphologically very similar, and if further taxonomic studies are made on them they should be directed through biological, biochemical or cytotaxonomical avenues.

Summary

The taxonomic conclusions reached in this study are listed below:

i) Nine redfin species are recognized, these being B.burchelli Smith 1841, B.afer Peters 1864, B.asper Boulenger 1911, B.burgi Boulenger 1911, Oreodaimon quathlambae (Barnard 1938), B.phlegethon Barnard 1938, B.tenuis Barnard 1938, B.calidus Barnard 1938 and B.erubescens Skelton 1974.

ii) O.quathlambae is a very distinct species with morphological adaptations for a high altitude mountain stream environment.

iii) B.phlegethon is a small distinct species with restricted distribution including an isolated population with divergent characters.

iv) The identity of B.tenuis is confirmed and the species is adapted to mountain tributaries.

v) B.erubescens is confirmed as a new species, isolated from B.calidus by a waterfall.

vi) The specific status of B.burgi is confirmed.

vii) B.burchelli appears to be a generalised redfin species.

viii) B.asper is restricted to the form from the larger rivers of the Gourits System and the Groot River of the Gamtoos System.

ix) B.afer is expanded to include the populations of B.asper (variant). This is a variable and widespread species found in perennial coastal rivers from the Sundays to the rivers of the Outeniqua coastal plain east of the Gourits System.

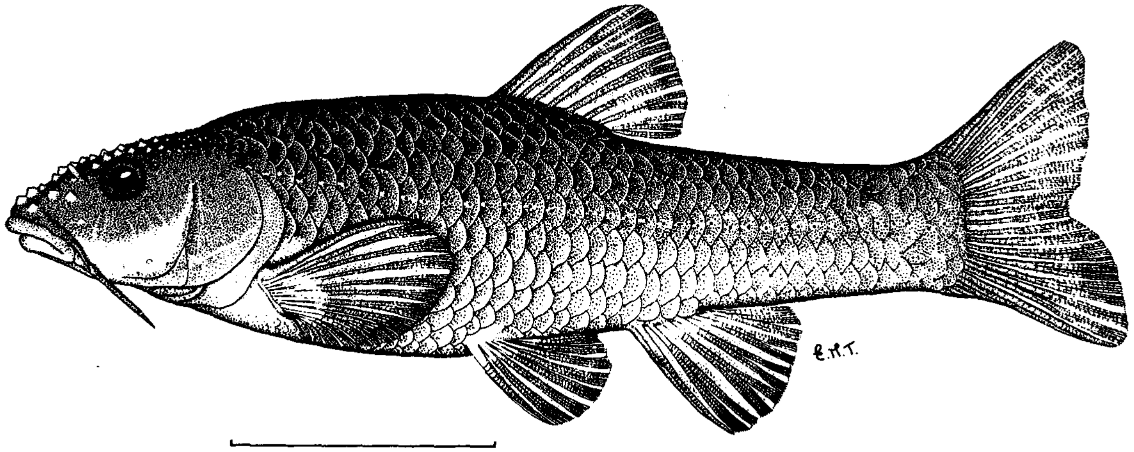


Fig. 3.51 Neotype of *Barbus burchelli* A. Smith 1841. AM/P 7223 A, ♂, 102 mm SL. Drawn by Elizabeth Tarr. Scale bar = 30 mm.

SPECIES ACCOUNTS

Barbus burchelli Smith, 1841

Fig. 3.51

Barbus (Pseudobarbus) burchelli A. Smith, 1841: pl. XI no.1; Günther, 1868: 96; Gilchrist & Thompson, 1913: 417-418 (in part, 2 specimens from Robertson, Cape); Jubb, 1965: 26-27, pl. VIII; Jubb, 1967: 97-99, Fig. 83, pl. 14.

?Barbus gobionides Valenciennes in Cuvier & Valenciennes, 1842: 189.

Gnathendalia vulnerata Castelnau, 1861: 57.

Barbus vulneratus. Boulenger, 1905b: 45; Boulenger, 1911: 148-149 (in part, only the 2 specimens from "Zonde Einde River"); Gilchrist & Thompson, 1913: 415-416 (in part, Fig. 73 and Zonde Einde River specimens only); Barnard, 1938b: 83, Fig. 18 B and C.

Material Examined: Neotype: AM/P:7223A; ♂ 102 mm SL. Fig. 3.51. Tradouw River, Breede River System, 33° 56' 50"S, 20° 42' 39"E, collected by S. Thorne, 13 December 1978. Other material recorded in Appendix 1.

Diagnosis: Redfin Barbus with last dorsal unbranched ray simple, slender and flexible; two pairs of well developed barbels longer than orbit diameter; breeding males with large conical tubercles in head 5-10 on either side of snout. Intestine involuted, moderately long, up to 2,8 times SL.

Description: Morphometric and meristic data are given in Table 3.20.

Medium-sized (up to 135 mm SL) fusiform cyprinid; predorsal length slightly longer than postdorsal length; head length sub-equal to body depth; eyes lateral to dorso-lateral; mouth sickle-shaped, sub-terminal and protrusible, lips moderately developed or retracted from rim of lower jaw; barbels well developed, larger than orbit diameter in adults.

Scales radiately striate, focus central, radii in all fields. Breast scales reduced and embedded, nape scales moderately crowded, pelvic axillary scale absent.

TABLE 3.20

Morphometric and meristic measurements of *B. burchelli* (N= 179)

Measurement	Range		Mode
	Max.	Min.	
Standard length (mm)	136.0	28.0	54.3
Head length (%SL)	33.1	24.7	27.0
Head depth (%HL)	76.8	62.2	69.9
Snout length (%HL)	41.5	30.6	36.0
Orbit diameter (%HL)	36.7	17.8	28.5
Postorbit length (%HL)	50.7	38.5	45.2
Interorbit length (%HL)	36.5	24.1	30.6
Predorsal length (%SL)	55.2	48.9	51.3
Postdorsal length (%SL)	51.4	44.9	48.8
Dorsal fin base (%SL)	15.6	11.2	13.4
Dorsal fin length (%SL)	26.6	19.0	23.2
Pectoral fin length (%SL)	25.0	18.6	21.7
Pelvic fin length (%SL)	19.2	14.0	16.6
Anal fin length (%SL)	25.0	17.3	20.3
Anal fin base (%SL)	13.5	7.1	10.7
Body depth (%SL)	29.3	22.8	25.5
Body width (%SL)	21.8	13.7	16.8
Caudal length (%SL)	28.0	21.3	24.8
Caudal peduncle depth (%SL)	17.7	10.9	12.3
Anterior barbel length (%OD)	115.0	3.7	55.2
Posterior barbel length (%OD)	166.0	3.7	94.7
Pectoral - pelvic length (%SL)	27.6	21.1	24.6
Pelvic - anal length (%SL)	17.1	11.9	14.3
Pharyngeal bones L/W (N = 120)	4.5	3.0	3.5
Length of intestine (N = 140)	280.5	73.4	159.2

Meristics		
Dorsal fin rays	III-IV (IV)	+ 6-8 (7)
Anal fin rays	III-IV (III)	+ 4-6 (5)
Pectoral fin rays	12-16 (14)	
Pelvic fin rays	7-9 (8)	
Vertebrae	34-38 (36-37)	
Precaudal vertebrae	17-20 (18-19)	
Caudal vertebrae	15-20 (17-18)	
Predorsal vertebrae	11-13 (12)	
Preanal vertebrae	18-22 (19-20)	
Lateral line scales	29-39 (36)	
Caudal peduncle scale rows	12-18 (12)	
Scale rows lat. line - dorsal	5-7 (6)	
Scale rows lat. line - pelvic	4-6 (4)	
Scale rows lat. line - anal	4-6 (4)	
Predorsal scale rows	14-22 (17-19)	
Primary scale radii ($\bar{M}$ to nearest whole no.)	10	
Pharyngeal teeth (mode)	2,3,5 - 5,3,2	

Paired fins sexually dimorphic; oval or rounded, longer and more expansive in males, reaching to within one or two scales of pelvic fin origin; shorter in females reaching to within four or five scales of pelvic fin origin; pelvic fins fan-shaped reaching to within one or two scales of anal fin base in males, or two or three scales (of anal fin base) in females; posterior edge of dorsal and anal fin straight or slightly rounded; caudal fin forked, lobe rounded. Dorsal fin origin slightly behind origin of pelvic fin.

Gill rakers 2-3 + 6-9 on leading arch. Pharyngeal bones falcate; pharyngeal teeth in three rows with oblique truncate crowns which are closely applied to each other. Intestine involuted with two to three secondary coils, up to 2,8 times the SL.

Conical tubercles on snout and top of head, arranged in specific pattern of bilateral groups (5-10 tubercles) on snout, bilateral arcs above nares and along dorsal side of orbit, and scattered over dorsal region of cranium. Bands of tubercles up to five or six deep over dorsal surface of pectoral fin rays, absent from leading ray; single rows of tubercles along free edge of scales of other fins. Single row of minute tubercles along free edge of scales of all regions. Tubercle buds develop on head of large breeding females.

Juveniles and sub-adults light brown to olive green with large dark blotches dorsally and laterally, a mid-lateral series of large spots with a large sub-triangular caudal mark. Larger adults darken to become bluish-black dorsally and laterally in breeding dress.

The proximal portion of fins scarlet, caudal fin, reddish in median portion of lobes in nuptial males only. Fin rays dark brown, membranes hyalin distally.

Lateral line along mid body complete or semi-complete (irregular suppression of tubules on a few scales). Cephalic lateral line with reduced mandibular canal, preopercle-mandibular canal disjunct.

Remarks: There has been confusion as to which of the two closely related species in the south-west Cape the original description of B.burchelli

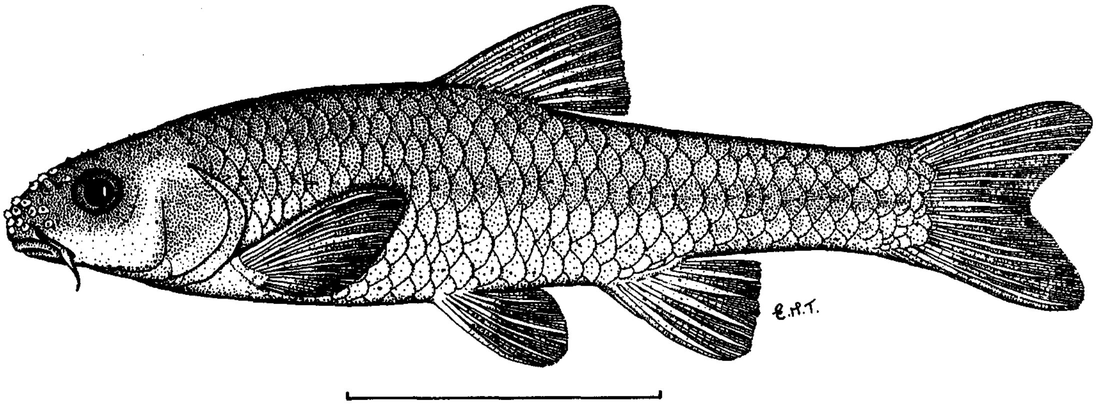


Fig. 3.52 *Barbus burgi* Boulenger, 1911, AM/P 6156, ♂, 85 mm SL. Drawn by Elizabeth Tarr. Scale bar = 30 mm.

by A. Smith (1841), actually referred to. There are no types as far as can be ascertained (Smith made no reference to his material; there is no reference to any collecting of redfins or "rooivlerks" in the account of his travels or of his party (Burrow, 1971) and searches in the South African Museum, the British Museum of Natural History (P.H. Greenwood, pers.comm.) or the Royal Scottish Museum (Swinney, in litt. 4 Feb. 1976)). The original description is inadequate and the accuracy of the artist unreliable (Barnard, 1943; Greenwood & Crass, 1959). The present nomenclature was settled by Jubb (1965) and although the reason for changing from the nomenclature adopted by Barnard (1938b, 1943) is not entirely justified there is no way, in the absence of types, of definitely proving that either is correct. In the interests of stability the status quo is therefore maintained and a neotype has been selected (Fig. 3.51) from recently collected material.

The type specimens of B. multimaculatus have not been examined but on the basis of the description and figure provided by Steindachner (1870) there is little doubt that this species is correctly placed in synonymy.

The identity of Barbus gobionides Valenciennes with no types available (Bauchot, in litt. 20 Oct. 1978) cannot be definitely established from the brief original description and (as pointed out by Barnard, 1943), this name is a nomen dubium.

Range: Details of collecting localities in Appendix 1. Map (fig 6.3) Chapter 6. B. burchelli is found in the Breede River System and the following independent rivers: the Kaffirkuils, the Duivenhoks, the Sout, the Kars and the Nieuwejaars.

Fig. 3.52

Barbus anoplus Weber, 1897: 152 (in part, the Frenchhoek specimen).

Barbus burchelli Boulenger, 1911: 164, Fig. 122 (in part, Eerste River specimens); Gilchrist & Thompson, 1917: 417-418 (in part, the Eerste and Berg River specimens), Fig. 75; Barnard, 1938b: 82-83; Barnard, 1943: 185-188, Fig. 18a.

TABLE 3.21

Morphometric and meristic measurements of *B.burgi* (N= 107)

Measurement		Range Max.	Min.	Mode
Standard length (mm)		109.0	34.0	59.4
Head length (%SL)		29.4	22.9	25.9
Head depth (%HL)		80.8	64.0	73.8
Snout length (%HL)		42.1	30.0	35.6
Orbit diameter (%HL)		37.5	22.3	29.1
Postorbit length (%HL)		53.0	38.7	47.1
Interorbit length (%HL)		40.0	27.8	33.5
Predorsal length (%SL)		53.8	44.6	48.9
Postdorsal length (%SL)		55.4	46.3	51.1
Dorsal fin base (%SL)		15.44	11.7	13.7
Dorsal fin length (%SL)		28.4	16.1	24.5
Pectoral fin length (%SL)		26.4	14.7	21.5
Pelvic fin length (%SL)		20.7	7.9	17.9
Anal fin length (%SL)		23.4	14.0	20.1
Anal fin base (%SL)		12.4	8.5	10.3
Body depth (%SL)		32.0	20.9	27.4
Body width (%SL)		18.6	9.8	15.2
Caudal peduncle length (%SL)		38.3	20.9	25.0
Caudal peduncle depth (%SL)		3.3	9.1	11.8
Anterior barbel length (%OD)		80.0	2.8	18.7
Posterior barbel length (%OD)		47.3	21.9	71.2
Pectoral - pelvic length (%SL)		32.0	16.5	24.7
Pelvic - anal length (%SL)		21.1	13.0	15.8
Pharyngeal bones L/W	(N = 58)	4.2	2.7	3.3
Length of intestine	(N = 81)	360.6	116.9	231.7

Meristics		
Dorsal fin rays	III-IV (III)	+ 6-8 (7)
Anal fin rays	II-IV (III)	+ 5-6 (5)
Pectoral fin rays	13-18 (14-15)	
Pelvic fin rays	7-9 (8)	
Total vertebrae	35-39 (36-37)	
Precaudal vertebrae	17-20 (19)	
Caudal vertebrae	16-20 (18)	
Predorsal vertebrae	10-12 (82)	
Preanal vertebrae	19-21 (88)	
Lateral line scales	28-37 (30-34)	
Caudal peduncle scale rows	12-16 (12)	
Scale rows lat. line - dorsal	4-6 (5)	
Scale rows lat. line - pelvic	3-5 (4)	
Scale rows lat. line - anal	3-5 (4)	
Predorsal scale rows	12-18 (15)	
Primary scale radii ($\bar{M}$ to nearest whole no.)	8	
Pharyngeal teeth (mode)	2,3,5 - 5,3,2	

Barbus burgi Boulenger, 1911: 147-148, Fig. 124; Gilchrist & Thompson, 1917, 419, Fig. 76.

Barbus afer. Boulenger, 1911: 178-179, Fig. 156 (non B.afer Peters, 1864).

Barbus bergi. Jubb, 1965: 27-28, Fig. 9 (unjustified emendation); Jubb, 1967: 99, Fig. 84.

Material examined: Lectotype BMNH 1901.2.11:14, 72 mm SL. Paralectotypes BMNH 1901.2.11: 15-16, 67 mm and 61 mm SL. Other material in Appendix 1.

Diagnosis: Redfin Barbus with last unbranched dorsal ray slender and flexible; two pairs of barbels, anterior pair only present in adults and very short (less than orbit diameter), pharyngeal teeth with truncated oblique crowns; intestine variable, up to 3,6 times the SL, involuted; mature males with large tubercles on head, body and fins, 10-15 on either side of snout.

Description: Morphometric and meristic data are given in Table 3.21.

A medium sized (up to 109 mm SL) fusiform cyprinid; sexes dimorphic. Predorsal length slightly shorter than postdorsal length; body depth greater than head length. Eyes lateral. Mouth sickle shaped, inferior and protrusible, lips moderate.

Scales radiately striate, radii few in all fields, focus centralized. Breast scales reduced and isthmus naked; pelvic axillary scale absent.

Paired fins sexually dimorphic, pectorals rounded, longer and more expansive in males, almost reaching to base of pelvics; pelvic fins rectangular almost reaching anterior base of anal fin in males; anal and dorsal fin posterior edges nearly straight; caudal forked with rounded lobes; origin of dorsal above origin of pelvics; dorsal. Gill rakers 2-4 + 6-10 on leading arch; Pharyngeal bones falcate; pharyngeal teeth in three rows.

Breeding males with tubercles on head in pattern as described in B.burchelli; bands of tubercles 3-4 deep over dorsal surface of pectoral fin rays except leading ray; tubercles in single rows on rays of dorsal, pelvic, anal and caudal fins; single rows of minute tubercles along free edge of all scales, inconstant on ventral scales in pectoral to pelvic region. Tubercle buds develop on large breeding females.

Colour of juveniles and sub adults: body light brown to dark olive green; a dark irregular lateral band along body ending in sub-triangular caudal mark; parallel series of faint wavy lines along length of body from head to caudal fin; occasional large blotches over dorso-lateral surface. In adults pigmentation is more uniformly dark laterally and dorsally; fins scarlet on basal half, fin rays dark, membranes hyaline. Orbit and operculum iridescent golden.

Lateral line canal straight along midbody, complete or semi-complete, cephalic lateral line with reduced mandibular canals; preoperculo-mandibular canal disjunct, no suprapreopercular tube on operculum.

Supraneurals vestigial or absent, anterior epineurals reduced, dermosphenotic with wide lateral flanges.

Remarks: Barnard (1938b)placed B.burgi in synonymy with B.burchelli and recognised the Breede River species as B.vulneratus. Jubb (1965) switched the status and placed B.vulneratus in synonymy with B.burchelli and resurrected B.burgi for the Berg River species (See introduction, Chapter 3 for reasons). Boulenger (1911) misunderstood the spelling of Berg River and consequently named the species B.burgi. This name is however valid as Boulenger's spelling was not inadvertent (his reference to Burg River or B.burgi is consistent in both Vol. II and Vol.VI (addendum) of the Catalogue).

Species Comparisons: Distinguished from B.burchelli by larger scales, short anterior barbels, anterior position of dorsal fin, fewer predorsal vertebrae, smaller more numerous head tubercles and larger dermosphenotic.

Range: Berg River system, Eerste River and Verlore Vlei River. Details in Appendix 1 and map in Chapter 6. (fig 6.3).

Recent searches for the species in the Eerste River (Gaigher, pers.comm.) have failed to produce signs of the species and it is probably extinct there. The discovery of B.burgi in the Verlorevlei River during the course of this study represents a new record.

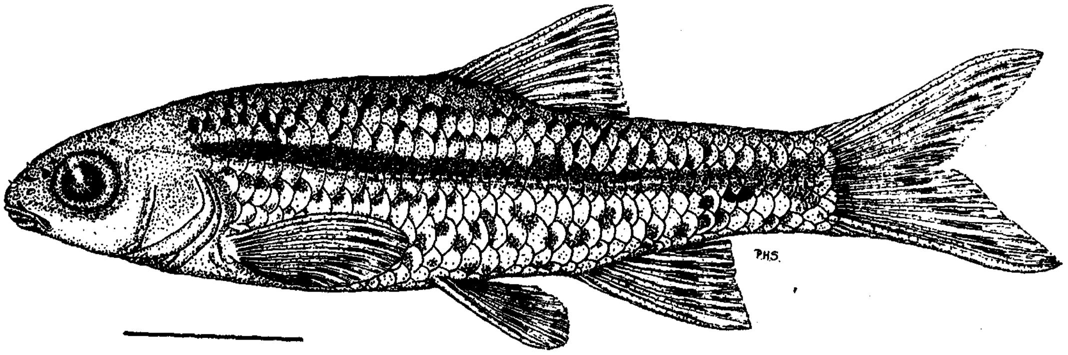


Fig. 3.53 *Barbus phlegethon* Barnard, 1938. AM/P 1399 ♂ , 45,5 mm SL. Drawn by P. Skelton. Scale bar 10 mm.

Barbus phlegethon Barnard, 1938

Fig. 3.53

Barbus phlegethon Barnard, 1938b: 87-88; Barnard, 1943: 204-206, Fig. 20; Jubb, 1965: 32, Fig. 13; Jubb, 1967: 97, Fig. 82.

Material examined: Lectotype: SAM 22484 ♂ 43 mm SL; 32 paralectotypes SAM 22484. Other material in Appendix 1.

Diagnosis: A small (less than 71 mm SL), redfin Barbus species with a flexible last unbranched dorsal fin ray; mouth small, inferior with a single pair of short barbels (usually less than half orbit diameter); adults with numerous irregular dark (brown-black) blotches; conical tubercles on head of male weakly developed.

Description: Morphometric and meristic data are given in Table 3.22. A fusiform species. Head length subequal to body depth. Eyes lateral. Mouth sickle shaped, sub-terminal and protrusible; lips moderate, frequently retracted from rim of lower jaw.

Scales cycloid,radiately striated with central focus. Breast scales reduced and embedded, pelvic axillary scale absent.

Paired fins sexually dimorphic; pectorals rounded, slightly longer and more expansive in males, usually not reaching base of pelvic fins; pelvic fins sub-rectangular; reaching anal fin in males; posterior edge of anal and dorsal fins straight or slightly concave; caudal fin forked, lobes narrowly rounded; dorsal fin origin above or slightly behind origin of pelvic fins.

Gill rakers 2 + 4-6 on anterior arch. Pharyngeal bones falcate, length to width ratio 2,9 - 3,9; pharyngeal teeth in three rows, 1,3,5 - 5,3,1; crowns oblique and truncated. Intestine involuted, up to 2.5 times SL.

Breeding males with few small conical tubercles on snout and top of head, bands of small tubercles over pectoral fin rays, excluding leading ray.

TABLE 3.22

Morphometric and meristic measurements of B.phlegethon (N= 92)

Measurement		Range Max.	 Min.	Mode
Standard length (mm)		59.5	27.5	43.3
Head length (%SL)		28.7	23.9	25.6
Head depth (%HL)		82.4	66.9	75.0
Snout length (%HL)		41.2	31.1	35.2
Orbit diameter (%HL)		36.3	25.3	30.2
Postorbit length (%HL)		57.1	43.1	46.4
Interorbit length (%HL)		38.8	27.2	32.8
Predorsal length (%SL)		55.2	49.0	52.4
Postdorsal length (%SL)		51.0	44.8	47.6
Dorsal fin base (%SL)		15.2	10.9	13.3
Dorsal fin length (%SL)		27.6	19.2	24.0
Pectoral fin length (%SL)		25.3	17.8	20.9
Pelvic fin length (%SL)		20.8	15.4	17.3
Anal fin length (%SL)		23.7	17.0	21.2
Anal fin base (%SL)		12.1	9.1	10.1
Body depth (%SL)		27.8	21.4	24.2
Body width (%SL)		17.6	11.7	14.4
Caudal peduncle length (%SL)		26.9	21.4	23.9
Caudal peduncle depth (%SL)		12.1	9.1	10.8
Anterior barbel length (%OD		-	-	-
Posterior barbel length (%OD)		50.0	2.6	26.9
Pectoral - Pelvic length (%SL)		31.9	23.3	27.4
Pelvic - Anal length (%SL)		18.9	12.0	14.7
Pharyngeal bones L/W	(N = 63)	3.9	2.9	3.4
Length of intestine	(N = 77)	244.0	78.1	142.4

Meristics		
Dorsal fin rays	III-IV (III)	+ 6-8 (7)
Anal fin rays	III-IV (III)	+ 5-6 (5)
Pectoral fin rays	11-15 (13-14)	
Pelvic fin rays	7-9 (8)	
Total vertebrae	35-37 (36)	
Precaudal vertebrae	17-19 (18)	
Caudal vertebrae	16-19 (17-18)	
Predorsal vertebrae	11-14 (12-13)	
Preanal vertebrae	18-21 (20)	
Lateral line scales	29-37 (35)	
Caudal peduncle scale rows	10-14 (12)	
Scale rows lat. line - dorsal	4-6 (5)	
Scale rows lat. line - pelvic	3-4 (4)	
Scale rows lat. line - anal	3-5 (3-4)	
Predorsal scale rows	14-20 (16-17)	
Primary scale radii ($\bar{M}$ to n ($\bar{M}$ to nearest whole no.)	12	
Pharyngeal teeth (mode)	1,3,5 - 5,3,1	

Juveniles with single dark lateral stripe; adults heavily blotched with dark pigment in addition to dark lateral band, white ventrally; proximal portions of fins brilliant scarlet; fin rays brown with a concentration of dark pigment in forks of branched rays giving banded effects; distal fin membranes hyaline; iris golden; cheek and operculum metallic silvery or golden.

Lateral line straight along midbody, complete. Cephalic lateral line without mandibular canal; preopercular canal disjunct. No supra-preopercular tube on operculum.

Supraneurals vestigial or absent, anterior epipleurals reduced. Neurocranium narrow and deep, hyomandibula with short dorso-anterior projections.

Species comparisons: *Barbus phlegethon* is not easily confused with other species. The small mouth, very short barbels, pigment pattern, long intestine and form of dorsal unbranched ray, will identify the species from the sympatric *B.calidus*. Juveniles may be recognised on the basis of pigmentation and having five branched anal fin rays and a single lateral stripe (juveniles of *B.calidus* are spotted).

Range: Cedarberg tributaries of Olifants River in the Clanwilliam Valley; one population from Driehoek tributary of Doring River. Details in Appendix 1; Ch. 6. (fig 6.3) and Fig 3.49.

Remarks: Barnard was not fastidious in designating or labelling type material and in consequence there is some doubt as to what his type material actually was (see also *B.tenuis* and *B.calidus*). In the absence of evidence to the contrary I have regarded that material which is known to have been available to Barnard before the date of publication of his species as the type material (International Code Article 72 b). In the case of *B.phlegethon* the samples concerned are SAM 18767; SAM 19003 and SAM 22484(?). These two samples were evidently combined and reaccessioned as SAM 22484 (P.A. Hulley, SAM, pers.comm. Nov. 1979) and labelled as syntypes. The lectotype was selected from this series on the basis of size and condition.

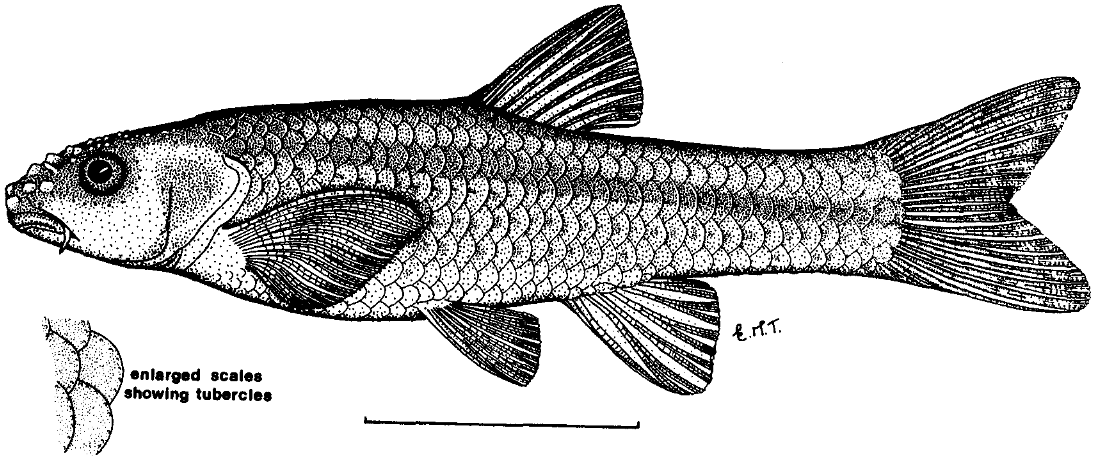


Fig. 3.54 *Barbus tenuis* Barnard, 1938. AM/P 3455 ♂ , 62,5 mm SL.
Drawn by Elizabeth Tarr. Scale bar = 30 mm.

Barbus tenuis Barnard, 1938

Fig. 3.54

Barbus anoplus, Gilchrist & Thompson 1913: 428 (*B. anoplus* non Weber, in part, specimens from le Roux River large).

Barbus tenuis Barnard, 1938b: 87, Barnard, 1943: 202-204 Fig. 19 b; Jubb, 1965: 31, Fig. 12; Jubb, 1967: 101, Fig. 87; Skelton 1976: (Fig. 10 b, new locality record).

Material Examined: Lectotype: SAM 18953, ♀ 74 mm SL. Paralectotypes SAM 10667, 18946, 18953, 18969, 18970. Other material given in Appendix 1.

Diagnosis: A terete redfin *Barbus* species with flexible last unbranched dorsal fin ray. Head length greater than body depth; single pair of short barbels less than orbit diameter; pharyngeal teeth in two rows 3,5 - 5,3; gut up to 1,3 times in SL with single flexure and slight secondary involution; seven pelvic fin rays.

Description: Morphometric and meristic data given in Table 3.23. A medium-sized (adults up to 80 mm SL), *Barbus* species; eyes dorsolateral. Mouth sickle shaped inferior and protrusible, lips moderate.

Scales cycloid, radiately striated with numerous radii, focus centralized. Breast scales reduced and embedded, nape scales reduced or absent; pelvic axillary scale absent.

Paired fins sexually dimorphic: shorter and less expansive in females, pectorals rounded, reaching to base of pelvics in males; pelvics rounded, reaching anal fin base in males; posterior edge of anal and dorsal fins straight or slightly rounded; caudal forked, lobes rounded; dorsal fin origin behind origin of pelvic fins.

Gill rakers 2 + 5-6 to 3 + 7-8 on anterior arch; pharyngeal bones falcate; length to width ratio 3 - 4,5; pharyngeal teeth crowns oblique with recurved tip.

Breeding males with large conical tubercles on snout and top of head, single rows of conical tubercles over rays of fins, and single rows of small conical tubercles along free edge of scales.

TABLE 3.23

Morphometric and meristic measurements of B.tenuis (N = 96)

Measurement	Range		Mode	
	Max.	Min.		
Standard length (mm)	80.0	30.0		
Head length (%SL)	30.0	24.6	26.7	
Head depth (%HL)	71.2	61.1	65.9	
Snout length (%HL)	42.4	30.7	35.0	
Orbit diameter (%HL)	30.2	20.6	26.0	
Postorbit length (%HL)	54.4	43.7	47.5	
Interorbit length (%HL)	35.7	25.3	30.1	
Predorsal length (%SL)	54.6	48.3	51.4	
Postdorsal length (%SL)	51.7	45.5	48.6	
Dorsal fin base (%SL)	14.3	11.0	12.6	
Dorsal fin length (%SL)	28.0	19.7	22.8	
Pectoral fin length (%SL)	24.3	16.7	21.0	
Pelvic fin length (%SL)	18.1	10.9	15.8	
Anal fin length (%SL)	24.1	16.9	20.1	
Anal fin base (%SL)	12.9	8.2	10.4	
Body depth (%SL)	26.8	18.8	22.4	
Body width (%SL)	20.4	13.3	16.6	
Caudal peduncle length (%SL)	29.2	23.1	26.3	
Caudal peduncle depth (%SL)	21.1	10.5	12.3	
Anterior barbel length (%OD)	27.8	7.7	16.8	
Posterior barbel length (%OD)	100.0	20.0	68.1	
Pectoral - pelvic length (%SL)	28.5	22.4	25.3	
Pelvic - anal length (%SL)	18.2	12.5	14.5	
Pharyngeal bones L/W (N = 72)	4.6	3.1	3.8	
Length of intestine (N = 23)	133.9	77.1	103.3	
Meristics				
Dorsal fin rays	III-IV (III)			+ 6-8 (7)
Anal fin rays	III-IV (III)			+ 5-6 (5)
Pectoral fin rays	12-16 (14)			
Pelvic fin rays	7-8 (7)			
Total vertebrae	33-38 (36-37)			
Precaudal vertebrae	17-19 (18)			
Caudal vertebrae	16-19 (18)			
Predorsal vertebrae	11-13 (12)			
Scale rows lat. line - dorsal	4-6 (5)			
Scale rows lat. line - pelvic4	3-5 (4)			
Scale rows lat line - anal	3-5 (4)			
Predorsal scale rows	14-22 (16)			
Primary scale radii (M̄ to nearest whole no.)	14			
Pharyngeal teeth (mode)	3,5 - 5,3			

Single, dark mid-lateral band from behind head to end of caudal peduncle, complete to incomplete middorsal stripe. Scarlet red on proximal portion of fins; fin rays brownish, distal membranes hyaline; iris golden; metallic silvery-golden operculum.

Lateral line straight, running along mid-body. Cephalic lateral line without mandibular canal; preopercular canal disjunct. No supra-preopercular tube on operculum.

Supraneurals vestigial or absent, anterior epineurals reduced; bones in anterior portion of neurocranium incompletely ossified; neurocranium broad and shallow; hyomandibula elongate and shallow; supraorbitals small and vestigal.

Species comparisons: Pigment pattern, larger scales with more radii, more slender profile, pharyngeal teeth and shorter intestine all distinguish this species from *B.asper* and *B.afer*.

Remarks: Jubb (1965) records that the type material of *B.tenuis* was lost. This is partly incorrect. The material available to Barnard before the publication of this species includes SAM 10667, 18946, 18953, 18969 and 18970. Of these SAM 18946, 18953 and 18969 have been examined, and although there is no label included which says they are type material they are considered here as type material (see *B.phlegethon*) and a lectotype has been selected from SAM 18953 collected by K.H. Barnard, C.W. Thorne and A.C. Harrison from between De Rust and Rust-en-vrede (Nels River?) on 24 October, 1937. The other samples mentioned above are apparently missing at present and are possibly lost.

Range: Mountain tributaries of Gourits River System, tributaries of Keurbooms River System. Details in Appendix 1 and Ch. 6. (fig 6.3).

Barbus afer Peters, 1864

Fig. 3.55

Barbus (Gapoeta) afer Peters, 1864: 395; Günther, 1868: 148; non Boulenger, 1911: 178, Fig. 156; non Gilchrist & Thompson, 1913: 430,

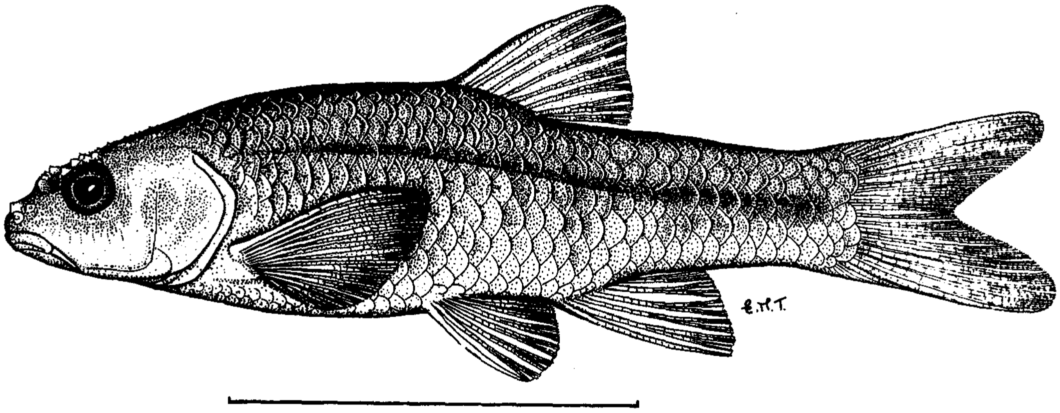


Fig. 3.55 *Barbus afer* Peters, 1864. AM/P 3785 ♂, 60 mm SL. Drawn by Elizabeth Tarr. Scale bar = 30 mm.

Fig. 88; Barnard, 1938, 85; Barnard, 1943: 217; Jubb,1965: 29-30, Fig. 11; Jubb, 1967: 101, Fig. 88.

Barbus anoplus. Boulenger, 1911: 177, Fig. 155 (in part, specimens from Baakens River, Port Elizabeth); Gilchrist & Thompson 1917; Fig. 87.

Barbus vulneratus. Gilchrist & Thompson 1913: 415-416 (in part, specimens from Baakens River and Swartkops River).

Barbus senticeps Smith 1936: 266-267, Fig. 3; Smith, 1937: 124-125, Fig. 2; Barnard, 1938: 84; Barnard, 1943: 200-202.

Barbus asper. Barnard, 1943: 196-200 (in part, specimens listed under (b) and (c) on p.197); Jubb, 1965: 28-29, Fig. 10 pl. VIII (in part, specimens from localities other than Gourits River System and Groot River, Gamtoos System); Smith & Smith, 1966; 154 Fig.

Material Examined: 3 syntypes in Berlin Museum (not examined). Material examined given in Appendix 1.

Diagnosis: A fusiform redfin *Barbus* with the last unbranched dorsal fin ray flexible, a single pair of (usually) well developed barbels, a moderately elongated and involuted intestine up to 2,3 times SL; scales moderately large.

Description: Morphometrics and meristics given in Table 3.24. A medium sized fusiform *Barbus* species (up to ± 110 mm SL); head length subequal to body depth. Eyes lateral. Mouth subterminal, sickle-shaped and protrusible: lips moderate; single pair of usually well developed barbels, longer than orbit diameter in adults.

Scales cycloid, radiately striated, focus centralized. Breast scales reduced and embedded; pelvic axillary scale absent.

Paired fins sexually dimorphic, longer and more expansive in males, reaching to or beyond (in western populations) base of pelvics; pelvics rounded (subrectangular) reaching anal fin base in males; anal and dorsal fin posterior edge straight or slightly rounded; origin of dorsal slightly behind origin pelvics; caudal forked, lobes narrowly rounded.

TABLE 3.24

Morphometric and meristic measurements of *B. afer* (N = 287)

Measurement	Range Max.	Min.	Mode
Standard length (mm)	104.0	43.0	
Head length (%SL)	30.4	25.4	27.9
Head depth (%HL)	79.4	62.1	71.5
Snout length (%HL)	41.8	29.7	34.9
Orbit diameter (%HL)	32.9	18.7	26.5
Postorbit length (%HL)	51.2	42.2	45.9
Interorbit length (%HL)	39.2	24.5	29.8
Predorsal length (%SL)	55.7	48.7	52.0
Postdorsal length (%SL)	50.9	44.3	48.0
Dorsal fin base (%SL)	15.8	11.0	13.4
Dorsal fin length (%SL)	26.9	17.6	23.4
Pectoral fin length (%SL)	26.1	16.1	18.5
Pelvic fin length (%SL)	20.4	14.2	17.4
Anal fin length (%SL)	23.5	16.6	20.8
Anal fin base (%SL)	12.2	9.0	20.8
Body depth (%SL)	30.6	22.5	26.3
Body width (%SL)	20.5	11.5	17.1
Caudal peduncle length (%SL)	27.6	21.3	24.6
Caudal peduncle depth (%SL)	14.7	10.3	12.4
Anterior barbel length (%OD)			
Posterior barbel length (%OD)	169.6	37.0	94.4
Pectoral - pelvic length (%SL)	28.2	19.5	24.2
Pelvic - anal length (%SL)	18.4	12.4	14.9
Pharyngeal bones L/W (N = 212)	4.3	2.7	3.5
Length of intestine (N = 180)	225.0	68.0	146.7

Meristics		
Dorsal fin rays	III-IV (IVO	+ 6-8 (7)
Anal fin rays	III-IV (III)	+ 5-6 (5)
Pectoral fin rays	13-17 (15)	
Pelvic fin rays	7-9 (8)	
Total vertebrae	35-39 (36-37)	
Precaudal vertebrae	17-20 (18-19)	
Caudal vertebrae	16-20 (18-19)	
Predorsal vertebrae	11-13 (12)	
Preanal vertebrae	18-21 (19-20)	
Lateral line scales	25-38 (32-37)	
Caudal peduncle scale rows	10-18 (16)	
Scale rows lat. line - dorsal	4-7 (5-6)	
Scale rows lat. line - pelvic	3-6 (4)	
Scale rows lat. line - anal	3-5 (4-5)	
Predorsal scale rows	13-22 (15-16)	
Primary scale radii ($\bar{M}$ to nearest entire no.)	12	
Pharyngeal teeth (mode)	2,3,5, - 5,3,2	

Gill rakers 2-3 + 6-8 on anterior arch. Pharyngeal bones falcate; length to width ratio 2,7 - 4,2; pharyngeal teeth usually 2,3,5 - 5,3,2 but 1,3,5 - 5,3,1 predominates in certain populations; crowns obliquely truncate and closely applied. Intestine involuted, up to 2.3 times in SL.

Breeding males with large conical tubercles on snout and head dorsum, patterns as described for B.burchelli but with fewer tubercles on snout region (3-4 per group), bands of minute conical tubercles up to three or four deep over pectoral fin rays, excluding the leading ray; single rows on rays in all other fins; single row of minute conical tubercles along free edge of scales.

Pigmentation variable but usually an unbroken thin lateral stripe from behind head to caudal fin; bilateral series of few rounded spots along predorsal region or less frequently a single more or less distinct mid-dorsal stripe. Breeding adults generally darkly pigmented as are those from deep stained habitats. Proximal portions of fins scarlet red; fin rays brown; distal membranes hyaline; ventral regions creamy white, iris golden; operculum metallic golden.

Lateral line straight, running along mid body, complete or nearly complete. Cephalic lateral line without mandibular canal (vestigial segments in few individuals); preopercular canal disjunct. No suprapreopercular tube on operculum.

Supraneurals vestigial or absent; anterior epineurals reduced.

Species comparison: Similar to B.asper from which it differs by having larger scales and a shorter intestine. Differs from B.tenuis in having a longer intestine and more pharyngeal teeth, deeper body and less distinctive pigmentation.

Remarks: The original locality of this species was given by Peters (1864) as "Cape of Good Hope". The specimens were collected by L. Krebbs who spent much time in the Uitenhage area (ffolliott & Liversidge, 1971). Liversidge discussed the question of the type locality with Jubb and they concluded that this was probably the Swartkops River System.

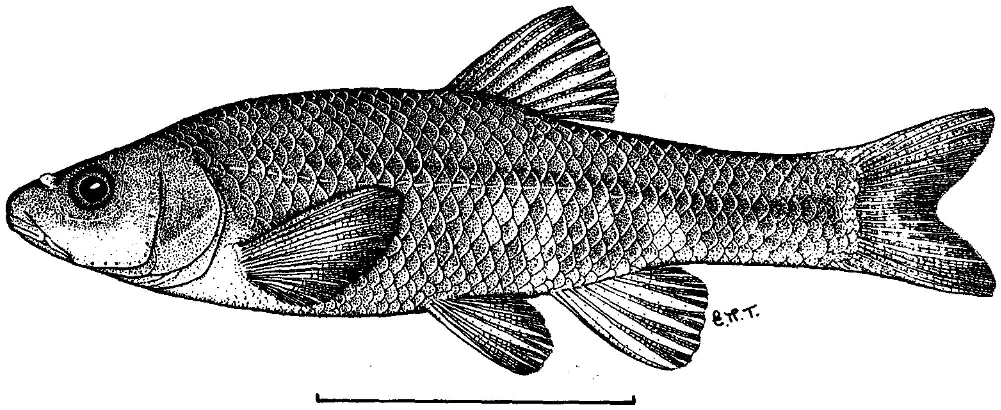


Fig. 3.56 *Barbus asper* Boulenger, 1911. AM/P 6033 ♂, 77,5 mm SL.
Drawn by Elizabeth Tarr. Scale bar = 30 mm.

Range: Coastal rivers between Gourits River System and Sundays River System. Single isolated population in Sundays River System. Details in Ch. 6 (fig 6.3) and Appendix 1.

Barbus asper Boulenger, 1911

Fig. 3.56

Barbus burchelli, Weber, 1897: 153 (in part, from the Buffels River, Laingsburg and the Kamanassie River).

Barbus asper Boulenger, 1911: 176-177, Fig. 154; Gilchrist & Thompson, 1913: 427-428 and 579, Fig. 86; Barnard, 1938: 84; Barnard, 1943: 196-200, Fig. 19a (in part, the specimens from locality (a) p. 197 except those from Haalkraal); Jubb, 1965: 28-29 (in part, only specimens from Gourits River System and Groot River, Gamtoos System); Jubb, 1967: 99 (in part, only specimens from Gourits River System and Groot River, Gamtoos System).

Material Examined: Holotype, BMNH 1909-12.8:1 ♂ 73 mm SL. Paratypes, BMNH 1909-12.8:6-9 ♀ 96 mm SL; ♂ 67 mm SL; 34 mm SL. One paratype (cotype) SAM 10644, extremely poor condition. Other material given in Appendix 1.

Diagnosis: Medium-sized (± 80 mm SL) fusiform *Barbus* with bright red fins, unbranched dorsal fin ray slender and flexible, single pair of barbels (less than or equal to orbit diameter), pharyngeal teeth with truncated oblique crowns, intestine long and involuted up to 3,8 times SL, scales small 35-45 in lateral line, crowded on nape.

Description: Morphometric and meristic data are given in Table 3.25. Head length subequal to body depth. Eyes lateral. Mouth subterminal-terminal, sickle-shaped; lips moderate; barbels not longer than orbit diameter in adults.

Scales cycloid, radiately striated, focus centralized. Breast and belly scales reduced and deeply embedded; nape scales reduced and crowded; pelvic axillary scale absent.

Paired fins sexually dimorphic, pectorals longer and more expansive in males, reaching base of pelvics; pelvics sub-rectangular reaching anal

TABLE 3.25

Morphometric and meristic measurements of **B. asper** (N = 110)

Measurement	Range		Mode	
	Max.	Min.		
Standard length (mm)	80.0	43.0	58.9	
Head length (%SL)	28.2	24.7	26.5	
Head depth (%HL)	76.4	66.8	71.7	
Snout length (%HL)	38.0	31.1	33.9	
Orbit diameter (%HL)	28.7	22.0	26.0	
Postorbit length (%HL)	52.1	37.8	47.0	
Interorbit length (%HL)	35.2	25.5	31.2	
Predorsal length (%SL)	54.6	47.8	51.0	
Postdorsal length (%SL)	52.2	45.5	49.0	
Dorsal fin base (%SL)	15.7	11.3	13.2	
Dorsal fin length (%SL)	27.9	18.9	23.0	
Pectoral fin length (%SL)	26.1	17.0	21.1	
Pelvic fin length (%SL)	21.8	12.6	16.6	
Anal fin length (%SL)	24.3	16.8	20.2	
Anal fin base (%SL)	13.3	8.5	10.2	
Body depth (%SL)	29.5	21.5	26.4	
Body width (%SL)	20.0	10.9	16.7	
Caudal peduncle length (%SL)	29.6	21.5	25.3	
Caudal peduncle depth (%SL)	13.2	9.6	11.6	
Anterior barbel length (%OD)	-	-	- -	
Posterior barbel length (%OD)	116.3	46.0	70.7	
Pectoral - pelvic length (%SL)	29.8	21.1	25.1	
Pelvic - anal length (%SL)	17.6	11.8	14.6	
Pharyngeal bones L/W (N = 74)	4.0	2.8	3.3	
Length of intestine (N = 81)	381.6	124.2	240.0	
Meristics				
Dorsal fin rays	III-IV (IV)			+ 6-8 (7)
Anal fin rays	III-IV (III)			+ 5-6 (5)
Pectoral fin rays	14-17 (15-16)			
Pelvic fin rays	7-9 (8)			
Total vertebrae	35-38 (36)			
Precaudal vertebrae	17-20 (19)			
Caudal vertebrae	16-19 (17-18)			
Predorsal vertebrae	11-13 (12)			
Preanal vertebrae	18-21 (19-20)			
Lateral line scales	35-45 (37-40)			
Caudal peduncle scale rows	16-22 (18-20)			
Scale rows lat. line - dorsal	6-9 (7-8)			
Scale rows lat. line - pelvic	5-8 (6)			
Scale rows lat. line - anal	5-8 (6)			
Predorsal scale rows	18-26 (21-22)			
Primary scale radii ($\bar{M}$ to nearest whole no.)	11			
Pharyngeal teeth (mode)	2,3,5 - 5,3,2			

fin base in males; posterior edge of anal and dorsal fins straight or slightly rounded; origin of dorsal behind origin of pelvics; caudal fin forked, lobes narrowly rounded.

Gill rakers 2-4 + 7-10 on anterior arch; pharyngeal bones falcate, length to width ratio 2,75-4; pharyngeal teeth 2,3,5 - 5,3,2; crowns obliquely truncated, closely applied.

Breeding males with large conical tubercles on snout and on top of head; pattern as in B.afer; bands of minute conical tubercles up to 3-4 deep on pectoral fin rays except first ray; single rows on rays in other fins; single row of minute conical tubercles along free edge of scales.

Uneven dark lateral band from behind head to posterior end of caudal peduncle; pigment in centre of scales form minute dots giving a "speckled hen" appearance. Overall colour silvery grey or brown, operculum golden, iris golden, proximal portion of fins scarlet; distal membrane hyaline, fin rays brown.

Lateral line incomplete, running straight along mid-body. Cephalic lateral line without mandibular canal; preopercular canal disjunct. No suprapreopercular tube on operculum. Supraneurals vestigial, anterior epineurals reduced.

Species comparisons: Close to B.afer from which it is distinguished by the smaller scales, having a longer more involuted intestine and by its pigmentation. Distinguished from B.tenuis by smaller scales, long involuted intestine, pharyngeal teeth formula and shape, deeper body.

Range: Groot River (Gamtoos River System) and larger tributaries of the Gourits River System. Details in Ch. 6 fig 6.3. and Appendix 1.

Barbus calidus Barnard, 1938

Fig. 3.57

Barbus serra. Gilchrist & Thompson, 1913: 404 (in part, 2 smallest Leipoldt specimens).

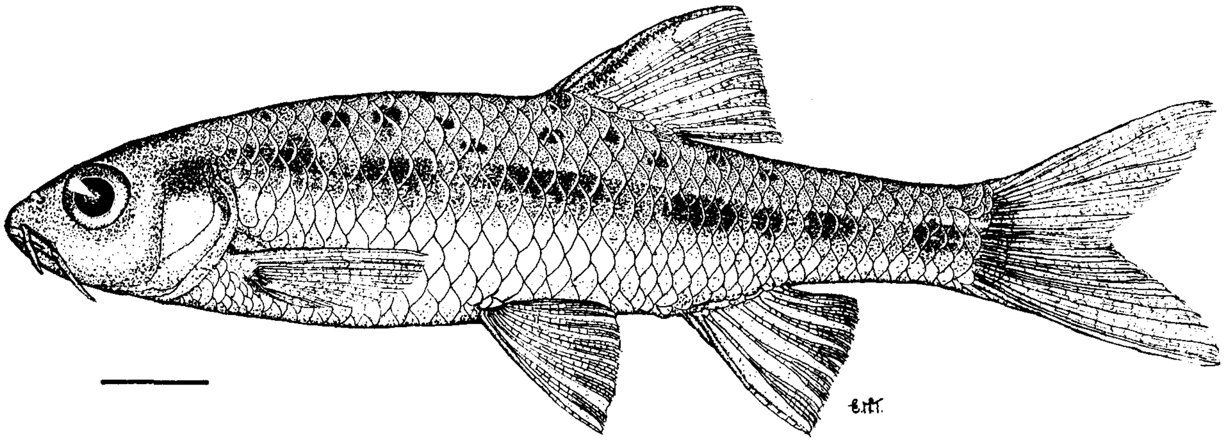


Fig. 3.57 *Barbus calidus* Barnard, 1938. AM/P 1371 ♂, 89 mm SL.
Drawn by Elizabeth Tarr. Scale bar = 10 mm.

Barbus calidus Barnard 1938: 86; Barnard 1943: 176-179, Fig. 15, a-c; Jubb, 1965: 25, Fig. 7; Jubb, 1967: 95, Fig. 80.

Material Examined: **Lectotype:** SAM 18605, ♂, 71 mm SL (new designation). Paralectotypes: SAM 18605; 18606; 18756. Other material in Appendix 1.

Diagnosis: A medium sized (± 82 mm SL) fusiform *Barbus* species with dorsal fin unbranched ray bony and serrated; original dorsal fin behind pelvics; six branched rays in the anal fin. Two pairs of well developed barbels (longer than orbit diameter in adults).

Description: Morphometric and meristic data given in Table 3.26. Head length greater than body depth. Eyes lateral, mouth terminal, U-shaped; lips thin.

Scales cycloid; radiately striated; focus placed in anterior half. Breast scales only moderately reduced; pelvic axillary scale present.

Pectorals slender, sub-falcate, nearly reaching base of pelvics; pelvics sub-rectangular; posterior edge of anal and dorsal fin straight; caudal forked, lobes narrow.

Gill rakers, 2 + 6-8 on anterior arch. Pharyngeal bones slender, falcate; length to width ratio 4,0 - 5,5; pharyngeal teeth 2,3,4, - 5,3,2; crowns slender, with recurved tips. Intestine short, less than or equal to SL with single flexure.

Breeding adults of both sexes (but more prominently males) with numerous minute eruptions (tubercles?) over head and predorsal scales; single rows of similar eruptions over fin rays of paired fins; exposed surface of dorsal and dorso-lateral scales scattered with similar eruptions.

Adults and juveniles with large irregular dark spots along dorsal and dorso-lateral surfaces; broad, more or less broken, lateral band from behind head to caudal fin, band of pigment adjacent to base of anal fin; in life a green to yellowish brown with cream or silvery ventral parts; Iris golden, operculum metallic silvery golden; fin rays dark; in adults proximal portions of fins scarlet, caudal fin with salmon tinge; distal fin membranes hyaline.

TABLE 3.26

Morphometric and meristic measurements of **B.calidus** (N = 280)

Measurement	Range		Mode	
	Max.	Min.		
Standard length (mm)	82.0	22.1		
Head length (%SL)	30.0	24.6	27.5	
Head depth (%HL)	76.7	60.9	68.2	
Snout length (%HL)	40.0	28.1	34.4	
Orbit diameter (%HL)	36.4	25.0	29.1	
Postorbit length (%HL)	53.3	38.2	43.6	
Interorbit length (%HL)	41.7	28.6	34.1	
Predorsal length (%SL)	57.5	50.0	54.3	
Postdorsal length (%SL)	50.0	42.6	45.7	
Dorsal fin base (%SL)	17.8	12.1	13.8	
Dorsal fin length (%SL)	26.0	18.8	22.2	
Pectoral fin length (%SL)	26.0	15.9	21.2	
Pelvic fin length (%SL)	23.2	15.5	18.8	
Anal fin length (%SL)	23.3	16.7	19.6	
Anal fin base (%SL)	22.1	9.1	13.4	
Body depth (%SL)	27.0	9.1	20.2	
Body width (%SL)	27.0	9.6	16.0	
Caudal peduncle length (%SL)	25.0	12.5	19.5	
Caudal peduncle depth (%SL)	25.0	7.9	12.2	
Anterior barbel length (%OD)	133.3	8.7	75.8	
Posterior barbel length (%OD)	157.1	41.7	107.8	
Pectoral - pelvic length (%SL)	150.0	18.8	41.7	
Pelvic - anal length (%SL)	26.5	14.9	19.4	
Pharyngeal bones L/W (N = 18)	5.5	4.0	4.6	
Length of intestine (N = 72)	124.3	43.3	89.1	
Meristics				
Dorsal fin rays	III-IV (IV)			+ 6-8 (7)
Anal fin rays	III-IV (III)			+ 5-7 (6)
Pectoral fin rays	11-15 (13-14)			
Pelvic fin rays	7-9 (8)			
Total vertebrae	36-39 (37-38)			
Precaudal vertebrae	17-20 (19)			
Caudal vertebrae	17-20 (18-19)			
Predorsal vertebrae	12-14 (263)			
Preanal vertebrae	20-22 (21)			
Supraneurals	5-9 (7)			
Lateral line scales	34-39 (37)			
Caudal peduncle scale rows	12-17 (14-16)			
Scale rows lat. line - dorsal	5-7 (6)			
Scale rows lat. line - pelvic	3-4 (3)			
Scale rows lat. line - anal	3-5 (4)			
Predorsal scale rows	14-21 (17-18)			
Primary scale radii ($\overline{M}$ to nearest entire no.)	9			
Pharyngeal teeth (mode)	2,3,5 - 5,3,2			

Lateral line complete, more or less straight along mid-body. Cephalic lateral line without disjunctions. Suprapreopercular tube on operculum.

Species comparison: Similar to *B.erubescens* but differs in having a strong serrated unbranched dorsal fin ray and six branched anal fin rays; more predorsal vertebrae; pharyngeal teeth five in the inner row and different in shape; intestine slightly longer; spotted pigmentation.

Remarks: The following material was available to Barnard at the time of publication of *B.calidus* (and in 1943 he indicates that he has used it all): SAM 215, 216, 2912, 2913-5, 18605, 18606, 18756, 19002 and 22499. Not all this material has been traced but SAM 18605, 18606 and 18756 have been examined and a lectotype selected from SAM 18605 which was collected by K. Barnard and C.W. Thorne from the Jan Diessels River in 1936.

Range: Clanwilliam Olifants River system within Fold Mountains. Details in Appendix 1; Chapter 6. (fig 6.2).

Barbus erubescens Skelton, 1974

Fig. 3.58

Barbus calidus. Jubb, 1967: 95-96 (in part, specimens collected by K.J. van Rensburg).

Barbus erubescens Skelton, 1974 b: 1-12, Figs 1,2,3.

Material Examined: Holotype and paratypes as recorded in Appendix 3. Other material recorded in Appendix 1.

Diagnosis: A medium sized (up to 95 mm SL), fusiform *Barbus* species with the last unbranched dorsal fin ray flexible and with vestigial serrations; anal fin with seven branched rays; two pairs of well developed barbels (longer than orbit diameter); without spots; males in breeding dress suffused with red.

Description: Morphometrics and meristics given in Table 3.27. Head length

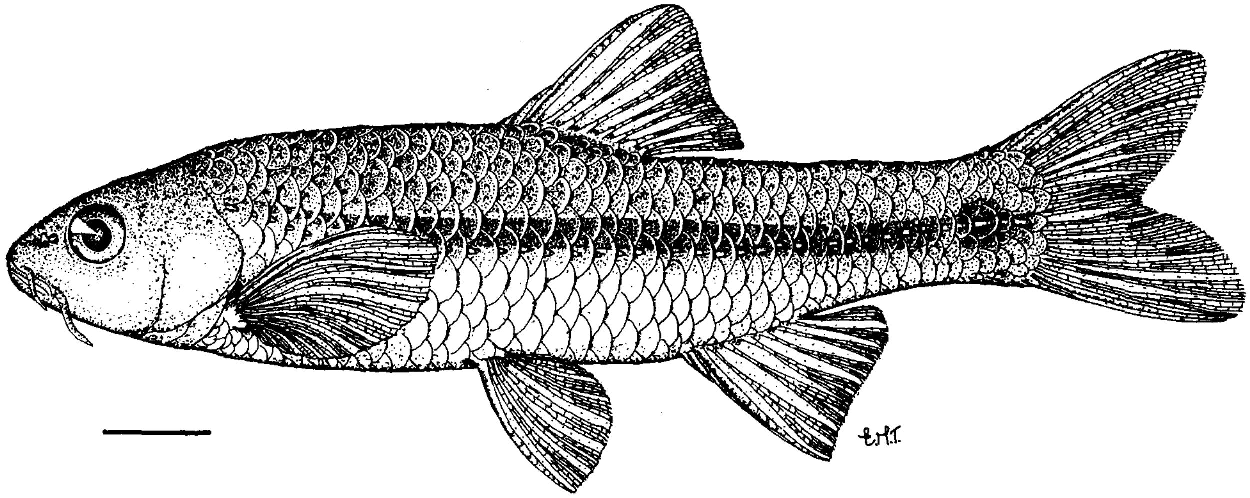


Fig. 3.58 *Barbus erubescens* Skelton, 1974. Holotype AM/P 2424, ♂, 84 mm SL. Drawn by Elizabeth Tarr. Scale bar = 10 mm.

greater than body depth, eyes lateral - dorso-lateral. Mouth large terminal, U-shaped, protrusible; lips thin; two pairs of well developed barbels (greater than orbit diameter in adults).

Scales cycloid, radiately striated, focus displaced anteriorly. Breast scales slightly reduced, not embedded; pelvic axillary scale present.

Pectoral fins rounded, almost reaching base of pelvics; pelvics rounded not reaching anal fin base; anal and dorsal posterior edges straight; dorsal origin behind origin of pelvics, over posterior edge of pelvic base; unbranched dorsal fin ray flexible with vestigial serrations. Caudal fin forked, lobes rounded.

Gill rakers 2 or 3 + 6-9 on anterior arch. Pharyngeal bones falcate; length to width ratio 4,4-5,7; pharyngeal teeth 2,3,4 - 4,3,2; crowns with terminal conical cusp. Intestine less than SL, with single flexure.

Adults in breeding condition with numerous minute erupted tubercles irregularly but densely scattered on head dorsum and dorso-lateral regions. Similar structures scattered on exposed surface of dorsal and dorso-lateral scales and in widely spaced single rows over fin rays.

Colour and pigmentation as in Appendix 3.

Lateral line complete, running straight or slightly curved to ventral side, along mid-body. Cephalic lateral line system without disjunctions or reductions. Suprapreopercular tube on operculum.

Species comparison: B.erubescens is similar to B.calidus from which it differs in the form of the unbranched dorsal fin ray, the number of dorsal and branched anal fin rays (dorsal fin 8 vs 7 in B.calidus; anal fin 7 vs 6 in B.calidus); the number and shape of pharyngeal teeth, the number of vertebrae before the dorsal fin, the number of scale radii, pigmentation, shape of the fins and size of the orbit.

Range: Twee River and tributaries, Clanwilliam Olifants River system. Appendix 1; Ch. 6. (fig 6.2).

TABLE 3.27

Morphometric and meristic measurements of B.erubescens (N = 110)

Measurement	Range Max.	 Min.	Mode
Standard length (mm)	95.0	30.5	64.6
Head length (%SL)	31.2	25.6	27.8
Head depth (%HL)	78.6	62.1	69.2
Snout length (%HL)	36.2	26.4	33.3
Orbit diameter (%HL)	32.4	22.2	26.7
Postorbit length (%HL)	50.0	40.8	46.0
Interorbit length (%HL)	37.9	24.6	31.9
Predorsal length (%SL)	55.7	50.3	53.1
Postdorsal length (%SL)	49.7	44.3	46.9
Dorsal fin base (%SL)	15.7	12.1	13.8
Dorsal fin length (%SL)	24.0	18.9	21.0
Pectoral fin length (%SL)	22.7	18.3	20.6
Pelvic fin length (%SL)	19.3	15.6	17.5
Anal fin length (%SL)	21.7	15.7	18.1
Anal fin base (%SL)	13.9	9.8	11.9
Body depth (%SL)	26.5	20.2	23.6
Body width (%SL)	18.3	12.0	15.5
Caudal peduncle length (%SL)	23.4	18.6	21.1
Caudal peduncle depth (%SL)	12.8	10.3	11.7
Anterior barbel length (%OD)	122.2	35.7	96.9
Posterior barbel length (%OD)	150.0	42.9	110.9
Pectoral - pelvic length (%SL)	26.5	10.0	23.5
Pelvic - anal length (%SL)	21.2	15.2	18.2
Pharyngeal bones L/W (N = 21)	5.7	4.4	4.9
Length of intestine (N = 58)	102.3	57.6	80.8

Meristics		
Dorsal fin rays	III-IV (IV)	+ 7-8 (8)
Anal fin rays	II-IV (III)	+ 6-8 (7)
Pectoral fin rays	11-16 (14-15)	
Pelvic fin rays	7-8 (8)	
Total vertebrae	36-39 (37-38)	
Precaudal vertebrae	18-20 (19)	
Caudal vertebrae	17-20 (18-19)	
Predorsal vertebrae	11-13 (12)	
Preanal vertebrae	20-22 (129)	
Supraneurals	6-8 (7)	
lateral line scales	35-40 (37-38)	
Caudal peduncle scale rows	15-19 (16)	
Scale rows lat. line - dorsal	5-6 (6)	
Scale rows lat. line - pelvic	3-5 (4)	
Pharyngeal teeth (Mode)	2,3,4 -4,3,2	

Oreodaimon quathlambae (Barnard, 1938)

Fig. 3.59

Labeo quathlambae Barnard 1938a: 525-528, Fig; Jubb 1966: 161-162; Jubb 1967: 115, Fig. 117A, B.

Oreodaimon quathlambae. Greenwood & Jubb 1967: 17-37, 17 figs; Pike & Tedder, 1973: 9-15 (new locality record); Skelton, 1974a (new morphological data); Skelton, 1976: 407-408 Fig. 10 A (new interrelationships data); Rondorf, 1976: (new locality data); Gephard, 1978: 105-111 Fig. 2 (geographic variation and new locality data).

Material Examined: Lectotype: SAM 19018 ♀, 80 mm SL. Paralectotypes: SAM 19018 (15 specimens 28-70 mm SL), NM 1416 (2) + 31; 30-38 mm SL. Other material as in Appendix 1.

Diagnosis: A medium-sized (up to 130 mm SL), terete redfin cyprinid with very small scales, a single pair of short barbels, pharyngeal teeth 3,4 - 4,3; intestine short, subequal to SL with single flexure.

Description: Morphometric and meristic data are given in Table 3.28. Head length greater than body depth. Eyes dorso-lateral. Mouth sub-terminal, sickle shaped and protrusible; lips moderate to well developed; barbels short, less than orbit diameter.

Scales cycloid, radiately striate, focus centralized. Breast and belly scales reduced and embedded; nape scales embedded; pelvic axillary scales absent; scales adjacent to dorsal, anal and pelvic fins embedded.

Paired fins sexually dimorphic, longer and more expansive in males; pectorals rounded, not reaching base of pelvics; pelvics rounded, not reaching anal fin; posterior edge of anal and dorsal fins straight or slightly rounded; last unbranched dorsal fin ray, flexible; origin of dorsal behind origin of pelvics; caudal forked lobes rounded; adipose (?) region at antero-dorsal base of caudal and dorsal fins.

Gill rakers 1-2 + 5-7 on anterior arch; pharyngeal bones falcate, length to width ratio 2,8 - 4,3; pharyngeal teeth crowns slender, oblique with recurved tips.

TABLE 3.28

Morphometric and meristic measurements of *O. quathlambae* (N = 32)

Measurement		Range		Mode
		Max.	Min.	
Standard length (mm)		102.0	46.0	
Head length (%SL)		27.1	22.7	24.8
Head depth (%HL)		69.4	59.9	64.3
Snout length (%HL)		39.3	33.3	36.8
Orbit diameter (%HL)		27.9	19.4	23.6
Postorbit length (%HL)		57.8	46.4	49.7
Interorbit length (%HL)		30.2	24.4	27.4
Predorsal length (%SL)		55.0	47.4	50.8
Postdorsal length (%SL)		52.6	45.0	49.3
Dorsal fin base (%SL)		13.5	10.5	11.9
Dorsal fin length (%SL)		22.0	17.7	19.8
Pectoral fin length (%SL)		21.7	15.5	18.8
Pelvic fin length (%SL)		16.7	12.8	15.1
Anal fin length (%SL)		20.0	15.1	17.5
Anal fin base (%SL)		12.1	8.9	10.2
Body depth (%SL)		25.5	20.0	22.0
Body width (%SL)		16.7	11.9	14.7
Caudal peduncle length (%SL)		28.2	22.8	25.3
Caudal peduncle depth (%SL)		12.1	9.9	11.0
Anterior barbel length (%OD)		-	-	-
Posterior barbel length (%OD)		80.7	34.2	56.3
Pectoral - pelvic length (%SL)		27.7	23.0	25.5
Pectoral - anal length (%SL)		17.5	12.7	14.9
Pharyngeal bones L/W	(N = 28)	4.3	2.7	3.2
Length of intestine	(N = 20)	114.3	77.4	96.2
Meristics				
Dorsal fin rays		III + 6-8 (7)		
Anal fin rays		III + 5-6 (5)		
Pectoral fin rays		15-17 (16)		
Pelvic fin rays		7-9 (8)		
Total vertebrae		38-40 (16)		
Precaudal vertebrae		19-22 (20-21)		
Caudal vertebrae		17-20 (18-19)		
Predorsal vertebrae		13-15 (14)		
Preanal vertebrae		20-22 (21)		
Lateral line scales		60-72 (65-67)		
Caudal peduncle scale rows		30-38 (32-36)		
Scale rows lat. line - dorsal		10-14 (11-12)		
Scale rows lat. line - pelvic		8-12 (10-11)		
Scale rows lat. line - anal		9-11 (9-10)		
Predorsal scale rows		28-40 (34-36)		
Primary scale radii ($\bar{M}$ to nearest whole no.)		10		
Pharyngeal teeth (Mode)		3,4 - 4,3		

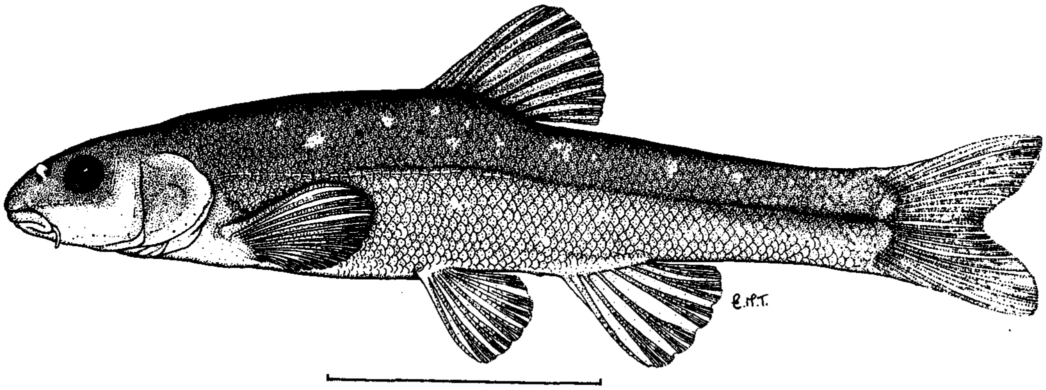


Fig. 3.59 Oreodaimon quathlambae (Barnard, 1938). AM/P 3473, ♂, 95 mm SL. Drawn by Elizabeth Tarr. Scale bar = 30 mm.

Sexually ripe adults with small conical tubercles on snout and top of head and lateral regions; bands of minute compressed tubercles up to six deep over pectoral fin rays excluding leading ray; single rows over rays of other fins; usually a single tubercle per scale on all scales except reduced ventral scales.

Pigmentation variable, usually dark lateral band from behind head to posterior end of caudal peduncle; dorsal surface plain or more frequently with a series of prominent bilateral spots or vermiculations. Body greyish brown to deep bluish black in breeding males, ventral region creamy white; iris golden, operculum metallic golden; in adults proximal portion of fins and adjacent body regions scarlet.

Lateral line complete, runs straight along mid-body. Cephalic lateral line without mandibular canal. Preopercular canal reduced distally, disjunct; no suprapreopercle tube on operculum.

Supraneurals vestigial or absent; anterior epineurals not ossified; bones of anterior portion of neurocranium incompletely ossified; supraorbitals vestigial; four infraorbitals including lachrymal; hyomandibular broad and shallow.

Range: Extinct, as far as known, in type locality - Umkomazana River, Natal. Known from three tributaries of Orange (Senqu) River in Lesotho (details in Appendix 1; Ch. 6).

Remarks: Natal Parks Board officials have expressed doubt that the species has ever existed in Natal (Geddes-Page 1977, Crass *in litt*. July 1977). They suggest that the recording of the species from the Umkomazana River was in error and the specimens were possibly collected in Lesotho. The evidence is however equivocal and the Umkomazana River must remain as the type locality until there is conclusive proof to the contrary.

CHAPTER 4

THE COMPARATIVE OSTEOLOGY OF THE REDFIN BARBUS SPECIES

The outstanding problem remaining in the taxonomy of the redfin Barbus species is whether the species form a monophyletic assemblage or not. Traditional characters have not yet provided the answer to this problem, and although a few of the newly explored characters in the previous chapter are suggestive, a study of the osteology, which is frequently of great value in unravelling the interrelationships of fishes (e.g. Greenwood et al., 1973) has been made to this end.

There are no full comparative accounts of the osteology of small Barbus species with radiately striated scales in the literature. For this reason a complete description of a redfin Barbus species is provided in this chapter. In so doing it is hoped to provide a basis for the comparative usage of osteological characters in the redfins and other Barbus species in general. The comparison with the redfin species is made in the present chapter. A comparison with other Southern African Barbus species is made in the following chapter.

Greenwood & Jubb (1967) provided a description of the osteology of O.quathlambae. Preliminary observations by Skelton (1976) suggested that this species was possibly related to certain redfin Barbus species. In the present chapter therefore a comparison of the osteology of O.quathlambae with the redfin Barbus species is included. The present objectives are purely to provide a comparative account of the osteology of the redfin Barbus species and O.quathlambae. The conclusions from this study will be drawn in Chapter 5. The taxonomic study (Chapter 3) indicated that the most generalised redfin species is probably Barbus burchelli and it has therefore been selected for the initial description.

In addition to the description of the osteology of O.quathlambae made by Greenwood & Jubb (1967) guidelines for comparative cyprinid osteology have been drawn from a number of sources. In particular the works of Harrington (1955), Ramaswami (1955 a & b) and Uyeno (1961) have been useful. A number of other accounts on cyprinids have included observations on

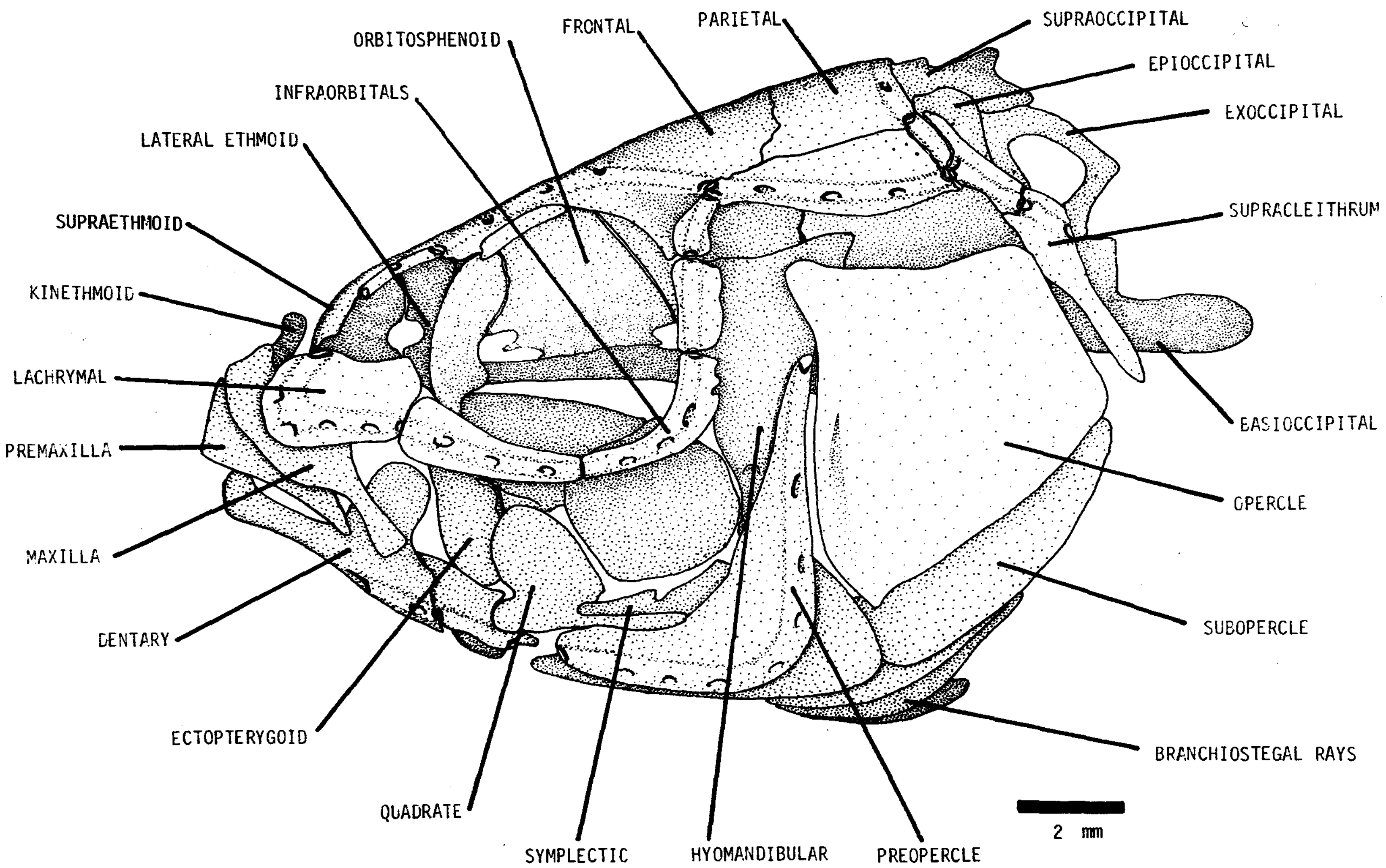


Fig. 4.1 Skull of B.burchelli (AM/P 3463)to show the orientation of the bones. Sclerous bones of eye removed. Only sufficient bones to provide orientation are labelled. Scale bar = 2 mm.

Barbus osteology although this is invariably on large Barbus or species other than those from Africa (Sagemehl, 1891; Vandewalle, 1977; Howes, 1978). More recently Barbour & Miller (1978) gave good illustrations of the neurocranium of the American cyprinid genus Algansea.

MATERIALS AND METHODS

Skeletons were prepared according to the method of Taylor (1967). Dissections were made in glycerine under a stereo-microscope and drawings were prepared using a camera lucida. Cartilage components were stained with Victoria Blue after dissection.

Osteological material examined is listed in Appendix 2.

The following description is divided into five main sections: the skull; pectoral girdle; pelvic girdle; the axial skeleton; unpaired fins. Osteological nomenclature is based on Weitzman (1962) with changes where necessary to bring the nomenclature into line with more recent terminology. In each section the order of presentation is the description of B.burchelli, followed by the comparison with other redfin species and O.quathlambae.

DESCRIPTION - SKULL

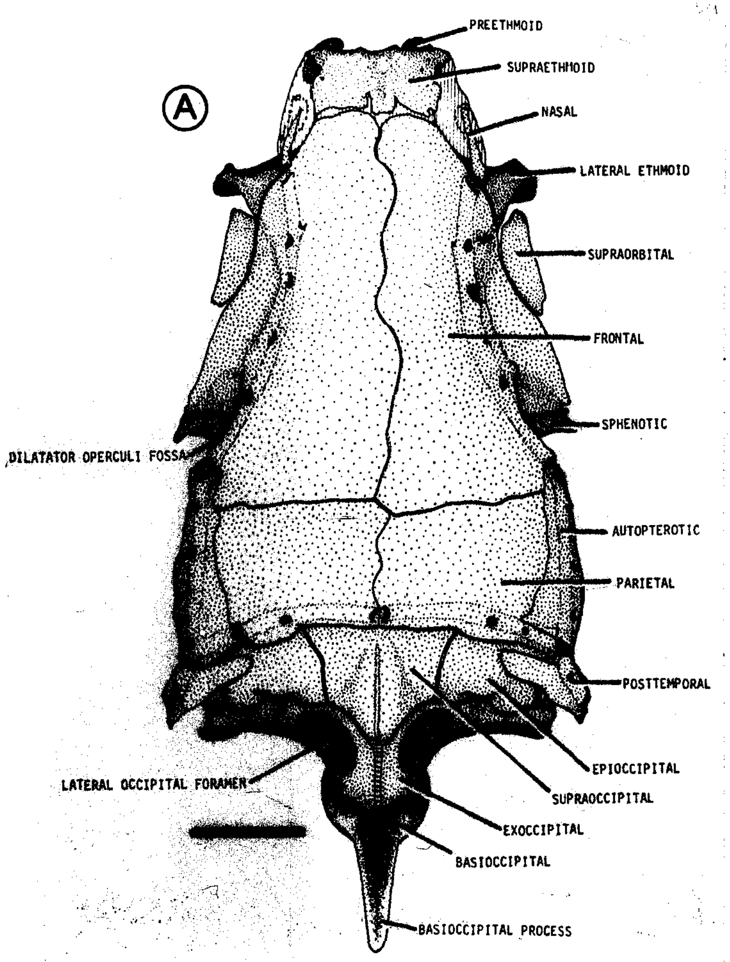
This description of bones of the skull is divided into two sections viz. neurocranium and branchiocranium. The orientation of individual cranial bones is provided in Fig. 4.1 which shows, in lateral view, the articulated skull of B.burchelli.

NEUROCRANIUM (Figs 4.2 A, B, C, D)

The neurocranium is most conveniently considered under four regions, viz. the ethmoid, orbital, otic-occipital and basicranial regions.

General proportions

There is no indication of sexual dimorphism in the redfin neurocranium. In dorsal view (Fig. 4.2 A) the neurocranium of B.burchelli is subrectangular in outline with the basioccipital process projecting as a prominent posterior spur. Viewed laterally it is triangular or wedge-shaped with the dorsal profile gently arched. The posterior



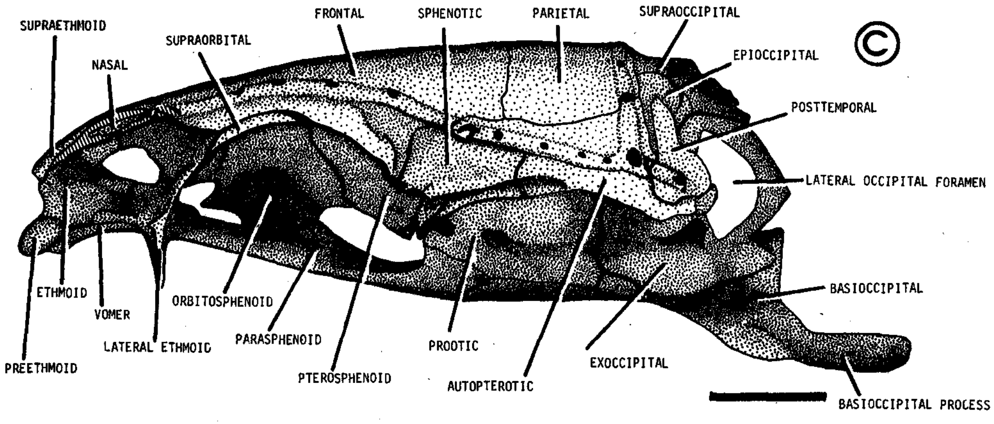
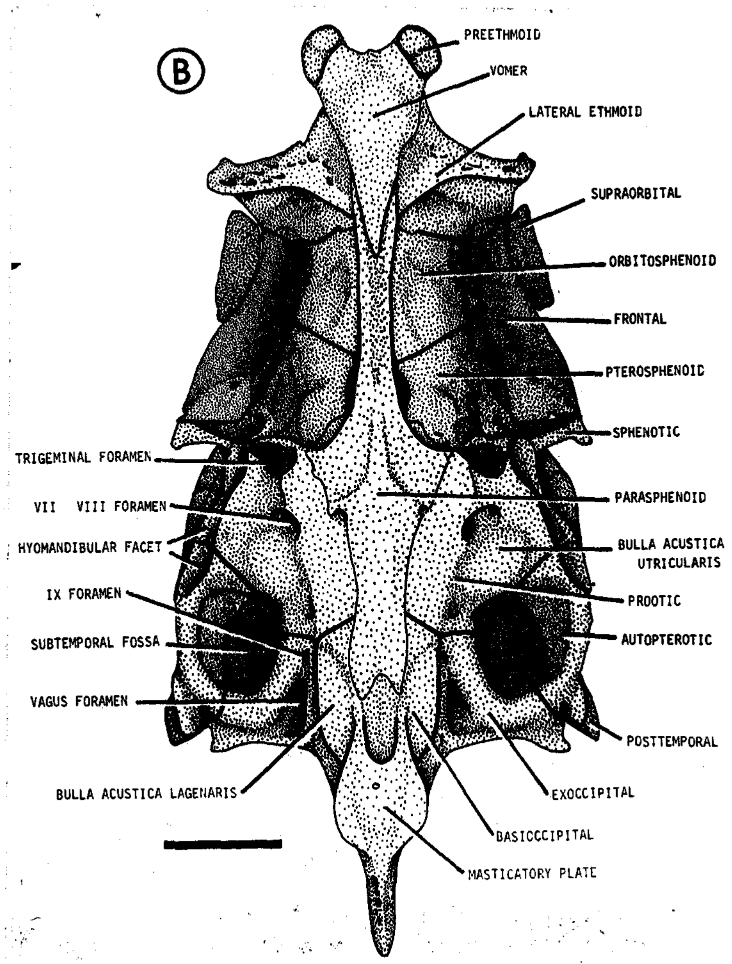
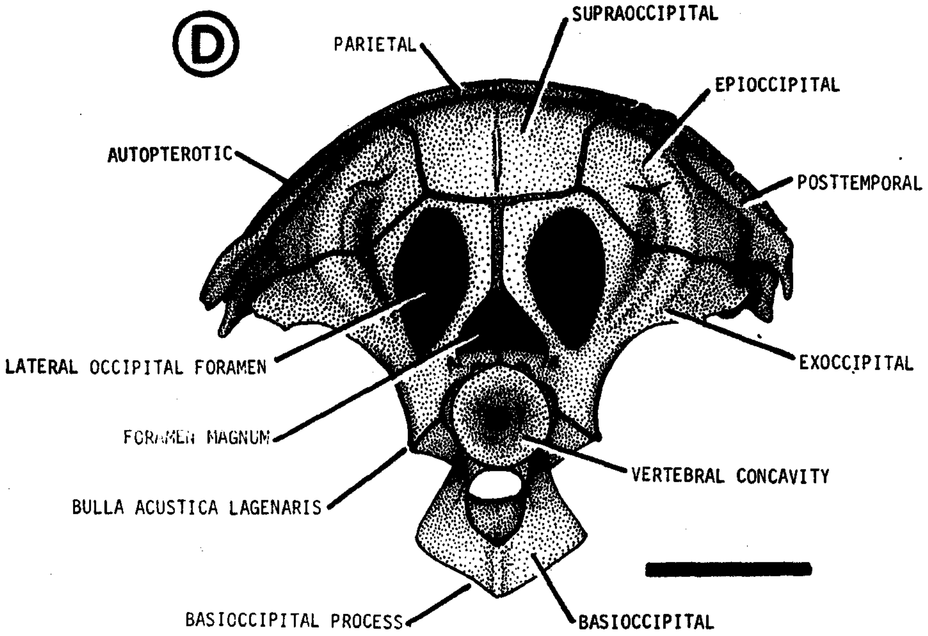


Fig. 4.2 Neurocranium of B.burchelli (AM/P 7443) (a) dorsal view. Note extrascapulars are possibly fused to autopterotic (left side) and parietal (right side) respectively. Nasal bones incompletely ossified. (b) ventral view, (c) lateral view from the left, (d) posterior view. Scale bar = 2 mm.


B
PREETHMOID
VOMER
LATERAL ETHMOID
SUPRAORBITAL
ORBITOSPHENOID
FRONTAL
PTEROSPHENOID
SPHENOTIC
TRIGEMINAL FORAMEN
PARASPHENOID
VII VIII FORAMEN
HYOMANDIBULAR FACET
BULLA ACUSTICA UTRICULARIS
IX FORAMEN
PROOTIC
SUBTEMPORAL FOSSA
AUTOPTEROTIC
VAGUS FORAMEN
POSTTEMPORAL
BULLA ACUSTICA LAGENARIS
EXOCCIPITAL
BASIOCCIPITAL
MASTICATORY PLATE


D
PARIETAL
SUPRAOCCIPITAL
EPIOCCIPITAL
AUTOPTEROTIC
POSTTEMPORAL
LATERAL OCCIPITAL FORAMEN
EXOCCIPITAL
FORAMEN MAGNUM
VERTEBRAL CONCAVITY
BULLA ACUSTICA LAGENARIS
BASIOCCIPITAL PROCESS
BASIOCCIPITAL

end is steeply truncated and the basioccipital process forms an angle of 30-40^{o} from the horizontal. The ventral surface (Fig. 4.2 B) is complex, without projections. There are two large subtemporal fossae. In posterior view the dorsal profile is semi-oval.

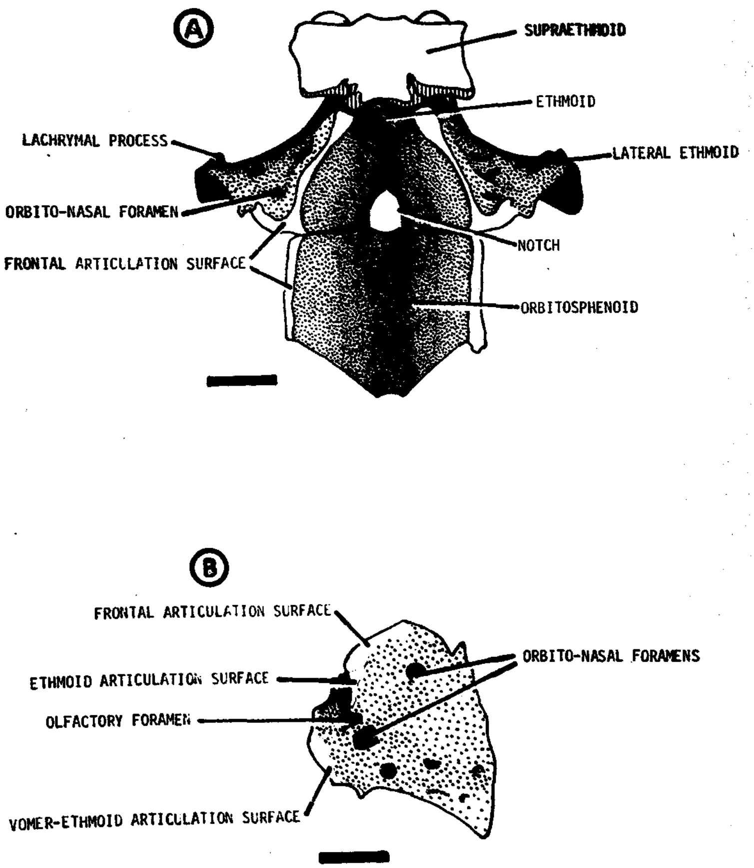
Ethmoid region

This comprises the anterior region of the neurocranium and includes the ethmoid-supraethmoid, the lateral ethmoids and the vomer. In addition the nasals lie adjacent to the supraethmoids above the nasal capsules and are therefore included here.

The majority of authors refer to the complex antero-dorsal bone of the neurocranium as the ethmoid and supraethmoid (Harrington, 1955). Patterson (1975) shows that this is in fact derived from a supraethmoid and rostrodermethmoid, but at the same time declines to advocate usage of these terms. In view of this the names ethmoid and supraethmoid are retained.

On the antero-ventral side the vomer also represents a complex fusion of the vomer and the ventral ethmoid (Patterson, 1975:514-515) but for simplicity and continuity the usual terminology of vomer is retained. Anteriorly there are two small spherical endoskeletal ossifications articulating with the ethmoid and vomer. These are well known in cyprinoids (Patterson, 1975:501) and are referred to as pre-ethmoids. The posterior portion of the region is formed by large paired lateral ethmoids. These are frequently considered to represent a fused compound of the lateral ethmoids and prefrontal bones (Harrington, 1955; Ramaswami, 1955 a, b; Greenwood & Jubb, 1967; Uyeno, 1961) but Patterson (1975:496, also 1977:97) finds that they are single ossifications (lateral ethmoid) with endo- and peri-chondral components.

The Supraethmoid (Fig. 4.2 A and C) is firmly fused to the horizontal plate-like ethmoid forming a deep T-shaped bone. This provides an anterodorsal roof (supraethmoids) and dividing septum (ethmoid) to the olfactory pits. On the dorsal side the supraethmoid is butterfly-shaped, sloping antero-ventrally with a gentle lateral curve from a shallow median valley. The lateral borders in juveniles are usually membranous or lightly ossified. The posterior edge lies in the same



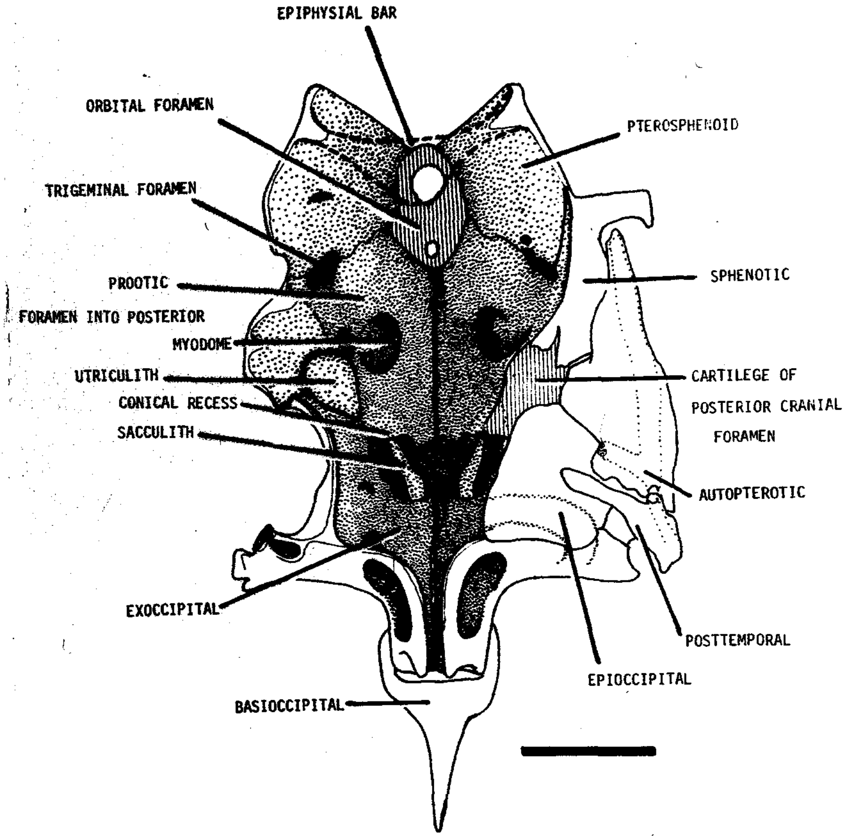


Fig. 4.3 (a) Dorsal view of anterior portion of the neurocranium of B.burchelli with frontal bones removed. (b) Anterior view of left lateral ethmoid of B.burchelli. Scale bar = 1 mm.

Left

Fig. 4.4 Dorsal view of posterior part of the neurocranium of B.burchelli with frontals, parietals, supraoccipital, left epiotic, left sphenotic, left autopterotic and left post-temporal removed. Scale bar = 2 mm.

Right

plane as the frontals and is separated from the latter by a narrow membraneous interspace.

The ethmoid (Fig. 4.2 C) forms the anterior internasal septum and is slightly emarginate (or in certain cases (partially divided) posteriorly to form the anterior rim of the olfactory foramina. On the ventral side the bone extends laterally and forms a synchrondral joint with the vomer. Each antero-lateral corner is truncated to accommodate in part the preethmoid ossifications.

The lateral ethmoids (Figs 4.2 A, B, C; 4.3 A, B) are large, complex bones in synchondrosis on the anterior side with the ethmoids, ventrally with the vomer and parasphenoid, dorsally with the frontals, medioventrally with each other and posteriorly with the orbitosphenoids. The shape and relationship of these bones in the neurocranium is illustrated in Figures 4.2 A, B. The anterolateral surface forms part of the nasal capsule (pit), the medial surface the walls of the anterior extension of the braincase and posterior surface the anterior walls of the orbit. An excavation on the anterior edge forms the major portion of the olfactory foramen. An orbito-nasal foramen passes dorso-laterally through each lateral ethmoid. The anterior surface is convex, forming primarily the curvature of the orbits. There is a small projection on the antero-lateral edge which forms the point of attachment for the lachrymal.

The ventral surface is honeycombed and shallowly excavated medially. Each lateral ethmoid is indented postero-medially to form a shallow anterior myodome. A notch on the angle of the indentation forms a gap in the roof of the myodome (Fig. 4.3 A).

The vomer (Fig. 4.2 B) is a flat,sub-triangular bone with a dorsal synchrondrosis with the expanded base of the ethmoid, the lateral ethmoids and the anterior part of the parasphenoid. The antero-lateral corners are thickened and truncated to form the ventral part of the preethmoid articulation sockets. There is a low medial dorsal ridge which fits into a ventral groove of the parasphenoid.

The preethmoids (Fig. 4.2 B) are kidney-shaped ossifications encased in cartilage and articulate in sockets formed by the ethmoid and vomer. The dual spheres of the preethmoids form articulation heads for the palatine (lateral) and a cartilage pad, or meniscus (Alexander, 1966), between the preethmoid and the maxilla.

The nasals (Fig. 4.2 A) are short tubular bones accommodating the anterior extremities of the supraorbital sensory canal. The bones lie in the cutis above the nasal capsule and their posterior edges rest on the dorsal surface of the frontals. The nasals are invariably incompletely ossified.

Orbital region

The posterior surface of the lateral ethmoids form the anterior walls of the orbit. Other bones surrounding the orbits include the orbitosphenoids, the pterosphenoids, part of the frontals and the supraorbitals. A portion of the sphenotics also contribute to the walls of the orbits themselves but these bones are considered under the otic-occipital region.

The orbitosphenoids (Figs 4.2 B, C; 4.3 A) are fused to form a single Y-shaped bone which provides the greater part of the median and dorsomedian walls of the orbit. It is sutured anteriorly to the lateral ethmoids, posteriorly to the pterosphenoids and dorsally to the frontals. The ventral flange overlaps a low dorsal ridge of the parasphenoid to form an interorbital septum. This flange is notched anteriorly and posteriorly to form in part interorbital fenestrae.

The pterosphenoids (Fig. 4.2 B, C) are paired pentagonal-shaped bones providing laterally the posterior walls of the orbit and medially the anteroventral floor of the braincase. Each forms synchrondral joints with the orbitosphenoids on the anterior side, the prootics posteroventrally, the sphenotics postero-dorsally and the frontals dorsally. The ventral edge forms the lateral rim of the orbital foramen (Fig. 4.4). The suture between the pterosphenoids and the prootic bones is broken by a notch in either bone to form the trigeminal foramen. A thin strut projects from the lateral side to form an arch over the trigeminal foramen. The pterosphenoids form a small part of the anterior wall of the hyomandibular facet.

TABLE 4.1

Variation in the number of infraorbital bones of B.burchelli.

No. of Infraorbitals		
Left	Right	No. of Specimens
5	5	12
4	5	1
6	5	2
6	6	2
5	6	1

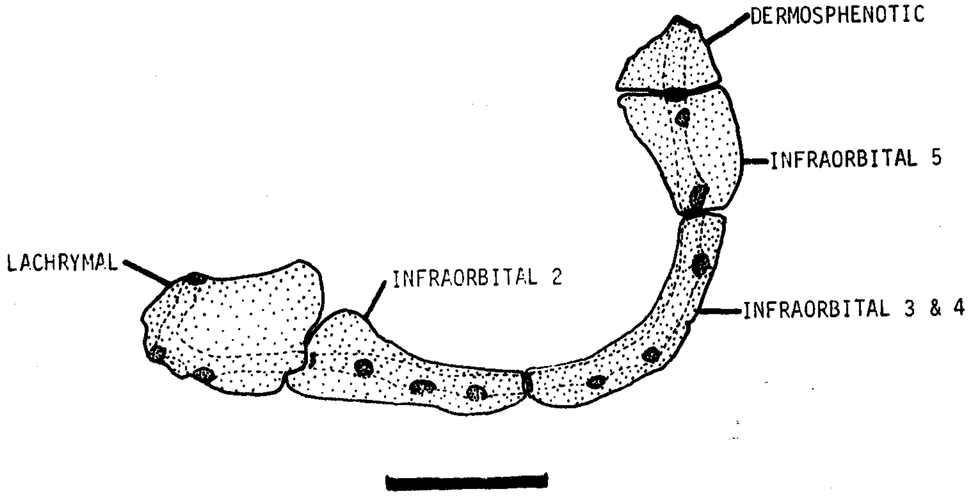


Fig. 4.5 The infraorbital bones of B.burchelli, left side lateral view. Scale bar = 2 mm.

The frontals (Fig. 4.2 A, B, C) are large thin triangular bones which curve gently from the midline to the lateral edges. Medially each forms a sinuous overlapping suture with the other. Posteriorly they overlap the parietals to form a straight margin at right angles to the longitudinal axis of the neurocranium. Each frontal is synchondrally sutured on the ventral side to the respective lateral ethmoid, orbitosphenoid, pterosphenoid and sphenotic bones. The passage for the supraorbital canal arcs above the orbit and separates a supraorbital shelf which curves ventral to abut a lateral spur on the sphenotic. The shelf is indented posteriorly to provide an attachment groove for the dilatator operculi muscle.

The supraorbitals (Fig. 4.2 A, B, C) are usually blunt and semi-rectangular in shape. They fit closely within a notch in the anterior region of the supraorbital shelf and also lie partly against the lateral ethmoids.

Infraorbitals (Fig. 4.5)

There are five infraorbital bones including the lachrymal and the dermosphenotic. Table 4.1 records the infraspecific variation in these bones from 18 cleared and stained B.burchelli specimens. Although a third of the specimens examined showed variation from the usual five infraorbitals on each side the variation was irregular. The variation tended to an increase in the number of bones and frequently this consists of a very short tubular unit intercalated between two normal infraorbitals (e.g. as in Fig. 4.20 I).

The lachrymal is rectangular with a low dorsal crest on the posterior side. The infraorbital sensory canal runs parallel to the anterior and ventral edges of the lachrymal and has two or three intermeidate pores along its length. Each lachrymal attaches to its lateral ethmoid and provides a wall for the nasal capsule.

The second infraorbital is shaped with the anterior end expanded and partly overlapping the lachrymal. The sensory canal with two or three pores passes longitudinally through the bone.

The third infraorbital (fused 3 + 4 according to Nelson, 1969 a) is a narrow curved bone and the longest in the series. The sensory canal has three or four pores.

The fourth infraorbital (=infraorbital 5) is relatively short with

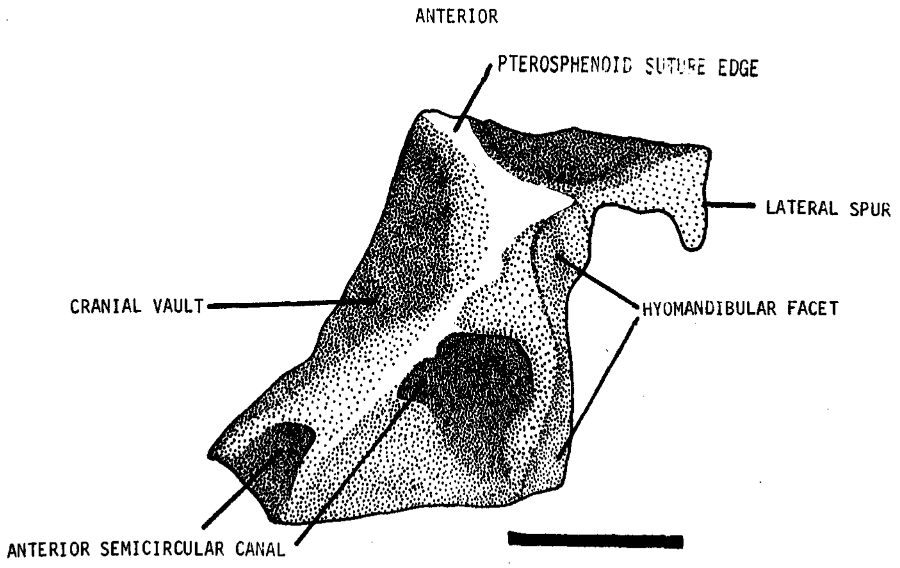


Fig. 4.6 Ventral view of disarticulated left sphenotic bone of B.burchelli. Scale bar = 1 mm.

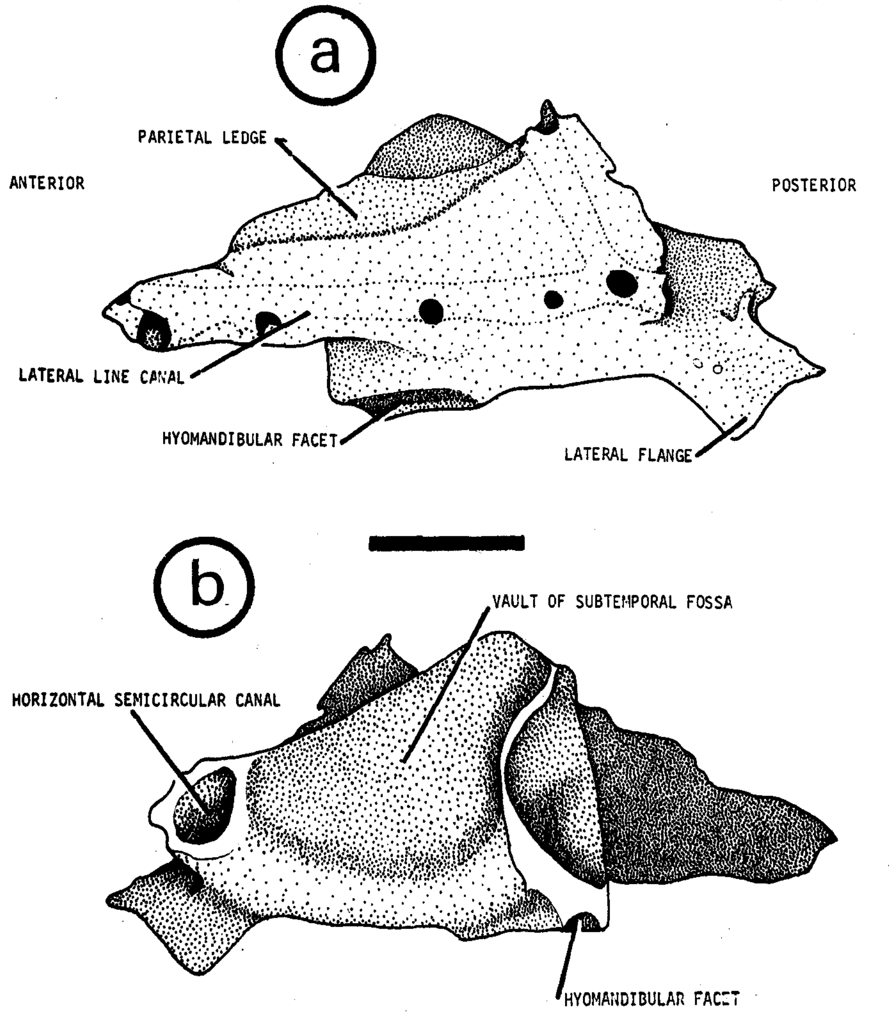


Fig. 4.7 The disarticulated autopterotic bone of B.burchelli, left side (a) lateral and (b) medial view. This particular example includes portion of the supratemporal sensory canal and therefore may include the extrascapular bone. Scale bar = 1 mm.

wider lateral flanges than either of the preceeding units. The sensory canal usually has only a single intermediate pore.

The dermosphenotic is small and triangular in shape with its base the width of the dorsal edge of the preceeding unit. The dermosphenotic meets the neurocranium opposite the junction of the pterotic and frontal bones. The sensory canal has a slight posterior angle and does not have any intermediate pores.

Otic Region

This region broadly encompasses the medio-posterior and dorso-posterior portion of the neurocranium which is deep and box-like, forming the major portion of the braincase. Bones of this region include the sphenotic, autopterotics, prootics, exoccipitals, epioccipitals, supraoccipitals, parietals, extrascapulars and for descriptive convenience, the posttemporals (see pectoral girdle). Use of the name epioccipitals in place of the epiotics is in accordance with Patterson (1975).

Each sphenotic (Figs 4.2 A, B, C; 4.6) forms a trapezoidal plate with a truncated lateral spur. They are sutured anteriorly with the pterosphenoids, ventrally with the prootics, posteriorly with the autopterotics, and dorsally in part with the frontals and a flange from the autopterotics. On the ventral side a broad ridge houses part of the anterior semi-circular canal. The ventral edge contributes to the hyomandibular facet.

The autopterotic (Figs 4.2 A, B, C; 4.7 A, B) is a complex bone sutured anteriorly to the sphenotic, postero-medially to the epioccipital, antero-ventrally to the prootic, and postero-ventrally to the exoccipital. The dorsal medial margin of each borders the cartilage sheet of the posterior cranial fontanelle. Anteriorly a lamellar portion abuts the postero-lateral corner of the frontals. The parietals overlap part of their medio-dorsal surface.

On the ventral side a smooth semicircular ridge marks the passage for the horizontal inner ear canal (Fig. 4.7 B) and forms part of the rim of the subtemporal fossa. A lamellar component (dermopterotic) is fused to the latero-dorsal side (Fig. 4.7 A), and projects forward to overlap the sphenotic.

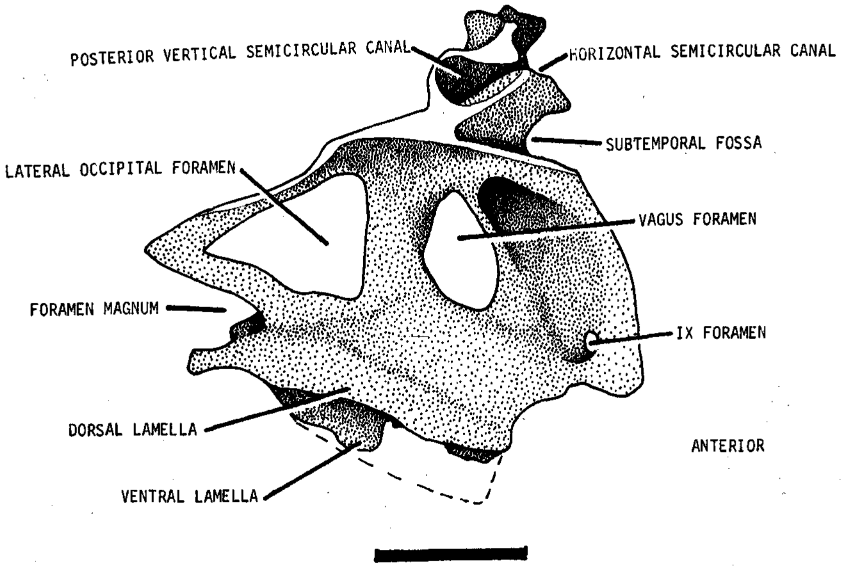


Fig. 4.8 Antero-medial view of disarticulated left exoccipital of B.burchelli. Scale bar = 1mm.

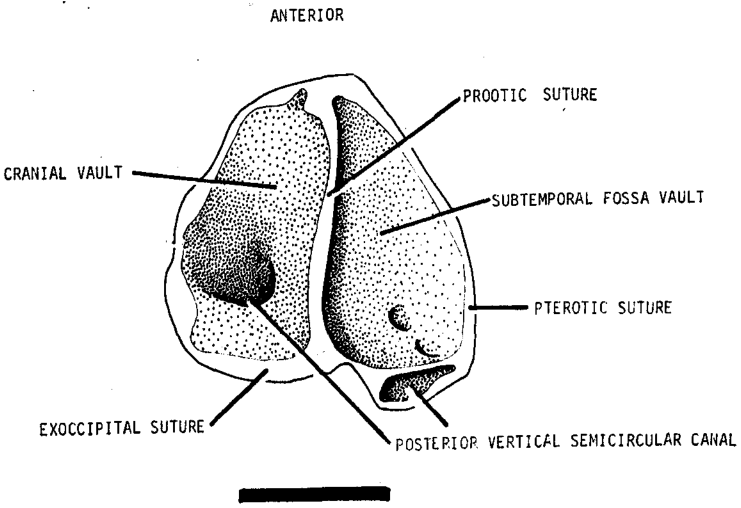


Fig. 4.9 Ventral view of disarticulated left epioccipital of B.burchelli. Scale bar = 1mm.

The prootics (Figs 4.2 B, C; 4.4) are large bones forming the lateral walls of the braincase. They are sutured anteriorly to the pterosphenoid (except for an interruption to form the trigeminal foramen), ventrally with the parasphenoid, and posteriorly with the exoccipital. On the dorsal side they suture anteriorly with the sphenotics and posteriorly with the autopterotics. The median antero-ventral corner forms the posterior border of the orbital foramen (Fig. 4.4).

Ventrally within the braincase each prootic divides into two lamellae, the upper ones meet and partly interdigitate in the midline to form the roof of the posterior myodome and the floor of the braincase (Fig. 4.3). A large foramen passes through the upper lamella of each prootic into the posterior myodome. A conical excavation in the posterior edge of the bone accommodates the anterior portion of the sagitta. The lapillus rests in a shallow basin which bulges externally to form the bulla acoustica utricularis.

Externally the prootic forms the anterolateral rim of the subtemporal fossa. The dorso-lateral margin meets the sphenotic within the hyomandibular facet. The lateral commissure forms a bridge over a recess on the ventral surface which marks the entrance of the passage to the trigeminal foramen. The foramina for the facial (VII) and acoustic (VIII) nerves occur within this recess (Mahy, 1975).

The exoccipitals (Figs 4.7 B, C, D; 4.4; 4.8) are large, complex bones suturing anteriorly with the prootics, dorsally with the epi- and supraoccipitals, laterally with the autopterotics, dorso-medially with each other, and ventro-medially with the basioccipital.

The shape and complexity of the exoccipitals is shown in Figure 4.8. Externally the bone provides part of the median and posterior rim of the subtemporal fossa. This rim is formed from the tubular passage of the horizontal semi-circular canal. The posterior part of this passage also accommodates the vertical semi-circular canal which passes dorsally to the epioccipitals.

There are three prominent foramina: a relatively small glossopharyngeal foramen anteriorly; behind this a large lateral vagus foramen, and postero-laterally the large lateral occipital foramen.

This latter foramen is bounded posteriorly by a thin strip of bone which, together with its counterpart, forms the dorsal border of the foramen magnum. In a similar fashion to the prootics and exoccipitals divide ventrally into two lamellae (Fig. 4.8). The upper lamellae meet in the midline (Fig. 4.4) to form the floor of the braincase and posteriorly the ventral border of the foramen magnum. The lower lamellae form the walls of the cavum sinus imparis (Harrington, 1955) which opens anteriorly into the braincase between the exoccipitals and the prootics.

The epioccipitals (Fig. 4.2 A, C, D; 4.4) are situated dorso-laterally on the posterior slope of the neurocranium. There are synchondroses antero-dorsally with the autopterotics, medially with the supraoccipitals, and ventrally with the exoccipitals. The parietals, extrascapulars and posttemporals lie over the antero-dorsal surface. The anterodorsal edge abuts the cartilage border of the posterior cranial fontanelle.

The epioccipitals are dome shaped (Fig. 4.7) and divided internally by a ridge into two halves which form respectively part of the subtemporal fossa vault and part of the roof of the braincase. The passage for the posterior horizontal canal is evident on the dorsal surface as a low rounded ridge.

The supraoccipital (Fig. 4.2 A, C) is a pentagonal, curved bone sutured laterally with the epioccipital, ventrally with the exoccipitals, and is overlain in part dorsally by the parietals. The anterodorsal corners join a cartilage sheet bounding the posterior cranial fontanelle. A thin low median lamella on the dorsal surface forms a supraoccipital crest.

There are no intercalars (opisthotics) in *B.burchelli*.

The parietals (Fig. 4.2 A) form the posterior roof of the neurocranium. Anteriorly on each a thin ledge fits beneath the posterior end of the frontals. Laterally the parietals overlap the autopterotics and posteriorly the supraoccipital and in part the epioccipitals. The

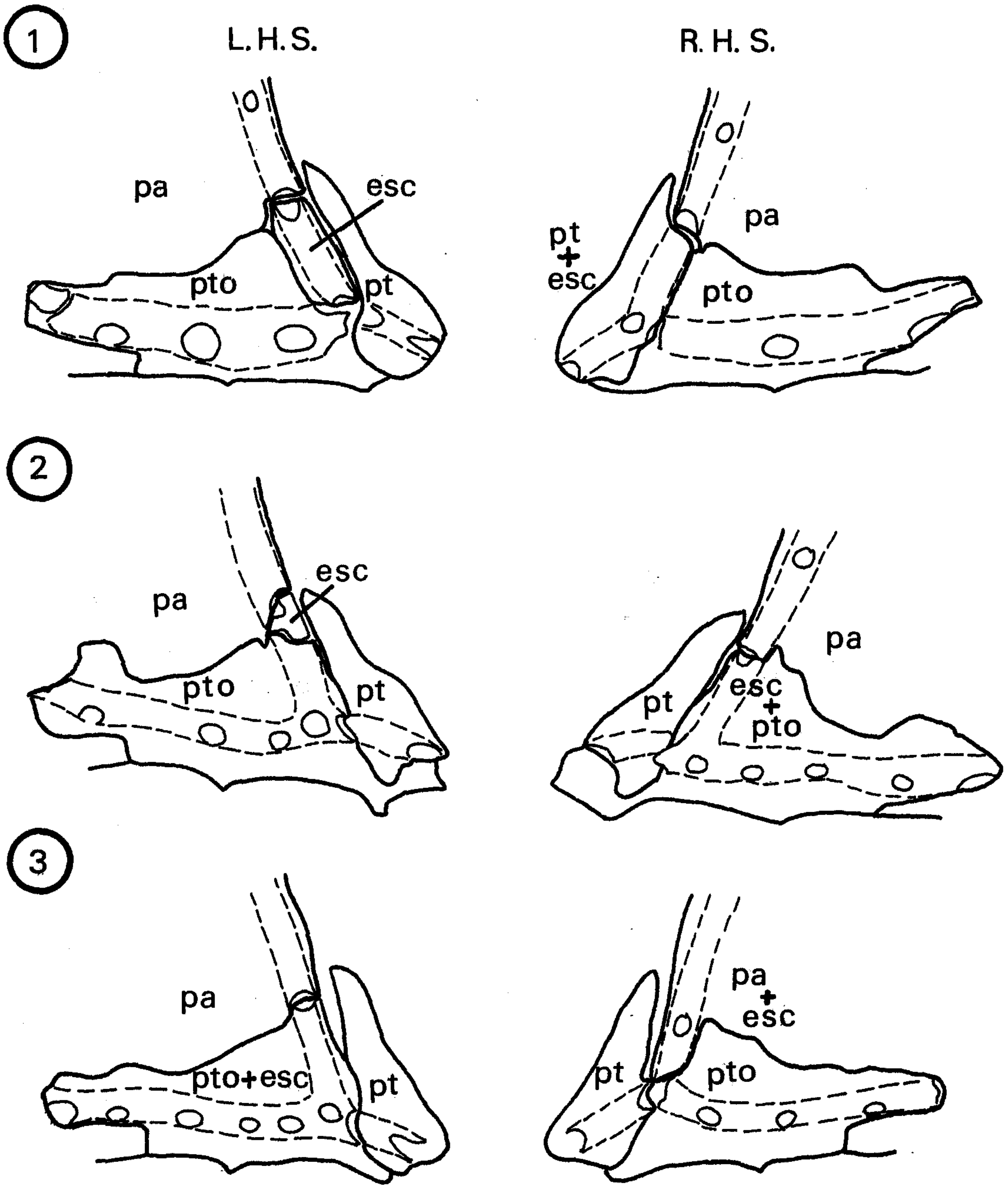


Fig. 4.10 Three examples illustrating the variation of the extrascapular bones on either side of the neurocranium of *B.burchelli*. Abbreviations: esc. - extrascapula; pa - parietal; pt - post-temporal; pto - autopterotic.

supratemporal sensory canal runs close and parallel to the posterior edge of the bones.

The extrascapulars (Figs 4.2 A; 4.8) develop either as separate entities, are absent, or are possibly incorporated with one or other dermal bone in the posterior region of the neurocranium. The interspecific arrangements in regard to this variation are endless and it is exceptional to find a bi-laterally symmetrical arrangement in the same individual. A few examples of such variation are illustrated in Figure 4.10. The extrascapulars are canal-bearing but extremely variable plate-like bones. They suture on the dorsal side of the epioccipital and auto-pterotic bones and may or may not include the junction of the supratemporal, cephalic lateralis and postocular commissure caphalic lateral line canals.

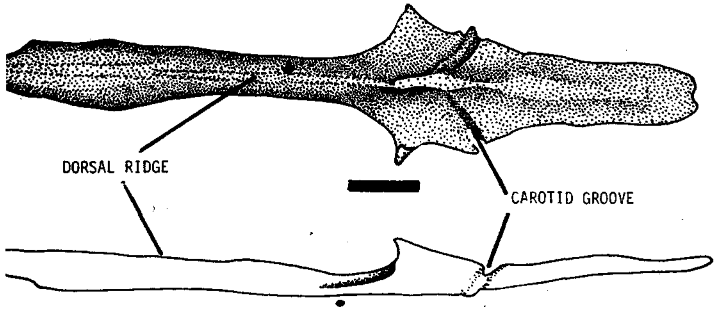
The flat, triangular posttemporals (Fig. 4.2 A) articulate on the dorsal surfaces of the epioccipitals and the pterotics. A strut basal section includes an oblique canal linking the cephalic lateral line with that of the trunk. Each has a slender vertical limb which lies adjacent to the posterior edge of its pterotic, extrascapular and a corner of its parietal.

Basicranial region

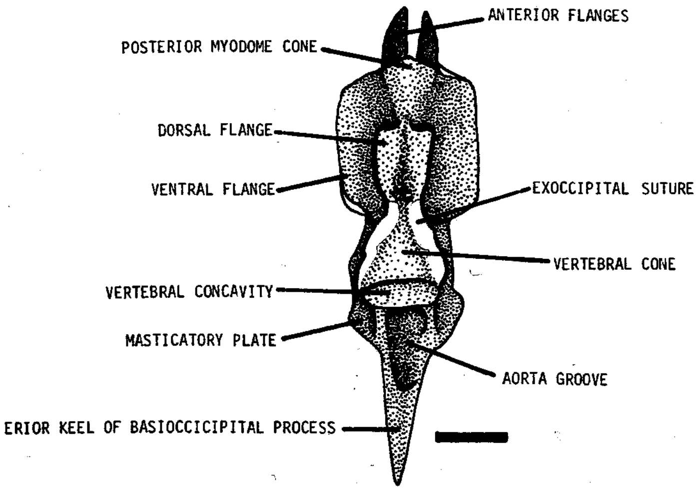
This includes the parasphenoid and the basioccipital bones.

The parasphenoid (Figs 4.2 B; 4.11) extends mid-ventrally from the ethmoid region to the basioccipital. It is a narrow, dagger-shaped bone with the anterior tip wedged between the vomer ventrally and the lateral ethmoids. A dorsal ridge on the vomer slots in with an antero-ventral groove on the parasphenoid. Dorsally a ridge rises to meet and overlap the ventral limb of the orbitosphenoid to form the interorbital septum.

Towards the posterior edge of the orbit the parasphenoid flares laterally to meet and suture with the prootic. It then tapers gradually posteriorly to terminate (usually as a bifurcation) on the ventral side of the basioccipital. A thick dorsal ridge in the midline opposite the point



.11 Disarticulated parasphenoid of B.burchelli, (a) dorsal view; (b) lateral view. Scale bar = 1 mm.



4.12 Dorsal view of the disarticulated basioccipital of B.burchelli. Scale bar = 1 mm.

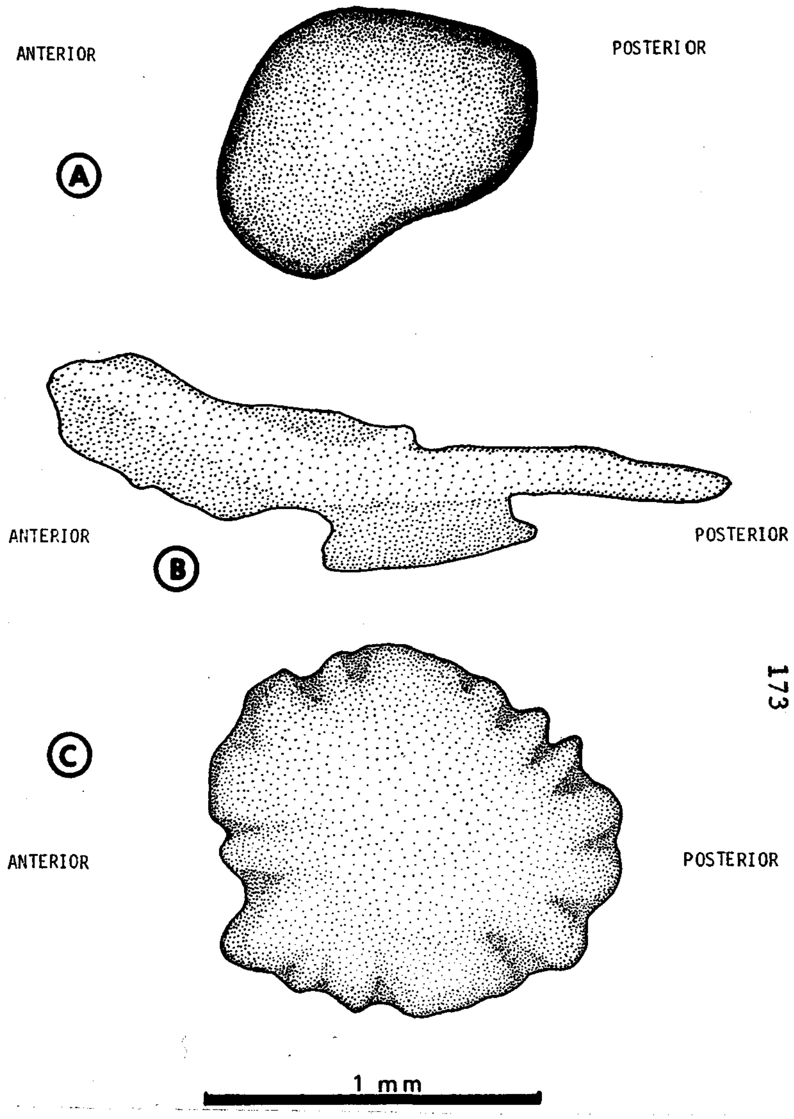


Fig. 4.13 Left otoliths of B.burchelli, (a) lapillus or utriculith, dorsal view; (b) sagitta or sacculith, lateral view; (c) asteriscus or lagenalith, lateral view. Scale bar = 1 mm.

where it flares laterally serves to divide the entrance of the posterior myodome. The parasphenoid forms the floor of the posterior myodome. Two oblique dorsal grooves run from the posterior base of this ridge to the edge of the bone where there are notches which provide foramina for the carotid arteries.

The basioccipital (Figs 4.2 A, B, C, D; 4.12) is a complex bone forming the posterior base of the neurocranium. It is sutured dorsolaterally to the exoccipitals and anteriorly to the prootics. The parasphenoid partly overlaps the anteroventral surface.

An anterior conical excavation in the basal block of the bone forms the posterior extremity of the posterior myodome (Fig. 4.12). Two slender triangular flanges extend forward from the base of the cone. On the dorsal side two other small flanges extend laterally to meet the flanges of the exoccipitals which divides the space between the bones into two compartments housing the posterior part of the sacculus (recessus sacculi) and the lagena (cavum sinus imparis). The latter cavum shows externally as the bulla acoustica lagenaris.

The prominent proatlas cone lies behind the small dorsal flanges and articulates with the first vertebra.

The basioccipital process extends caudad from beneath the proatlas cone at an angle of 30-40°. The ventral surface of the process forms a shallow, concave masticatory plate from which extends a caudad projecting, laterally compressed "keel". A large passage for the aorta passes beneath the vertebral concavity and extends in a dorsal groove on the basioccipital process.

Otoliths (Fig. 4.13)

The utriculus is smooth and kidney-shaped. The asteriscus, the largest of the otoliths, is disc-shaped with a flat medial surface, a convex lateral surface and a low serrated margin and antirostrum. The sagitta is arched and rod like with thin flanges developed from the ventral side. The anterior portion lies in a conical excavation in its prootic.

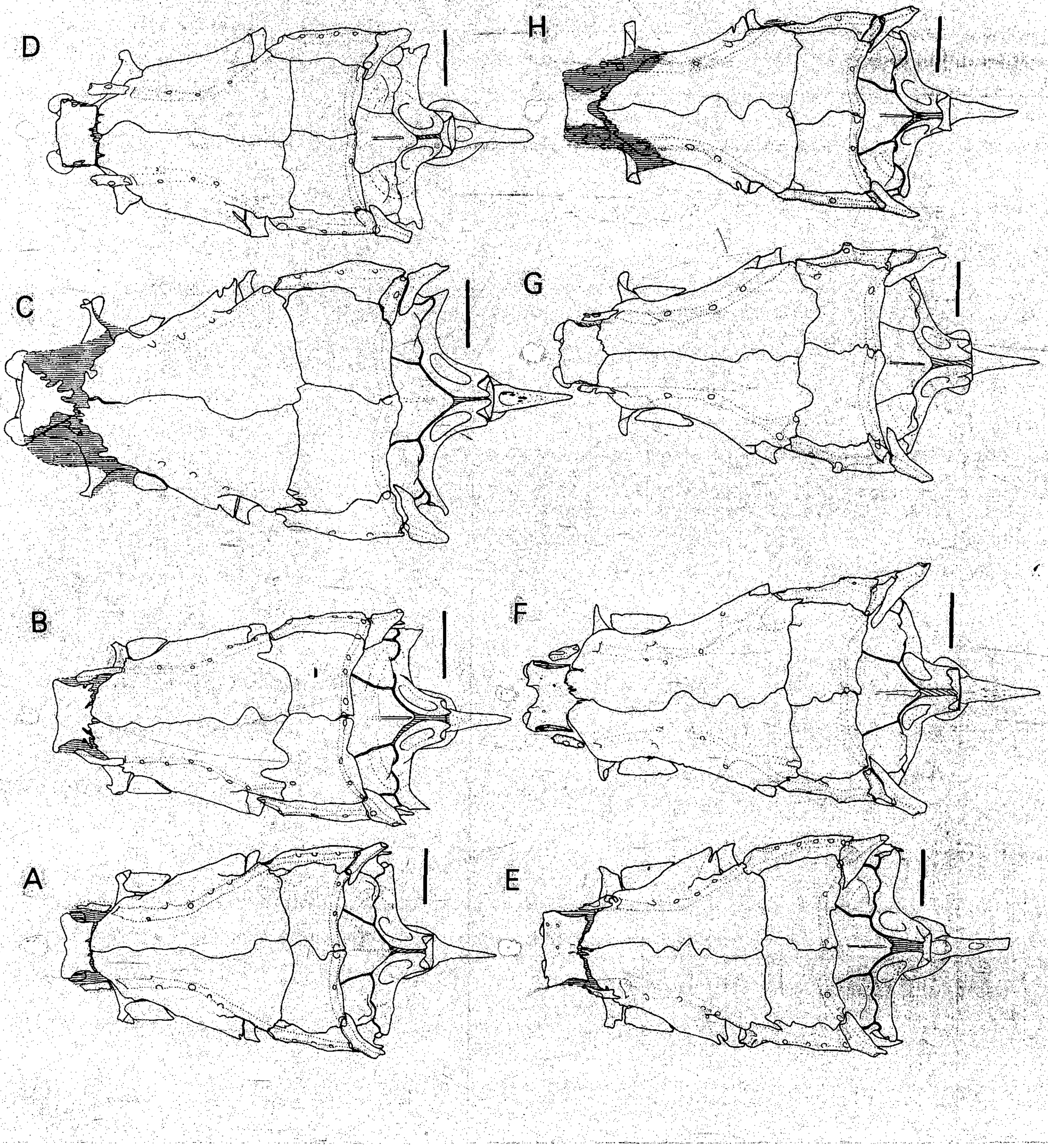


Fig. 4.14 Dorsal view of neurocrania of redfin *Barbus* species and *O.quathlambae*. A - *B.burgi*; B - *B.phlegethon*; C - *B.tenuis*; D - *B.afer*; E - *B.asper*; F - *B.calidus*; G - *B.erubescens*; H - *O.quathlambae*. Scale bar = 2 mm.

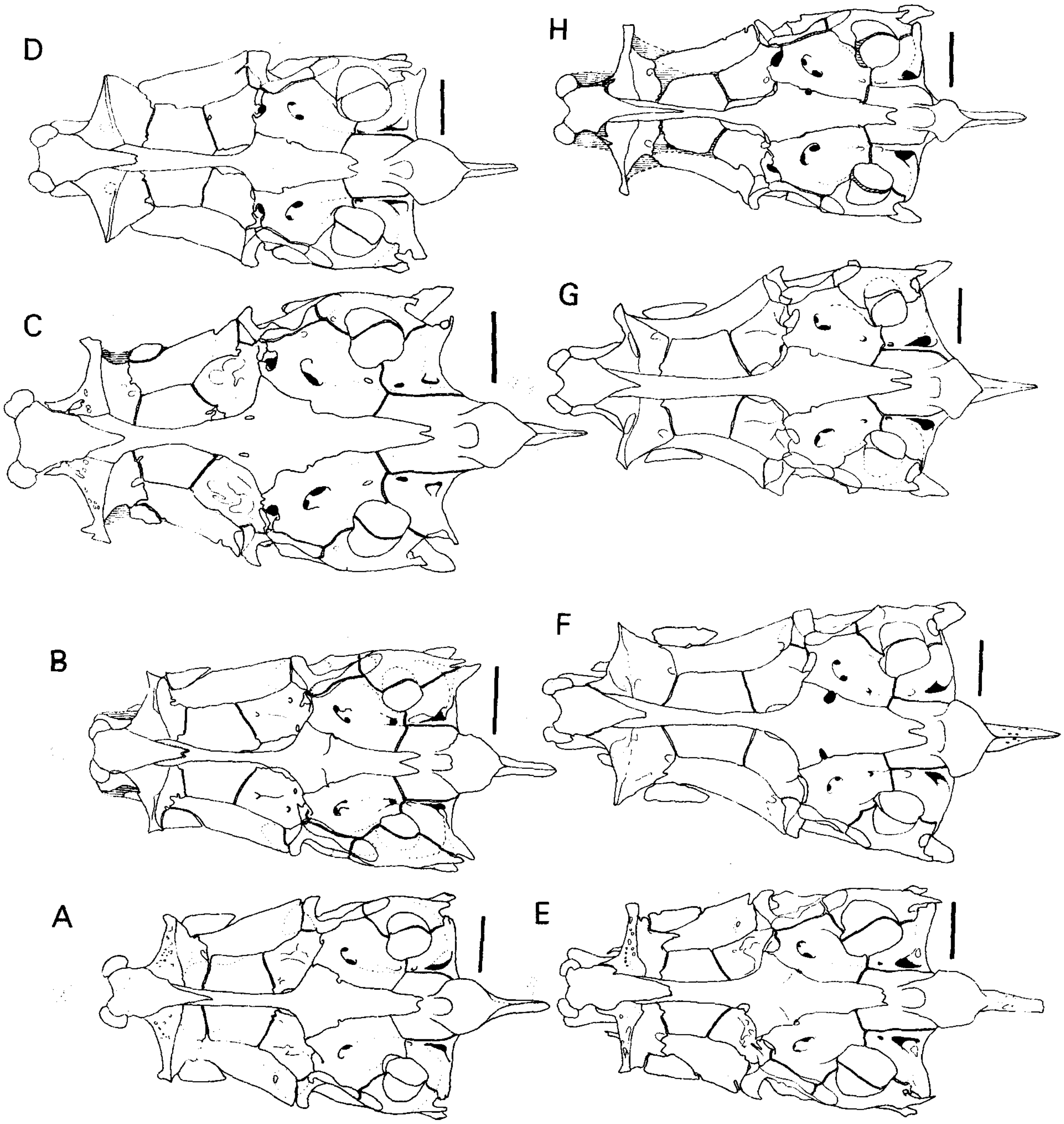


Fig. 4.15 Ventral view of neurocrania of redfin *Barbus* species and *O.quathlambae*. A - *B.burgi*; B - *B.phlegethon*; C - *B.tenuis*; D - *B.afer*; E - *B.asper*; F - *B.calidus*; G - *B.erubescens*; H - *O.quathlambae*. Scale bar = 2 mm.

Comparisons - neurocranium

In general proportions the neurocrania of B.tenuis and B.phlegethon differ most from that of B.burchelli (Figs 4.14-4.17). In B.tenuis it is broad and relatively shallow whereas in B.phlegethon it is relatively narrow and deep. In posterior view (Fig. 4.17) the neurocrania of these two species reflect these differences. B.tenuis has a flat dorsal profile, whereas B.phlegethon has a particularly rounded one.

Although the differences between the remaining species and B.burchelli are not outstanding it is evident that B.burgi, B.afer, B.asper and B.erubescens tend to have generally deeper neurocrania (similar to B.burchelli) and B.calidus and O.quathlambae are more shallow in this respect.

In B.calidus and B.erubescens the basioccipital process descends at an angle of between 50-60° from the horizontal; in the flexible-rayed species this angle is between 30°-40°. The shape of the masticatory plate also differs between species. In the flexible-rayed redfins the plate is flat or slightly concave, and in species with truncated pharyngeal teeth, more rounded and broad. In B.calidus and B.erubescens the plate is more concave and generally tends to be more cardiform. The area of the plate is relatively small in O.quathlambae.

Ethmoid region

The supraethmoid differs in several respects between the redfin species. In all flexible-rayed species the posterior border of this bone is separated from the anterior border of the frontals. The frontals only slightly overlap the posterior dorsal edge of the ethmoid in these species. In B.calidus and B.erubescens the frontals overlap the supraethmoid and there is no "gap" between the two bones.

The supraethmoid of B.calidus and B.erubescens is fairly deeply grooved to receive the kinethmoid bone when the jaws are retracted. There are also two anterior "buttresses" more or less well developed on either side of this notch in these species. In the flexible-rayed species the median groove is shallow and the bone is usually flatter on the dorsal side.

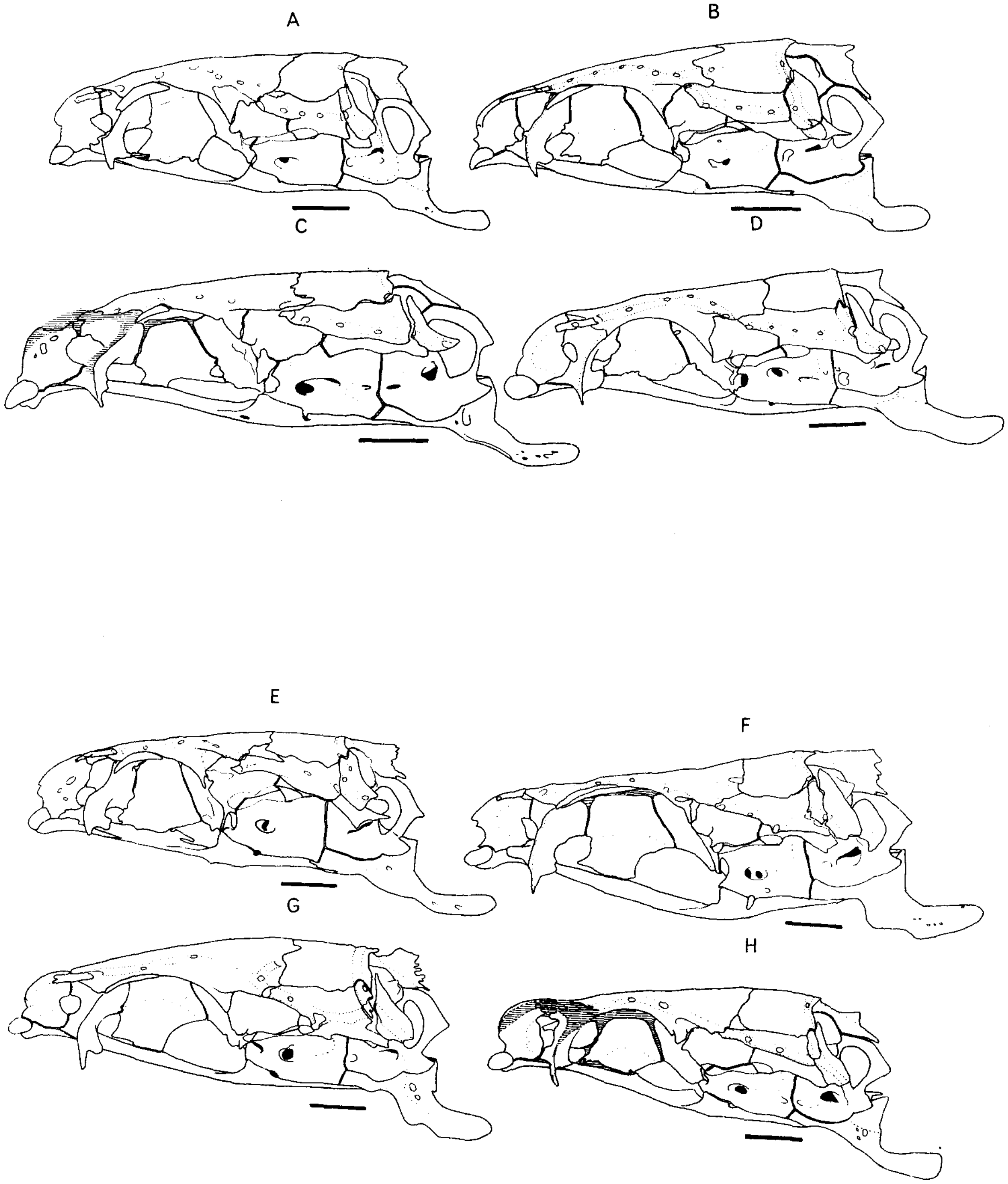


Fig. 4.16 Lateral view of neurocrania of redfin *Barbus* species and *O.quathlambae*. A - *B.burgi*; B - *B.phlegethon*; C - *B.tenuis*; D - *B.afer*; E - *B.asper*; F - *B.calidus*; G - *B.erubescens*; H - *O.quathlambae*. Scale bar = 2 mm.

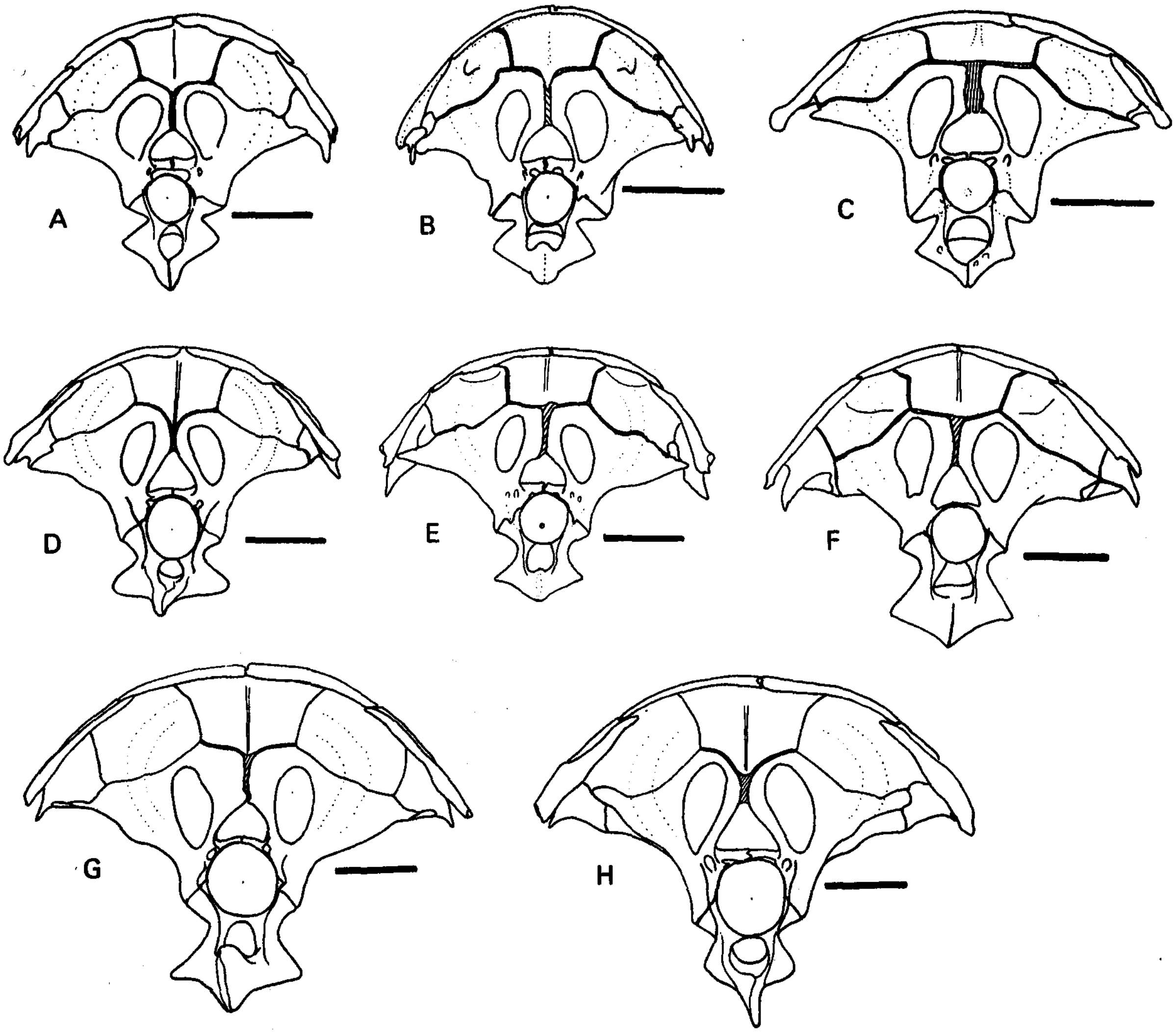


Fig. 4.17 Posterior view of neurocrania of redfin Barbus species and O.quathlambae. A - B.burgi; B - B.phlegethon; C - B.tenuis; D - B.afer; E - B.asper; F - B.calidus; G - B.erubescens; H - O.quathlambae. Scale bar = 2 mm.

In *B.tenuis* and *O.quathlambae* the supraethmoids remain poorly ossified even in adults, as do the margins of adjacent bones in the ethmoid region viz. the lateral ethmoids, frontals, and nasals. These conditions occur only in the juveniles of the other redfins. The nasals of flexible-rayed species usually remain partly unossified.

Articulation facets for the entopterygoids are developed regularly on the ventral surface of the lateral ethmoids of *B.calidus* and *B.erubescens*. Similar articulation facets are present on the lateral ethmoids of some specimens of the flexible-rayed species but they are always small and poorly developed. There are no facets on the entopterygoid as observed by Howes (1978) for certain cyprinids.

The olfactory foramina are formed by notches in the posterior margin of the ethmoid and the anterior margin of the lateral ethmoid bones in all the redfins. In *B.tenuis* and *O.quathlambae* the foramina are frequently large, e.g. the illustration of *O.quathlambae* neurocranium in Greenwood & Jubb (1967, Fig. 2). In certain populations of *B.afer* (e.g. Homtini R.) the foramina are almost entirely enclosed by the lateral ethmoids.

The flexible-rayed redfins have a distinct postero-medial concavity on the lateral ethmoids which in conjunction forms a shallow anterior myodome (see also the description of the neurocranium of *O.quathlambae* by Greenwood & Jubb, 1967). In *B.calidus* and *B.erubescens* the concavities are absent.

Orbital region

The supraorbital shelf of *B.burchelli*, *B.burgi*, *B.phlegethon*, *B.afer* and *B.asper* is wide. In these species the supraorbital bones are relatively broad and stout with a straight lateral and arcuate mesial edge. The supraorbitals fit into a notch in the supraorbital shelves which is antero-dorsally placed in respect of the orbit. The supraorbital bones are generally well developed in the above species with the exception of *B.afer* and *B.asper* where they may be vestigial or entirely absent (e.g. Fig. 4.14 D).

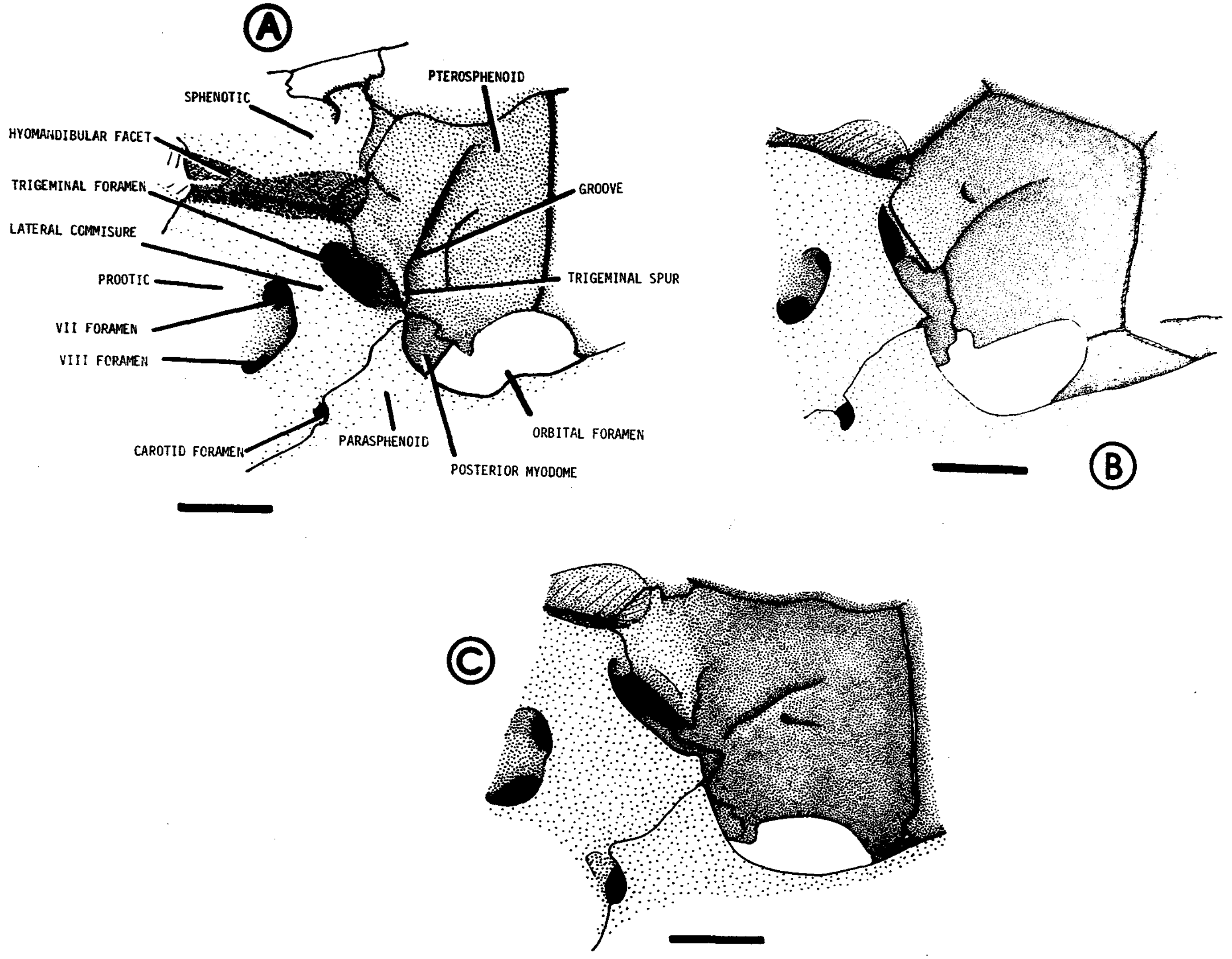


Fig. 4.18 Right latero-ventral view of part of neurocranium of (a) *B.burchelli*, (b) *B.calidus*, (c) *B.erubescens* showing trigeminal foramen, prootic-pterosphenoid suture and part of orbital foramen. Note right pterosphenoid meets left pterosphenoid in *B.calidus* and *B.erubescens*. Scale bar = 1 mm.

The supraorbital shelf of *B.calidus* and *B.erubescens* is relatively narrow. The supraorbital bones of the two species are well developed but their shape (elongated and narrow) differs from that of the other redfins. In addition the supraorbital shelf is only marginally indented to receive the supraorbitals in the two serrated-rayed species.

There are slight differences in the development of the groove for the dilatator operculi on the frontals and sphenotic bones. Again the major difference is between the flexible-rayed species and the serrated-rayed species. In the former the supraorbital shelves are broad (except in *B.tenuis*) and narrow in *B.calidus* and *B.erubescens* and consequently the dilatator operculi groove is relatively small in *B.tenuis*, *B.calidus* and *B.erubescens*. In *B.burgi* the groove is roofed by the expanded dermosphenotic.

The pterosphenoids of the flexible-rayed species do not meet and suture antero-medially, but do so in *B.calidus* and *B.erubescens* (Fig. 4.18). Thus in these latter species the orbitosphenoids are excluded from the orbital foramen.

In *B.calidus* the trigeminal foramen is enclosed entirely by the prootic (Fig. 4.18 B). In *B.erubescens* (Fig. 4.18 C) and other redfins the pterosphenoids form the anterior rim of the foramen. The strut in front of the foramen described for *B.burchelli* also occurs in the other redfins, but is variable in development, often different on each side of a specimen.

The interorbital septum (orbitosphenoid) is generally similar in the species with the exception of *B.tenuis*. In this species it is lower and shorter.

Otic occipital region

Few noteworthy differences have been found in this region of the neurocranium. The extrascapular bones are more regular in form and development in *B.calidus* and *B.erubescens* than in the flexible-rayed redfins. In the serrated-rayed species the extrascapulars agree with the description of those bones by Greenwood & Jubb (1967), viz. "a

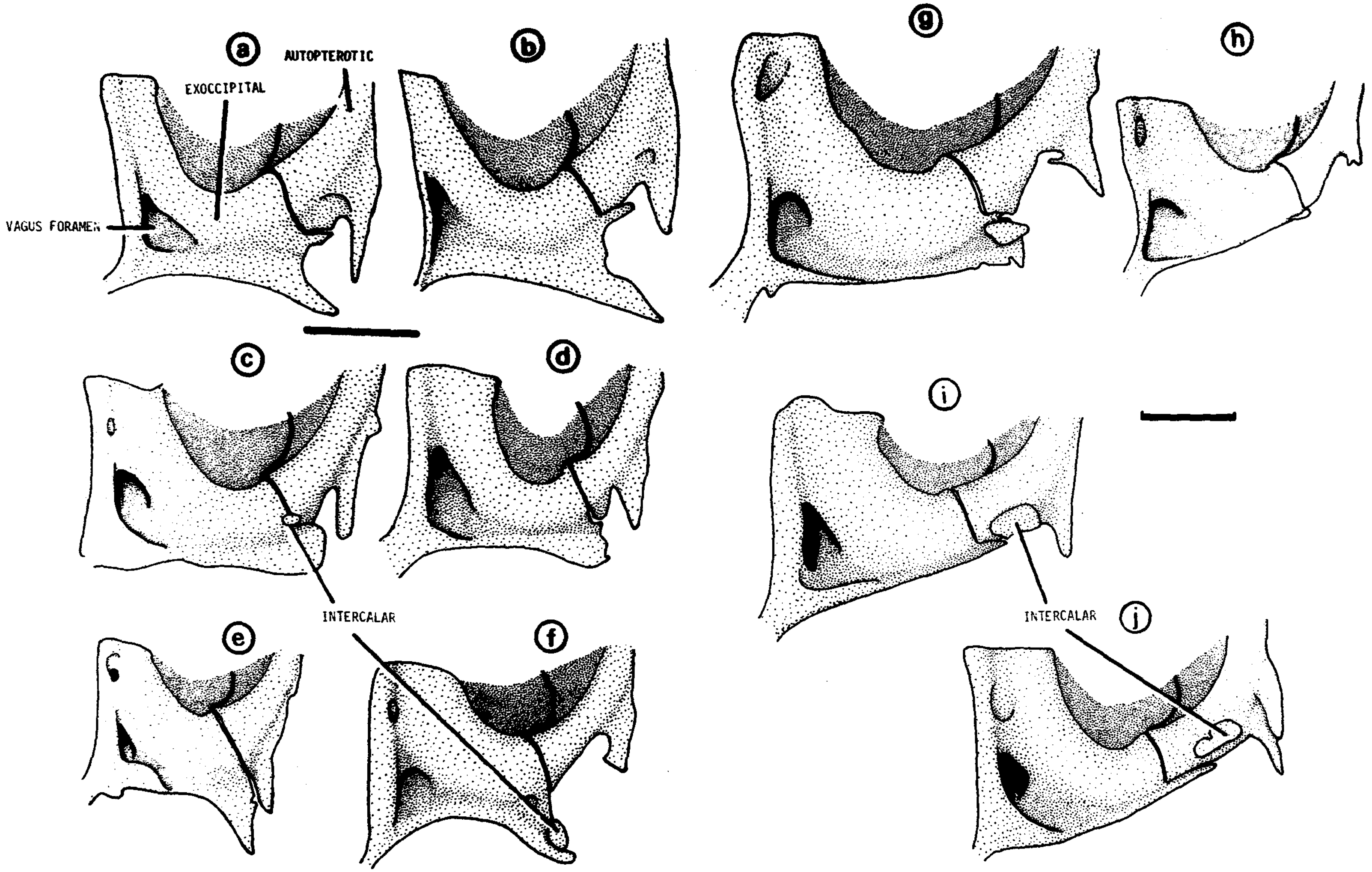


Fig. 4.19 Ventral view of left postero-ventral part of the neurocrania of redfin *Barbus* species and *O.quathlambae* showing the development of flanges on the exoccipital and autopterotic bones as well as the intercalar bones. Labels for all as on A. A - *B.asper*; B - *B.afer*, C - *B.burgi*, D - *B.burchelli*, E - *B.phlegethon*, F - *B.tenuis*, G and H - *O.quathlambae*, I - *B.calidus*, J - *B.erubescens*. Scale bar = 1 mm.

broad blunt triradiate bone carrying the Y-shaped but very unequally armed supratemporal canal".

Intercalars are regularly present in B.calidus and B.erubescens as small irregular discs overlying the ventral postero-medial surface of the autopterotics (Fig. 4.19 I, J). Intercalars are usually vestigial or absent from flexible-rayed species. When these bones are present in the flexible-rayed species they are extremely small and are located over the junction of the exoccipital and pterotic bones.

In B.burchelli and B.burgi (Fig. 4.19, C, D) there is a broad posterior flange on the exoccipitals, which is separated by a narrow gap from a postero-lateral flange of the autopterotic. The autopterotic flange forms a prop for the supracleithrum. B.asper and B.afer are similar to B.burchelli but have the exoccipital flange extended laterally to form a pointed process. B.phlegethon also has a well-developed exoccipital flange which lies much closer to the autopterotic prop than in other redfins (Fig. 4.19 E).

In O.quathlambae the exoccipital rim is only slightly expanded to form a small posterior flange (as e.g. in Fig. 4.19 H). This flange is widely separated from the prop or flange on the autopterotic bone which itself is usually pointed and poorly developed. The exoccipitals form a slender postero-lateral flange in B.tenuis (Fig. 4.19 F), and, as in O.quathlambae, this flange is widely separated from the autopterotic prop.

Basicranial region

In the basicranial region the main difference between the species lies in the form of the basioccipital process. The masticatory plate is flat and broad in the species with truncated pharyngeal teeth (B.burchelli, B.burgi, B.phlegethon, B.afer, B.asper) and relatively less expanded in B.tenuis, O.quathlambae, B.calidus and B.erubescens. In B.calidus and B.erubescens the masticatory plate is slightly concave whereas in the flexible-rayed species it tends to be flat. There is another difference between the serrated-rayed and flexible-rayed species in the basioccipital process. In the former species the process descends at an angle of greater than 55° from the horizontal, but usually at 30° to 40° in the flexible-rayed species.

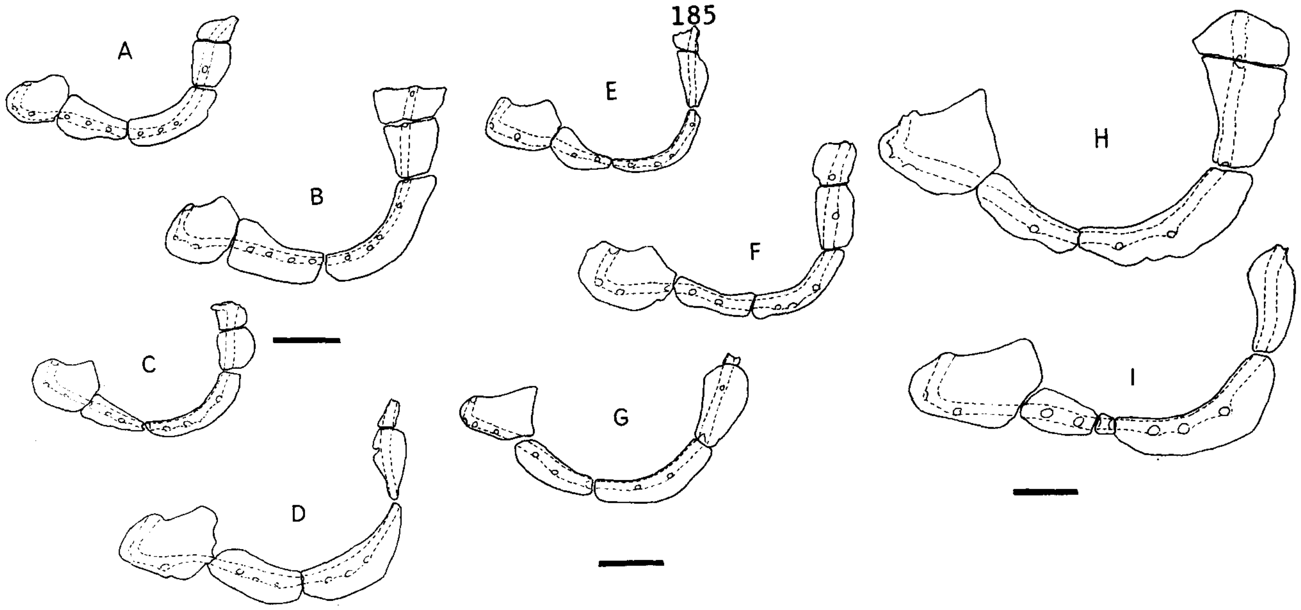


Fig. 4.20 Examples of infraorbital bones of redfin Barbus species and O.quathlambae. A - B.burchelli, B - B.burgi, C - B.phlegethon, D - B.tenuis, E - B.afer, F - B.asper, G - B.calidus, H - B.erubescens, I - O.quathlambae. Scale bar = 2 mm.

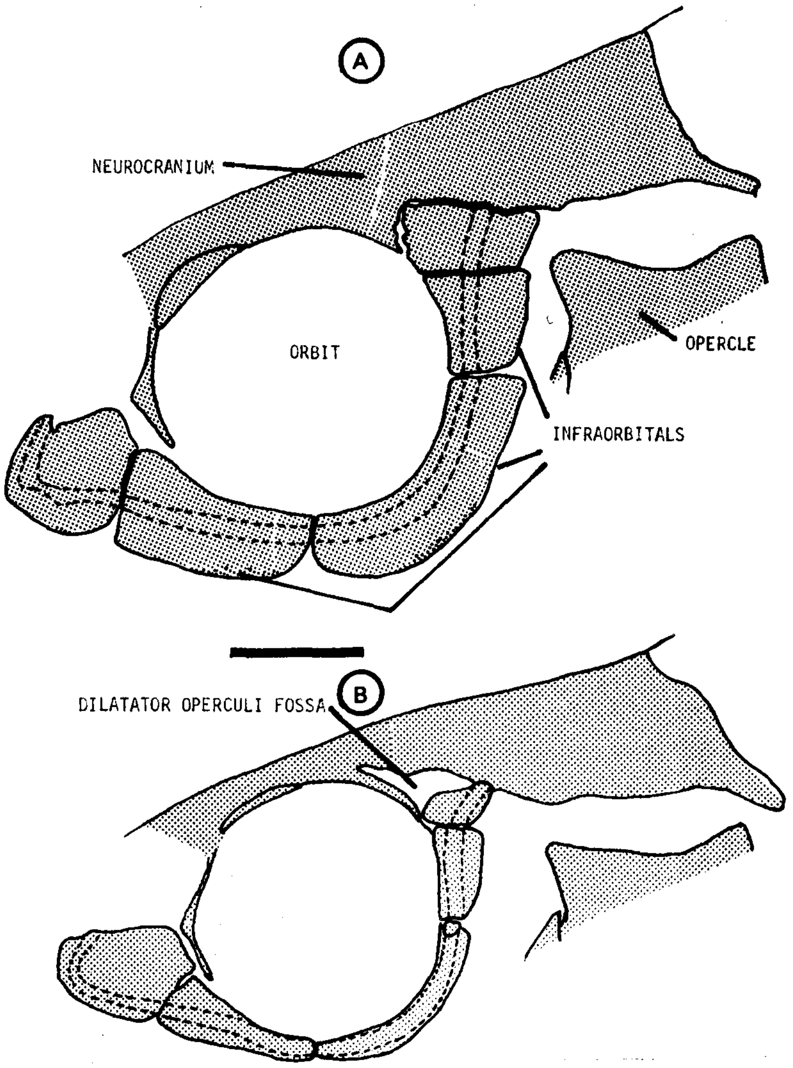


Fig 4.21 Differences between the infraorbital bones of B.burchelli and B. burgi. A. B.burgi; note infraorbitals broad, especially the dermosphenotic which covers the dilatator operculi fossa. B. B.burchelli. Scale bar = 2mm.

The parasphenoid of B.tenuis is generally broader than that of other redfins.

Infraorbitals (Fig. 4.20). Redfin species normally have five infraorbitals except for O.quathlambae which has four (Greenwood & Jubb, 1967). Infraspecific variation in the shape of these bones is usually quite large but B.burgi has distinctly broad infraorbitals (Fig. 4.20). The dermosphenotic of B.burgi forms a roof over the dilatator operculi groove (Fig. 4.21 A) which is diagnostic for the species.

The shape of the lachrymals differs consistently between the serrated-rayed and the flexible-rayed species (Fig. 4.20). In B.calidus and B.erubescens there is a high acute peak on the dorsal side but is usually low and indistinct in the flexible rayed species.

The infraorbitals of B.tenuis are weakly ossified and the dermosphenotic and infraorbital 5 are usually reduced to narrow tubular units.

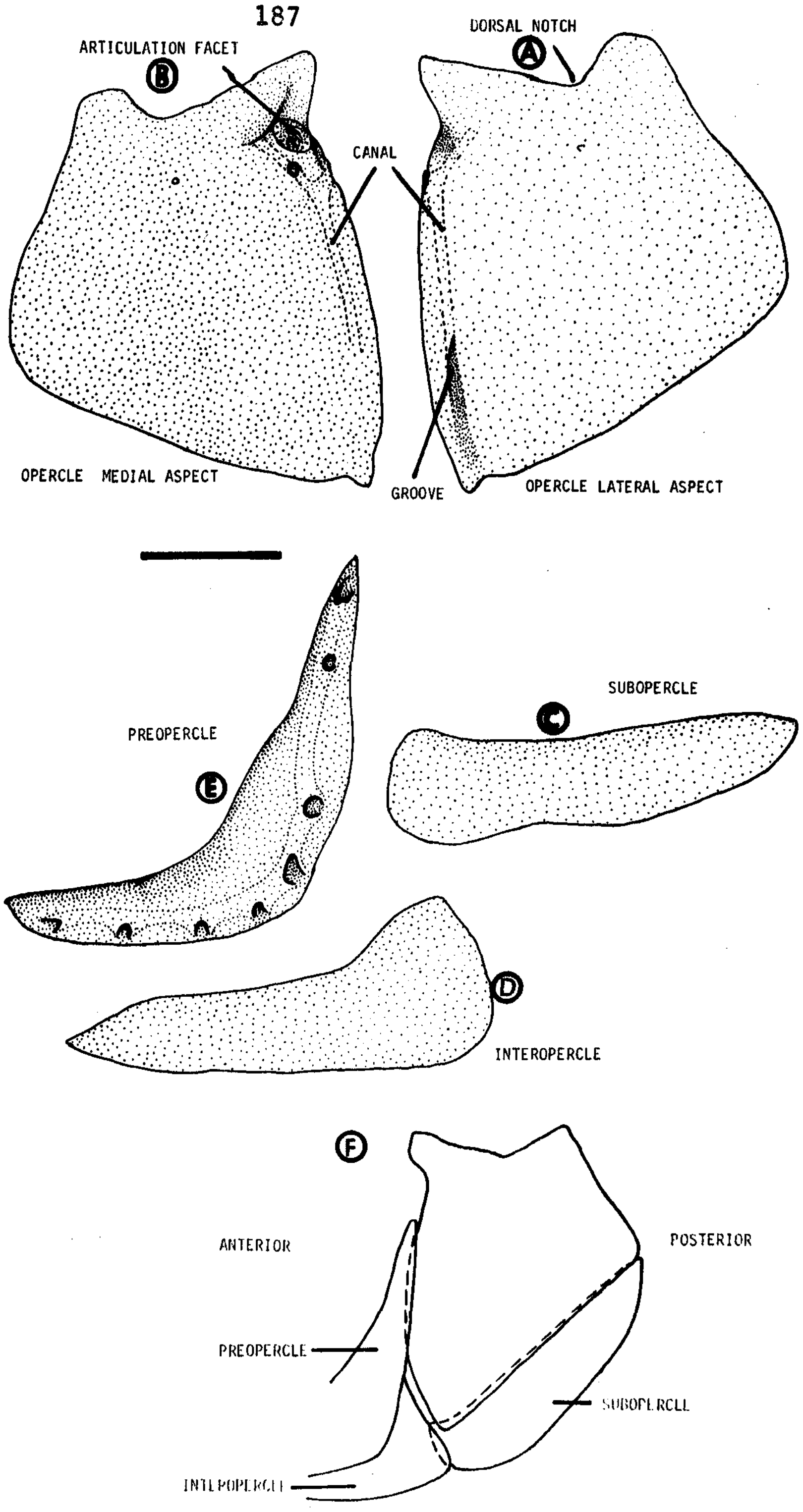
BRANCHIOCRANIUM

This region is divided into five sections: opercular series, suspensorium, mandibular arch, hyoid arch and the branchial arch. Each section will be described for B.burchelli and compared with other redfins before dealing with the following section.

Opercular series (Fig. 4.22)

This comprises four large, flat bones which together form the gill cover: these are the opercle; the subopercle; the interopercle and the preopercle.

The opercle of B.burchelli is a large flat bone with an articulation socket sub-dorsally on the antero-medial surface. There is no canal (suprapreopercular bone?) on the lateral antero-dorsal angle. A vertical canal for the ramus opercularis superficialis branch of the facial nerve (Harrington, 1955) passes from the anterior edge below the articulation socket to emerge and continue as a groove on the



(E) lateral view of preopercle; (F) [illegible]
opercle series. Scale bar = 2 mm.

lateral surface of the bone. A postero-dorsal branch of the canal passes through the base of the articulation socket. The dorsal margin of the bone has a prominent indentation.

The *subopercle* is elongated and tapered posteriorly. It fits below and behind the opercle and is overlapped anteriorly by the interopercle.

The *interopercle* is tapered anteriorly and truncated posteriorly. There is a low postero-dorsal expansion which covers the space between the opercle and the preopercle. The bone lies in front of the subopercle and below the preopercle and is attached anteriorly by a large ligament to the retroarticular.

The *preopercle* is lunate and has a low lateral convex flexure. The preopercular sensory canal passes medially from the dorsal extremity to the antero-ventral extremity and has six or seven intermediate pores which open on the postero-ventral side of the canal. The anterior edge of the vertical limb fits into a groove on the hyomandibular and posteriorly overlaps the opercle. The dorsal edge of the horizontal limb fits into a groove on the quadrate bone.

Comparisons

The opercles of some redfin species (Fig. 4.22) differ in certain respects from that of *B.burchelli*. *B.calidus* and *B.erubescens* have a fused suprapreopercular forming a canal over the lateral antero-dorsal angle (the small bone at the ventral end of the suprapreopercular of *B.erubescens* is not generally characteristic of that or any other redfin species).

B.tenuis, in particular, and *O.quathlambae* have elongated opercles (subject to a certain amount of intraspecific variation). In *B.phlegethon* the opercle is relatively short and deep. The notched dorsal edge is not as characteristic in *B.tenuis*, *O.quathlambae* or *B.asper* as in other redfins.

The opercles of *B.calidus* and *B.erubescens* differ from each other in the following respects: the dilatator process is more prominent in

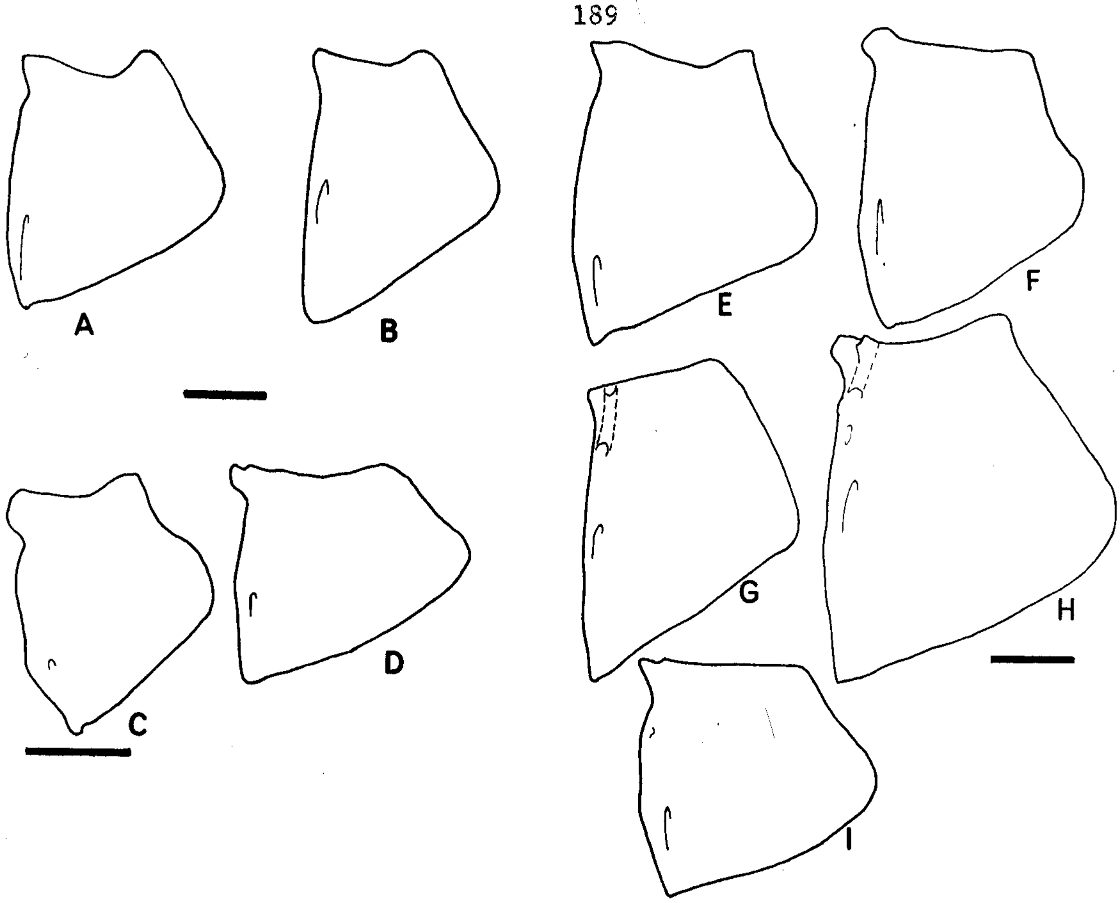


Fig.4.23 Left opercle bones of redfin *Barbus* species and *O.quathlambae*. A - *B.burchelli*, B - *B.burgi*, C - *B.phlegethon*, D - *B.tenuis*, E - *B.afer*, F - *B.asper*, G - *B.calidus*, H - *B.erubescens*, I - *O.quathlambae*. Scale bar = 2 mm.

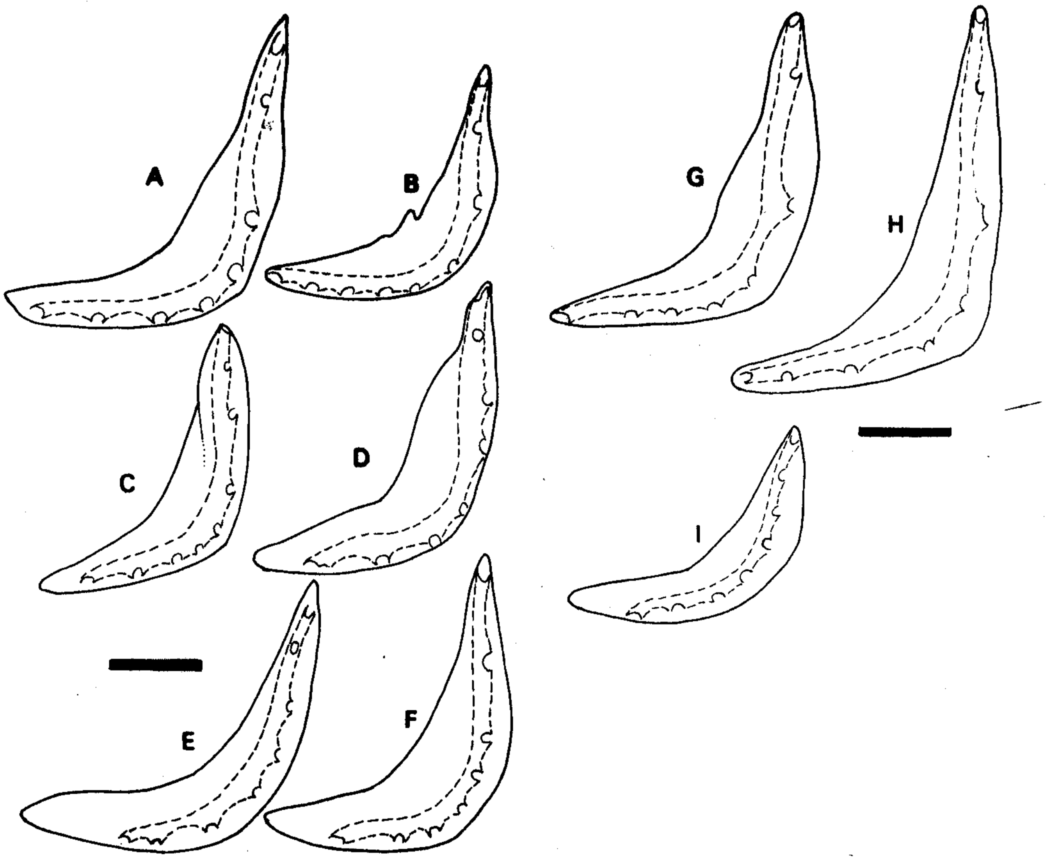


Fig. 4.24 Left preopercle bones of redfin *Barbus* species and *O.quathlambae*. A - *B.burchelli*, B - *B.burgi*, C - *B.phlegethon*, D - *B.tenuis*, E - *B.afer*, F - *B.asper*, G - *B.calidus*, H - *B.erubescens*, I - *O.quathlambae*. Scale bar = 2 mm.

B.erubescens, the dorsal edge is less indented in B.calidus and the postero-ventral angle is more rounded than angular in B.erubescens.

There are no outstanding differences between the sub- and interopercles of the redfins. The preopercle of O.quathlambae (Fig. 4.24) forms a more gentle arc than it does in the other species. The sensory canal terminates on the ventral side of the horizontal limb in all the species except B.burchelli, B.burgi, B.calidus and B.erubescens. This feature is correlated with the development of the mandibular canal.

Suspensorium (Fig. 4.25)

The suspensorial bones are taken here to include the hyomandibular, symplectic, quadrate, metapterygoid, ectopterygoid and the palatine.

The hyomandibular is a tall triangular bone with a moderately thick T-strut base which is flanked with lamellae anteriorly and posteriorly. The oblique dorsal edge is rounded and encapsulated by cartilage to form a dual-headed articulation condyle. A second spherical condyle (opercular articulation facet) protrudes from the posterior edge.

A canal for the facial nerve runs from the mesial surface ventrad to open ventro-laterally. A smaller branch passes posteriorly to emerge in front of the opercular articulation facet.

A cartilage connects the ventral edge of the hyomandibular to the strut-like symplectic. Anteriorly the symplectic fits into a mesial groove on the quadrate. There is usually a notch on the dorsal side of the symplectic to allow a branch of the facial nerve to pass between it and the metapterygoid.

The quadrate forms a ventral horizontal strut surmounted antero-dorsally by a large plate-like flange. The anterior end of the ventral strut forms the articulation condyle for the lower jaw. The dorsal flange in part laterally overlaps the ectopterygoid and endopterygoid. Posterodorsally it meets the metapterygoid edge to edge.

The metapterygoid is a large, plate-like, laterally convex bone which partly overlaps the ectopterygoid anteriorly. The dorsal edge is notched and convex in profile.

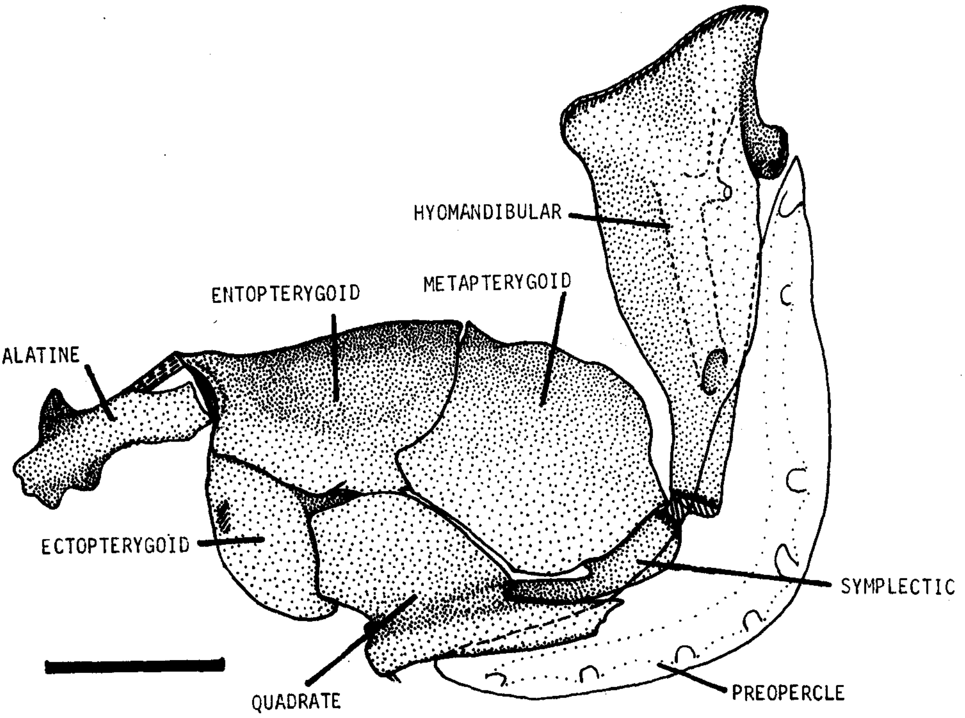


Fig. 4.25 Lateral view of left suspensorium of B.burchelli. Outline of preopercle given to show in situ position. Scale bar = 2 mm.

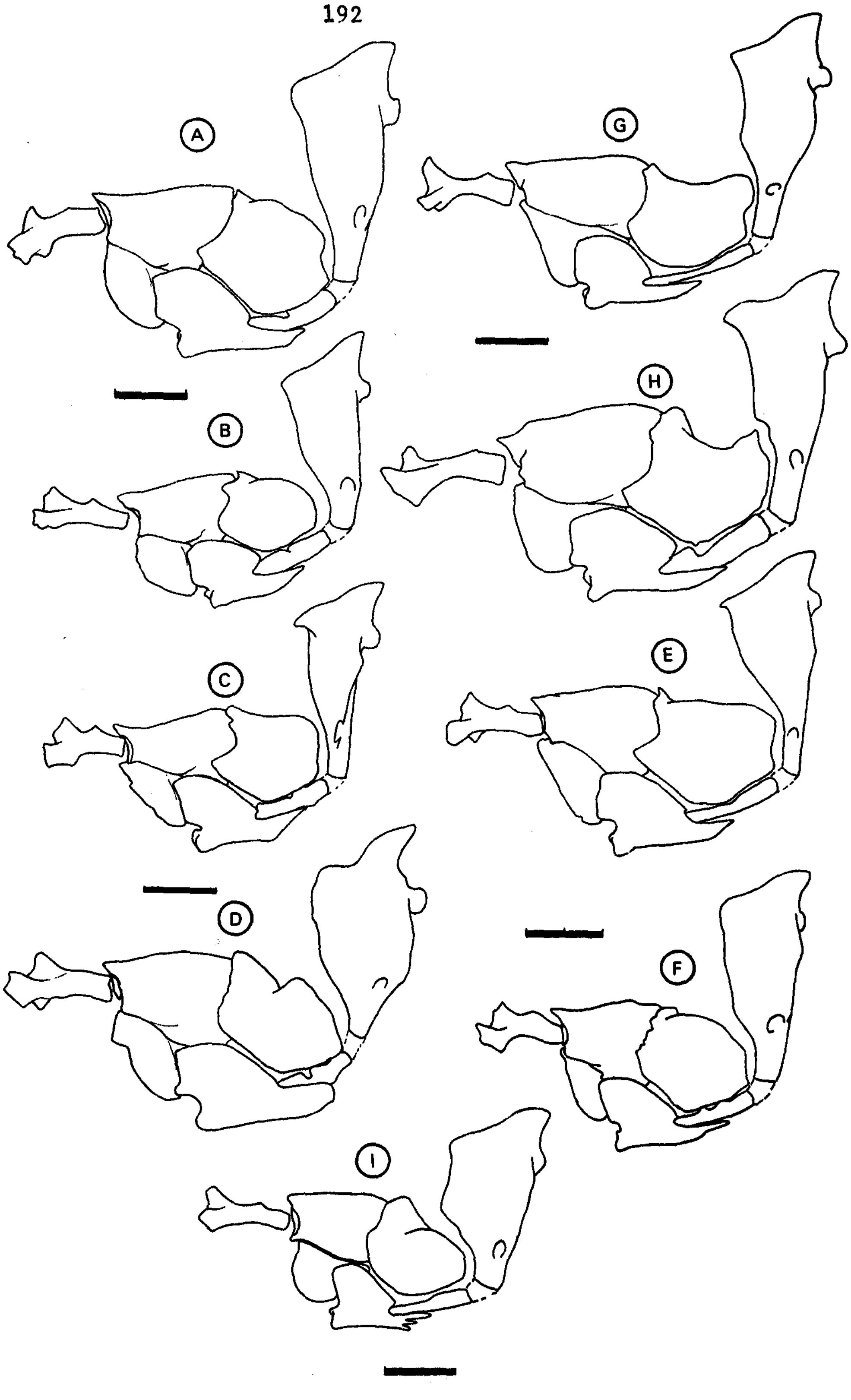


Fig. 4.26 Suspensoria of redfin Barbus species and O.quathlambae.
A - B.burchelli, B - B.burgi, C - B.phlegethon, D - B.tenuis,
E - B.afer, F - B.asper, G - B.calidus, H - B.erubescens,
I - O.quathlambae. Scale bar = 2 mm.

The *entopterygoid* is elongated and trapezoidal with a thickened anterior socket for the palatine. Posteriorly the entopterygoid lies mesial to the metapterygoid and ventrally lateral to the ectopterygoid. A ligament from the anterodorsal surface suspends the bone from the lateral ethmoid.

The rod-like *palatine* articulates posteriorly with the entopterygoid. A ligament attaches from the dorsal edge to the dorsal rim of the entopterygoid socket. Anteriorly the palatine expands to form a mesial bracket with which it articulates with the preethmoid. There is also a antero-lateral projection providing an attachment base for a ligament which inserts on the maxilla.

Comparisons

There are no differences in the architecture of the suspensorium although differences in proportions and details of bones are recorded in Fig. 4.26.

The hyomandibular of *B.phlegethon* is relatively tall and narrow and differs from other species in having a small projection at the anterior base of the dorsal articulation facet. In *B.tenuis* and *O.quathlambae* the hyomandibula is short and broad. In *B.calidus* and *B.erubescens* the anterior flange of the hyomandibula is reduced from the ventral side.

There is a distinction between the metapterygoid bones of the serrated- and flexible-rayed species. In the former the dorsal edge of the metapterygoid is concave whereas in the flexible-rayed species this edge is convex and is usually notched to form two flanges. In *B.tenuis* and *O.quathlambae* this notch is deeper and consequently the two flanges are more pronounced than in the other redfins.

In *B.calidus* and *B.erubescens* the quadrate has an excavation on the ventral side just behind the mandibular articulation facet. This excavation provides space for the posterior process of the angulo-articular when the mouth is open. In the flexible-rayed species there is merely a smooth indentation in this region of the quadrate.

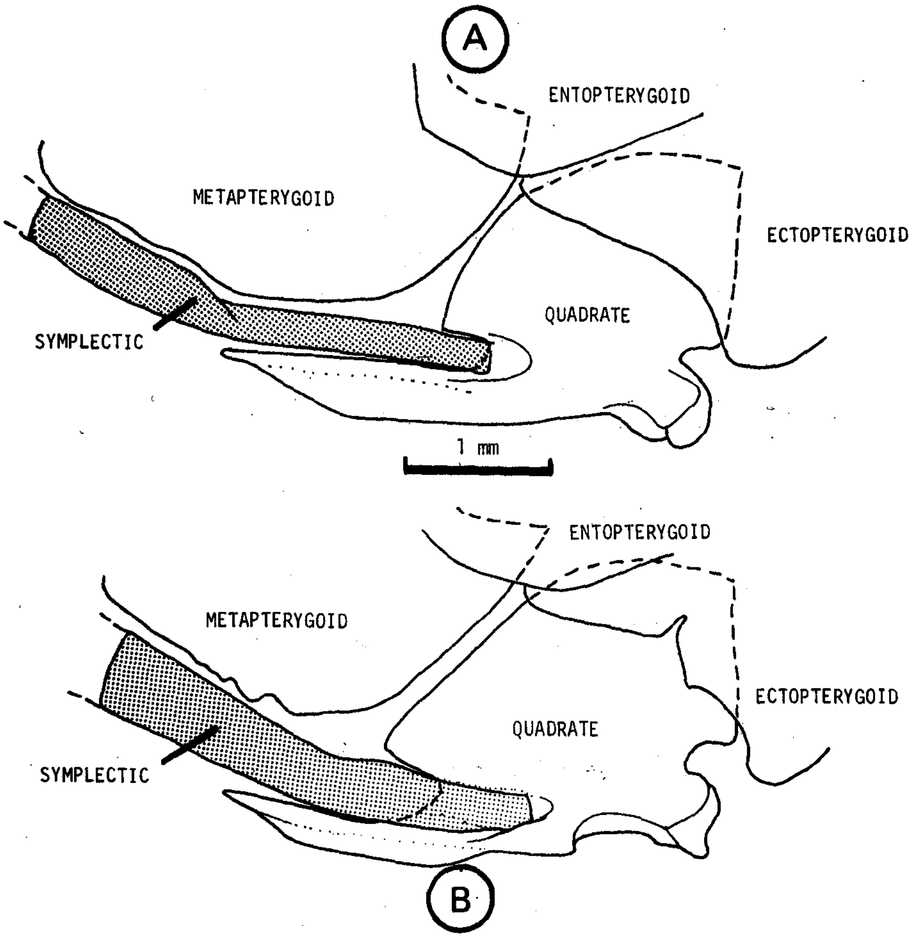


Fig. 4.27 Medial view of part of suspensorium of (A) B.calidus and (B) B.erubescens to illustrate differences between symplectic and thesymplectic-quadrate position of each species. Scale bar = 1 mm.

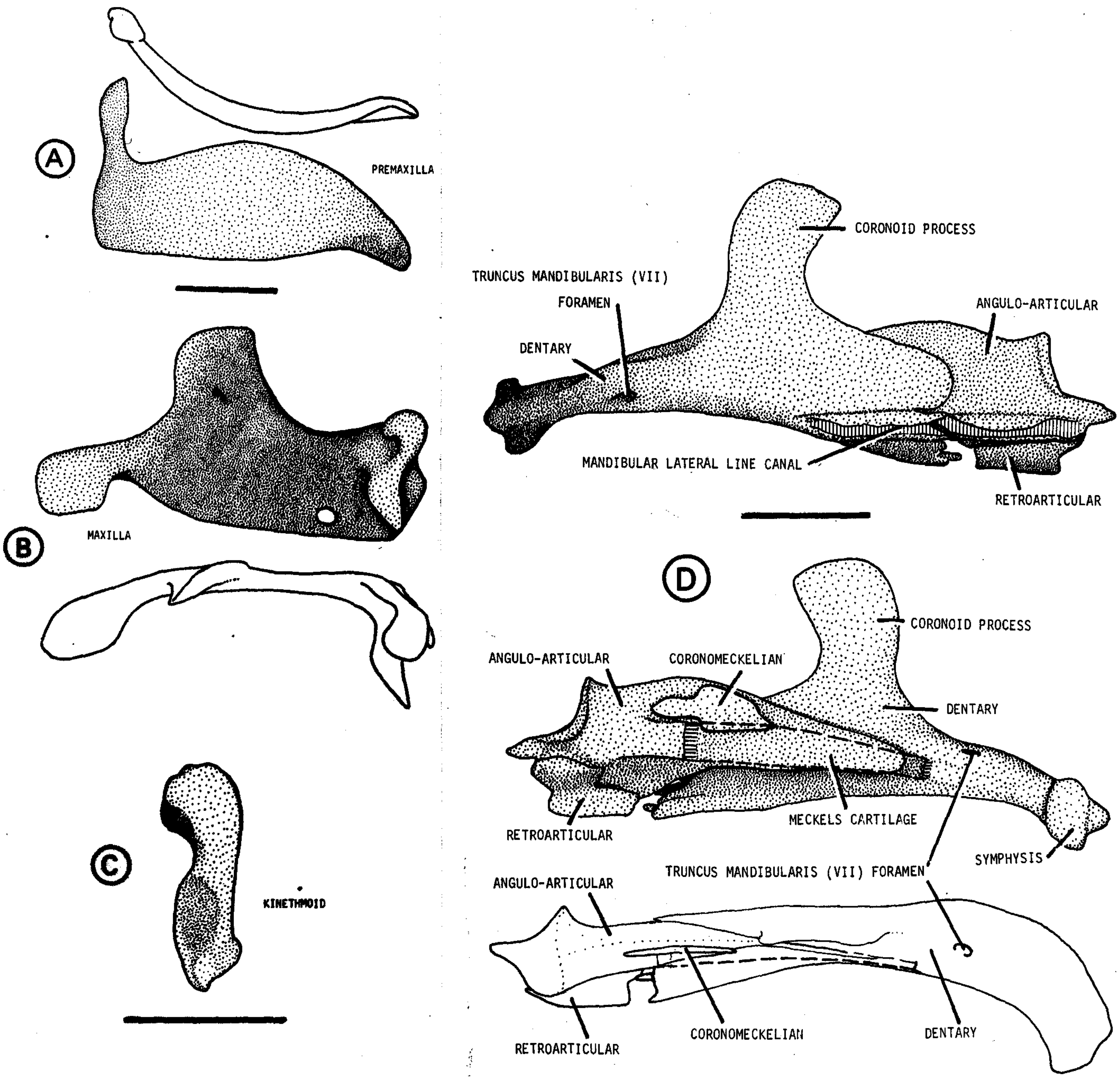


Fig. 4.28 Left mandibular bones of B. burchelli. A - lateral and dorsal views of premaxilla, B - medial and dorsal views of maxilla, C - lateral view of kinethmoid, D - lateral, medial and dorsal views of lower mandible. Scale bar = 1 mm.

Differences between the symplectic-quadrate junction are recorded between B.calidus and B.erubescens. In B.erubescens the symplectic is broader and slots further into the groove on the quadrate than in B.calidus (Fig. 4.27).

Mandibular Arch (Fig. 4.28)

This comprises the bones of the upper and lower jaws and includes the median kinethmoid, premaxillae, maxillae, dentaries, coronomeckelians, angulo-articulars and retroarticulars.

The median kinethmoid (Fig. 4.28 C) is small and club-like. It expands anteriorly on the dorsal side and on the ventral side is laterally compressed. The large sigmoid ligament (Matthes, 1963) joins the dorsal surface to the ascending processes of the premaxillae. A ventral ligament joins to the ethmoid, and two smaller ligaments pass obliquely from the lateral surfaces to the maxillae.

The premaxilla (Fig. 4.28 A) is broad and curves gently mesiad to taper posteriorly. There is a slender ascending process at the anterior end at the base of which the bone forms a symphysis with the opposite premaxilla. The anterior processes of each premaxilla is attached to the kinethmoid by the sigmoid ligament (Harrington, 1955).

The maxilla (Fig. 4.28 B) is broad with a large dorsal ascending process. On the dorso-medial side of the anterior end there is a thick rounded condyle (boss) which articulates with a cartilagenous meniscus. This meniscus is sandwiched between the condyle and the preethmoid. A stout tapered rostral process joins the ventral side of the condyle and forms a catch for the retracted premaxilla. The lateral surface is smooth except for a narrow ledge and shallow excavation below it which provide for the insertion of the ligament from the palatine and the adductor mandibulae muscle respectively. Beneath the ledge a foramen occurs for the nerve to the anterior barbel. Posterior to the dorsal process the maxilla narrows and forms a mesial curved flange.

The dentary (Fig. 4.28 D) has a stout, moderately depressed, curved anterior arm which terminates in an expanded symphyseal head. At

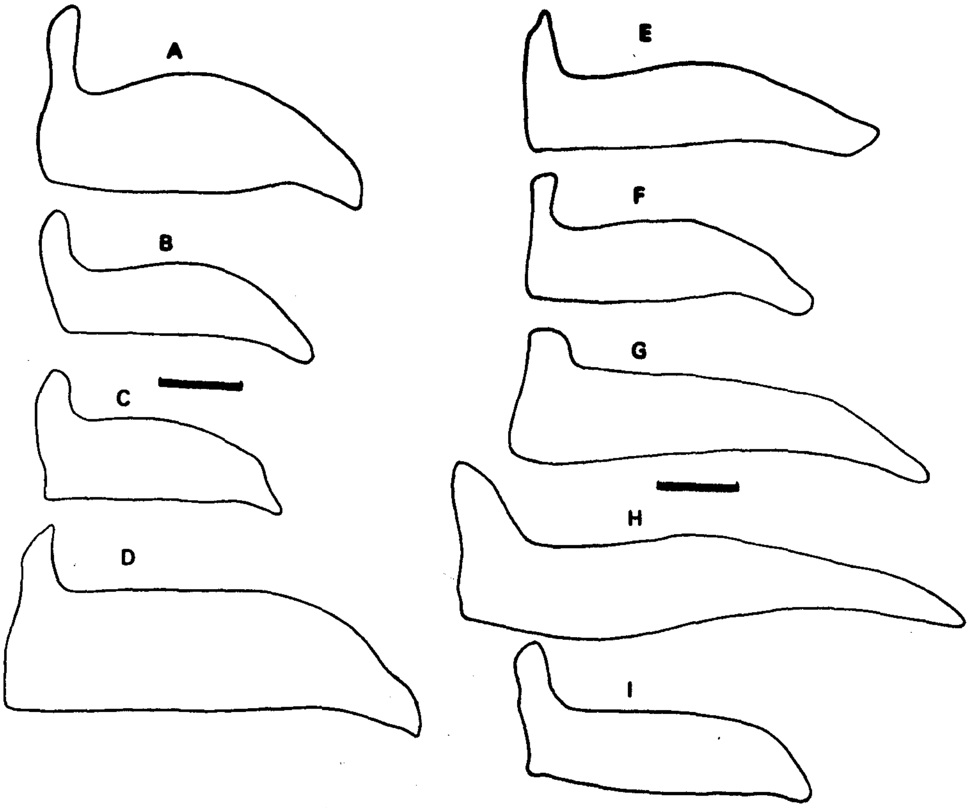
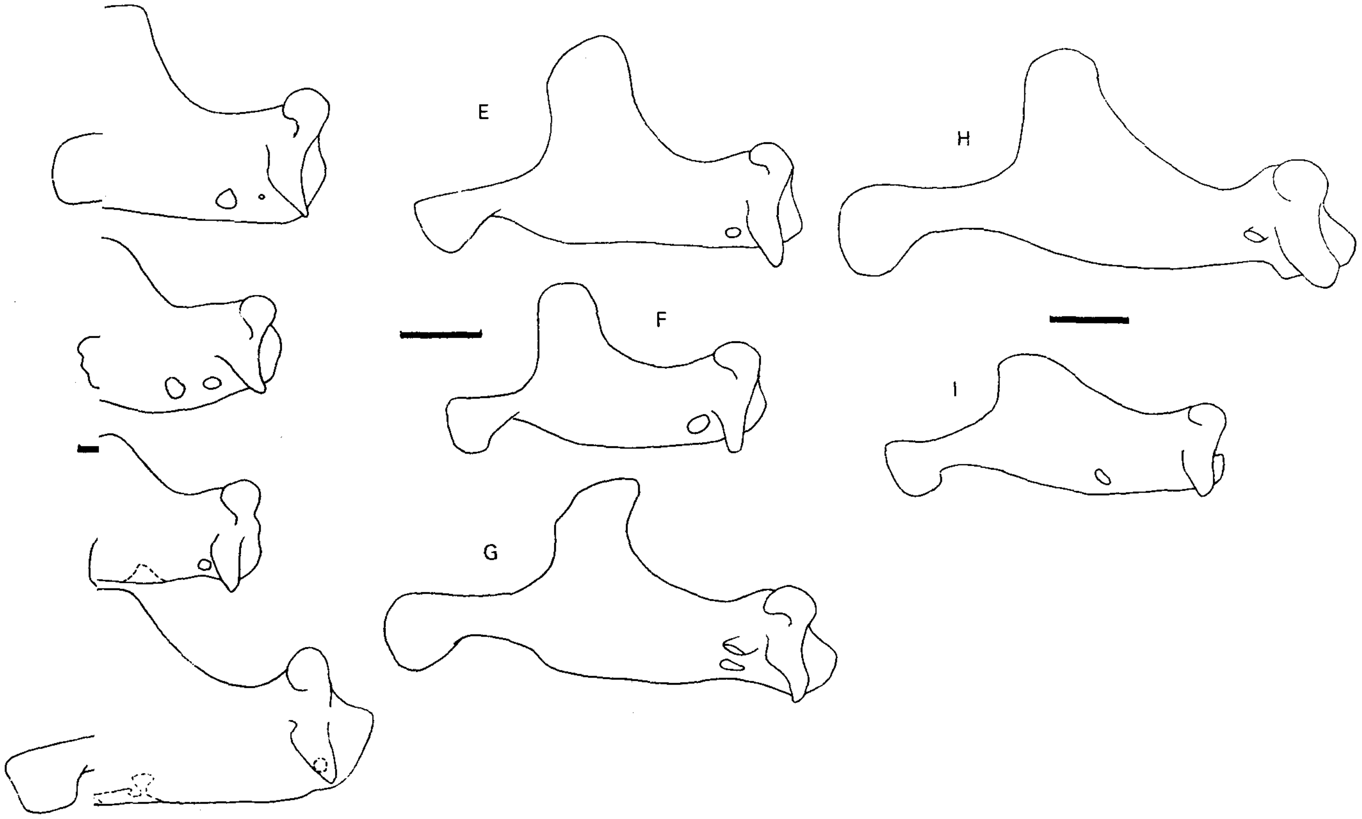


Fig. 4.29 (i) The left premaxillae of redfin *Barbus* species and *O.quathlambae* (lateral view). A - *B.burchelli*, B - *B.burgi*, C - *B.phlegethon*, D - *B.tenuis*, E - *B.afer*, F - *B.asper*, G - *B.calidus*, H - *B.erubescens*, I - *O.quathlambae*. Scale bar = 1 mm.



. 4.29 (ii) Left maxillae of redfin *Barbus* species and *O.quathlambae*. (medial view). A - *B.burchelli*, B - *B.burgi*, C - *B.phlegethon*, D - *B.tenuis*, E - *B.afer*, F - *B.asper*, G - *B.calidus*, H - *B.erubescens*, I - *O.quathlambae*. Scale bar = 1 mm.

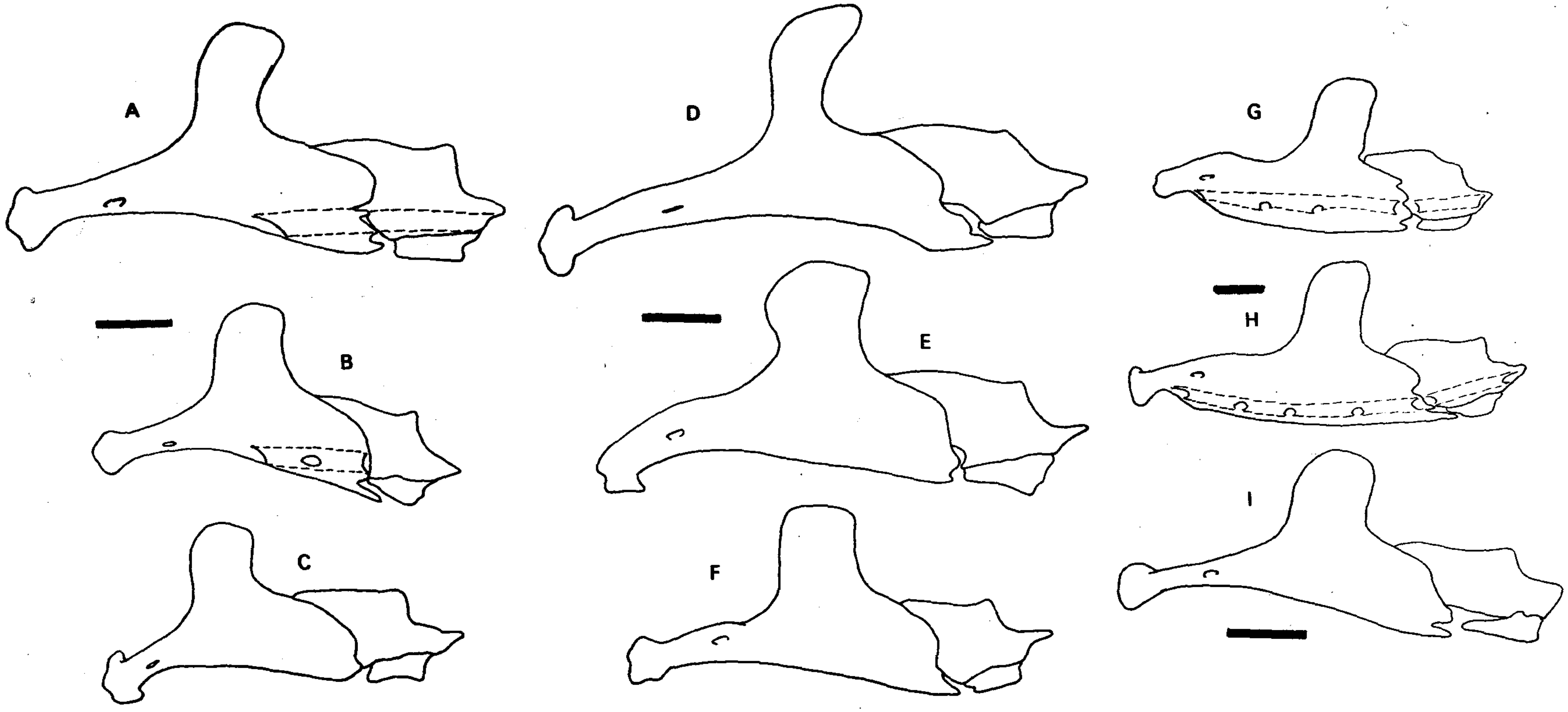


Fig. 4.29 (iii) Left mandible of redfin *Barbus* species and *O.quathlambae* (lateral view). A – *B.burchelli*, B – *B.burgi*, C – *B.phlegethon*, D – *B.tenuis*, E – *B.afer*, F – *B.asper*, G – *B.calidus*, H – *B.erubescens*, I – *O.quathlambae*. Scale bar = 1 mm.

the base of the tall, laterally compressed coronoid process there is a medial groove which accommodates the angulo-articular and coronomeckelian. Meckel's cartilage extends from a ridge at the anterior end of the groove. A short tube for the mandibular sensory canal occurs postero-ventrally on the lateral side. A foramen for the truncus mandibularis branch of the facial nerve passes obliquely in front of the coronoid process (Mahy, 1975).

The angulo-articular is flattened anteriorly and articulates within the medial groove of the dentary. Meckel's cartilage lies on the medial side of this anterior portion and joins a ridge on the stout posterior part of the bone. There is a large postero-dorsal articulation facet with a small posterior process. There is a latero-ventral tube for the mandibular sensory canal.

The small irregular coronomeckelian articulates behind the medial ridge and Meckel's cartilage.

The retroarticular is small and roughly L-shaped, and sutures to the postero-ventral surface of the angulo-articular. A ligament joins from the posterior surface to the interopercle.

Comparisons (Fig. 4.29)

There is a distinct difference in proportion in the upper jaws between the serrated-rayed and flexible-rayed redfin species. Both the premaxillae and maxillae of *B.calidus* and *B.erubescens* are more slender and elongated with lower ascending processes than those of the flexible-rayed redfins. The maxillary foramina of these two species are directed obliquely (postero-ventral) through the bone and not simply at right angles as in the flexible-rayed redfins.

The lower jaws of *B.calidus* and *B.erubescens* have an extensive ventral flange on the lateral part of the dentary which bears a tube for the mandibular sensory canal. The tube passes anteriorly beyond the coronoid process and has two or three intermediate pores. Of the flexible-rayed redfins only *B.burchelli* and *B.burgi* have the mandibular lateral line canal. This is however restricted to the posterior portion of the dentary and the angulo-articular, or in the case of *B.burgi* from the Berg River System, to only the dentary.

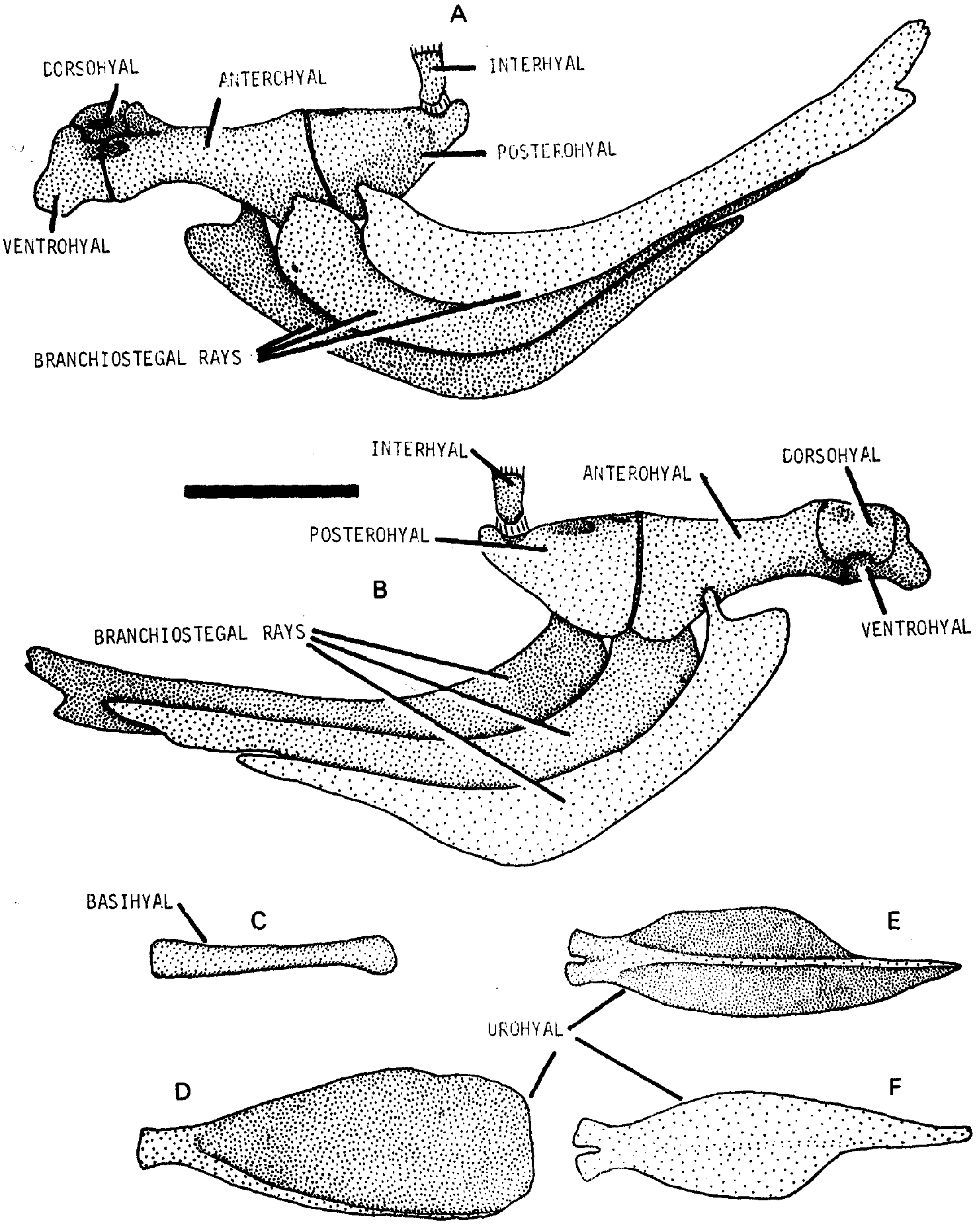


Fig. 4.30 Hyoid arch of B.burchelli excluding hyomandibula. A - lateral view of part of hyoid arch, B - medial view of part of hyoid arch, C - disarticulated basihyal, D - lateral view of urohyal, E - dorsal view of urohyal, F - ventral view of urohyal. Scale bar = 2 mm.

The coronoid process is tall and slender in *B.tenuis* and the anterior limb is elongated. The anterior limb of the dentary of *O.quathlambae* is also elongated. The dentary of *B.phlegethon* has a short, stout anterior limb.

Hyoid arch (Fig. 4.30)

As the hyomandibular has already been included in the suspensorium the hyoid arch is here taken to include the interhyal, posterohyal, anterohyal, ventro- and dorsohyals and the urohyal, as well as three branchiostegal rays. The terminology used follows Nelson (1969 b).

The *interhyal* is a small cylindrical bone suspended vertically between the cartilage at the ventral end of the hyomandibular and the latero-dorsal end of the posterohyal (=epihyal).

The *posterohyal* is a laterally compressed triangular bone sutured anteriorly with the anterohyal. The interhyal articulates in a notch on the lateral-dorsal edge. The posterior (3rd) branchiostegal ray articulates on the lateral surface.

The *anterohyal* is a laterally compressed elongated bone, which anteriorly forms a dual articulation head for the dorso- and ventrohyals. A small notch on the antero-dorsal edge forms the attachment point of a ligament from the basihyal.

The *ventro*- and *dorsohyal* (hypohyals) are short L-shaped blocks sutured posteriorly with the anterohyal and anteriorly with each other. The hyoid foramen is formed by the junction of the hypohyals with the anterohyal.

The *basihyal* is a depressed, club-like bone which is attached to both anterohyals by ligaments.

The *urohyal* forms an oblong horizontal plate surmounted by a vertical medial plate. The anterior end is thickened and divided to form two lateral heads for ligaments attaching to either ventrohyal. Posteriorly the horizontal plate is usually asymmetrically tapered in *B.burchelli*.

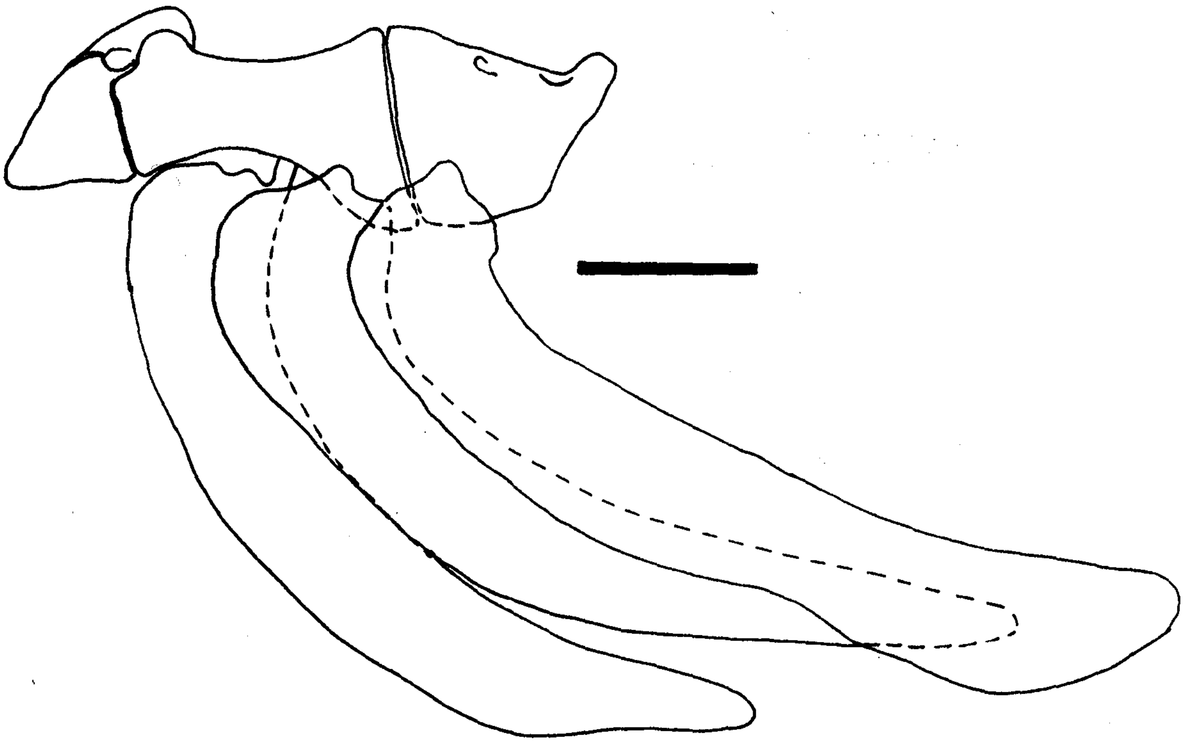


Fig. 4.31 Lateral view of part of the hyoid arch of B.phlegethon.
Scale bar = 1 mm.

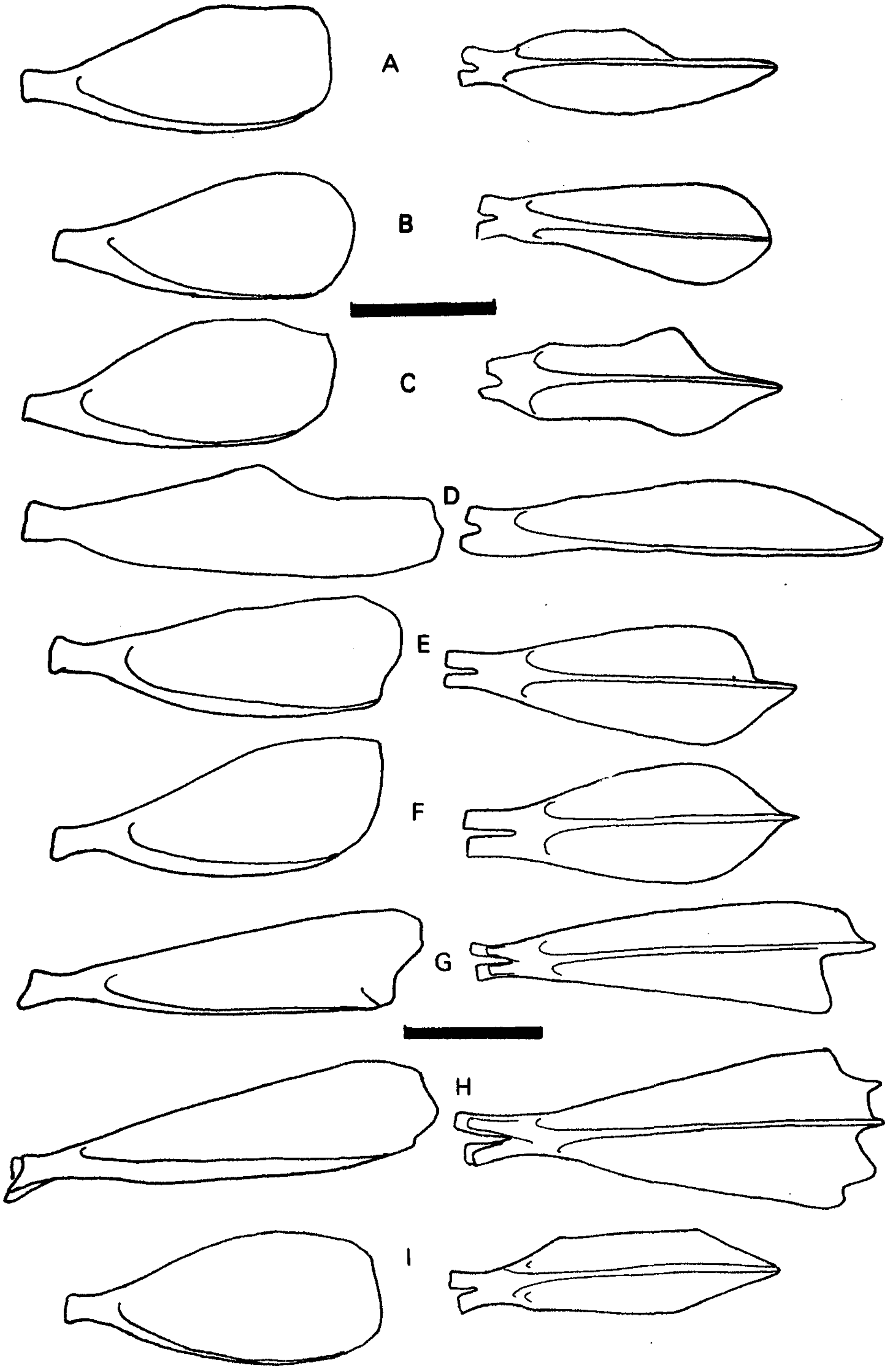


Fig. 4.32 Lateral and dorsal views of the urohyal of redfin *Barbus* species and *O.quathlambae*. A - *B.burchelli*, B - *B.burgi*, C - *B.phlegethon*, D - *B.tenuis*, E - *B.afer*, F - *B.asper*, G - *B.calidus*, H - *B.erubescens*, I - *O.quathlambae*. Scale bar = 2 mm.

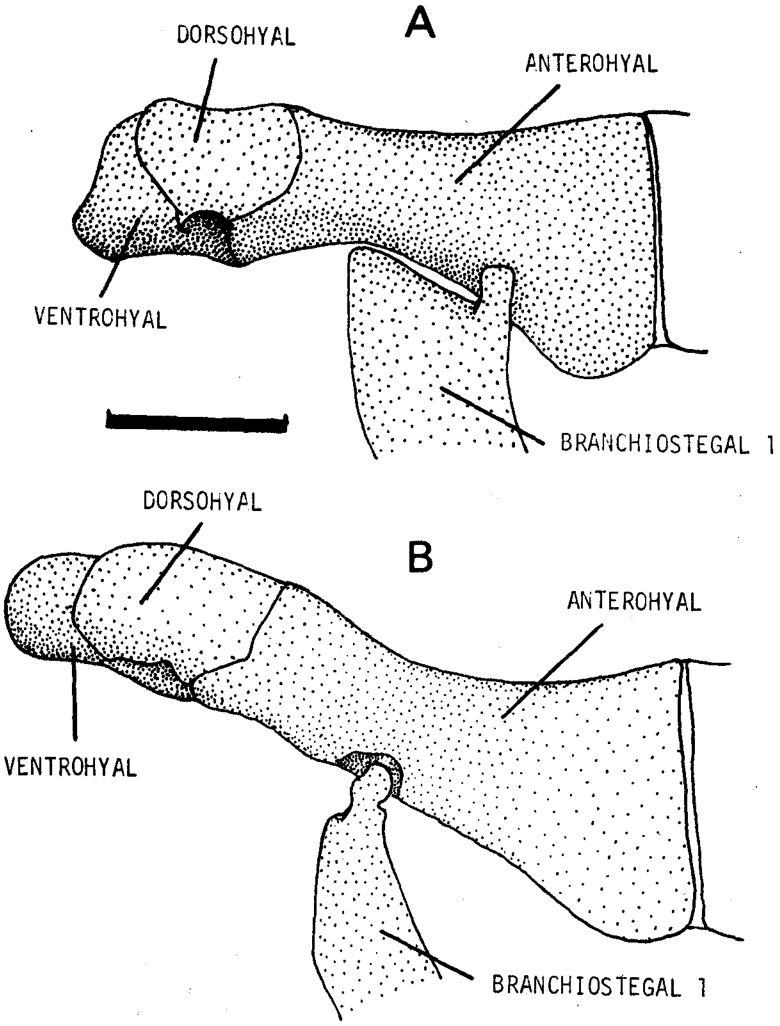


Fig. 4.33 Articulation of first branchiostegal ray and anterohyal of (a) B.burchelli and (b) B.erubescens. Scale bar = 1 mm.

There are three curved, spathiform branchiostegal rays articulating as in Figure 4.30. The first ray has a posterior process which slips behind the anterohyal. The second and third rays have "clupeoid" projections (sensu McAllister, 1968) and articulate over expanded surfaces of the postero- and anterohyals.

Comparisons

Although the hyoid arch may vary slightly in proportions (e.g. it is short in B.phlegethon, Fig. 4.31) there are only a few minor differences between the redfin species. The hyoid foramen is large in O.quathlambae and in B.erubescens it is frequently reduced to a small foramen in the dorsohyal.

The basihyal is usually broad in B.tenuis compared to other redfins. The urohyal is subject to much intraspecific variation in the development of the horizontal flanges and in some specimens the flange may be entirely reduced on one side (e.g. B.tenuis in Fig. 4.32). The urohyal of B.calidus and B.erubescens differs from the flexible-rayed redfins in that posteriorly the horizontal flanges are truncated whereas in the flexible-rayed species they tend to taper (Fig. 4.32).

The serrated-rayed species differ too in the articulation of the first branchiostegal (Fig. 4.33). There is a certain amount of variation in the form of this articulation and the difference is not always as clear-cut as shown in Figure 4.33.

Branchial skeleton (Fig. 4.34 A, B)

The branchial skeleton consists of four pairs of gill arches and a modified fifth pair of gill arches. The bones included here are the infrapharyngobranchials, epibranchials, ceratobranchials, hypobranchials and basibranchials in an arrangement similar to that described for other cyprinids (e.g. Harrington, 1955; Ramaswami 1955; Mahy, 1975). The terminology adopted here follows that of Nelson (1969 b).

There are two pairs of ossified infrapharyngobranchials which Nelson (1969 b) identified in cyprinids as the second and third infrapharyngobranchials respectively. There are also a pair of cartilage pads at the posterior end of the third infrapharyngobranchials which are

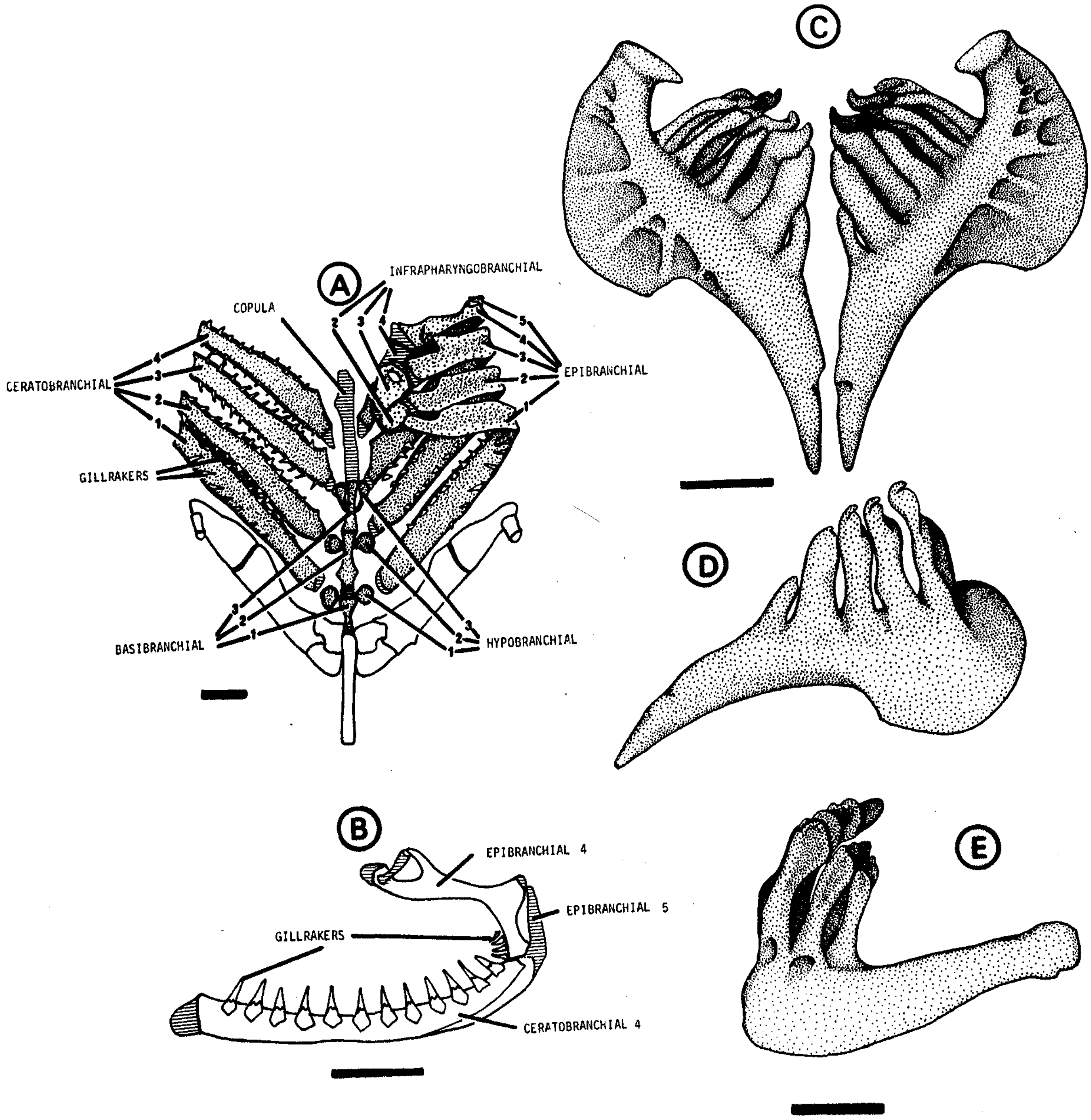


Fig. 4.34 Branchial arches of *B.burchelli*. (A) dorsal view of branchial arches excluding pharyngeal bones, (B) part of fourth and fifth branchial arches, (C) antero-dorsal view of pharyngeal bones (=ceratobranchial 5), (D) side view (postero-lateral) of right pharyngeal bone as laid on its pitted surface, (E) dorsal view of right pharyngeal bone. Scale bar = 1 mm.

identified as the fourth infrapharyngobranchials. The bones are small and relatively flat and are attached by ligaments to the ventral side of the neurocranium. The third infrapharyngobranchials are the larger of the bones and usually have a foramen as illustrated (Fig. 4.34 A).

The epibranchials are varied in shape, arching ventro-laterally. The first, second and third are broad with a trough on the dorsal side and notched medially from the posterior end. The fourth epibranchial (Figs 4.34 A, 4.34 B) is thinner than the preceeding three and bears two dorsal processes: a thin filamentous projection on the anterior side close to the medial end, and a relatively stout posterior process nearer the lateral end. A finger of cartilage connects the tip of the process with the end of the 4th ceratobranchial. According to Nelson (1969 b, p.510) this cartilage represents the 5th epibranchial.

There are four pairs of narrow, arched, trough-like ceratobranchials (the pharyngeal bones represent the fifth ceratobranchials). A series of conical gillrakers are embedded in the epidermis along the antero- and postero-dorsal surface of each ceratobranchial. The gill rakers, reduced in size, continue onto the epibranchials (Fig. 4.34). The leading edge of the first ceratobranchial has six or seven rakers, but all other rows have from 11 to 15. The ceratobranchials articulate medially with the basibranchials. A small cartilage pad encapsulates the median end of each ceratobranchial.

The pharyngeal bones (fifth ceratobranchials) (Fig. 4.34 D, C, E) are attached by muscles to the posterior part of the ventral surface of the neurocranium, to the pectoral girdle and are connected antero-ventrally via a cartilagenous copula (fourth basibranchial) to the median series of basibranchial bones. The pharyngeals are moderately broad, falcate bones with a rounded latero-dorsal contour, an enlarged lateral pitted surface and a tapered ventral limb. There are three rows of pharyngeal teeth as described in Chapter 3.

Paired hypobranchials (Fig. 4.34 A) lie adjacent to the mesial ends of the first, second and third ceratobranchials. The first and second hypobranchials are small spherical bones; the third is comma-shaped with the tails arching ventrally.

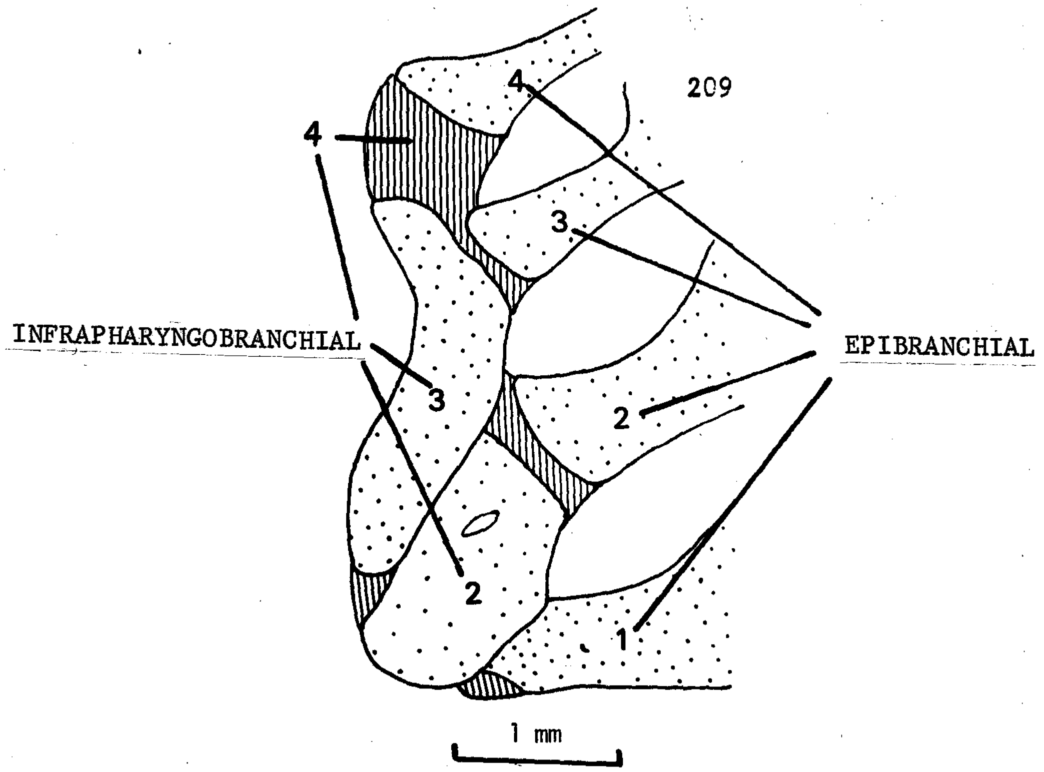


Fig. 4.35 Infrapharyngobranchials of O.quathlambae, left side, dorsal view.

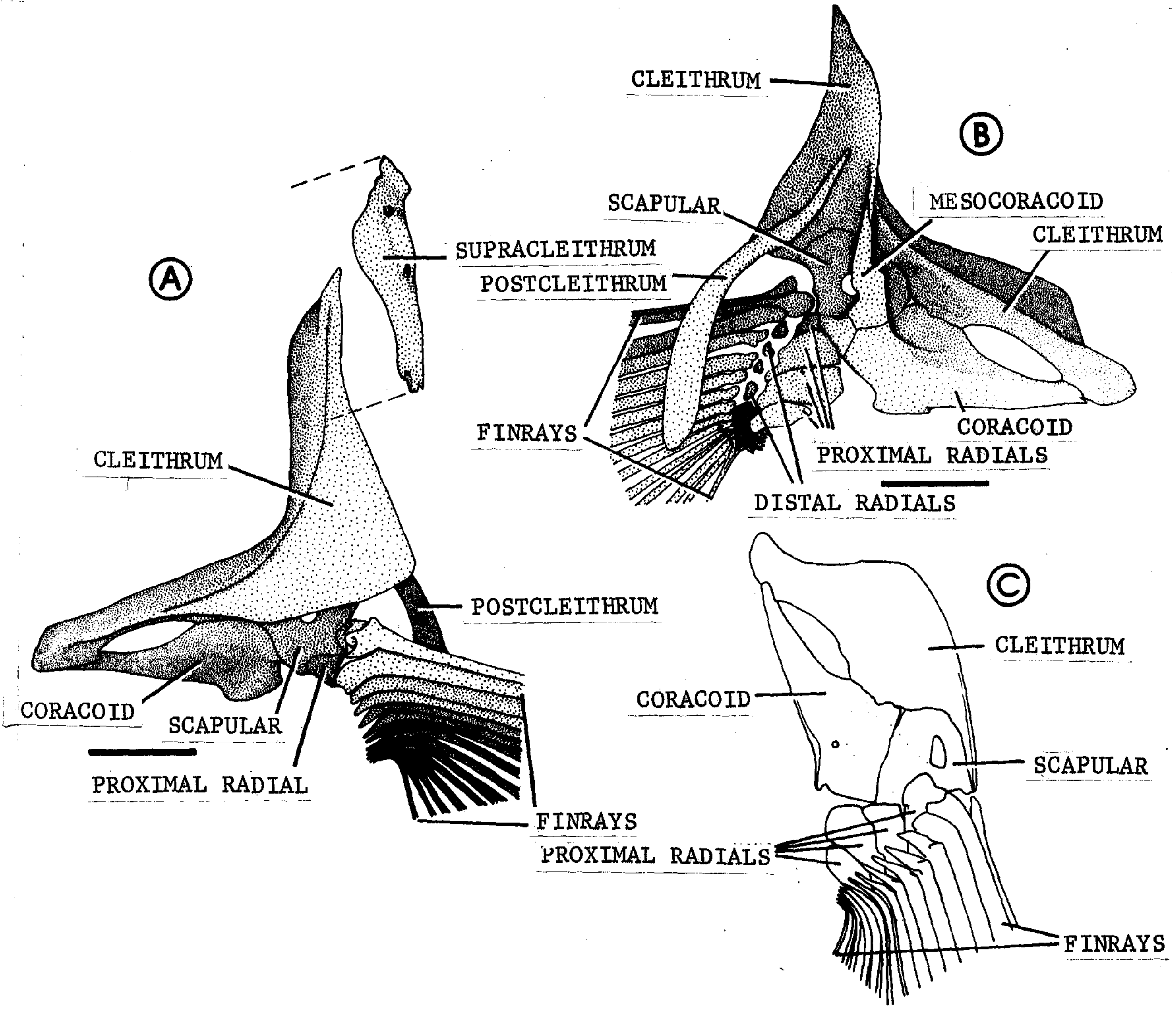


Fig. 4.36 Pectoral girdle of B.burchelli, (A) lateral view, (B) dorso-medial view, (C) ventral view. Scale bar = 2 mm.

There are three ossified *basibranchials* and a cartilage copula representing the fourth basibranchial (Nelson 1969 b) which links the basibranchials to the pharyngeal bones. The first basibranchial is a small tear-shaped unit between the basihyal and the second basibranchial. The second basibranchial is an elongated rod of similar proportions to the third rod-like basibranchial.

Comparisons

There are only a few slight differences between the branchial skeletons of the redfin species. The third infrapharyngobranchial of *O.quathlambae* is elongated and boot-shaped (Fig. 4.35) without a foramen. *O.quathlambae* also has slightly fewer gill rakers than the other redfin species (7-9 vs 9-12). The gill rakers of *B.calidus* and *B.erubescens* are larger and generally better ossified than the flexible-rayed species. There are slight proportional differences in the length of the epi- and ceratobranchials of the species in accordance with head proportions (e.g. the bones are relatively short in *B.phlegethon* and relatively long in *B.tenuis*).

PECTORAL GIRDLE (Figs 4.36 A, B, C; 4.37 A, B)

The pectoral girdle includes the post-temporal which is more or less firmly attached to the neurocranium with which it was included for descriptive purposes. The rest of the pectoral girdle consists of the supracleithrum, cleithrum, coracoid, scapula, mesocoracoid and postcleithrum.

There is sexual dimorphism in the pectoral girdles and fins of the flexible-rayed redfins. The extent of this dimorphism is evident from Figure 4.37 which illustrates girdles of equal sized male and female *B.burchelli*. The bones are broader and more robust in the male and this is especially notable in the mesocoracoid and the proximal radials.

The blade-like *supracleithrum* is stout posterodorsally with a ledge on the anterodorsal side. This provides a fit for the bone between the posttemporal and the autopterotic flange. On the medial side the ventral arm articulates with the dorso-lateral surface of the cleithrum. There is a short oblique tube latero-dorsally for the sensory canal.

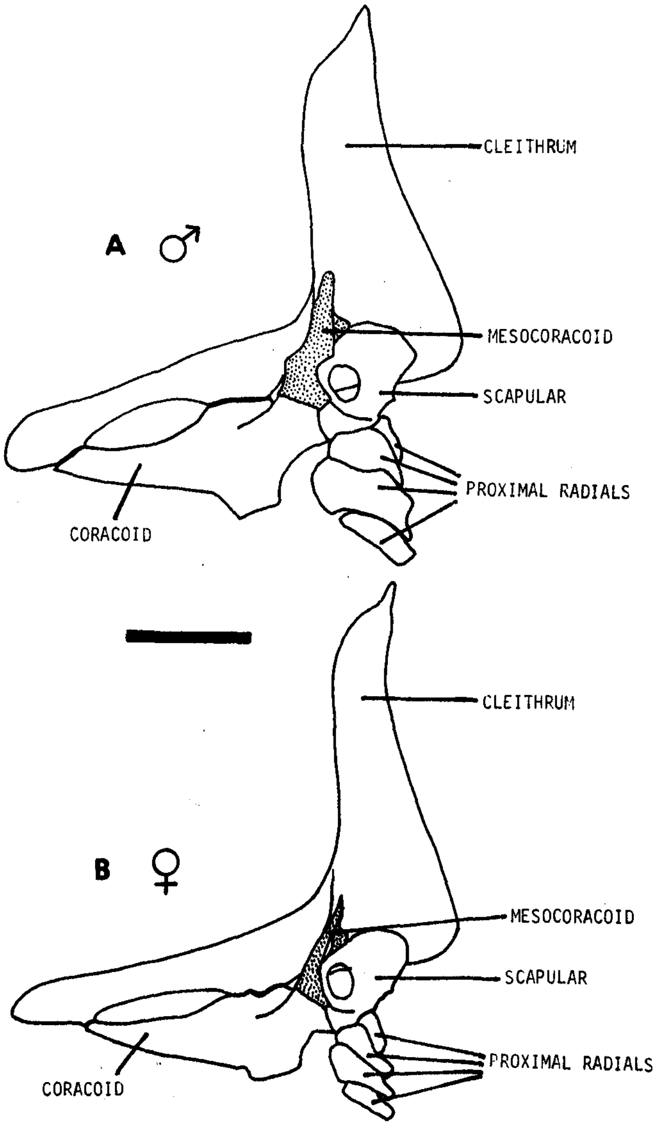


Fig. 4.37 Medial view of right pectoral girdle of (A) male and (B) female *B.burchelli* of the same size (59 mm SL). Scale bar = 2 mm.

The large L-shaped cleithrum articulates dorso-laterally with the supracleithrum and medially with the postcleithrum. On the medio-ventral surface the cleithrum is sutured to the coracoid, the scapula and the mesocoracoid. The vertical limb is divided into a lateral and medial flange. The horizontal limb forms a broad shelf divided by a ridge into a narrow medial strip and a broad lateral surface. The anterior end is obliquely emarginate (Fig. 4.36 C).

The coracoid articulates on the antero-medial edge of the cleithrum, and the anterior edge of the scapula. It is plate-like and notched laterally to form an intercleithro-coracoid foramen. A posterior dorsal ridge forms part of the basal support for the mesocoracoid.

The scapula is thick and disc-shaped, articulating laterally with the cleithrum, anteriorly with the coracoid and dorsally with the mesocoracoid. There is a large central foramen. On the posterior edge there are saddle-like articulation facets for the leading fin ray and the first proximal radial. The second proximal radial also articulates on this edge. A prominence on the dorsomedial side forms part of the base for the mesocoracoid.

The mesocoracoid forms a strut across the internal angle of the girdle. On the ventral side it articulates with the scapula and coracoid while on the dorsal side it meets a ridge on the cleithrum and curves ventrally to form an expanded head which reaches to the edge of the scapula. In males the mesocoracoid is curved whereas in females it is usually a straight strut (Fig. 4.41).

The postcleithrum is attenuated and twisted, articulating on the medial surface of the vertical arm of the cleithrum. The dorsal end is tapered to a point, the ventral end flattened and paddle-like.

There are two series of radials, four larger proximal and a variable number of small distal elements. Of the proximal radials the first and second articulate with the scapula. The second radial has an anterior V-notch for this purpose. The third and fourth elements are irregular and compressed and articulate on the posterior edge of the coracoid. The distal radials are spherical elements located between the divided bases of the fin rays.

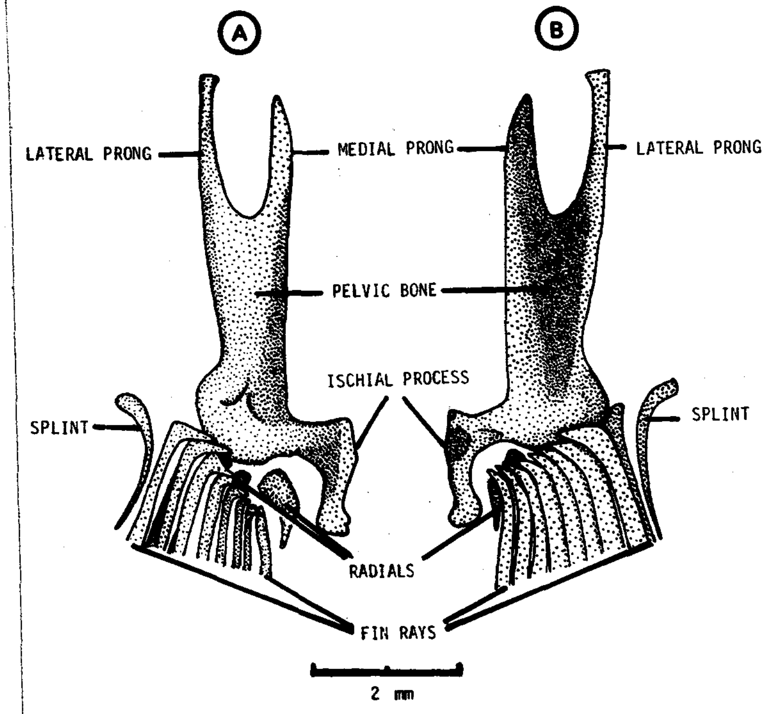


Fig. 4.38 Right pelvic skeleton of *B.burchelli* (A) ventral view, (B) dorsal view.

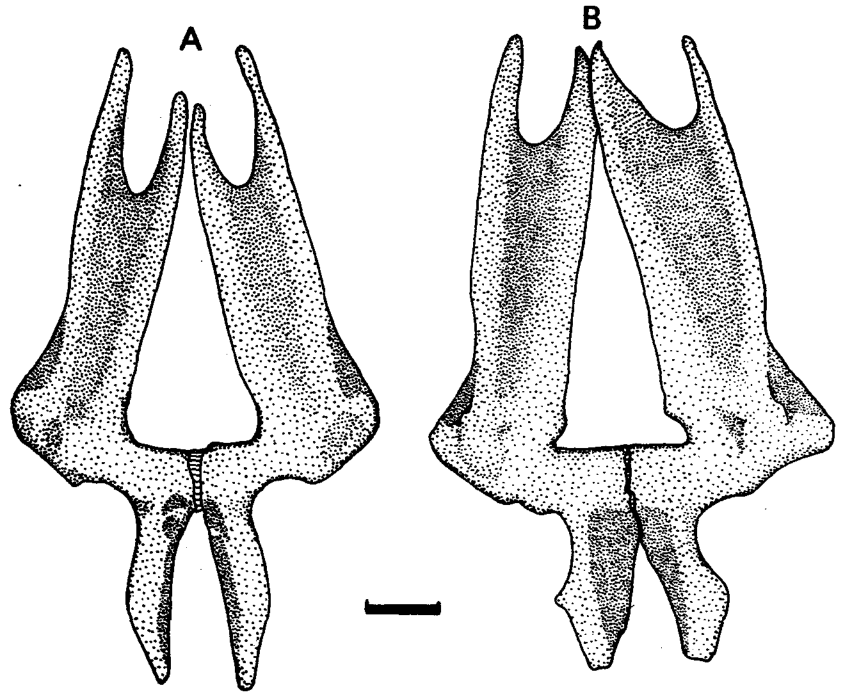


Fig. 4.39 Dorsal view of pelvic bone of (A) *B.erubescens* and (B) *B.calidus* showing taxonomic differences in development of the medial prong and ischial process. Scale bar = 1 mm.

There is considerable intraspecific variation in the development of the pectoral girdle, a factor which tends to mask interspecific characters.

The intercleithro-coracoid gap is generally small in B.phlegethon, B.calidus and B.erubescens. The coracoid is narrow in B.tenuis and O.quathlambae and the gap usually large. The vertical limb of the cleithrum is short in B.tenuis and O.quathlambae but long in B.phlegethon.

The scapula is small in B.calidus and B.erubescens. The postcleithrum of B.erubescens frequently has small projecting spurs which are, however, inconsistent.

The pectoral girdle of B.burgi, B.afer and B.asper is similar to that of B.burchelli.

PELVIC GIRDLE (Fig. 4.38)

This consists of paired pelvic bones and a series of radials. Each pelvic bone is elongated and forked anteriorly. The two bones are concave ventrally and form a symphysis at the antero-medial base of the posterior ischial process which is simple and truncate. There are three radials: two small, spherical, lateral units and a larger, curved, pear-shaped medial unit. The lateral rays articulate against the pelvic bone and the medial rays against the pearshaped radial. There is a curved splint at the base of the leading ray similar to that described by Gosline (1961) for many lower teleostean groups.

Comparisons

The basic form of the pelvic girdle is similar in all the redfin species. There are useful differences between the bones of B.calidus and B.erubescens (Fig. 4.39). The ischial process and the medial anterior prong of the pelvic bones of B.erubescens are longer and more slender than in B.calidus.

AXIAL SKELETON

The axial skeleton is divided into the following sections: the Weberian apparatus, precaudal vertebrae, caudal vertebrae, caudal skeleton, supraneurals and intramuscular bones.

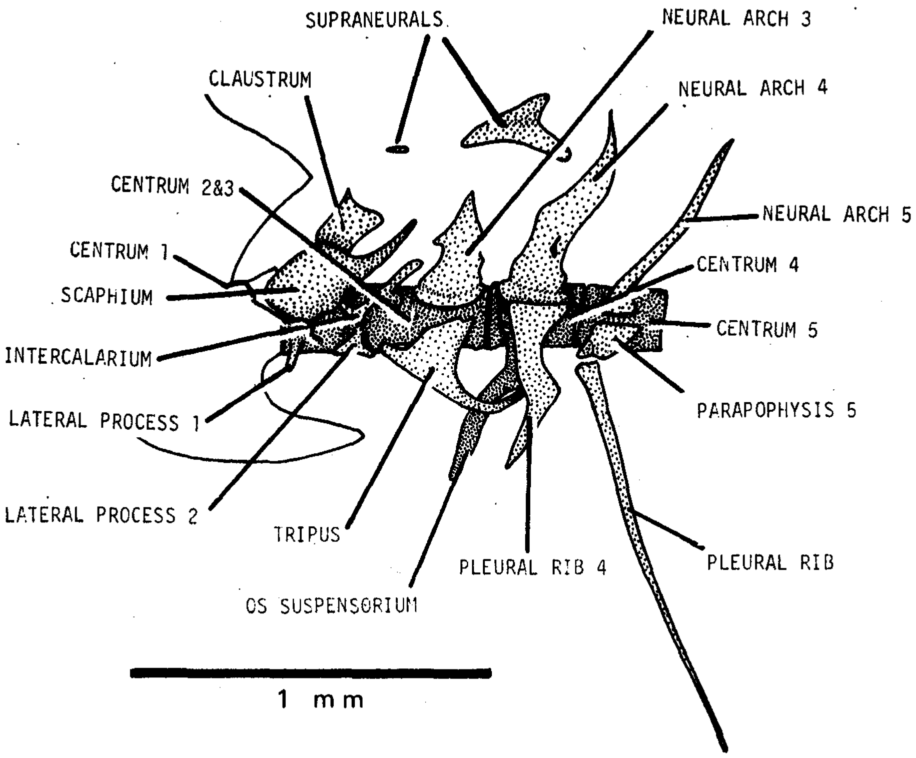


Fig. 4.40 Weberian vertebrae of the juvenile <u>B. afer</u> (AM/P 2652, SL 14 mm) indicating derivation of components of Weberian apparatus.

The Weberian Apparatus (Figs 4.40; 4.41)

Rosen & Greenwood (1970) provided a homology of the components of the characoid Weberian apparatus. The cyprinoid Weberian complex differs in certain respects from that of the characoids. Thus the second and third centra in cyprinoids are fused and in addition there is a plate-like bone in front of the "neural complex" (cf. Weitzman, 1962). According to Rosen & Greenwood (1970) the neural complex is most probably derived from a supraneural bone. The additional unit in cyprinoids is usually referred to as the "neural arch of the second vertebra" (e.g. Nelson, 1948; Ramaswami, 1955; Greenwood & Jubb, 1967). Howes (1978) calls this the "neural plate" of the second vertebra.

Watson (1939) established that during development in Cyprinus carpio "the basidorsals of the second, third and fourth vertebrae fuse with the first three interspinous bones (=supraneurals) to form a massive arch of cartilage which later gives rise to the neural arches". Rosen & Greenwood (1970) suggest the intercalaria are derived from the neural spine, neural arch and prezygapophyses of the second vertebra, the neural spine being later resorbed. If this homology is correct and applies to cyprinoids as well, then it is unlikely that the anterior dorsal unit in cyprinoids is a "neural arch of the second vertebra".

A similar study to that by Rosen & Greenwood (1970) on very small specimens of Brycon sp., was made on small specimens of Barbus afer (Fig. 4.40). The results (Fig. 4.40) show that the homology suggested by Rosen & Greenwood (1970) for Brycon applies equally well to B.afer. However the presence of a tiny splint of bone in front of the crested precursor of the adult "neural complex" suggests this is the additional anterior unit in the adult cyprinid Weberian apparatus. It appears then that this unit is derived from a supraneural bone and not the "dorsal arch of the second vertebra". A more appropriate name for it is therefore "anterior neural complex".

The Weberian apparatus of B.burchelli (Fig. 4.41) is associated with the first four centra. The first and fourth are discreet and the second and third fuse to form a compound centrum.

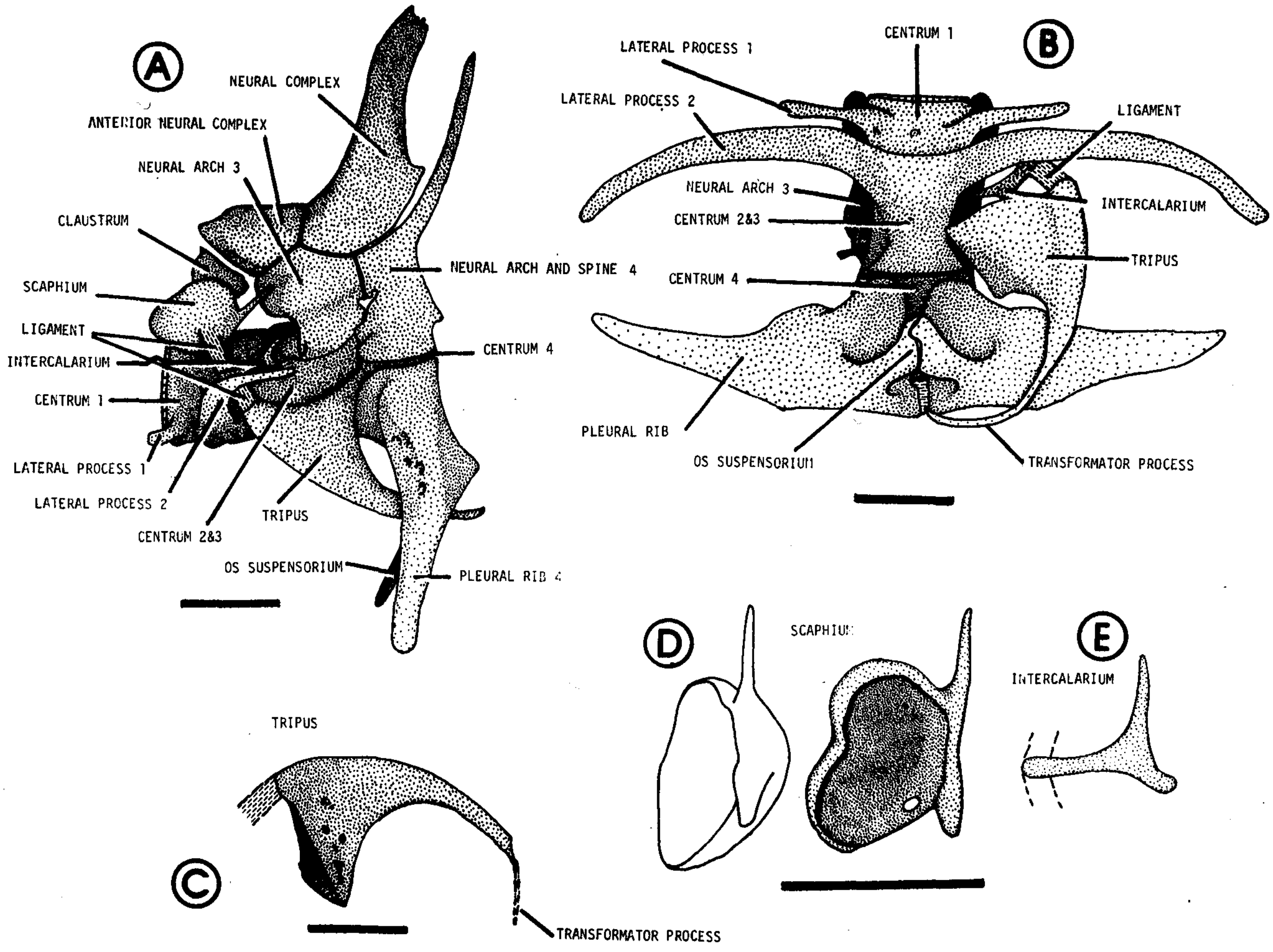


Fig. 4.41 Weberian apparatus of B.burchelli, (A) lateral view, (B) ventral view with right tripus and intercalarium removed, (C) dorsal view of right tripus, (D) postero-medial and medial views of right scaphium, (E) anterior view of right intercalarium. Scale bar = 1 mm.

The *first centrum* is narrow and has slender bilateral processes from the ventral side. A ligament connects these processes to the medial surface of the cleithrum. Conical excavations on the lateral dorsal surface provide hinge sockets for the scaphia.

The *compound second and third centra* are deeply constricted latero-ventrally and latero-dorsally. The ventral constrictions provide articulation grooves for the tripodes, the dorsal constrictions form sockets for the pyramidal bases of the neural arch and spine. There are large curved bilateral processes on the base of the second centrum.

The *fourth centrum* is also constricted latero-dorsally and latero-ventrally to accommodate the pyramidal bases of the neural arches and pleural rib complexes respectively. The *pleural rib* is stout and blunt with the lamellar os suspensoria extending from the medio-ventral surface. The *neural arches* unite to form a spine behind the supraneural complex.

The *anterior neural complex* is a curved plate-like hexagon, articulating with the posterior neural complex and the neural arch and spine of the third vertebra. The *posterior neural complex* has a tall crest which provides a useful taxonomic character in different *Barbus* groups. In *B.burchelli* the crest is simple but the shape is usually variable with an irregular blunt end.

The *claustrum* is a small platelet articulating with the anterior neural complex. The *scaphium* (Fig. 4.41) is a hollow hemisphere with hinge projections which articulate in the socket on the first centrum and against the antero-lateral surface of the third neural arch. A ligament joins the outer surface of the hemisphere with the distal part of the intercalarium.

The *intercalarium* (Fig. 4.41 E) is an unequally-armed Y-shaped ossicle which articulates within a small excavation on the latero-dorsal side of the compound centra. Ligaments connecting the intercalarium with the scaphium and tripus are attached distally. The *tripus* (Fig. 4.41 C) has a thick articulation ridge at right angles to the plane of a short anterior arm and a posterior tapered, crescentic transformator process.

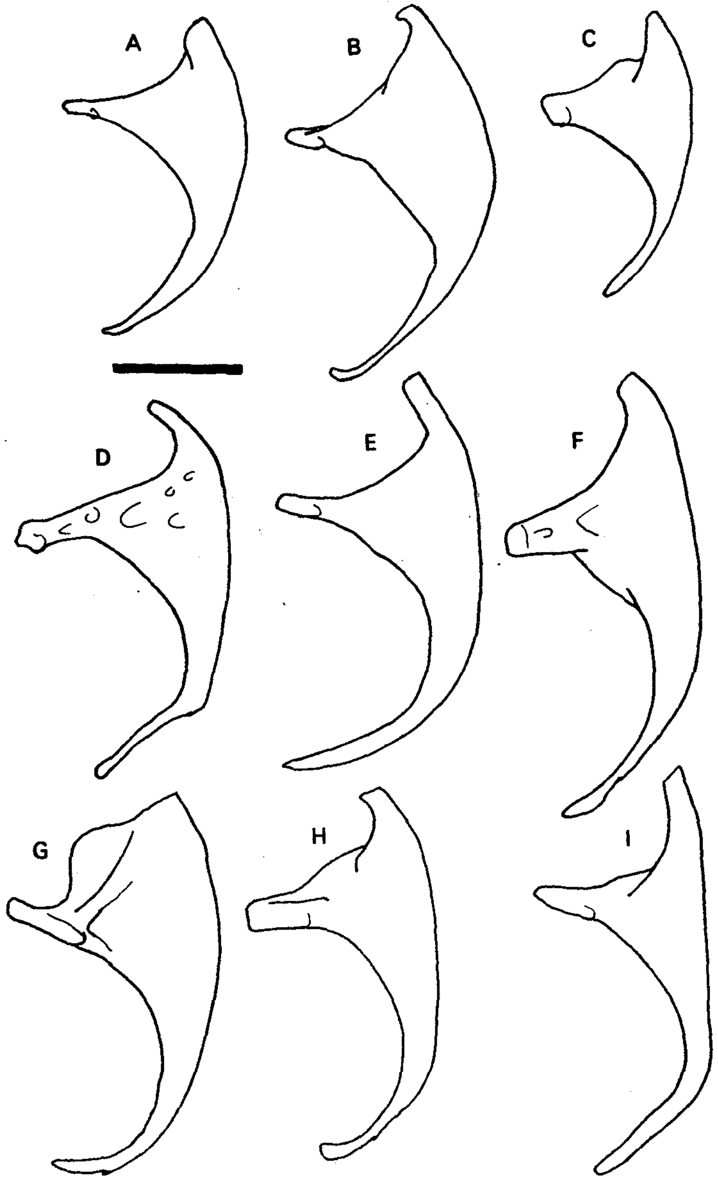


Fig. 4.42 The tripus of redfin *Barbus* species and *O. quathlambae*, (A) *B. burchelli*, B – *B. burgi*, C – *B. phlegethon*, D – *B. tenuis*, E – *B. afer*, F – *B. asper*, G – *B. calidus*, H – *B. erubescens*, I – *O. quathlambae*. Scale bar = 1 mm.

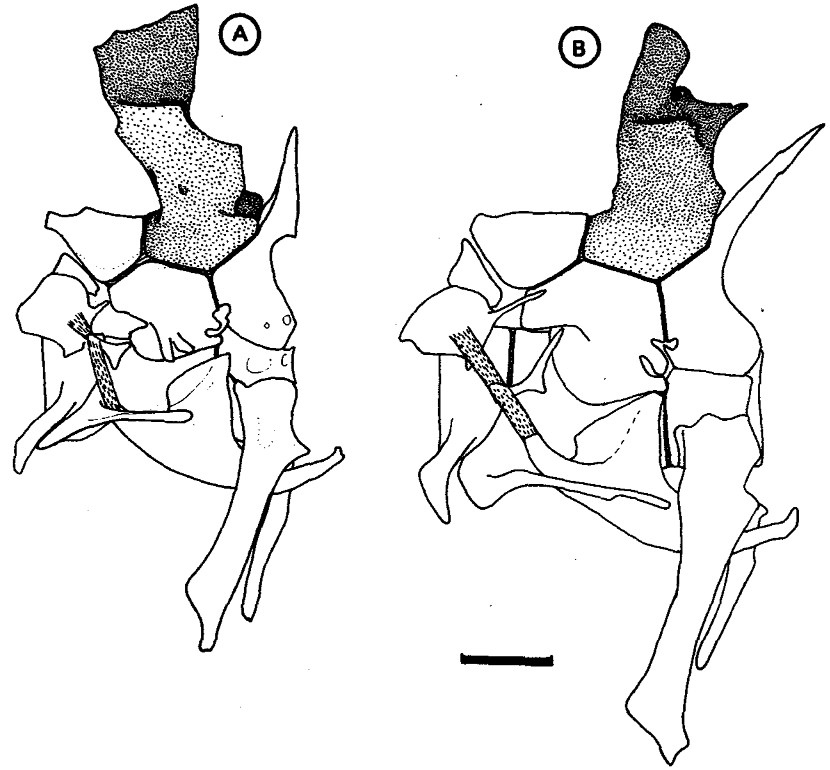


Fig. 4.43 Left lateral view of the Weberian apparatus of (A) *B. calidus* and (B) *B. erubescens*. Scale bar = 1 mm.

Comparisons

There is much intraspecific variation in the precise shape of the ossicles and other more prominent features of the Weberian apparatus (e.g. the supraneural crest and the lateral processes). Thus no specific differences are noted between the Weberian apparatus of the majority of the flexible-rayed redfin species. O.quathlambae differs generally in the shape of the tripus (Fig. 4.42) which is more slender and elongated than in the other species.

The shape of the crest of the posterior neural complex differs in the serrated-rayed redfins and the flexible-rayed species. In B.calidus and B.erubescens there are bi-lateral flanges on this crest as illustrated in Fig. 4.43 A and B, and it is also notched distally on the posterior side.

Vertebrae (Fig. 4.44)

Precaudal vertebrae

The neural arches of the precaudal vertebrae have broad and stout neural spines before the dorsal fin. From opposite the base of the dorsal fin and posteriorly the neural spines decrease in robustness. The precaudal vertebrae have both pre- and postneurapophyses; the prezygapophyses are large in the predorsal vertebrae and decrease in size opposite the base of the dorsal fin and posteriorly; the postzygapophyses arise from the centra and are broad and irregular in shape.

There are well developed parapophyses on the precaudal vertebrae where the pleural ribs articulate. In the last few precaudal vertebrae the parapophyses become pointed and progressively longer, eventually fusing to form the haemal arch of the caudal vertebrae. The pleural ribs are large and antero-posteriorly compressed and become progressively more slender and rounded posteriorly. The pleural ribs articulate on the lateral surface of the parapophyses of the more anterior vertebrae but in the last few precaudal vertebrae this articulation lies on the posterior edge of the parapophyses. Small spur-like posthaemapophyses only develop on the last one or two precaudal vertebrae.

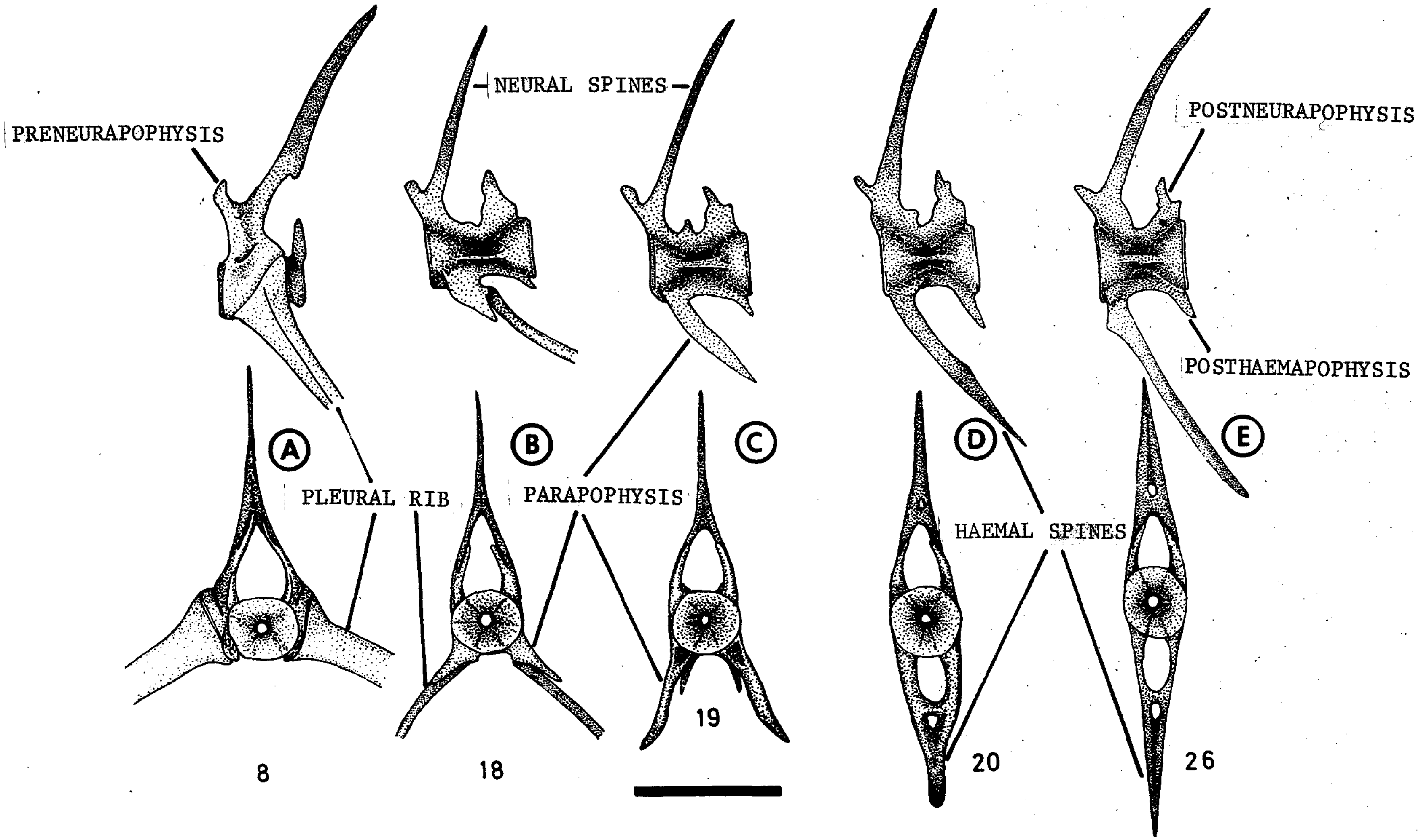


Fig. 4.44 Lateral and anterior views of sample vertebrae of B.burchelli (A) a predorsal vertebra, (B) vertebra (18), (C) vertebra 19 (last precaudal vertebrae), (D) first caudal vertebra, (E) typical caudal vertebra. Scale bar = 2 mm.

Caudal vertebrae

The first caudal vertebra is taken as that with a closed haemal arch. Frequently the distal part of the developing haemal arches have not yet fused into a single spine and remain as two separate spurs. The preneurapophyses remain relatively small and the postneurapophyses are prominent flanges on top of the centra. There are small slender posthaemapophyses and very small prehaemapophyses. The neural and haemal dorsal spines are directed posteriorly on the caudal peduncle. The spines of the last two (sometimes the third) caudal vertebrae are stout and laterally compressed and directed strongly posteriorly to provide support for the caudal fin, and an articulation base for the procurrent rays (Fig. 4.45).

Comparisons

There are no major differences in the vertebrae of the redfins.

Caudal Skeleton (Fig. 4.45)

There are usually two caudal vertebrae involved in the caudal skeleton (representing the PU_2 and PU_3 centra respectively) in that their neural and haemal spines are bent posteriorly and provide articulation bases for some of the procurrent fin rays. The haemal spine of the PU_2 vertebrae is broad and stout and the haemal arch forms a pyramidal base which articulates within a ventral concavity on the centrum.

The compound ural centrum ($PU_1 + U_1$ - Buhan, 1972) is fused to the second hypural and the first and second uroneurals (urostyle) to form a V-base for the skeleton. There is an irregular dorsal flange on top of the centrum. On the ventral side the united parhypural and first hypural articulate within a pyramidal concavity. The parhypural has small bilateral hypurapophyses. Hypurals three to six articulate within a ventral groove on the urostyle. A pair of small third uroneurals occur in some specimens at the base of the principle caudal ray. There is a single broad epural above the urostyle.

Comparisons

The structure of the caudal skeleton is conservative for all the species under consideration.

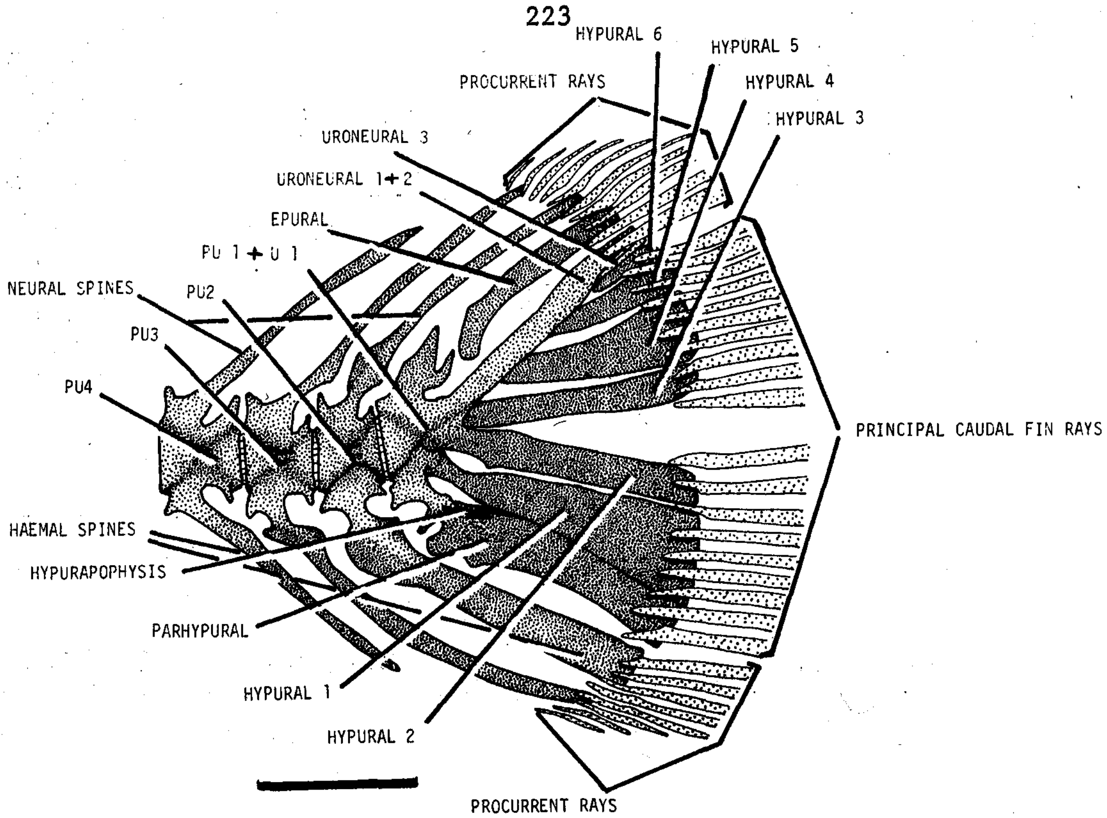


Fig. 4.45 Caudal fin skeleton of B.burchelli, lateral view. Abbreviations: Pu - preural centrum, u - ural centrum. Scale bar = 2 mm.

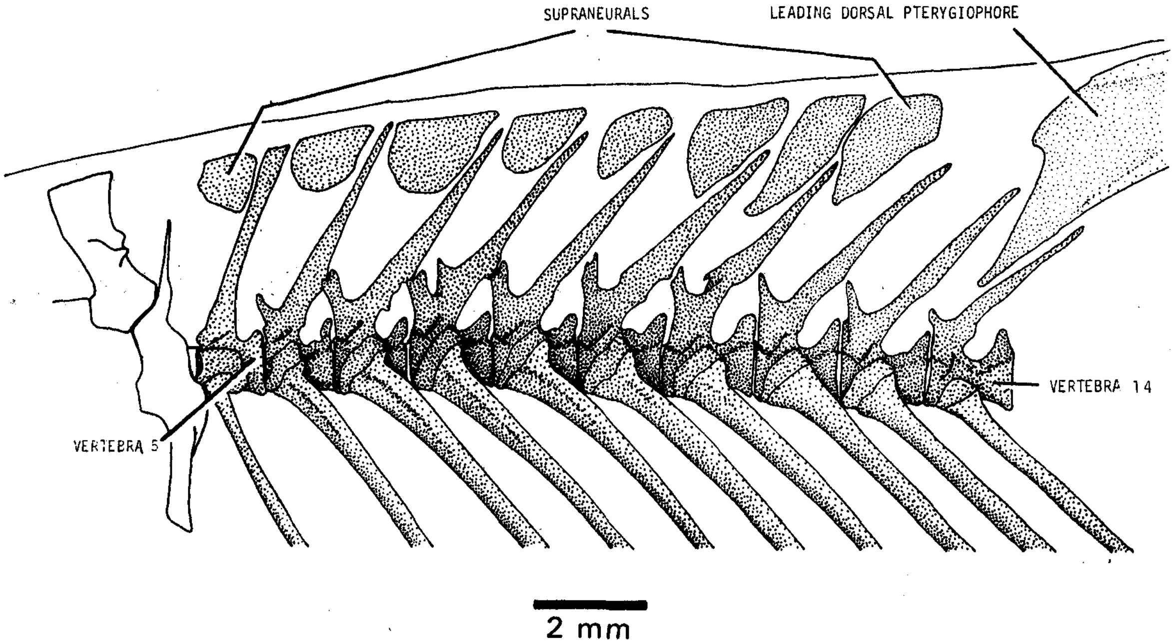


Fig. 4.46 Predorsal vertebrae and supraneurals of B.calidus. Scale bar = 2 mm.

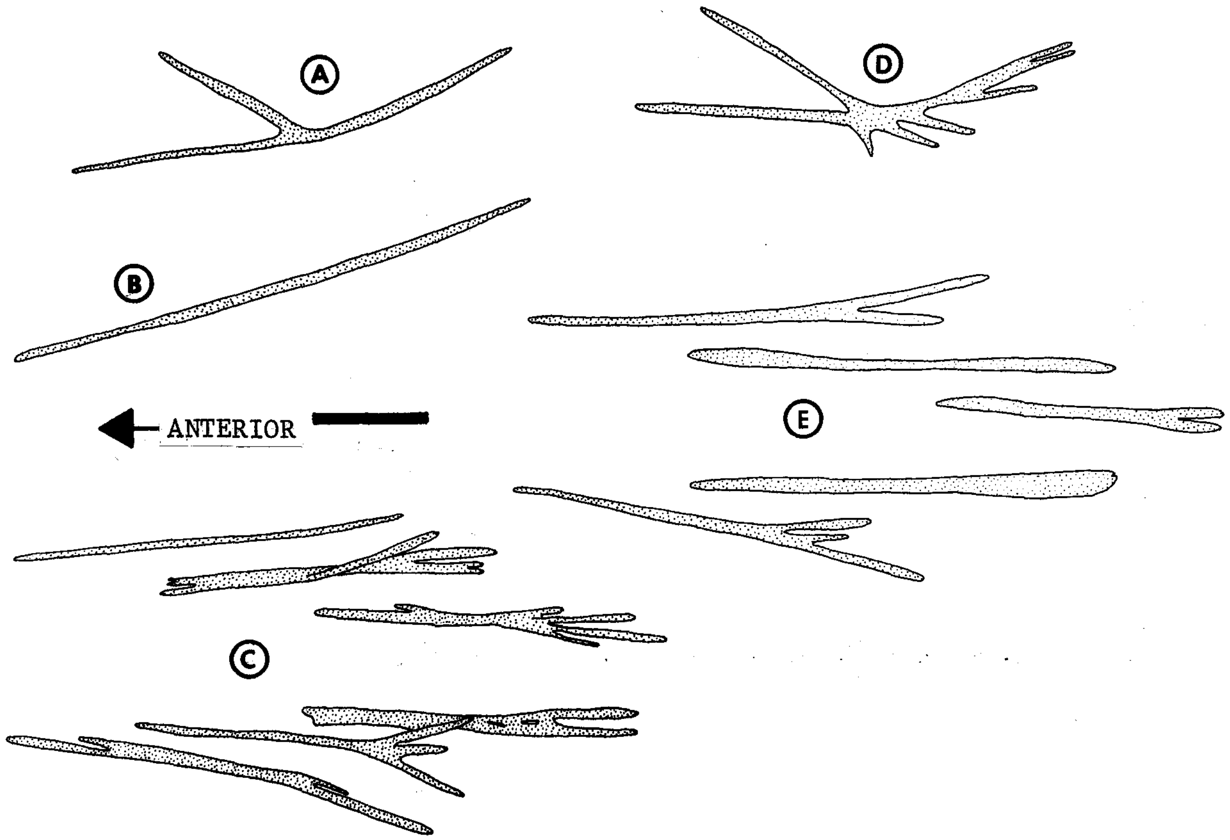


Fig. 4.47 Examples of intramuscular bones from redfin Barbus species. (A) epineural of B.burchelli, (B) caudal epineural of B.burchelli, (C) intramuscular bones opposite the ural and two or three preural certebrae, (D) epineural of B.calidus, (E) intramuscular bones opposite the ural and two or three preural vertebrae of B.calidus. Scale bar = 1 mm.

Supraneurals (Fig. 4.46)

B.calidus and B.erubescens are the only redfins with well developed supraneural bones. The flexible rayed species have vestigial supraneurals in certain individuals only.

Intramuscular bones (Fig. 4.47)

In adult B.burchelli the epineural intramuscular bones are not ossified ahead of the dorsal fin. The epineurals posterior to the fin lie obliquely in the epaxial muscles and are in the form of tri-radiate rods (Fig. 4.47 A) except on the caudal peduncle where they are simple rods (Fig. 4.47 B). The last few intramusculars lie horizontally over the ural and preceeding three or four centra. These are thicker bones and have a more complex form than those of the trunk (Fig. 4.47 C). The epipleurals develop posteriorly from opposite the anterior base of the anal fin. They parallel the form of the adjacent epineural intramusculars.

Comparisons

The intramuscular bones of the flexible rayed species are similar to those of B.burchelli although in B.tenuis and O.quathlambae they are more weakly developed and seldom assume more than a rod-like form. The intramusculars of B.calidus and B.erubescens are well developed (polyradiate) and ossified from opposite the fifth or sixth vertebra in adults. By way of contrast the last few intramusculars of B.calidus and B.erubescens are relatively simple structures with blunt lobes (Fig. 4.47 D, E).

UNPAIRED FINS (Fig. 4.48 A, B)

The architecture of the dorsal and anal fins is similar to that described by Weitzman (1962) for Brycon meeki. In the dorsal fin (Fig. 4.48 A) the first three pterygiophores have only a proximal and distal radial. The fourth and subsequent pterygiophores also have a median radial. The anal fin (Fig. 4.48 B) has six pterygiophores, the anterior two with a proximal and distal radial, the posterior four with a full complement of three radials. There is an end piece or stay in both fins.

There are three or four unbranched dorsal and anal rays the last of which is segmented and flexible. The last branched ray in each fin is divided to the base.

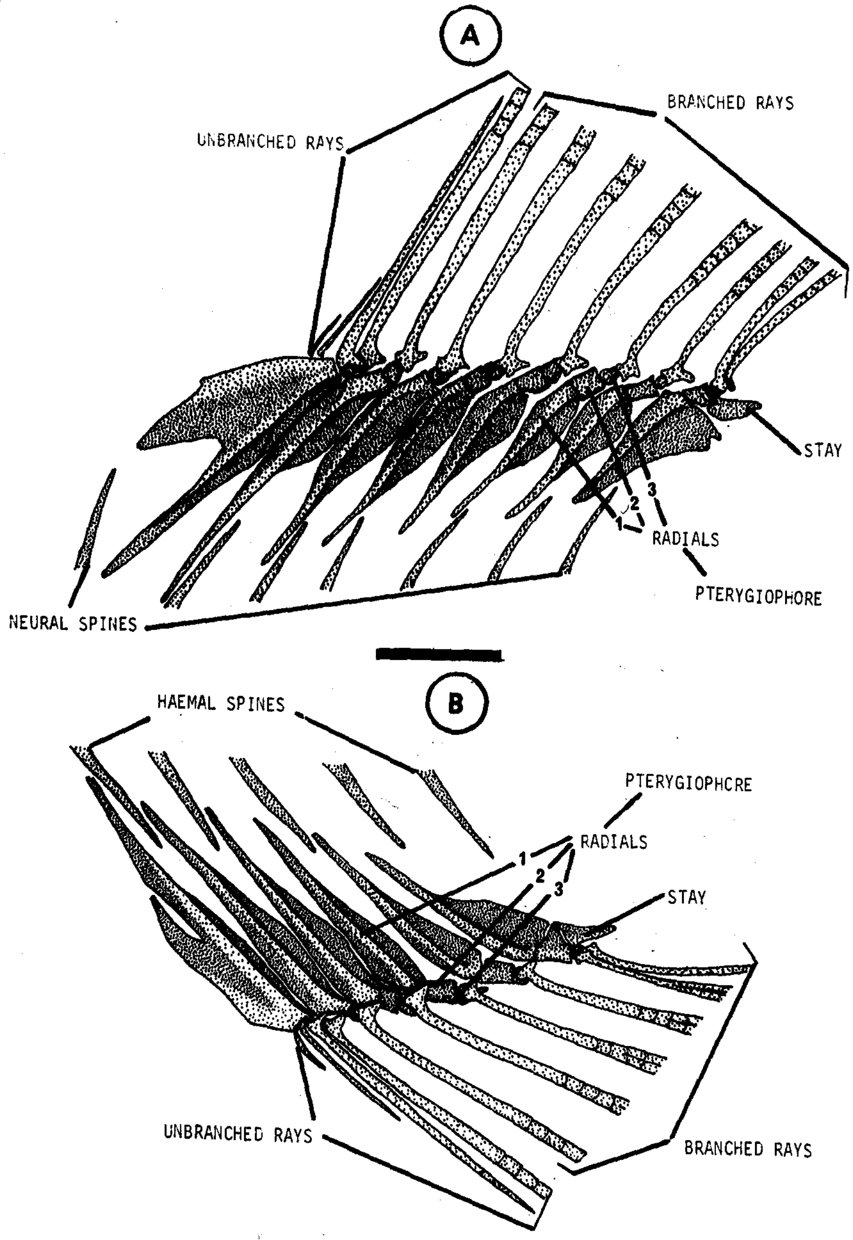


Fig. 4.48 Dorsal fin and anal fin skeletons of B. burchelli, (A) dorsal fin, (B) anal fin. Scale bar = 2 mm.

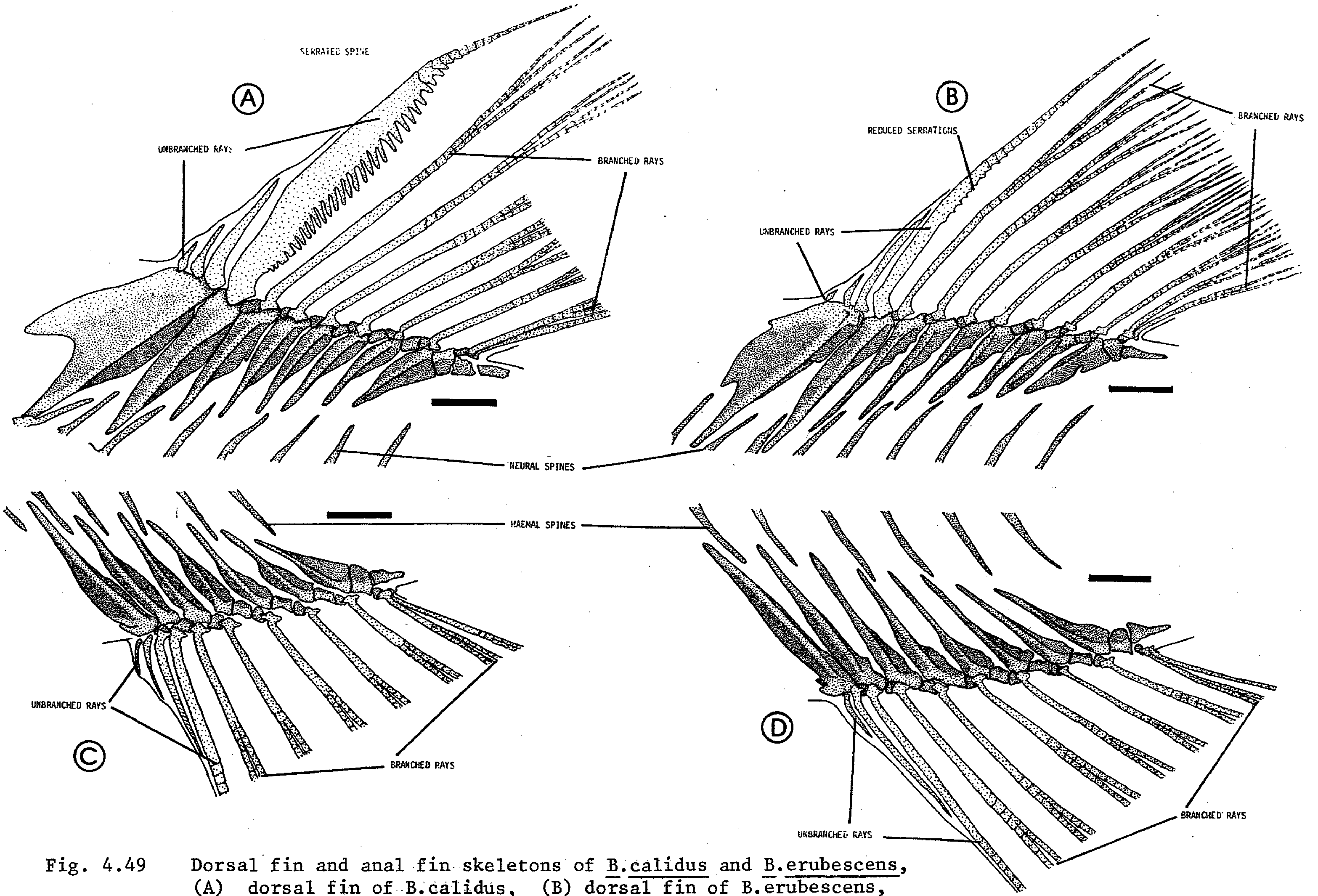


Fig. 4.49 Dorsal fin and anal fin skeletons of *B. calidus* and *B. erubescens*, (A) dorsal fin of *B. calidus*, (B) dorsal fin of *B. erubescens*, (C) anal fin of *B. calidus*, (D) anal fin of *B. erubescens*. Scale bar + 2 mm.

Comparisons

The dorsal and anal fins of all the flexible-rayed fins are similar to those of B.burchelli. The form of the last unbranched ray is different in B.calidus and B.erubescens (Fig. 4.49 A, B) and this difference has already been described in Chapter 3. In accordance with the development of a stout, serrated, unbranched ray in B.calidus the anterior pterygiophores in the dorsal fin of this species are proportionately more robust than in B.erubescens or the flexible-rayed species. There is an additional branched ray and pterygiophore in the dorsal fin of B.erubescens.

B.calidus (Fig. 4.49 C) has an additional pterygiophore in the anal fin and B.erubescens (Fig. 4.49 D) two additional pterygiophores to accommodate the respective increase in anal branched rays reported for these species.

General Summary

It is evident that the main osteological differences lie between the serrated-rayed and the flexible-rayed redfin species. Although these differences are not always of great magnitude they combine to present a quite different facies for the two groups. In these observations it is also evident that the osteology of O.quathlambae falls within the bounds of the flexible-rayed species.

Besides the differences recorded in form or shape of the bones there is a qualitative difference in the osteological development of certain bones of the species of each group. The bones of the serrated-rayed species are well developed and robust without evidence of reduction. There is a recurrent trend of reduction and lack of robustness in certain bones of the flexible-rayed species. This is most clearly evident in the epineural intramuscular bones and the supraneural bones but also finds expression in cranial bones e.g. the intercalars, and the bones of the anterior region of the neurocranium, especially the supraethmoid. In bones such as the extrascapulars which are variable in form that of the serrated-rayed redfins are nevertheless more predictable in form than those of the flexible-rayed species.

TABLE 4.2

A comparative summary of aspects of osteology of redfin species.

	B.burchelli	B.burgi	B.phlegethon	B.tenuis	B.afer	B.asper	B.calidus	B.erubescens	O.quathlambae
anium shape	moderately deep subrectangular	deep subrectangular	deep, narrow subrectangular	shallow, broad subrectangular	moderate subrectangular	moderate subrectangular	moderate subtriangular	moderate subtriangular	moderate subtriangular
hmoid	shallow groove	shallow groove	shallow groove	unossified shallow groove	shallow groove	shallow groove	deep groove	deep groove	unossified shallow groove
ethmoid, entopterygoid s, postero-ventral vomer,	concave	concave	concave	concave	concave	concave	condyles not concave	condyles not concave	concave
henoids	divided	divided	divided	divided	divided	divided	joined	joined	divided
bitals	stout	stout	stout	reduced - irregular	stout (when present)	stout (when present)	slender	slender	vestigial irregular
bital shelf	wide notched	wide notched	wide notched	narrow - notched (?)	wide notched	wide notched	narrow	narrow	wide notched
bitals (a) lachrymal	low peak	low peak	low peak	low peak	low peak	low peak	high peak	high peak	low peak
(b) dermosphenotic	triangular	broad - square	triangular	reduced - triangular	triangular	triangular	triangular variable	triangular variable	?
itals	flanged	flanged	flanged	slender process	flanged	flanged	no process	no process	slender process
lars	vestigial, irreg.	vestigial, irreg.	vestigial, irreg.	vestigial, irreg.	vest. (irreg.)	vestig (irreg.)	disc. well dev.	disc. well dev.	vestig (irreg.)
apulars	irregular	irregular	irregular	irregular	irregular	irregular	regular (?)	regular (?)	irregular
ipital process	flat; 30-40°	flat; 30-40°	flat; 30-40°	flat; 30-40°	flat 30-40°	flat 30-40°	concave 50-60°	concave 50-60°	flat 30-40°
e	moderate	moderate	moderate	broad	moderate	moderate	suprapreopercular	suprapreopercular	broad
rcular canal	complete	complete	reduced	reduced	reduced	reduced	complete	complete	reduced
dibular			narrow, tall	short, broad					short, broad
erygoid (dorsal edge)	convex	convex	convex	convex, deep notched	convex	convex	concave	concave	convex deep notched
te	shallow excav.	shallow excav.	shallow excav.	shallow excav.	shallow excav.	shallow excav.	deep excav.	deep excav.	shallow excav.
illa	deep	deep	deep	deep	deep	deep	slender	slender	deep
a	deep	deep	deep	deep	deep	deep slender	slender	slender	deep
jaw	short flange	short flange					long flange	long flange	
l	deep, tapered	deep, tapered	deep, tapered	slender, tapered	deep tapered	deep tapered	slender truncate	slender truncate	deep tapered
geals	broad	broad	broad	broad	broad	broad	slender	slender	broad
al girdle male vs female	dimorphic	dimorphic	dimorphic	dimorphic	dimorphic	dimorphic	monomorphic	monomorphic	dimorphic
c girdle							processes short	processes long	
ian neural crest	simple, irreg.	simple,irreg.	simple,irreg.	simple, irreg.	simple irreg.	simple irreg.	flanged	flanged	simple irreg.
neurals	absent (vestig.)	absent (vestig.)	absent (vestig.)	absent (vestig.)	absent (vestig.)	absent (vestig.)	large	large	absent (vestig.)
muscular bones	reduced	reduced	reduced	reduced	reduced	reduced	well developed	well developed	reduced
l fin (unbranched ray, pterygiophores)	slender (8)	slender (8)	slender (8)	slender (8)	slender (8)	slender (8)	stout serrated (8)	moderate (9)	slender (8)
fin (pterygiophores)	6	6	6	6	6	6	7	8	6

Within either of the two groups the main differences between the species are due to relatively minor specializations and not to basic architectural changes. Thus in spite of a certain degree of adaptive radiation in the flexible-rayed species there remains remarkable similarity in particular bones. For example, the pharyngeal teeth and character of the intestine indicates a fairly wide range of trophic adaptation but nevertheless the proportions of the upper jaw bones, the pharyngeal bones themselves, the angle of the basioccipital process and the surface of the masticatory plate are all basically similar between the species.

The main points of comparison of the osteology of the redfin species are summarized in Table 4.2. Further discussion and comparison with other *Barbus* species is given in the next chapter.

CHAPTER 5

PHYLOGENY AND CLASSIFICATION OF THE REDFINS

One of the functions of systematics is the classification of organisms (Mayr, 1969; Crowson, 1970; Nelson, 1971). To the majority of biologists classification depends on the phyletic interrelationships of the organisms. The interrelationships of the redfin species and of the group to other cyprinids have, to date, not received much attention. Both Barnard (1943) and Jubb (1965, 1967) refer to the redfin "group" implying that there may be some relationship between the species.

There is no strict "classification" of African Barbus species in use at present. The closest approximation is the categorization of the African Barbus by certain key characters of Boulenger (1911). The major division in the key is based on whether the scales are parallel or radiately striated. Secondary divisions are based on the form of the last unbranched dorsal fin ray. The form of this ray has three ideal characteristics: simple, enlarged and spinous; simple, not enlarged and flexible; and serrated, enlarged and spinous.

The redfins all have radiately striated scales. However certain redfin species have a simple, flexible unbranched dorsal fin ray and others have serrated unbranched dorsal fin rays. This challenges the concept of categorizing African Barbus species according to these characters. One of the tasks of this present chapter then, is to establish whether or not the group as a whole is monophyletic.

A further task of the chapter is to determine the in-group and, as far as possible, the out-group relationships of the redfins. This is not only important for classification (Hennig, 1966; Mayr, 1969; Nelson, 1971,1972 a; Brundin, 1972) but is an essential prerequisite for an assessment of the biogeography of the species (Nelson, 1974; Croizat et al., 1974; Rosen, 1978). The need to know the interrelationships of the redfins has become more necessary since Skelton (1976) suggested that O.quathlambae was related to at least some of the redfins. Not only does the generic status of the redfins thus require revision, but O.quathlambae has a relict distribution isolated from other redfins. The classification and phylogeny will be handled in the present chapter, and the biogeography will be discussed in the following chapter.

Methods

There are at least three possible approaches to systematics (Michener, 1970), a phenetic approach, a cladistic approach and a evolutionary or gradistic approach. Of these approaches the latter two are based on the theory of evolution of organisms originally proposed by Darwin. The pheneticists are not concerned with phylogenetic interrelationships of taxa but only on the degree of similarity between them.

The gradistic approach to systematics is dealt with in detail by Mayr (1969). Relationships between organisms include both ancester-descendant relationships and those of common ancestry (an explanation of these concepts is given by Nelson, 1972 a). The philosophy presents no strict formalisations on how relationships between organisms are established but this is usually based on the degree of weighted similarity and the evolutionary grade of the organisms concerned.

The cladistic approach is based on a philosophy propounded by Hennig (1950, 1966) and is often referred to as "Hennigian". This approach has since been considerably refined (e.g. Brundin, 1972; Nelson, 1970, 1971, 1972 a & b; 1973), and may be presented as it is currently accepted in the form of the following model (Cracraft, 1974):

(a) Ancestors cannot be recognised or identified but can only be hypothesised;

(b) Species originate by allopatric speciation and phylogenies are usually assumed to be dichotomous branching sequences;

(c) Related taxa are clustered into lineages on the bases of shared derived characters (synapomorphies). This means that there is a definite concept of relationship based on the common ancestry of the organisms viz. a taxon A is more closely related to taxon B than either is to a third taxon C if, and only if, the first two taxa (A and B) share a common ancestor which is not shared by the third taxon (C).

Cracraft (1974) compared the gradist and cladist systematic models and concluded that the cladist model is to be preferred on the grounds that the premises on which it is based are precisely formulated and provide for logical construction and consistency. The successful application of the model in numerous studies in recent years is testimony of the attraction of these qualities for systematists. It is also for these reasons that the cladistic approach is adopted in this study.

One of the fundamentals of cladistic philosophy has been that species originate in dichotomous branching sequences (Hennig, 1966; Nelson, 1971; Brundin 1972; Cracraft, 1974). This particular concept has been rejected by opponents to the philosophy (e.g. Darlington, 1970) who point out that there are numerous known examples where there are several isolated populations of species which could in time become full species and thus constitute multiple splitting. The cladists counter the argument with the fact that the recognition of dichotomous splitting is based on the unlikely probability that such isolates will all attain species status at precisely the same time. The need to consider multiple speciation is only entertained after the alternatives for dichotomous speciation have been exhausted (Brundin, 1972; Cracraft, 1974).

It has been recently shown by Bremer & Wanntorp (1979) that cladistic analysis does not in fact necessarily determine the sequence of speciation in the sense of reproductive isolation, but rather it provides a sequence of geographic isolation of the taxa concerned. This is important because, as these authors demonstrate, multiple splitting of species is probably a far more common occurrence than is presently recognised. Bremer & Wanntorp (*op.cit.*) also point out that the biological species concept is not a suitable basis for cladistic philosophy, and suggest rather the application of the "evolutionary species" concept as conceived by Wiley (1978).

In spite of these necessary adjustments to the cladistic philosophy, the fundamental concept of establishing the relationships between taxa on the basis of shared derived characters is still valid. It has been pointed out above that cladists have recognised that there are limits to any analysis, and that relationships are not always successfully established since the necessary synapomorphies have not been recognised. To this should be added that the absence of synapomorphies between taxa may also be explained by multiple splitting of an ancestral species. In cases where further analysis of sister groups is not possible due to the sensitivity of analysis, the taxa with unresolved interrelationships remain clustered in groups which are defined on the basis of the last recognisable synapomorphy(-ies). An excellent example of such a state of affairs is given by Greenwood (1979) for the "*Haplochromis*" cichlid species.

The terms "primitive" and "derived" are necessarily only relative to an alternative state in the same character set (homologous characters). From this it is evident that the same character may be either primitive or derived depending on the level of comparison to which it is applied. The following terminology for particular character states has been coined by Hennig: plesiomorph (primitive), symplesiomorph (shared primitive), apomorph (derived), synapomorph (shared derived), autapomorph (derived in one lineage only).

The most essential preliminary step in Hennigian methodology is the sorting out of homologous characters into a series of plesiomorphic and apomorphic states. Hennig (1966) suggested four means by which a character state might be adjudged plesiomorph or apomorph. These are

(a) geological character precedence - a character which appears earlier in the geological record is relatively primitive;

(b) chronological progression - the derived character will appear in the daughter species which has departed farther geographically or ecologically from the ancestral species;

(c) ontogenetic character precedence - ontogeny recapitulates phylogeny, and

(d) the criterion of correlated series transformations.

Nelson (1973) rejects both the recapitulist and the palaeontological arguments on the basis that neither are founded on justifiable assumptions nor on the principle of parsimony. Cracraft (1972) points out that primitive characters may appear at an earlier time, but because of the incompleteness of the fossil record there is no guarantee that primitive character states do not appear at a later time than the derived state.

The criterion of correlated series transformations is of course subject to certain limitations - one of the correlated character states must be known with reasonable certainty. This of course must be established without recourse to the correlated characters - i.e. circular reasoning must be avoided. Thus ultimately one depends on other criteria for determining a character state.

The assumptions on which the criterion of chorological progression depend, i.e. that speciation involves dispersal or ecological change, are not justified. Croizat et al. (1974) show that dispersal is not a necessary adjunct to speciation.

Other criteria for character evaluation have been suggested or implicitly used. Cracraft (1972) considers that there are no objective criteria for a character state evaluation other than a comparative analysis. Several authors have proposed guidelines for evaluations on this basis. According to Crowson (1970), a condition which occurs in related forms outside the group is probably primitive within it, provided the related forms are not actually derived from members of the first group.

Kluge (1976) crystallized the informal procedures which most systematists have used over the years for determining the primitive character state into a set of rules. The primitive state of a character is frequently observed (a) among the groups related to the one being studied (i.e. Crowson's criterion), and (b) within the group chosen for study. Secondly it is exhibited by that taxon which is considered primitive on the basis of other evidence.

These rules have been successfully applied in similar cyprinoid studies (e.g. Smith & Koehn, 1971; Barbour & Miller, 1978) and appear to be reasonably formulated. Consequently they will be the criteria adopted in this study. The usual criteria of parsimony will also apply viz. minimum parallel evolution and minimum reversal of evolutionary trend (Nelson, 1970).

The first part of this chapter will be devoted to a character analysis based on a comparison with other southern African Barbus species. The reasons for considering this comparison sufficiently broad to establish the character states in the redfins are firstly the Southern African Barbus species are sufficiently diverse and numerous (Jubb, 1967) to include representatives of most categories of African Barbus species. Secondly, the closest relatives of the redfins are most likely to occur in adjacent geographic regions rather than in distant regions ("Jordans Law", vide Hubbs, 1943). Tables 5.1 - 5.5 summarize comparative characters in southern African Barbus species.
The character states are summarised in Table 5.6, using a code similar to that applied by Barbour & Miller (1978). In the code the number 0 denotes the primitive state and 1 and 2 denote the form and sequence of the morphocline.

TABLE 5.1

Comparison of certain characteristic morphological features of southern African *Barbus* species. Data derived from personal observations and Jubb (1967).

SPECIES	SIZE +	SCALES	SQUAMATION +		BARBELS	DORSAL FIN	
		Radii (No)	Breast Scales	Pelvic axillary		Form of Unbranched Ray	No. of Branched Rays
B.capensis	large 150 mm	parallel	reduced	present	2	Bony non-serrate Spine	8-10
B.holubi	large	parallel	reduced	present	2	Bony non-serrate Spine	8-10
B.kimberleyensis	large	parallel	reduced	present	2	Non-serrate Spine	8-10
B.marequensis	large	parallel	reduced	present	2	Non-serrate Spine	8-10
B.natalensis	large	parallel	reduced	present	2	Non-serrate Spine	8-10
B.polylepis	large	parallel	reduced	present	2	Non-serrate Spine	8-10
B.andrewi	large	radiate <15	reduced	present	2	Bony Serrated	8
B.serra	large	radiate <15	reduced	present	2	Bony Serrated	8
B.mattozi	large	radiate <15	normal	present	2	Bony Serrated	8
B.poechii	moderate	radiate <15	normal	present	2	Bony non-serrate Spine	8
B.trimaculatus	moderate	radiate <15	normal	present	2	Bony non-serrate Spine	8
B.afrohamiltoni	moderate	radiate <15	normal	present	2	Serrated	8
B.afrovernayi	small	radiate <15	normal	present	-	Serrated	7
B.argenteus	moderate	radiate <15	normal	present	2	Serrated	8
B.eutaenia	moderate	radiate <15	normal	present	2	serrated	8
B.hospes	moderate	radiate <15	reduced	absent	2	serrated	8
B.manicensis	moderate	radiate <15	normal	present	2		
B.multilineatus	small	radiate <15	normal	present	2	serrated	8
B.paludinosus	moderate	radiate <15	normal	present	2	serrated	8
B.tangandensis	small	radiate <15	normal	present	2	serrated	8
B.trevelyani	moderate	radiate <15	normal	absent	2	(serrated)	8
B.annectens	small	radiate >15	normal	present	2	flexible	8
B.anoplus	moderate	radiate <15	reduced	absent	1 or 2	flexible	7
B.barnardi	small	radiate <15	normal	present	1 or 2	flexible	8
B.barotseensis	small	radiate <15	normal	present	2	flexible	8
B.bifrenatus	small- moderate	radiate <15	normal	present	2	flexible	8
B.brevipinnis	small	radiate <15	normal	present	1 or 2	flexible	8
B.fasciolatus	small	radiate <15	normal	present	2	flexible	8
B.gurneyi	moderate	radiate <15	normal	absent	2	flexible	7
B.haasianus	small	radiate <15	(small)	?	-	flexible	8
B.lineomaculatus	small	radiate <15	normal	present	2	flexible	8
B.motebensis	moderate	radiate <15	reduced	absent	2	flexible	7
B.neefi	small	radiate <15	normal	present	2	flexible	8
B.pallidus	small	radiate <15	normal	present	2	flexible	8
B.puellus	small	radiate <15	normal	present	1	flexible	7
B.radiatus	moderate	radiate <15	normal	present	2	flexible	8
B.toppini	small	radiate <15	normal	present	1	flexible	8
B.treurensis	moderate	<15	normal	present	2	flexible	8
B.thamalakanensis	small	<15	normal	present	2	flexible	8
B.unitaeniatus	moderate	<15	(reduced ?)	present	2	flexible	8
B.viviparus	small - moderate	<15	normal	present	2	flexible	8

\+ Notes: (i) Size: large = >150 mm general maximum
moderate = > 50<150 mm general maximum
small = 50 mm or less general maximum

(ii) squamation: reduced means scales are notably smaller and often embedded
normal means although smaller than body scales they are still well developed on the breast.

(iii) pelvic axillary scale: an enlarged distinctly trianguloid scale in the axil of these fins.

(iv) dorsal fin: spine = bony non-serrated unbranched ray
serrated = bony serrated unbranched ray
flexible = soft flexible unbranched ray
No of branched rays: modal counts.

It was readily evident at an early stage in the analysis that there were in fact two separate redfin lineages present. This evidence is derived from certain characters where (e.g. pharyngeal teeth) it was not possible to fit the character state of each redfin species into a single morphocline. In these cases the character state has been differentiated by suffixing a further code (A) to the state.

CHARACTER STATE ANALYSIS

Red fin colouration

Both Barnard (1938, 1943) and Jubb (1965, 1967) laid great stress on the red fin colour of these species, and this forms the prime basis for considering the species related. There is little doubt that this character is distinctive relative to other southern African Barbus species, and at this stage, without considering the results from other characters the redfins, is regarded as synapomorphous.

Reference to several regional studies indicates that red pigment on the fins is common to many cyprinid species (e.g. Hubbs & Lagler, 1958; Scott & Crossman, 1970; Maitland, 1977). There are other southern African Barbus species which have red pigment on the fins albeit not as distinctive as in the southern coastal redfins. Of these other species the most similar to the redfins in red pigment are B.argenteus and B.gurneyi (Crass, 1964; Jubb, 1967; Pienaar, 1978). The point to be made from these observations is that although the red pigment is prominent in the redfins the tendency to develop red colouration is widespread in the genus and family so that the possibility of convergence in the group cannot be ruled out. The function or functions of the red colour in the redfins has not yet been established.

Barbels

Approximately 90% of non-redfin southern African Barbus species have two pairs of barbels (Table 5.1). Four of the redfin species have two pairs of barbels, and this is thus regarded as plesiomorphic.

In B.burgi the anterior pair of barbels only develops at a late stage, and the barbels are never very long compared to the other species with anterior barbels. This condition could be interpreted as an apomorphic step towards the loss of barbels in other species.

Scale morphology

The number of scale radii in Barbus species with radiately striated scales has been assessed by the arbitrary examination of certain specimens. The majority of southern African species generally have fewer than about 12 primary radii per scale. Fewer scale radii are therefore taken to be plesiomorph and the most derived (or apomorph) species in this regard is B.tenuis.

Squamation

(i) Scale size. The majority of redfin species have a similar scale size (approx. 30-38 in lateral line; 12-16 around caudal peduncle) except B.asper which has relatively small scales. This is considered apomorphic as the only other equivalently small scaled southern African Barbus species are the large "yellowfish" which have parallel striated scales. The extremely small scales of O.quathlambae are quite clearly apomorphic (Greenwood & Jubb, 1967).

(ii) Pelvic axillary scale. This scale is commonly present in southern African Barbus and other cyprinid genera. (Table 5.1). It is however reduced or absent in a few species other than the flexible-rayed redfins. (B.hospes, B.trevelyani, B.anoplus, B.motebensis, B.gurneyi) which represent at most 12.5% of non-redfin Barbus species in the region. This suggests that the reduced condition in the flexible-rayed species is synapomorphic.

(iii) Breast region. Reduction of scales in the breast region is only partially dependent on scale size - the smaller scaled species have a greater area of reduced scales. Smaller scales on the breast region is characteristic of the large yellowfish (parallel striated scaled species) and the two large species with radiately striated scales, B.andrewi and B.serra, from the south-west Cape. The significance of the reduction of scales in this region is not entirely understood but it is notable that all the species mentioned above have relatively long involuted intestines and are basically bottom feeders. The flexible-rayed redfin species all have subterminal or inferior mouths suggesting they too are bottom feeders. The majority of small or medium sized Barbus in southern Africa do not have a marked reduction in breast scale size (exceptions are B.hospes, B.anoplus, B.motebensis and B.unitaeniatus). Two of these viz. B.hospes and B.unitaeniatus also have inferiorly positioned mouths and there is thus a possible correlation between breast scale reduction and feeding habits. The character is entrenched in the flexible-rayed redfins which suggests it should be tentatively considered as a synapomorphic character.

(iv) Nape scales. Barbus tenuis, B.asper and O.quathlambae have reduced or crowded scales in the nape region. Hubbs (1941) has observed that reduction and loss of nape scales is characteristic of many rheophilic fishes. Both the small scales of B.asper and O.quathlambae facilitate crowding on the nape. B.tenuis has relatively larger scales. Barnard (1943) observed that a naked nape patch was variable within populations of B.tenuis. At this stage no genetic significance is attached to this character.

Unbranched dorsal fin rays

The majority of southern African Barbus species with radiately striated scales have simple, flexible last unbranched dorsal fin rays (Table 5.1). Although the proportion of each species which each character will vary in other regions, in southern Africa the ratio of simple rayed to serrated rayed species is five to three. The majority of the lower teleostean fishes have simple,flexible dorsal fin rays and this is the usual condition in the majority of the African cyprinid genera. It is reasonable to assume therefore that the simple,flexible condition is plesiomorphic and the serrated condition apomorphic.

The state of the character in B.erubescens is intermediate between the flexible and simple condition and that found in B.calidus where the serrations are well developed. Theoretically the character state in B.erubescens could be interpreted as being a first stage apomorphic step from the simple condition to the serrated condition. However there is little evidence for this and it is more likely that the unbranched dorsal fin ray of B.erubescens represents a reduction from the condition in B.calidus. Similar cases of loss of serrations and of ossification of this fin ray in other Barbus have been reported in the literature (e.g. Jubb, 1965, 1967; Bell-Cross, 1967; Poll, 1976). From these cases it is evident that a simple, flexible unbranched dorsal fin ray in Barbus species need not necessarily be plesiomorph to a serrated ray state in all cases. In B.erubescens the character state is apomorph to the serrated ray of B.calidus.

Branched dorsal fin rays

The majority of southern African *Barbus* species have eight or more branched dorsal fin rays (Table 5.1). The few species with seven such rays include *B.afrovernayi*, *B.anoplus*, *B.gurneyi*, *B.motebensis* and *B.puellus*. From this it may be considered that the seven branched dorsal fin rays in the redfin species, except *B.erubescens*,is a synapomorphy. The eight branched rays in *B.erubescens* is probably plesiomorphic.

Branched anal fin rays

The extreme conservative nature of the number of branched rays in the anal fin of certain cyprinid genera has long impressed systematists. Hora (1937:312) wrote "It may here be noted that in a great majority of cyprinoid genera there are only five branched rays in the anal fin. Any variation from this standard is, therefore, of special significance". Boulenger (1907 pp 198-199) remarked of *Barbus* species in the Nile River "I have been much impressed by the absolute constancy of the number (5) of branched rays in the anal fin...". Gosline (1978) indicates that a key character of two large cyprinid subfamilies (Cyprininae and Gobioninae) is that the branched anal fin rays are restricted to 5, 6 or rarely 7. Whether or not Gosline's concept of these subfamilies is accepted (*vide* Howes, 1978) is not relevant to this discussion - the impressive number of cyprinid species with this conservative character remains the same. The importance attached to the conservativeness of this character is shown by Brittan (1954) who erected a sub-genus for the single *Rasbora* species in south-east Asia with six in place of the usual five branched anal fin rays.

The only southern African *Barbus* species with six or more branched anal fin rays are *B.andrewi*, *B.calidus* and *B.erubescens*. As in southern Africa, the majority of the African *Barbus* species have five branched anal fin rays. A few Moroccan species have six branched anal rays. Banister & Clark (1977) found two of three *Barbus* species from the Arabian peninsula with six branched anal fin rays and considered that this was indicative of relationship between the species.

B.andrewi, *B.calidus* and *B.erubescens* all occur in close proximity in the south-west Cape and Skelton (1976) argued that the branched anal fin ray indicated a synapomorphy for the species. However a subsequent study of *B.andrewi* suggests this species has a closer relationship with *B.serra*, also from the south-west Cape. *B.serra* has only five branched anal fin

TABLE 5.2

Occurrence of tubercles in southern African Barbus species

Species	Description and Source
B.capensis	Minute erupted tubercles scattered on lachrymal plate and beneath orbit. (AM/P 1974).
B.holubi	Minute erupted tubercles scattered on snout and top of head and on branched rays of anal fin. (Barnard, 1943); Jubb, 1965).
B.kimberleyensis	Minute erupted tubercles scattered over top of head and snout.
B.polylepis	Minute erupted tubercles scattered on top of head and snout as well as sides (Fig. 5.1). Single rows on branched rays of anal fin. (AM/P 1919).
B.natalensis	Minute erupted tubercles scattered over top of head and snout and predorsal scales. (AM/P 163).
B.marequensis	Minute erupted tubercles scattered on top of head. (AM/P 2022; Groenewald, 1958).
B.serra and B.andrewi	Minute erupted tubercles scattered over top and sides of head and snout(Fig.5.1); single rows over fin rays of all fins including leading edge of pectoral (both sexes). (AM/P 2041; AM/P 1976).
B.hospes	Minute erupted tubercles (0.2 mm diam.) scattered densely (10-12/mm^2) on top and sides of heat, snout and predorsal region. Rows 2-3 deep conical tubercles over pectoral fin rays. (Both sexes). AM/P 1834; Barnard, 1943).
B.multilineatus	Bands - conical tubercles over fin rays of pectoral fins: males. (AM/P 3277).
B.afrohamiltoni	Bands 3-4 deep over fin rays of pectoral fins; males. (AM/P 4408).
B.argenteus	Minute erupted tubercles scattered on top and sides of head; scattered over exposed scale surfaces over entire body; weak bands 2-3 deep on leading and subsequent 5-6 pectoral fin rays; males. (AM/P 602).
B.trevelyani	Minute erupted tubercles over entire head and body (exposed scale surfaces); single spaced rows over pectoral and pelvic fins; males. (AM/P 2587; Gaigher, 1976).
B.anoplus	Bands 2-3 deep conical tubercles over pectoral fin rays; males. (AM/P 585).
B.motebensis	Conical tubercles (0,3 mm basal diam.) on snout, chin, lower jaw rami, base of barbels and cheeks and top of head; bands 3-4 deep over pectoral fin rays; occasionally present on free edge of few scales; males. (AM/P 889; Jubb, 1967, 1968).
B.gurneyi	Conical tubercles (0,5 mm basal diam.) on snout, top of head especially anteriorly. Also on sides of head behind orbit; few scattered on cheeks and lower jaw rami; bands 3-4 deep over pectoral fin rays including leading ray. (AM/P 1013; AM/P 847; Crass, 1964; Jubb, 1967).
B.annectens	Minute conical tubercles widely scattered on top of head; bands up to 4 deep over pectoral fin rays; males. (AM/P
B.brevipinnis	Bands of conical tubercles - deep on pectoral fins. Males only. (AM/P
B.lineomaculatus	Minute conical tubercles scattered on top of head and 1-2 on lower jaw rami; bands 5-6 deep over pectoral fin rays excluding leading ray; males. (AM/P 1982).
B.viviparus	Minute conical tubercles scattered over top and sides of head; bands up to 5 or 6 deep over pectoral fin rays. Males. (AM/P
B.unitaeniatus	Minute conical tubercles scattered on top of head and below orbit; bands 3-4 deep over leading and other pectoral fin rays. Males. (AM/P 6380).
B.barnardi	Small conical tubercles over lachrymal bones and snout also rami of lower jaw; bands 5-6 deep over pectoral fin rays; males. (AM/P 3267; Jubb, 1965).
B.toppini	Minute conical tubercles on snout and top of head, also rami of lower jaw; bands 5-6 deep over pectoral fin rays; males. (AM/P 4426).
B.macrotaenia	Small conical tubercles on lachrymal bones, snout and top of head, below orbit and rami of lower jaw; bands 5-6 deep over pectoral fin rays, males; vestigial in females. (AM/P 2138).
B.trimaculatus	Erupted mounds over top of head; bands up to deep over pectoral fin rays. (P.F.I., I/69).

rays which suggests that *B.andrewi* and *B.calidus* have independently derived six branched anal fin rays. On the other hand the six and seven branched anal rays of *B.calidus* and *B.erubescens* are almost certainly synapomorphic.

Tubercles

Tubercles represent one of the more outstanding characters of the flexible-rayed redfin species. These structures have generally received little attention in literature on *Barbus* species, although originally pointed out by Günther in 1868. A survey of southern African *Barbus* species (Table 5.2) suggests that the occurrence of tubercles is perhaps more common than is realized. The reason for this apparent lack of attention is probably twofold, because in *Barbus* they are usually found only on males in ripe breeding condition, and because they are usually extremely small structures which are frequently not evident. A microscopic examination is often required to identify tubercles. The few species with larger or otherwise more prominent tubercles have usually been reported on in literature.

The survey (Table 5.2) showed that several different tubercle patterns are represented in various *Barbus* species. The following patterns are recognised.

I. Small (< 0.5 mm diameter), erupted tubercles (referred to by Barnard (1943) as "pimples") scattered densely over snout, on the dorsum and sides of the head or part thereof, on the exposed surfaces of the predorsal scales, and as single rows on the fin rays. These tubercles develop on both sexes. The category may be divided into two groups.

   i) tubercles absent on all fins except the anal.
   ii) tubercles present on all fins or on the pectoral and pelvic fins only.

   The yellow fishes, i.e. large *Barbus* species with parallel striated scales (*B.capensis*, *B.holubi*, *B.kimberleyensis*, *B.polylepis* Fig. 5.1), *B.natalensis* and *B.marequensis* are included in the first group. Groenewald's (1957) Figs 14 and 20 illustrate the head of a specimen of *B.marequensis* (= *Varicorhinus brucii*) on which tubercles are evident. In many of these species the tubercles are not well developed and are restricted in their distribution on the head.

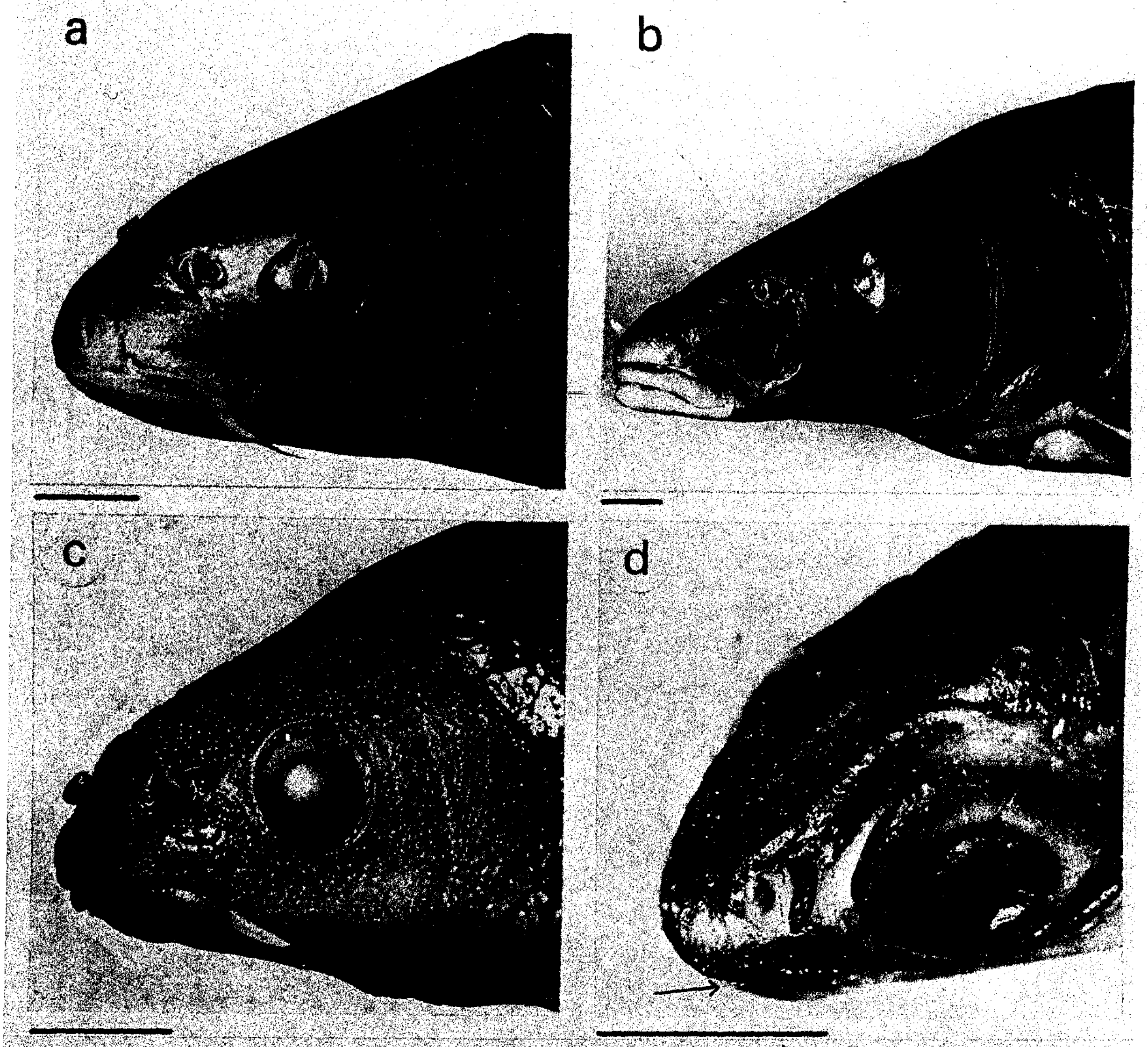


FIGURE 5.1. Head tubercles of four southern African *Barbus* species.
(a) *B.polylepis* SL 225 mm AM/P 919. Scale bar 10 mm.
(b) *B.serra* SL 305 mm AM/P 2041. Scale bar 10 mm.
(c) *B.trevelyani* SL 56 mm AM/P 2587. Scale bar 5 mm.
(d) *B.barnardi* SL 30 mm AM/P 3267. Scale bar 2.5 mm.
(arrow directs to tubercles).

To the second group belong *B.serra* (Fig. 5.1, 5.2), *B.andrewi*, *B.calidus*, *B.erubescens*, *B.trevelyani* (Fig. 5.1, 5.2). The tubercles are generally better developed in these species than in the yellow fishes and frequently cover much of the head and the body surface. There are usually relatively widely spaced single rows of tubercles (e.g. Fig. 5.3) over the rin rays, particularly of the pectoral fins.

II. Small (< 0.5 mm diameter), erupted tubercles on the head region with conical tubercles on the pectoral fins. A few species have been found with such a pattern: *B.trimaculatus*, *B.hospes* (Fig. 5.3) and *B.argenteus*.

III. Small (< 0.5 mm diameter), conical tubercles on the head with bands of conical tubercles on fins. There are several groups which can be recognised here.

  (i) Bands of conical tubercles on the fins only e.g. *B.multilineatus*, *B.afrohamiltoni* and *B.brevipinnis*.

  (ii) Tubercles sparsely scattered mainly on top of the head, bands on pectoral fins. Here included are *B.annectens*, *B.lineomaculatus*, *B.viviparus* and *B.unitaeniatus*.

  (iii) Tubercles concentrated anteriorly on the head, especially on snout, bands on pectoral fins: *B.toppini*, *B.barnardi* and *B.macrotaenia*.

  (iv) Large (> 0.5 mm basal diameter), conical tubercles on head and bands on pectoral fins: *B.anoplus*, *B.motebensis* (Fig. 5.3) and *B.gurneyi* (Fig. 5.3). *B.anoplus* is distinguished from *B.motebensis* on the grounds that the males do not develop tubercles (Jubb, 1967; 1968). Gaigher (1976) found that certain populations of *B.anoplus* do develop head tubercles and personal observations indicate that development of pectoral fin tubercles is consistent in the species.

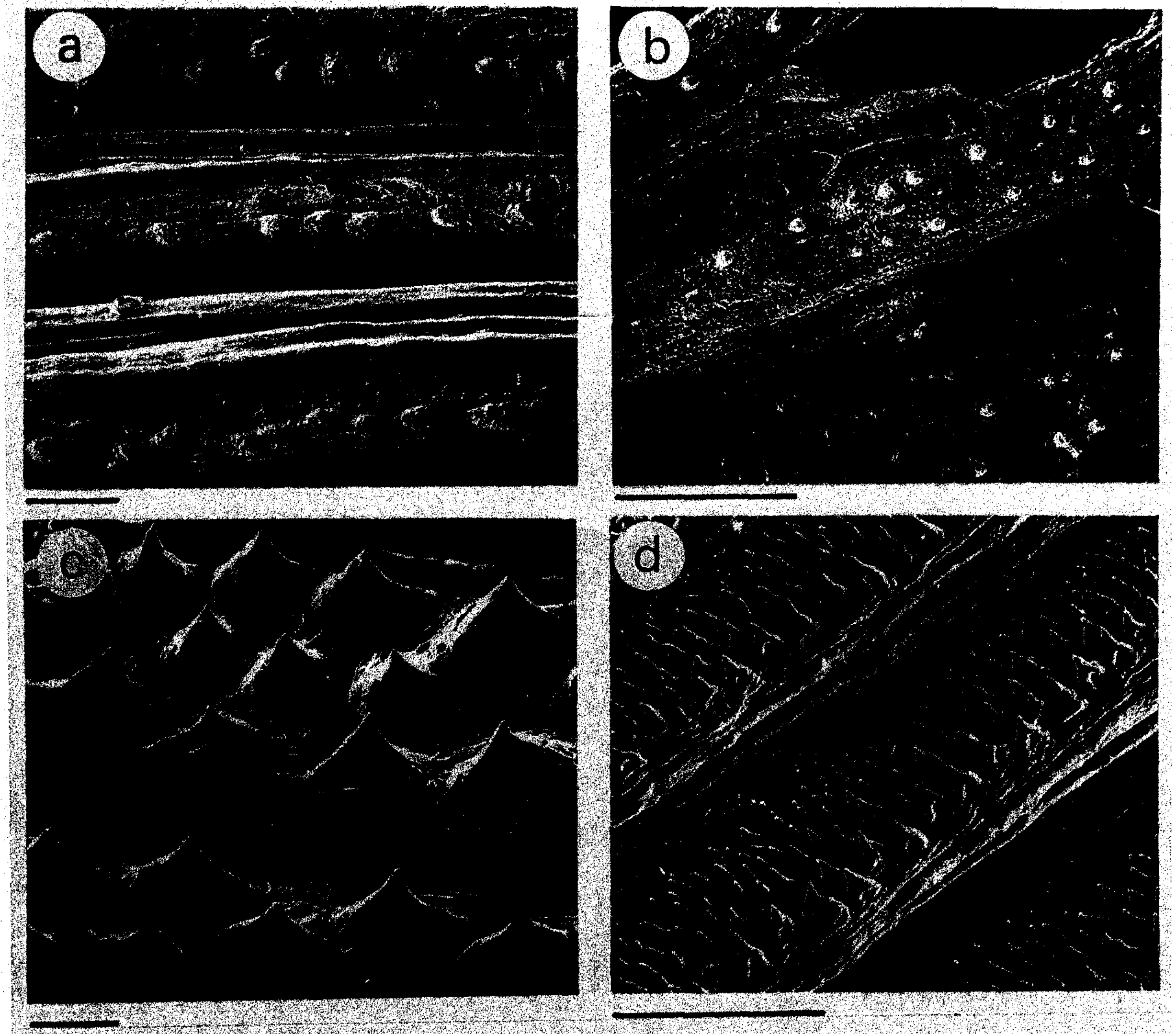


FIGURE 5.2. Tubercles on pectoral fins of four southern African Barbus species.

(a) B.serra SL 305 mm AM/P 2041. Scale bar 0.5 mm.

(b) B.trevelyani SL 73 mm AM/P 3703. Scale bar 0.5 mm.

(c) B.hospes SL 63 mm AM/P 1834. Scale bar 0.05 mm.

(d) B.macrotaenia SL 29,5 mm AM/P 2138. Scale bar 0.25 mm.

(v) The flexible-rayed redfin pattern (Chapter 3). The major features of comparison with the other patterns are: the much larger size of these tubercles; the regularity and form of the pattern, and the development of regular rows on the borders of the scales.

(vi) There are other distinct patterns of tubercles in African Barbus - e.g. described by Poll (1961, 1976) for the Clypeobarbus. This pattern is noteworthy in that large conical tubercles are present on the lips of these fishes as well as the snout and chin. Bands of conical tubercles also occur on the pectoral fins of C.pseudognathodon (pers.obs.).

(vii) Banister & Bailey (1979) described Barbus papilio with relatively large tubercles below the orbit and over the post-orbital region. This again is a different pattern to those described above.

The development of tubercles of the size and pattern found in B.burchelli, B.burgi, B.afer, B.asper, B.tenuis and vestigially in B.phlegethon is quite clearly unique in the African context and represents a very distinct synapomorphy. The tubercles of O.quathlambae can be included in this group without much difficulty and are interpreted as derived from the condition in the redfin Barbus species (see below). The small scattered "erupted" tubercles on the head and scale surfaces of B.calidus and B.erubescens is found in several other southern African Barbus species. With regard to the tubercles of B.calidus and B.erubescens it is noted that all other small Barbus species with radiately striated scales (except B.trevelyani) have bands of conical tubercles on the pectoral fins. Like B.calidus and B.erubescens, B.trevelyani has single rows of erupted tubercles only on the pectoral fin rays.

Lachner & Jenkins (1971) have found that cyprinids with unspecialized breeding habits generally tend to have small tubercles distributed over the head in no particular pattern. This is recorded for B.calidus and B.erubescens and is regarded as plesiomorphic for the redfins. It is however quite evident that there is little in common between the tubercles of the serrated-rayed and flexible-rayed redfin species. In view of this the tubercles of the two redfin groups are not considered a homologous character series.

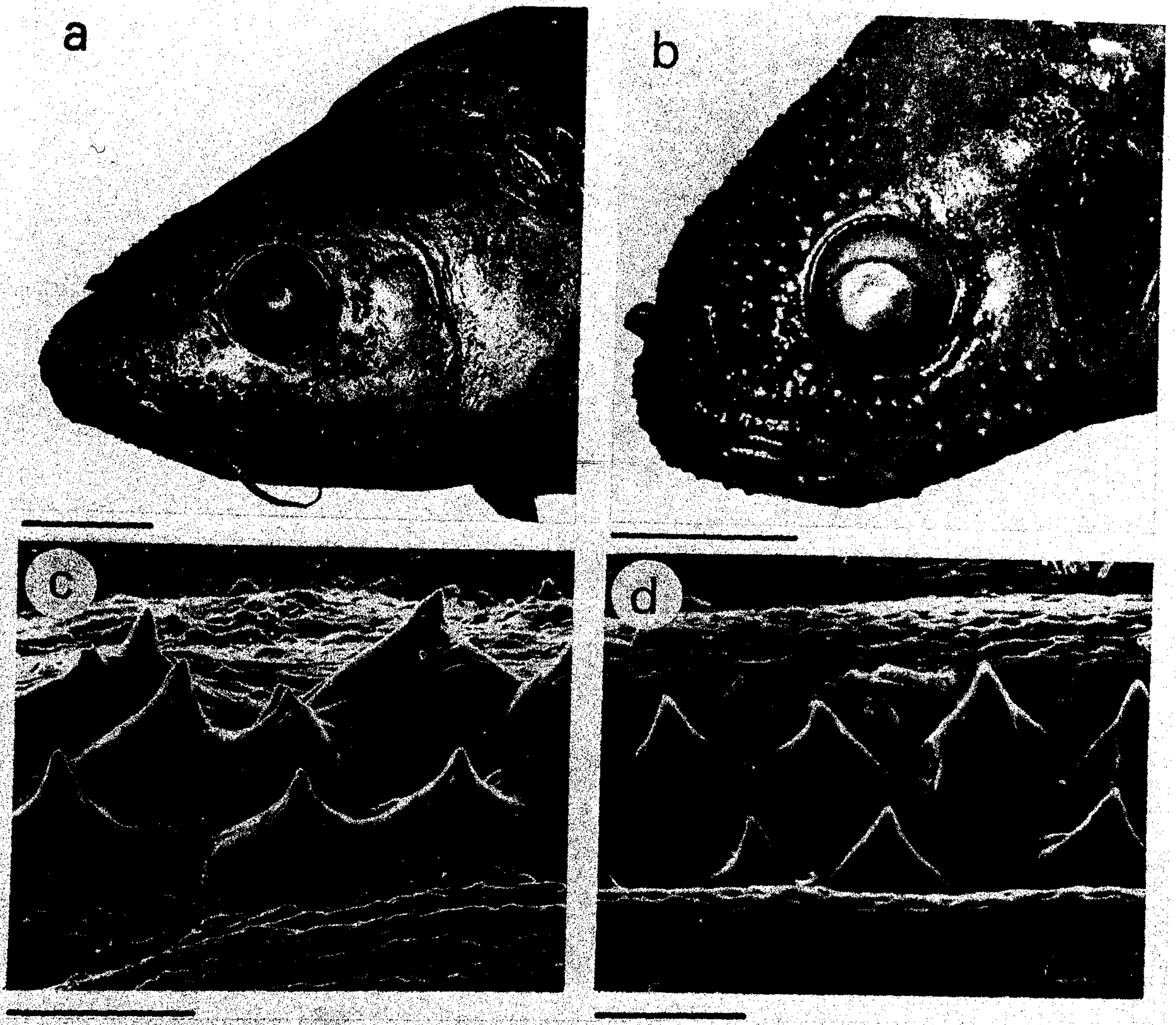


FIGURE 5.3. Aspects of tubercles of B.gurneyi and B.motebensis.
(a) Lateral view of head of male B.gurneyi SL 70,5 mm AM/P 1013. Scale bar 5,0 mm.
(b) Antero dorsal view of head of B.motebensis. SL 48 mm AM/P 842. Scale bar 5,0 mm.
(c) Scanning electron micrograph of portion of band of tubercles on pectoral fin of B.gurneyi SL 54 mm. AM/P 847. Scale bar 0.05 mm.
(d) Scanning electron micrograph of portion of band of tubercles on pectoral fin of B.motebensis SL 46,5 mm AM/P 889. Scale bar 0.05 mm.

Given that tubercles in Barbus species are generally small, there is the possibility that the small tubercles of B.burgi or O.quathlambae are plesiomorphic. Although the tubercles of O.quathlambae are small and to a certain extent less definitely organized on the head (Skelton, 1974a), there are two indications that they are derived from the pattern found in the redfin Barbus species and not ancestral to it. In spite of the small size the number of snout tubercles in O.quathlambae is low. Individuals with best developed tubercles (Skelton, 1974a: Fig. 2), have a maximum of five tubercles in each snout group. Secondly the tubercles on the scales and fins of this species both suggest a condition derived from that found in the flexible-rayed redfins. If the extremely small scales of O.quathlambae are autapomorphic then it is likely that the reduction in tubercle number per scale in this species is also autapomorphic. The pectoral fin tubercles are more compressed than in any of the Barbus species examined.

In addition to the above, the specialization of the tubercles in O.quathlambae can be explained in terms of the spawning habits of the species suggested by Gephard (1978). Fishes from crevice habitats are generally attenuated in form with smooth profiles. They usually do not have large projections. The large head tubercles found in the flexible-rayed redfin Barbus species would not be suitable for manoeuvering in the confines of rocky crevices.

The tubercles of B.burgi are considered to represent the plesiomorph condition for the flexible-rayed species. The character is best viewed in terms of the number of tubercles on the snout. In large mature males of B.burgi there are more than 10 tubercles per group on the snout. The transformation of the character proceeds initially by reduction in number before an increase in size. The next stage is represented by B.burchelli which has between six and ten tubercles per group on the snout. There is a further reduction in number to between three and five tubercles in B.asper and B.afer. In these species they are again relatively larger.

The three autapomorphic states of tubercles of B.phlegethon, B.tenuis and O.quathlambae can be derived from that of B.asper and B.afer. B.phlegethon has reduced tubercles; B.tenuis has reduced pectoral fin tubercles. In O.quathlambae the reduction in tubercle size on the head, reduction of number on the scales and the specialization of bands on the pectoral fins has occurred.

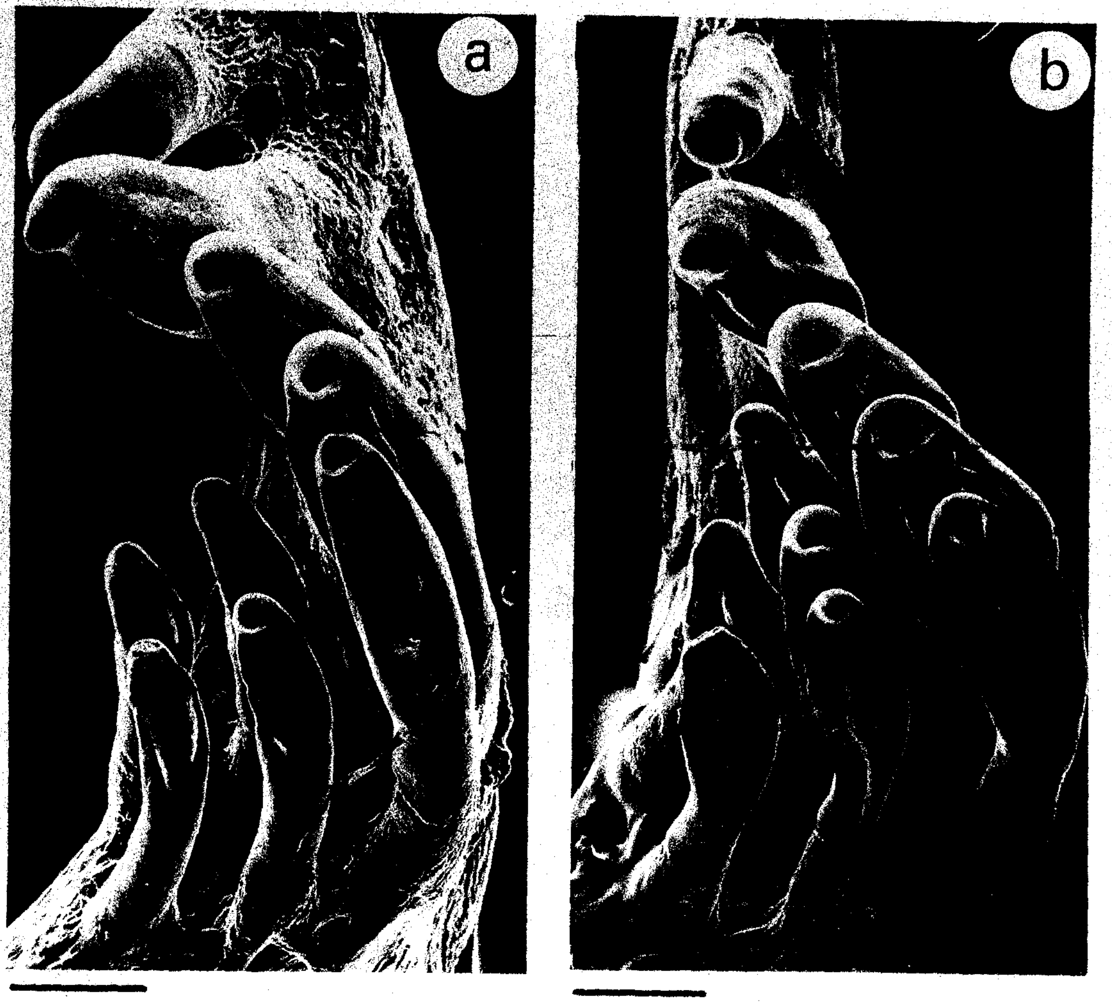


FIGURE 5.4. Occlusal view of the pharyngeal teeth from juveniles of two large southern African Barbus species (scanning electron micrographs). Scale bar = 0.5 mm.

(a) B.capensis SL 105 mm AM/P 1370

(b) B.serra SL 95 mm AM/P 1361

Pharyngeal bones and teeth

The pharyngeal bones and teeth of cyprinids can provide valuable systematic characters (Chu, 1935), but to date have not been used in the systematics of southern African Barbus species.

Chu (1935) demonstrated that the length to width ratio of the pharyngeal bones of cyprinids could be correlated with diet. Carnivorous species tend to have more slender pharyngeal bones, while herbivorous species have relatively shorter and broader bones. In Chinese Cyprininae the length to width ratio of pharyngeal bones varies from 2:1 to 5:1 (Chu, 1935).

In B.calidus and B.erubescens there is a relatively high length to width ratio of 4-5,5:1, whereas in all the flexible-rayed species the ratio is somewhat lower - ±3-4:1. No interspecific differences were found in the latter group.

B.tenuis shows an unusual degree of specialization in the degree of loss of pharyngeal teeth which is however not matched by a change in the proportions of the pharyngeal bones. This applies to O.quathlambae as well.

Although there is no comparative data available for non-redfin Barbus species, measurements of the pharyngeal bones of one or two individuals of a number of species indicate that the ratios given above for redfin species fall within the range for other small radiately striated scaled Barbus species.

Although it is not possible at this stage to evaluate this character as apomorphic or plesiomorphic, the conservativeness of the length to width ratio in flexible-rayed species and the difference between the two groups lends support to the concept of two distinct lineages of redfins.

Most of the Barbus species investigated have small teeth in the minor row with sub-cylindrical stems and bent depressed crowns which have small, recurved terminal cusps (Fig. 5.4, 5.5). Middle row teeth are larger but generally modelled on the same pattern. Outer, major row teeth are heterodont. The first and second teeth are relatively slender, their stems cylindrical or slightly ovoid, and the crown is bent and compressed usually with a recurved, terminal conical cusp. The third tooth is stouter, the crown less bent and the terminal cusp large and conical.

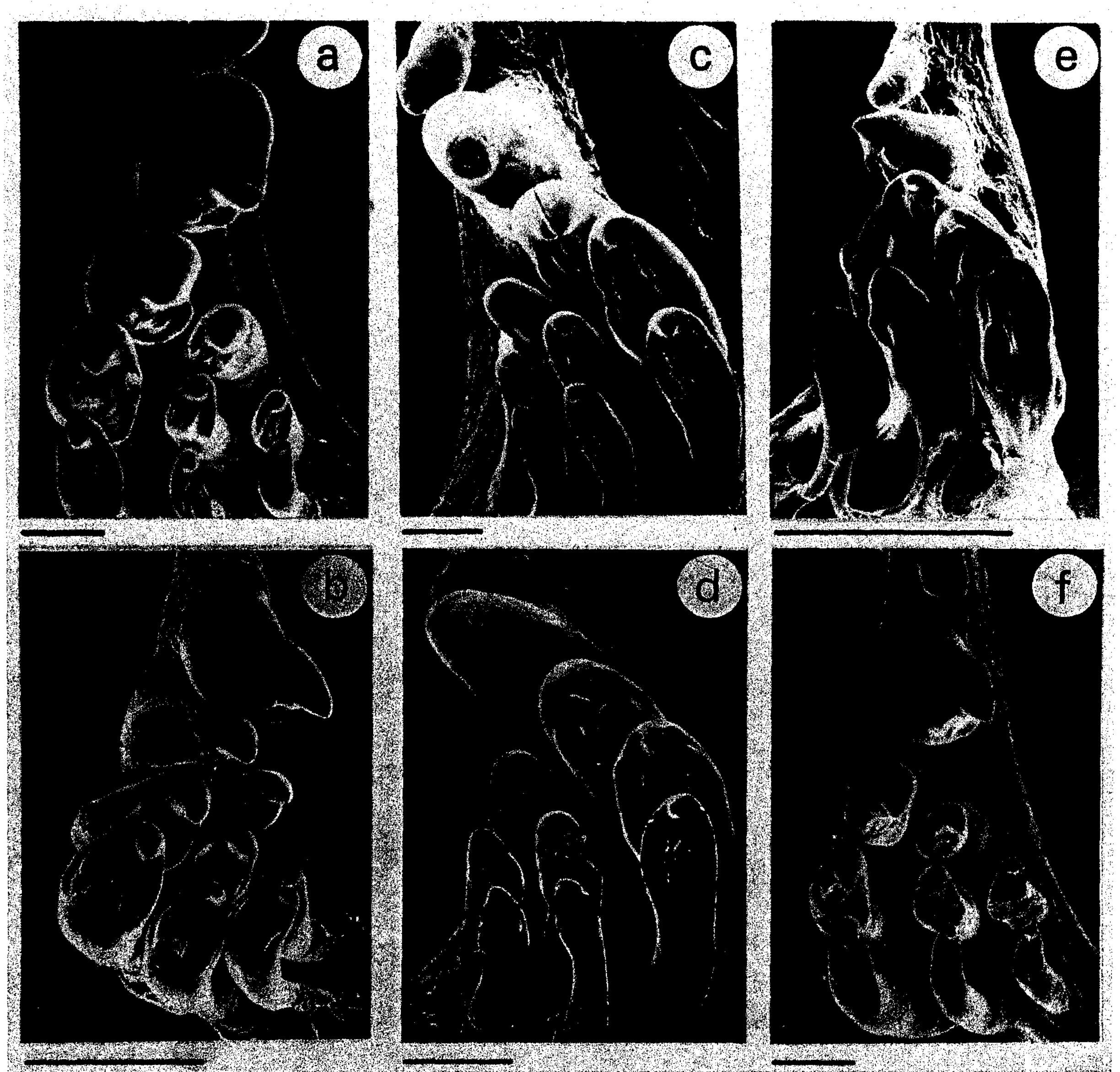


FIGURE 5.5. Occlusal view of the pharyngeal teeth of several southern African *Barbus* species. Scale bar = 0.5 mm.

(a) *B.trimaculatus* SL 63 mm AM/P 550, right arch ;
(b) *B.trevelyani* SL 55 mm AM/P 2587, right arch ;
(c) *B.paludinosus* SL 68 mm AM/P 425, left arch ;
(d) *B.afrohamiltoni* SL 50 mm, left arch ;
(e) *B.afrovernayi* SL 30 mm AM/P 3313, left arch ;
(f) *B.gurneyi* SL 67 mm AM/P 1013, right arch.

The fourth tooth is the largest tooth in the row, the stem is usually compressed and has a large conical crown on the ventral half.

In the juveniles of large *Barbus* species (e.g. *B.capensis*, *B.serra* (Fig. 5.4) the tooth shape is similar to other species of both large and small *Barbus* (Fig. 5.5). In the adults of the large species the pharyngeal teeth frequently become progressively stouter and in certain cases semi-molariform. Similar developments in the pharyngeal teeth of large *Barbus* species from East Africa have been given by Banister (1973).

The pharyngeal tooth form of the flexible-rayed redfins (Chapter 3) is, as far as is known, comparable to only one other southern African *Barbus* species, *B.afrovernayi* (Fig. 5.5d). The salient comparative features are the oblique wear on the crowns and the lateral placement of the cusps. *B.afrovernayi* is one of very few small, radiately striated southern African *Barbus* species with the alimentary tract involuted beyond the simple S-form (see below). This distinctive, small tropical species is without any other similarities to the redfin species and it is more than likely that the similarity of the pharyngeal teeth is due to convergence and is not synapomorphous.

It has been shown in Chapter 3 that the flexible-rayed redfin species and *O.quathlambae* all have a basic pattern in the shape of the pharyngeal teeth. This has been modified in accordance with the inferred feeding habits of each species. The basic shape,which emphasizes an oblique crown and cusps on the medial side, is relatively unusual in southern African *Barbus* species and is therefore considered to be a synapomorphy for the flexible-rayed redfins. The shape is most pronounced in those species with a relatively long and involuted intestine (*B.burchelli*, *B.burgi*, *B.asper* and *B.afer* and *B.phlegethon*), and this state is taken to be the plesiomorph condition in the lineage.

The shape of the teeth of *B.tenuis* and more especially *O.quathlambae* is convergent with the shape of the teeth of *B.calidus* (Fig. 3.38). In *B.tenuis* and *O.quathlambae* the shape of the pharyngeal teeth is regarded as synapomorphic. The shape of the teeth of *B.calidus* is similar to several other southern African *Barbus* species. The teeth of *B.erubescens* are more caniniform and are apomorphic relative to those of *B.calidus*.

It is generally accepted that three rows of pharyngeal teeth is the primitive condition in cyprinids (Chu, 1935; Nelson, 1969b; Eastman & Underhill, 1973). All southern African Barbus species except B.tenuis have trisereal pharyngeal teeth and this, as far as is known, is the usual condition in other African Barbus species. The usual tooth formula for southern African Barbus is 2,3,5 - 5,3,2 (pers.obs.) and again this appears to apply to other African species (Matthes, 1963; Banister, 1973). A few southern African species (e.g. B.toppini and B.trevelyani) have only four teeth in the major (inner) row on each arch (pers.obs.). The plesiomorph state in the redfin species is thus accepted as trisereal, with a formula 2,3,5 - 5,3,2. This is characteristic for B.calidus, B.burchelli, B.burgi, B.asper and B.afer.

Transformation to the character state in other redfin species has occurred via reduction in two areas. The reduction of teeth in the outer (minor) row is a synapomorphy shared by B.phlegethon, B.tenuis and O.quathlambae. There is only a partial reduction of the row in B.phlegethon so that the total reduction of the row in B.tenuis and O.quathlambae is considered synapomorphic for these two species. Reduction of a tooth in the major row occurs in two species, B.erubescens and O.quathlambae. This is unlikely to represent a synapomorphy for two reasons. It would invalidate the synapomorphy of B.phlegethon and B.tenuis with O.quathlambae (which is the more parsimonious interpretation) and the shape of the teeth of B.erubescens and O.quathlambae does not appear to be homologous at this level of phylogeny. This suggests that the loss of a major row tooth is an independant derivation for each species.

It is logical to interpret the pharyngeal teeth shape and formula of B.erubescens (2,3,4 - 4,3,2) as derived from the state found in B.calidus (2,3,4 - 5,3,2) (Skelton, 1974b).

Intestine

The relative length and degree of coiling of the intestine does not seem to have evoked much interest in African Barbus systematics. Differences here can however be put to good use as a systematic character in cyprinids, provided they are seen in the correct perspective (Kafuku, 1958; Barbour & Miller, 1978). The few studies on the intestine of African Barbus species available (e.g. Matthes, 1963; Kruger & Mulder, 1973) report on

TABLE 5.3

Length and involution of intestine in southern African *Barbus* species

Species	AM/P	GL x $\frac{1}{SL}$	Form	(N)
B.capensis	1370	1,94	involuted	(3)
B.holubi	163	1,64	involuted	(1)
B.kimberleyensis	3922	1,21	involuted	(3)
B.polylepis	283	1,61	involuted	(3)
B.natalensis	40	2,33	involuted	(2)
B.andrewi	SAM 18936	1,53	involuted	(3)
B.serra	1361	1,3	involuted	(2)
B.mattozi	3722	0,75	short-s-flexured	(1)
B.poechii	3252	0,87	short-s-flexured	(3)
B.trimaculatus	550	0,92	short-s-flexured	(3)
B.afrohamiltoni	4408	0,98	short-s-flexured	(5)
B.afrovernayi	3313	1,20	involuted	(3)
B.argenteus	3577	0,85	short-s-flexured	(5)
B.eutaemia	358	0,74	short-s-flexured	(2)
B.hospes	1834	0,95	short-s-flexured	(3)
B.multilineatus	734	0,72	short-s-flexured	(3)
B.paludinosus	976	0,82	short-s-flexured	(6)
B.tangandensis	3311	0,78	short-s-flexured	(3)
B.trevelyani	11	1,26	involuted	(3)
B.annectens	3854	0,90	short-s-flexured	(3)
B.anoplus	2705	0,79	short-s-flexured	(3)
B.barnardi	3237	0,88	short-s-flexured	(3)
B.barotseensis	3381	0,77	short-s-flexured	(3)
B.bellcrossi	1714	1,0	short-s-flexured	(1)
B.bifrenatus	1320	0,96	short-s-flexured	(3)
B.brevipinnis	1716/35	0,97	short-s-flexured	(1)
B.fasciolatus	3352	0,62	short-s-flexured	(3)
B.gurneyi	1013	0,96	short-s-flexured	(3)
B.haasianus	3156	0,82	short-s-flexured	(3)
B.lineomaculatus	747	0,79	short-s-flexured	(3)
B.manicensis	671	0,83	short-s-flexured	(1)
B.motebensis	889	1,01	short-s-flexured	(3)
B.neefi	1546	0,83	short-s-flexured	(3)
B.pallidus	1404	0,87	short-s-flexured	(3)
B.puellus	1195	0,91	short-s-flexured	(1)
B.radiatus	2410	0,85	short-s-flexured	(3)
B.toppini	4438	0,77	short-s-flexured	(3)
B.trewensis		0,84	short-s-flexured	(3)
B.thamalakanensis	3417	0,82	short-s-flexured	(3)
B.unitaeniatus	30	0,81	short-s-flexured	(3)
B.viviparus	1346	0,86	short-s-flexured	(3)

the length of the gut but not on its pattern of coiling. Where known, the relative length and form of the intestine of African Barbus species is basically conservative, without remarkable interspecific differences.

A survey of gut length and coiling of southern African Barbus species (Table 5.3) showed that the large yellow fish all have involuted intestines which may be between two and three times standard length. The pattern of coiling is similar to that reported for the redfin Barbus species in Chapter 3. An exception is the predator B.mattozi which has a short, single flexured, S-shaped intestine, more or less equal to the SL. The majority of the small and moderately sized radiately striated, scaled Barbus species have a short intestine equal to or less than the standard length. The tract forms a simple recurved S-pattern within the body cavity. Only two species, B.trevelyani and B.afrovernayi show any degree of further involution and have a slightly longer tract than the other small Barbus species. In these two species the intestine involutes on a similar pattern to the redfins, but is not as extensive as, for example, that of B.burgi or B.asper.

It appears that the plesiomorph condition of the intestine for small Barbus species with radiately striated scales is a short single flexured tract more or less equal to the standard length. This state is characteristic of B.calidus, B.erubescens and O.quathlambae and to a lesser extent B.tenuis. For B.calidus and B.erubescens there is no reason to believe that the character is other than plesiomorph. As noted in Chapter 3, the intestine is relatively shorter in B.erubescens than in B.calidus. This correlates with the reduction in pharyngeal tooth number and more caniniform teeth. The tooth formula and shape in B.calidus is closer to that more commonly observed in Barbus species which suggests that B.erubescens is relatively more specialized.

Based on the circumstantial evidence of the character state of other structures associated with trophic function, the short intestine of B.tenuis and O.quathlambae can be derived from that of other flexible-rayed redfins. The paucity of small Barbus species with involuted intestines longer than the standard length suggests that the relatively long and involuted intestine in the flexible-rayed redfins is a synapomorphy. This agrees with the synapomorphous form of the pharyngeal teeth of these species. If the short intestine of *B.tenuis* and *O.quathlambae* was plesiomorphic one could expect that the pharyngeal teeth of the species also to be plesiomorphic but, as noted, they are clearly derived. The morphology of structures associated with trophic function of these two species is closely integrated with the same structures of other flexible-rayed redfin species. All have subterminal or inferior mouths, relatively broad upper jaw bones, and basioccipital processes at a similar angle to the neurocranium. These structures all appear to be specialized relative to other small *Barbus* species. It is therefore probable that the short intestine of *B.tenuis* and *O.quathlambae* is synapomorphic for the two species and convergent with the plesiomorphic state found in a majority of small *Barbus* species, including *B.calidus* and *B.erubescens*.

It is not possible at present to evaluate the differences in the length of the gut of *B.asper*, and, in part, *B.burgi*, compared with the slightly shorter tracts of *B.burchelli*, *B.afer* and *B.phlegethon*. There is a wide degree of intraspecific variation in this character, and the evidence is equivocal as to whether these differences are phenotypic or genotypic.

Osteology

In many respects this is a pioneering attempt to provide a Hennigian evaluation of *Barbus* osteology. Greenwood & Jubb (1967) made it clear that it was then still too early to make full use of osteological characters in cyprinids because the osteology of too few species was known. Little has changed since 1967 and, as far as is known, there have been no specific studies of this kind made of any African *Barbus* species.

Two recent studies on other cyprinids have used osteological characters and Hennigian methods viz. Barbour & Miller (1978) and Howes (1978). The study of *Luciobrama macrocephalus* by Howes (1978) considered a large number of cyprinid genera at an intergeneric and subfamilial level. Barbour & Miller (1978) by way of contrast concerned themselves with the phylogeny of the relatively small and geographically restricted genus, *Algansea*. This latter study is more akin to what is being attempted here. Howes' (1978) work is valuable. It illustrates just how difficult it is to provide clear cut decisions on cyprinid characters. The value of broad comparisons is not underestimated. Barbour & Miller's (1978) work nevertheless also has important implications, showing as it does the value and importance of drawing conclusions from within the circumscribed group.

In order to provide the necessary comparative basis to evaluate redfin osteological characters, examples of virtually all the southern African *Barbus* species as well as representatives of other cyprinid genera have been cleared, stained and examined (Appendix 2). A complete review and description of *Barbus* osteology is beyond the scope of the present study. Only characters which are of some value in helping to establish the state of particular characters in redfin species are dealt with. Frequently a decision on the status of a character is taken predominantly from its occurrence in redfin species rather than on its appearance in other *Barbus* species of the region. This amounts to the adoption of Kluge's alternative criterion (p. 235).

In several instances where there are distinct character differences between species and which otherwise would probably form useful characters for determining phylogeny, it has been found that such character states are widely encountered in other *Barbus* species. In certain cases it is felt that it is not possible to make a reasonably unequivocal evaluation of the state of these characters at present, and they have therefore not been taken into consideration.

Vertebrae

It is well known that environmental factors can influence the number of vertebrae in fishes (Barlow, 1961; Tatarko, 1968; Fowler, 1970). Lindsey (1976) has found that there is a definite correlation between the maximum body size and the number of vertebrae (pleomerism) in many fish genera including *Barbus*. That author also discussed Jordan's rule that there is an increase in the vertebral count of related taxa with an increase in latitude, and found that the rule does apply to many fish groups. It is thus difficult to provide a simple phylogenetic evaluation of characters state for the number of vertebrae in the redfin *Barbus* species. The evaluations are therefore only tentatively made and must await experimental proof before confirmation.

TABLE 5.4

Frequency distribution of vertebrae and supraneural bones in southern African *Barbus* species.
(A) Total vertebrae; (B) Precaudal vertebrae; (C) Caudal vertebrae.

SPECIES	(N)	VERTEBRAE (A)															PRECAUDAL VERTEBRAE (B)										CAUDAL VERTEBRAE (C)								
		31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	15	16	17	18	19	20	21	22	23	24	15	16	17	18	19	20	21	22	23
B.capensis	21													14	7									4	11	6					3	12	4	2	
B.holubi	23													11	10	2								4	12	7					2	10	10	1	
B.kimberleyensis	7													1	5	1								4	3								4	2	1
B.species	9										1	1	7									1	2	5	1						2	5	2		
B.marequensis	33								3	11	7	11	1								4	16	10	3							8	18	7		
B.natalensis	14										5	9											8	6							11	3			
B.polylepis	27										2	18	7										19	7	1						6	19	2		
B.andrewi	33								4	25	4									5	22	5	1							1	8	16	8		
B.serra	15									1	10	4										7	5	2	1					2	6	6	1		
B.mattozi	8								5	3											7	1									6	2			
B.poechii	20				16	4													6	14									6	14					
B.trimaculatus	29				1	23	5												1	21	7								1	21	7				
B.argenteus	18					6	12												1	14	3								9	8	1				
B.afrohamiltoni	12			1	11													2	10									1	9	2					
B.afrovernayi	6			4	2												3	3											2	3	1				
B.eutaenia	27			3	23	1													21	6								9	17	1					
B.hospes	28						9	18	1										12	15	1								1	4	16	7			
B.manicensis	7	1	6															2	5								1	1							
B.multilineatus	9	1	6	1	1												2	6	1									7	1	1					
B.paludinosus	50			1	21	25	3											4	33	12		1						4	26	14	3				
B.tangandensis	38	1	32	5													3	32	3								2	31	5						
B.trevelyani	29					3	14	12													16	13					2	4	19	4					
B.annectens	12		7	5														8	4									8	4						
B.anoplus	35			1	11	22	1												5	25	5							13	21	1					
B.barnardi	32			1	11	20												8	22	2								1	9	18	4				
B.gurneyi	22			1	18	3												1	7	14								12	9	1					
B.motebensis	9				1	8													1	4	4							4	5						
B.macrotaenia	17			10	6	1												6	11									6	8	3					
B.neefi	20		4	15	1												1	10	7	2							2	9	9						
B.pallidus	45		5	25	6													3	33	8	1						14	25	6						
B.puellus	7	5	2														1	5	1								5	2							
B.thamalakanensis	17		2	7	8													6	7	4							3	7	3	4					
B.toppini	12			4	8													8	4									2	4	6					
B.treurensis	3					1	2													2	1							2	1						
B.unitaeniatus	34				3	11	18	2											5	27	2							2	11	18	3				
B.viviparus	38			30	8													1	24	12	1						9	25	4						
B.radiatus	20	3	11	5	1													15	5								4	11	5						

TABLE 5.4

Frequency distribution of vertebrae and supraneural bones in southern African *Barbus* species. (D) Predorsal vertebrae; (E) Preanal vertebrae; (F) Supraneural bones.

SPECIES	(N)	PREDORSAL VERTEBRAE (D)									PREANAL VERTEBRAE (E)														SUPRANEURAL BONES (F)								
		8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	3	4	5	6	7	8	9	10	11
B.capensis	21					1	13	7													1	18	2						1	8	10	2	
B.holubi	23								14	9												12	11									13	10
B.kimberleyensis	7							7													2	4	1								5	2	
B.species	9						7	2											1	1	6	1									8	1	
B.marequensis	33			12	19	2												1	14	7	11							16	17				
B.natalensis	14				1	13														11	3								12	2			
B.polylepis	27				18	9														9	17	1						1	25	1			
B.andrewi	33			13	20											8	25										17	16					
B.serra	15				1	11	3									1	5	9											7	8			
B.mattozi	8		4	4												2	5	1									8						
B.poechii	20		20											13	7											1	19						
B.trimaculatus	29		24	5									2	16	2												12						
B.argenteus	18		1	17											6	17											+	+					
B.afrohamiltoni	12		12										12														12						
B.afrovernayi	6		5	1							5	1															6						
B.eutaenia	27		21	6									18	9												2	4						
B.hospes	28						1	19	8						19	9														2	25	1	
B.manicensis	7		7									7														+	+						
B.multilineatus	9		8	1								7	2														8	1					
B.paludinosus	50			41	9							12	34	3	1												2	44					
B.tangandensis	38	1	27	10							7	30	1													2	25	9					
B.trevelyani	29			2	25	2								4	23	2									5	10	12	2					
B.annectens	12	5	7								1	10	1												1	10	1						
B.anoplus	35			1	24	10					1	1	22	10	1										1	3	4	8					
B.barnardi	32		16	16							1	11	18	1											+	+							
B.gurneyi	22			15	7									21	1											1	4	7					
B.motebensis	9			1	8								2	7													+	+					
B.macrotaenia	17		8	9								14	3													2	15						
B.neefi	20		3	14	3						1	15	3	1												+	+	+					
B.pallidus	45			40	5							13	28	4											1	4	12	5					
B.puellus	7		6	1							1	5														+	+						
B.thamalakanensis	17		14	3								5	10	2												5	12						
B.toppini	12		4	8								11	1														+	+					
B.treurensis	3			1	2										3												+						
B.unitaeniatus	34		17	17									2	31	1										+	+	+	+					
B.viviparus	38	7	14	17								9	23	6													+	+					
B.radiatus	20	15	5								3	12	5													17	1						

Note: + denotes apparent number of supraneurals when radiographs are not sufficiently clear to be certain of exact number.

Total vertebral counts: There is a distinct difference in the number of vertebrae in large Barbus species and the smaller species from southern Africa (Table 5.4 a - e). The difference agrees with Lindsey's (1976) concept of pleomerism. Small or medium sized species have from 31 to 38 vertebrae. The majority have fewer than 36. The redfin species usually have between 36 and 38 vertebrae which is more than most other small Barbus with radiately striated scales from southern Africa. O.quathlambae has 38 or 40 vertebrae which is higher than any other "small" Barbus with radiately striated scales but similar to the "large" Barbus with radiately striated scales.

There is no indication that the relatively high number of vertebrae in the redfins is due to pleomerism. Several of the other "small" Barbus examined, such as B.trimaculatus, B.poechi, B.argenteus and B.manicensis and B.paludinosus all attain a comparable or larger size than the redfins (pers.obs.). An alternative explanation could be that the higher vertebral count in the redfins is in accordance with Jordan's rule (Lindsey, 1976) viz. that the redfins are endemic to higher latitudes than other small African Barbus species with radiately striated scales. In so far as this might represent an adaptational specialisation of the redfins to a temperate environment as compared with the great majority of African smaller Barbus species, the high vertebral numbers may be considered as synapomorphous for the group.

O.quathlambae inhabits higher altitudes than any of the other redfins, and the consequently cooler climates, particularly in the past, may further account for this species' high number of vertebrae. Furthermore, if, as suggested by Gephard (1978) the species is a crevice spawner, it would be advantageous to have greater bodily flexibility. This demand may have been functionally catered for by an increase in number of vertebrae.

Whatever the reasons for this increased count, it is likely that it is an adaptation to the high altitude stream environment of O.quathlambae, and the character is then autapomorphic for the species.

Precaudal vertebrae: The redfin species have from 17 to 20 precaudal vertebrae (Table 3.11b) with modal counts of 18 or 19, except

O.quathlambae which has from 19 to 22 and a mode of 20 or 21. Other small southern African Barbus species have from 15 to 20 precaudal vertebrae and the majority have a mode of between 16 and 18 (Table 5.4b). B.trevelyani is unusual and has 19 or 20 precaudal vertebrae. From the figures in Table 5.4b, it appears that the slightly higher total vertebral counts in the redfins is a result of an increase in precaudal vertebrae. This character would not add a new synapomorphy for the redfin species.

Caudal vertebrae: The redfins have from 15 to 20 caudal vertebrae (Table 3.11c) with modal counts of 17 or 18 except for B.calidus, B.erubescens and O.quathlambae which have a mode of 18 or 19 caudal vertebrae. Other small Barbus species in southern Africa have from 15 to 20 caudal vertebrae. The majority have a mode of 16 to 18 (Table 5.4c). B.hospes is unusual and has a high mode at 19. There are insufficient differences in caudal vertebral counts to provide taxonomically useful characters.

Predorsal vertebrae: Small Barbus species with radiately striated scales in southern Africa usually have 8 - 11 predorsal vertebrae (Table 5.4d). Barbus hospes, endemic to the lower Orange River System, is exceptional, and has 13 - 15 predorsal vertebrae. This species does not have a particularly high number of either precaudal or caudal vertebrae, and the high predorsal vertebral count is clearly a reflection of the posterior displacement of the dorsal fin. The redfin Barbus species have from 11 (B.burgi) to 12 or 13 predorsal vertebrae (Table 3.11d) which is above average for small Barbus with radiately striated scales. O.quathlambae has 13 or 14 predorsal vertebrae which again is relatively high compared to other small Barbus species. Because the above average counts in the redfins and O.quathlambae are all from a particular portion of the vertebral column it suggests that these high counts may reflect a synapomorphic character.

Preanal vertebrae: Small Barbus with radiately striated scales have usually 17 - 20 preanal vertebrae (Table 5.4e). There are a few exceptions to this, notably B.argenteus, B.hospes, and B.trevelyani (and possibly B.treurensis), which have 21 or 22 preanal vertebrae. The flexible-rayed

TABLE 5.5

A preliminary survey of osteological characters of southern African Barbus species. Characters referred to explained in notes. This classification of characters is based on a subjective qualitative assessment. The table is therefore intended as a preliminary guide to Barbus osteological characters and it is not considered a definitive statement of character state. In many cases intraspecific variation is considerable and the assessment requires further confirmation.

Species	Dilator gap	Pterosphenoids meet	Exoccipital border	Intercalars	Frontals - supraethmoids	Suprapre-opercle	Supraorbital canal	Metapterygoid	*Ectopterygoid	Upper jaws	Dermosphenotic	Infraorbital 5	Infraorbital 3+4	Lachrymal	Cleithro-coracoid gap	Urohyal	Weberian crest
B.capensis	Large	Yes	±	P	I	P	P	V	O	B	M	E	-	I	P	B	E
B.holubi	Large	Yes	±	P	I	P	P	V	O	B	M	E	-	I	P	B	E
B.kimberleyensis	Large	Yes	±	P	I	P	P	V	O	N	M	E	-	I	P	N	E
B.marequensis	Large	Yes	±	P	I	P	P	V	O	B	M	E	-	I	P	B	E
B.natalensis	Large	Yes	±	P	I	P	P	V	O	B	M	E	-	I	P	B	E
B.polylepis	Large	Yes	±	P	I	P	P	V	O	B	M	E	-	I	P	B	E
B.andrewi	Large	Yes	1	P	I	P	P	V	O	I	M	(E)	-	II	P	B	I
B.serra	Large	Yes	1	P	I	P	P	V	O	I	M	(E)	-	II	P	N	I
B.mattozi	-	Yes	2	P	I	P	P	C	O	N	S	-	-	III	P	N	I
B.poechii	-	Yes	2	P	O	P	-	V	O	N	S	-	-	III	P	B	I
B.trimaculatus	-	Yes	2	P	O	P	-	V	O	N	S	-	-	III	P	B	I
B.afrohamiltoni	-	No	2	P	O	P	-	C	O	I	M	-	-	III	P	B	I
B.afrovemayi	-	No	2	P	O	-	-	C	C	B	S	-	-	III	-	B	I
B.argenteus	-	No	2	P	O	P	P	C	O	N	M	-	-	III	P	N	I
B.eutaenia	-	No	2	P	O	P	P	X	O	N	M	-	-	III	P	N	I
B.hospes	-	Yes	2	P	O	P	P	X	O	B	S	-	-	I	P	N	A
B.manicensis	-	No	2	P	O	P	P	C	O	N	S	-	-	III	P	B	I
B.multilineatus	-	No	2	P	O	P	-	C	O	N	S	-	-	III	P	B	I
B.paludinosus	-	No	1	P	O	P	-	C	O	N	M	-	-	III	P	B	I
B.tangandensis	-	No	2	P	O	P	-	C	O	N	S	-	-	III	P	N	I
B.trevelyani	-	No	(1)	P	I?	P	-	C	O	B	-(L?)	E	E	III	P	B	I
B.annectens	-	No	2	P	O	P	P	V	O	N	S	-	-	III	-	B	I
B.anoplus	-	No	2	(P?)	N	-	-	C	C	N	S	-	-	III	P	B	I
B.barnardi	-	Yes	2	P	O	-	-	C	O	N	S	-	-	III	P	B	I
B.barotseensis	-	No	2	P	O	P	P	C	O	N	S	-	-	III	P	B	I
B.bifrenatus	-	No	2	-	O	P	-	C	O	N	S	-	-	III	P	B	I
B.brevipinnis	-	No	2	-	O	-	-	C	O	N	S	-	-	III	A	B?	I
B.fasciolatus	-	No	2	-	O	-	-	C	O	N	-	-	-	III	-	B	I
B.gurneyi	-	No	2	-	N?	-	-	C	C		M	-	-	III	-	B	I
B.haasianus?	-	No	2	-	O	-?	-?	C	O	N	?	-	-	III	?	B	I
B.lineomaculatus	-	No	2	-	O	P	-	C	O	N	S	-	-	III	P	B	I
B.motebensis	-	No	2	-	N	-	-	C	C(?)	N	M	-	-	III	P	B	I
B.neefi	-	No	2	-	O	P	-	C	O	N	S	-	-	III	1?	B	I
B.pallidus	-	No	2	-	O	P	-	C	O	N	M	-	-	III	-?	B	I
B.puellus	-	No	2	-	O	-	-	C	O	N	L	E	E	I	-	B	I
B.radiatus	-	Yes	2	-	O	P	P	C	O	N	S	-	-	III	-	B	I
B.toppini	-	No	2	-	O	-	-	C	O	N	-	-	-	III	P	B	I
B.treurensis	-	No	2	-	O	P	-	C	O	N	S	-	-	III	P	N	I
B.thamalakanensis	-	No	2	-	O	-	-	C	O	N	S	-	-	III	-	B	I
B.unitaeniatus	-	Yes	2	-	O	P	-	V	O	B	S	-	-	III	-?	B	I
B.viviparus	-	No	2	-	O	-	-	C	O	N	S	-	-	III	-	B	I

Notes on characters referrred to.

Dilator gap:	refers to foramen in frontal bone at head of dilator groove. Dash indicates there is no substantial foramen.
Pterosphenoids meet:	refers to whether left and right pterosphenoids suture in midline or not.
Exoccipital border:	refers to the presence of a broad flange on this bone as described for redfin species (Ch. 4). 1 = flange broad 2 = flange narrow.
Intercalars:	present = P, dash if absent.
Frontals - supraethmoid:	refers to overlap (o), non-overlap (N), interdigitation of these bones (I). N may be a presumptive stage of I?
Supraopercle:	canal present (P) or absent (-) on opercle bone.
Supraorbital canal:	refers to whether this sensory canal has a secondary median branch (P) or not.
Metapterygoid:	refers to dorsal edge, V = convex, C = concave.
Ectopterygoid:	refers to extent which this bone contacts the quadrate. O = marginal contact, C = substantial contact.
Upper jaws:	refers to estimated relative proportions. Broad (short and deep) = B; Narrow (long and slender) = N; Intermediate (?) = I.
Dermosphenotic:	Refers to size: S = small; M = moderate; L = large.
Infraorbital 5:	refers to size: E = expanded; dash is not expanded.
Infraorbital 3+4:	refers to size: E = expanded; dash is not expanded.
Lachrymal:	I = moderate with low dorsal peak; II - very long with low dorsal peak; III - relatively short with a high dorsal peak.
Cleithro-coracoid gap:	P = present; - no gap.
Urohyal:	refers to estimate proportions: N = slender and narrow; B = broad and deep.
Weberian crest:	E = expanded distally; I = irregular; A = expanded anteriorly.

redfin species have 19 or 20 preanal vertebrae (Table 3.11e) which is similar to most small Barbus examined. B.calidus, B.erubescens and O.quathlambae usually have 21 preanal vertebrae which is slightly more than other small Barbus species from southern Africa.

Supraneural bones

Supraneural bones occur regularly in the cypriniformes and other lower teleostean fishes. They are present in all non-redfin Barbus species which have been examined and are usually well developed. In B.anoplus and B.motebensis the supraneurals are frequently reduced in size.

There is usually a single supraneural located between pairs of neural spines so that the number of supraneural bones per individual usually depends on the number of predorsal vertebrae. The larger Barbus with parallel striated scales have more predorsal vertebrae than the majority of radiately striated scaled species and they also have more supraneurals (Table 5.4f). B.hospes is an exception and has a very high number of predorsal vertebrae and supraneural bones compared to other small or medium sized Barbus with radiately striated scales. The majority of small Barbus with radiately striated scales have only four to six supraneurals. B.calidus and B.erubescens have from six to eight and this is considered to be a synapomorphy. The reduction and loss of these bones in the flexible-rayed redfin Barbus and O.quathlambae is also considered to be synapomorphous.

Intramuscular bones

The epineurals from the fifth or sixth vertebra of medium and large Barbus species from southern Africa are usually well ossified in adults. In specimens of B.anoplus and B.motebensis examined the epineurals before the dorsal fin were not well ossified. In B.gurneyi they were not ossified until opposite the ninth or tenth vertebra. The reduction of these bones in the flexible-rayed redfin Barbus and O.quathlambae is considered to be synapomorphous.

Neurocranium (refer to Table 5.5).

The frontals of teleosts usually overlap or interdigitate with the supraethmoids (Starks, 1926). In a large number of cyprinid genera

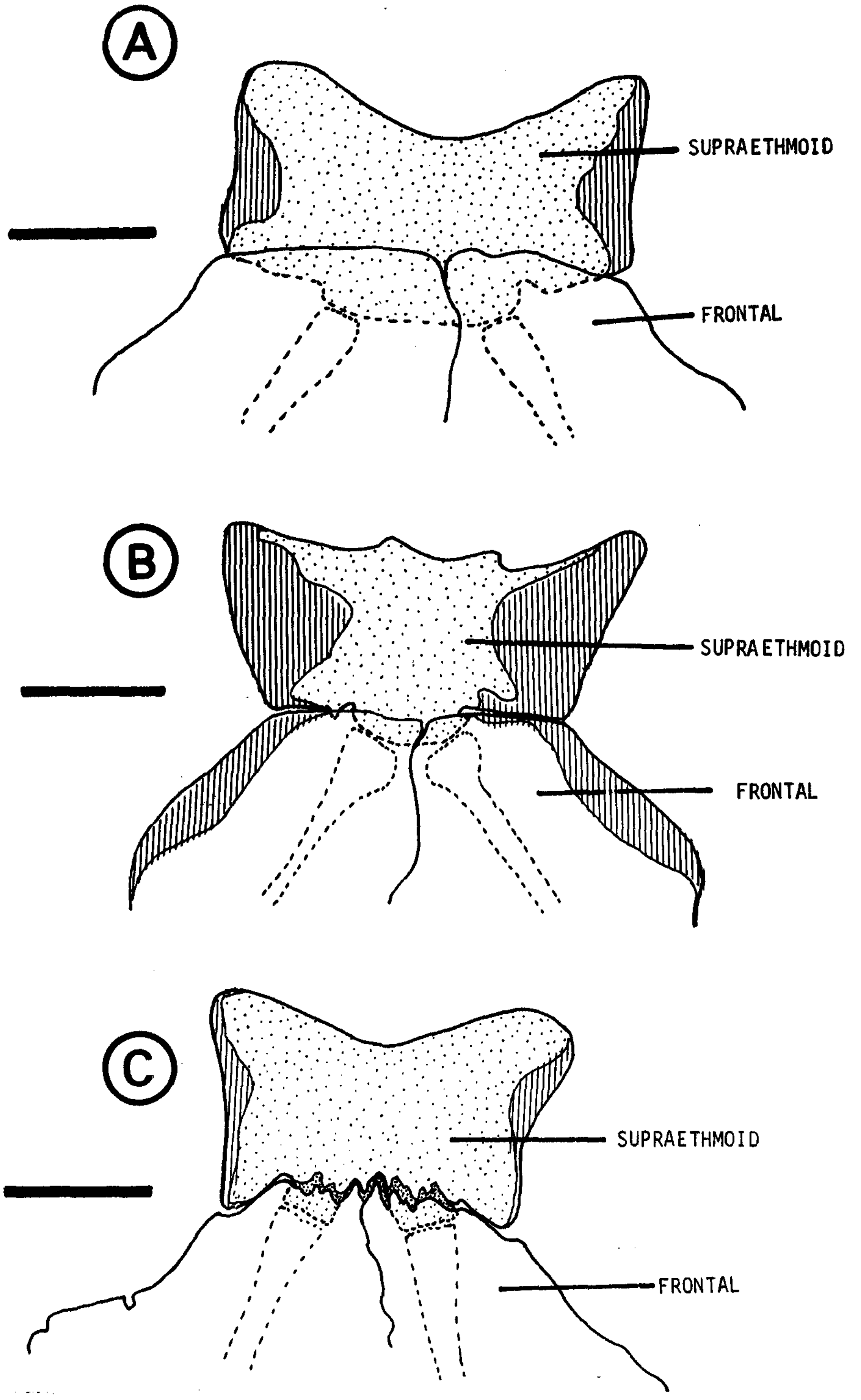


Fig. 5.6 Dorsal view of anterior portion of neurocranium of three small *Barbus* species to show relationship between the frontals and the supraethmoid (a) *B.trimaculatus*, frontals overlap supraethmoid (b) *B.motebensis*, frontals abut supraethmoid (c) *B.trevelyani*, frontals abut and interdigitate with supraethmoid. Scale bar = 1 mm. Lined region represents cartilagenous or unossified portion of bones.

the frontals usually interdigitate with the supraethmoid (Howes, 1978). In relatively few genera the frontals overlap the supraethmoid and this was considered by Howes (op.cit.) to be apomorphic. In the larger *Barbus* species studied the frontals interdigitate with the supraethmoid, but interdigitation does not appear to be a common feature of the smaller southern African species. In all the smaller species examined the frontals overlap the postero-dorsal part of the ethmoid. In the smaller species the frontals usually overlap the greater part of the posterior edge of the supraethmoid (e.g. in *B.trimaculatus* Fig. 5.6a). This is the condition found in *B.calidus* and *B.erubescens* and is considered to be plesiomorphic.

In the flexible-rayed redfins and *O.quathlambae* the frontals abut the posterior edge of the supraethmoid. This is also found in a few other southern African species e.g. *B.motebensis* (Fig. 5.6 b), *B.anoplus*, *B.treurensis* and *B.hospes*. This condition may more closely approach interdigitation than the overlap condition found in *B.calidus* and *B.erubescens*, which suggests that abutment could be relatively primitive to overlapping in terms of cyprinid osteology. Abutment is consequently apomorphic to interdigitation and is synapomorphous for the flexible-rayed redfins.

The reduction of ossification of bones at the anterior end of the neurocranium of *B.tenuis* and *O.quathlambae* is striking. Similar conditions are only found in the juveniles of other southern African *Barbus* species. In *O.quathlambae* and *B.tenuis* the reduction occurs in large adults and the feature is regarded as synapomorphous.

The pterosphenoids of *B.calidus* and *B.erubescens* meet anteriorly to exclude the orbitosphenoid from the orbital foramen. In the flexible-rayed redfins the orbitosphenoid divides the pterosphenoids anteriorly. Both conditions are found in the *Barbus* examined. The large, parallel striated scaled species *B.andrewi* and *B.serra* as well as in the radiately striated scaled *B.trimaculatus*, *B.poechii*, *B.hospes*, *B.unitaeniatus*, *B.barnardi* and *B.radiatus* all have the pterosphenoids meeting. All the other radiately striated scaled *Barbus* have the orbitosphenoid separating the pterosphenoids. In *B.puellus* the orbitosphenoids almost exclude the pterosphenoid from the orbital foramen.

Uyeno (1961) found an identical situation in the genus Gila and species from related genera. In certain species the pterosphenoids meet but not in others. The studies of Harrington (1955), Ramaswami (1955a, b), Mahy (1975) and Howes (1978) all indicate that the pterosphenoids are usually separate in cyprinids.

Although it is probable that there has been convergence in the character (separated or united pterosphenoids), in many cyprinids united pterosphenoids appear to be the less frequent condition. In B.calidus and B.erubescens, which are almost certainly closely related, the character is probably synapomorphous.

The development of a flange on the posterior border of the exoccipitals of the flexible-rayed redfins is a useful character. The flange is correlated with the form of the pharyngeal teeth and the length of the intestine (Chapter 4). It serves as part of the site of origin for the posterior levator muscle. This muscle attaches to the pharyngeal bones and serves to raise them, bringing the pharyngeal teeth in contact with the masticatory pad (Matthes 1963). The species with well worn teeth probably require a stronger, and therefore larger, muscle for the grinding action, causing tooth wear. The larger flanges observed in these species provide larger attachment surfaces for these muscles.

The variation in the form of the exoccipitals in southern African Barbus species is given in Table 5.5. Juveniles of the large species have relatively narrow flanges whereas the adults develop broad ones. The adults of these species all have longer, more involuted alimentary tracts (Table 5.3) and in some the pharyngeal bones may become stout and the teeth partly molariform. B.mattozi is a predator with a short intestine (Kruger & Mulder, 1973) and does not have broad flanges on the exoccipitals. Flanges are rarely found in the smaller or moderately sized Barbus species. This agrees with the form of the pharyngeal teeth of these species which are designed more for a raking than a scraping action.

The development of the exoccipital flange in the flexible-rayed redfins is sufficiently unusual among the small southern African Barbus species that it is considered to be synapomorphic. There are two basic forms of this flange (Fig. 4.19): a simple, squarish flange in B.burgi and

B.burchelli, and a triangular projection as in *B.afer*, *B.asper*, *B.phlegethon* and *B.tenuis*. The flange is vestigial in *O.quathlambae*. Purely from the point of view of number of species it could be reasoned that the triangular projection is plesiomorphic to the squared flange. However this form not only appears to be the more complex structure, but both *B.phlegethon* and *B.tenuis* are apomorphic in pharyngeal tooth characters. If the functional explanation for the flange suggested above is correct it seems even more likely that the triangular projection is the derived form and the squarish flange of *B.burgi* and *B.burchelli* the plesiomorphic condition.

Intercalars are usually present in *Barbus*,overlying the postero-ventral surface of the pterotics. They are present as in *B.calidus* and *B.erubescens*, but are absent in *B.motebensis*. They were found in three specimens of *B.anoplus* which is closely allied to *B.motebensis*. Ramaswami (1955) considered these bones normally absent from cyprinids, but Howes (1978: 39) found them in several cyprinid genera and "some *Barbus* species". The loss or reduction of the intercalars has probably occurred independantly in several cyprinid lineages. Nevertheless the trend to reduction of these bones in a reasonably circumscribed group such as the redfins and *O.quathlambae* is sufficiently unusual among southern African *Barbus* species that this trend is considered synapomorphic.

The shape of the neurocranium is a useful character for the flexible-rayed redfins. *B.burchelli*, *B.burgi*, *B.afer* and *B.asper* have a similar, moderately deep and broad neurocranium. The proportions are generally characteristic of the neurocrania of smaller and moderately sized *Barbus* species and are regarded as plesiomorphic. *B.phlegethon* has a deep and narrow neurocranium which is autapomorphous. The relatively shallow broad neurocranium of *B.tenuis* is also unusual and apomorphic for the species.

The infraorbital series provides several useful taxonomic characters in different *Barbus* species. The series usually consists of five units representing six bones (Nelson, 1969b): a lachrymal, the second infraorbital, a fused third and fourth, the fifth infraorbital and a dermosphenotic. A few species have the series reduced to four units either through loss or further fusion. Thys (1971) reports reduction of the series to but one or two elements in *Barbus carens* and *B.jae*.

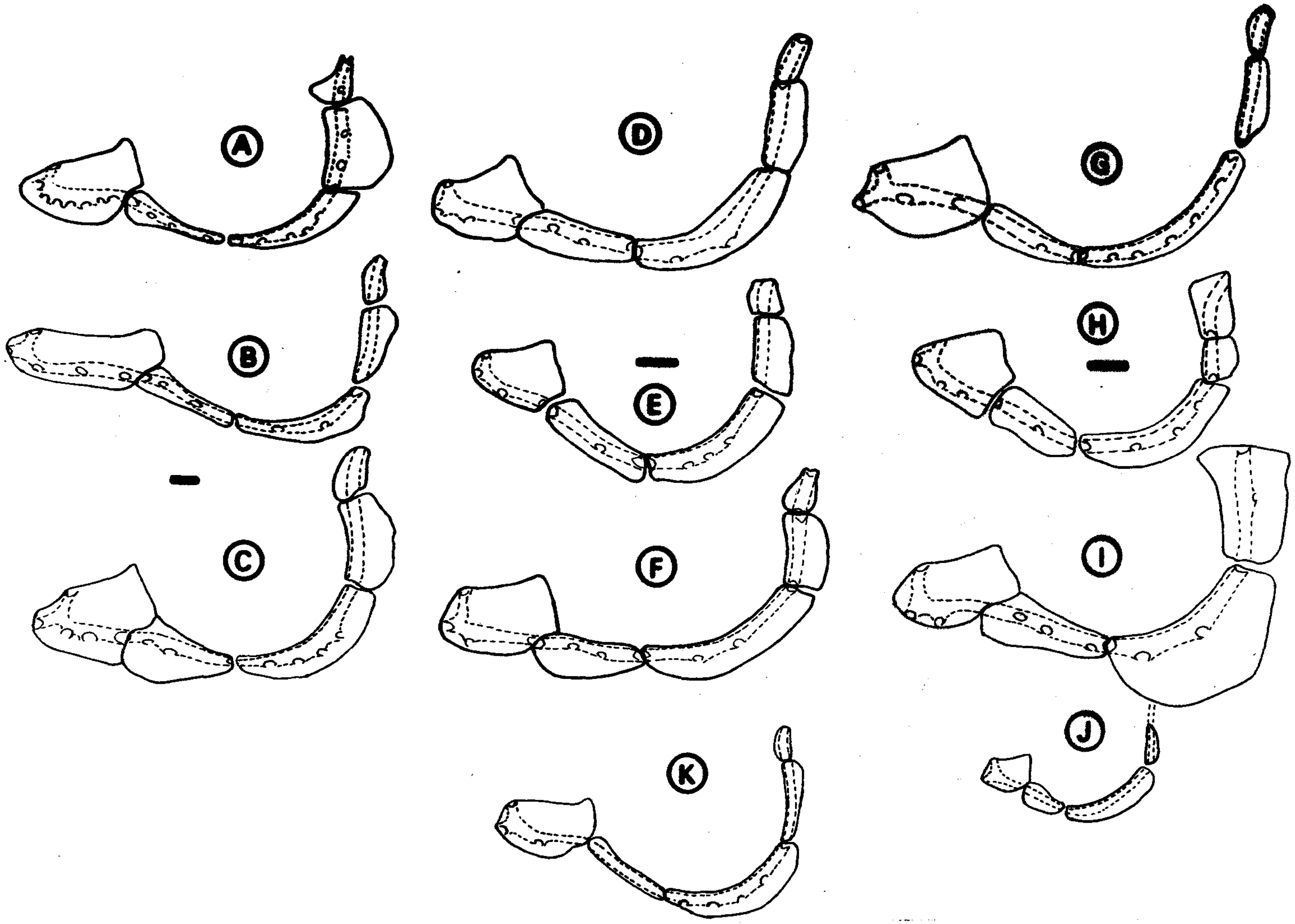


Fig. 5.7 Examples of the infraorbital series from certain Barbus species.
a) B.holubi, b) B.serra, c) B.mattozi, d) B.trimaculatus,
e) B.eutaenia, f) B.unitaeniatus, g) B.radiatus, h) B.motebensis,
i) B.trevelyani, j) B.toppini, k) B.hospes. Scale bar = 1 mm.

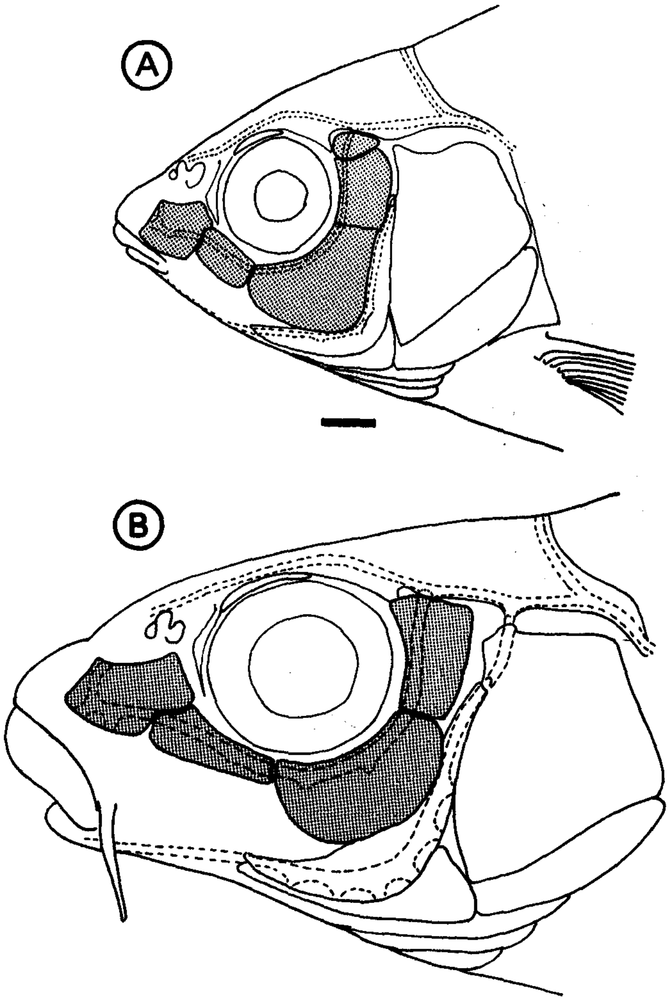


Fig 5.8 The infraorbital series of (a) *B.toppini* and (b) *B.trevelyani* *in situ* to show extent of coverage provided by infraorbitals to cheek. Scale bar = 1 mm.

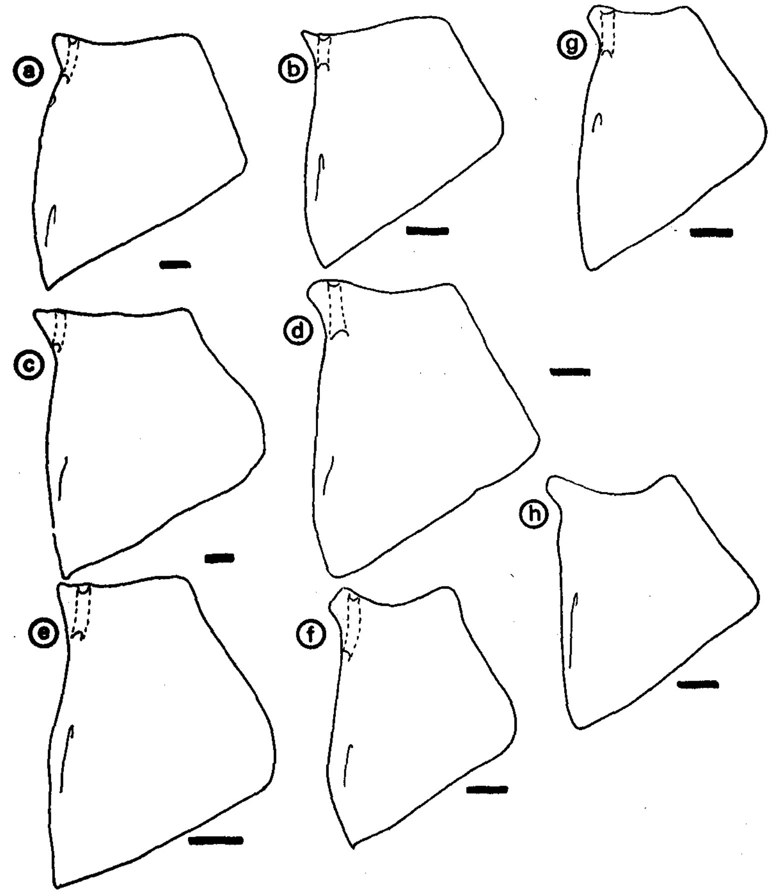


Fig 5.9 Examples of the opercle of certain *Barbus* species a) *B.holubi*, b) *B.serra*, c) *B.mattozi*, d) *B.trimaculatus*, e) *B.eutaenia*, f) *B.unitaeniatus*, g) *B.radiatus*, h) *B.motebensis*. Scale bar = 1 mm.

In addition to *O.quathlambae*, *B.trevelyani* and *B.toppini* have been found to have only four infraorbitals.

The shape of particular units is characteristic either for a particular species, or frequently for distinctive species groups. The large, parallel straited, scaled southern African *Barbus* (Fig. 5.9a) have a moderately elongated lachrymal with numerous pores in the lateral line canal. The second and fused third and fourth infraorbitals are tubular, the fifth is expanded and the dermosphenotic is small.

A second characteristic series is that found in the two large, radiately striated, scaled species from the south western Cape, *B.andrewi* and *B.serra* (Fig. 5.7b). The lachrymal is elongated, similar to that of *B.barbus* (pers.obs.; Vandewalle, 1977) and unlike any other African *Barbus* as far as is known.

The lachrymal of small or moderate sized *Barbus* is short, with the dorsal edge usually forming a prominent angle. In *B.hospes* this bone is relatively elongated with a low dorsal angle (Fig. 5.7k).

The remaining infraorbitals of the small and moderate sized *Barbus* are narrow or relatively narrow bones without prominent flanges. Boulenger's (1911) definition of the genus states that the infraorbitals do not cover the cheek (e.g. as they do in many characins - Weitzman, 1962). In two *Barbus* species from southern Africa, *B.trevelyani* and *B.puellus*, the infraorbitals 3+4 and 5 are broad and cover the cheek (Fig. 5.8).

The following deduction may be made from the form of the infraorbitals of the redfins. The lachrymal of the flexible-rayed species has a characteristic, relatively low dorsal angle and is considered synapomorphic. The comparatively well developed dermosphenotic of *B.burgi* is unusual and is probably autapomorphic. The four infraorbitals in *O.quathlambae* is characteristic (Greenwood & Jubb, 1967) and is considered autapomorphic. The infraorbitals of *B.tenuis* are narrow, similar to those of *O.quathlambae*, and the dermosphenotic is reduced in size and usually poorly ossified. This may represent an intermediate character state in a transformation from the plesiomorphic state found in the other flexible-rayed redfins to the apomorphic state in *O.quathlambae*.

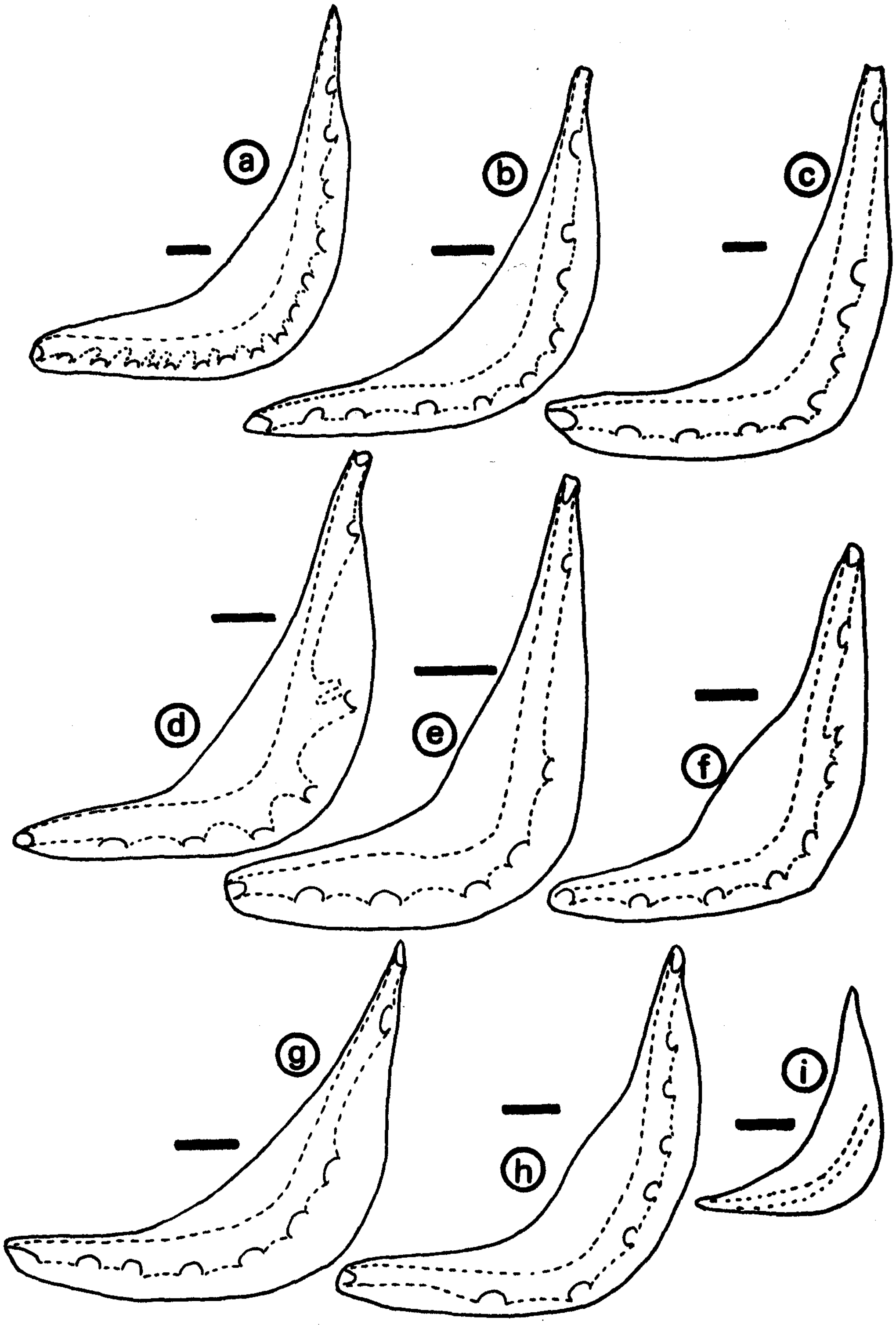


Fig 5.10 Examples of preopercles of certain *Barbus* species a) *B.holubi*, b) *B.serra*, c) *B.mattozi*, d) *B.trimaculatus*, e) *B.eutaenia*, f) *B.unitaeniatus*, g) *B.radiatus*, h) *B.motebensis*, i) *B.toppini*. Scale bar = 1 mm.

Branchiocranium

Opercle. The Barbus opercle is generally similar to that of the redfin species (Fig. 5.9) and is characterised by the presence or absence of the suprapreopercle (the bony canal) on the antero-dorsal corner. The presence or absence of this canal is usually consistent within a species, although extraordinary variation was found in a sample of four specimens of B.pallidus from the eastern Cape. (The canal was present in one specimen absent in two and vestigial in the fourth.) Approximately 70% of southern African Barbus species have this canal on the opercle. This is almost certainly the plesiomorphic state. The opercular canal is present only when the preopercular mandibular canal is connected to the post-ocular commissure. A break in this connection has probably occurred independently in different cyprinid lineages (Gosline, 1974) but there is no reason to suspect that this is not synapomorphous in the flexible-rayed redfin species. It is also possible that this synapomorphy is shared with other southern African Barbus species.

The shape of the opercle is relatively unusual in B.tenuis and O.quathlambae. This is therefore regarded as synapomorphous for these two species.

Preopercle: The shape of the preopercle is conservative in Barbus (Fig. 5.10) and it presents no outstanding character for the redfins or any other species. The reduction of the preopercular sensory canal from the tip of the anterior limb of the bone is however a unique character shared by B.asper, B.afer, B.phlegethon, B.tenuis and O.quathlambae. This is essentially part of the general reduction of the mandibular sensory canal in the flexible-rayed species (see below) and represents an advanced synapomorphic character for these particular species.

Lower jaws: The lower jaws of the redfins and of O.quathlambae are all of a basic Barbus type. The development of a broad ventral flange on the dentary as described for B.calidus and B.erubescens is characteristic of all the Barbus species examined (examples given in Fig. 5.11). The reduction of this flange and the mandibular sensory canal on the dentary and angulo-articular of the flexible-rayed redfins and O.quathlambae is an outstanding feature of the species and is clearly synapomorphous.

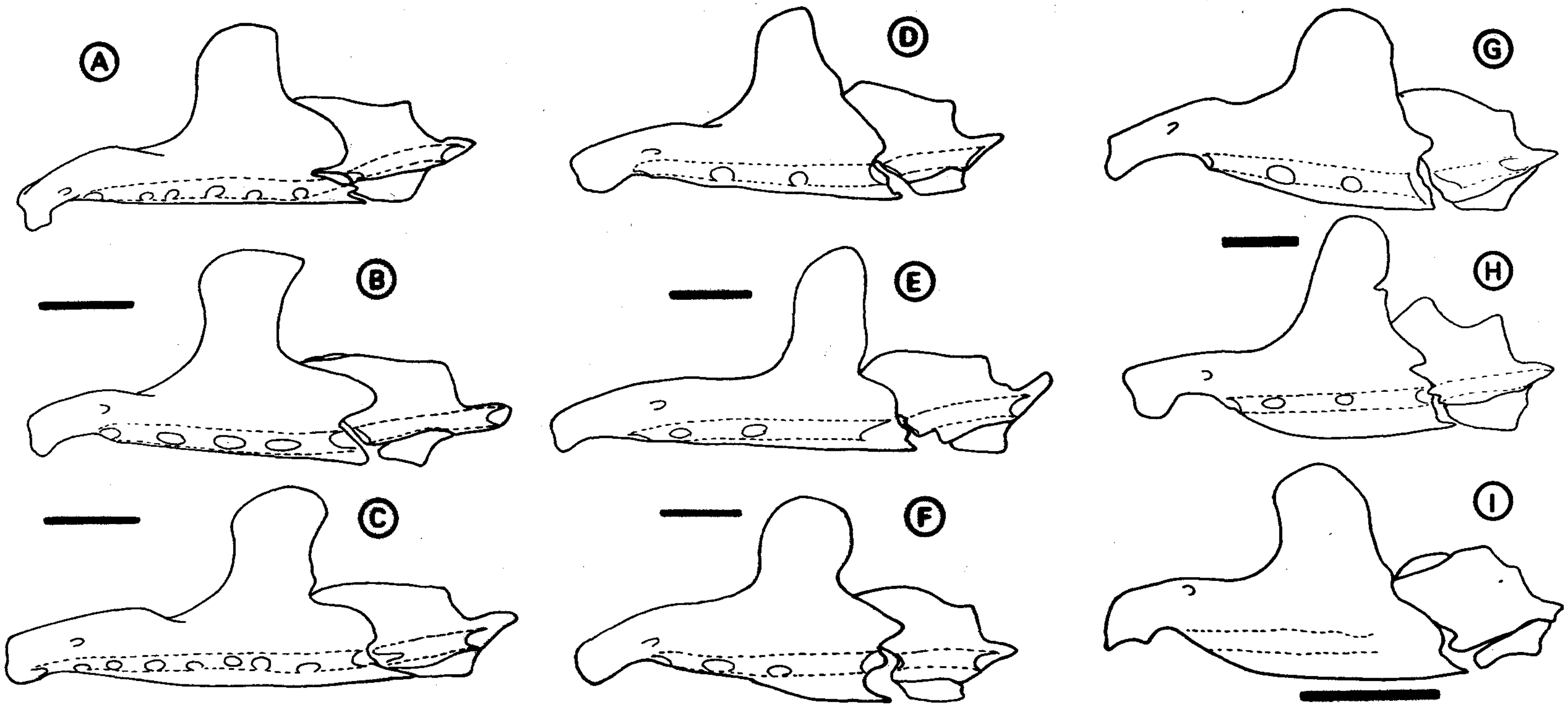


Fig 5.11 Examples of the lower mandible of certain Barbus species (left mandible lateral view). a) B.holubi, b) B.serra, c) B.mattozi, d) B.trimaculatus, e) B.eutaenia, f) B.unitaeniatus, g) B.radiatus, h) B.motebensis, i) B.toppini. Scale bar = 1 mm.

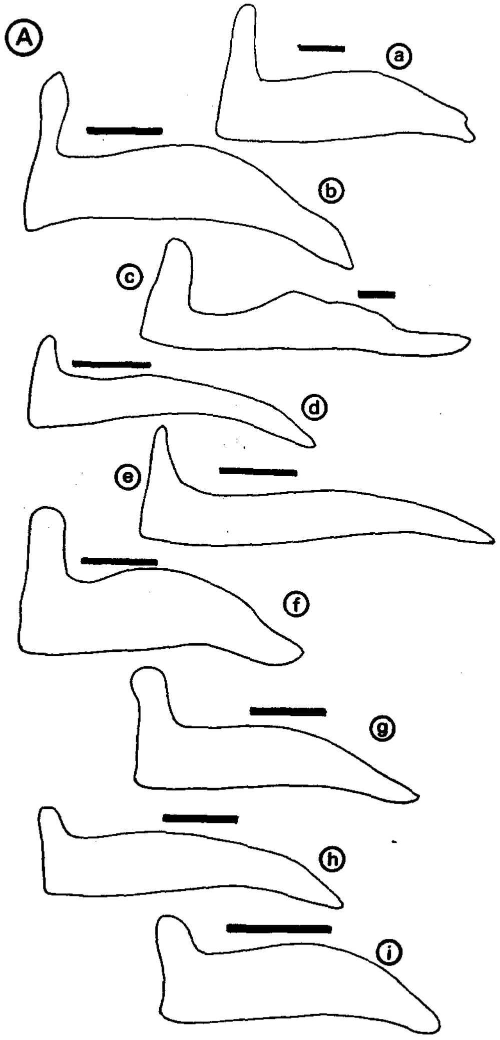


Fig 5.12a Examples of premaxillae of Barbus species (lateral view).
a) B.holubi, b) B.serra, c) B.mattozi, d) B.trimaculatus,
e) B.eutaenia, f) B.unitaeniatus, g) B.radiatus, h) B.motebensis,
i) B.hospes. Scale bar = 1 mm.

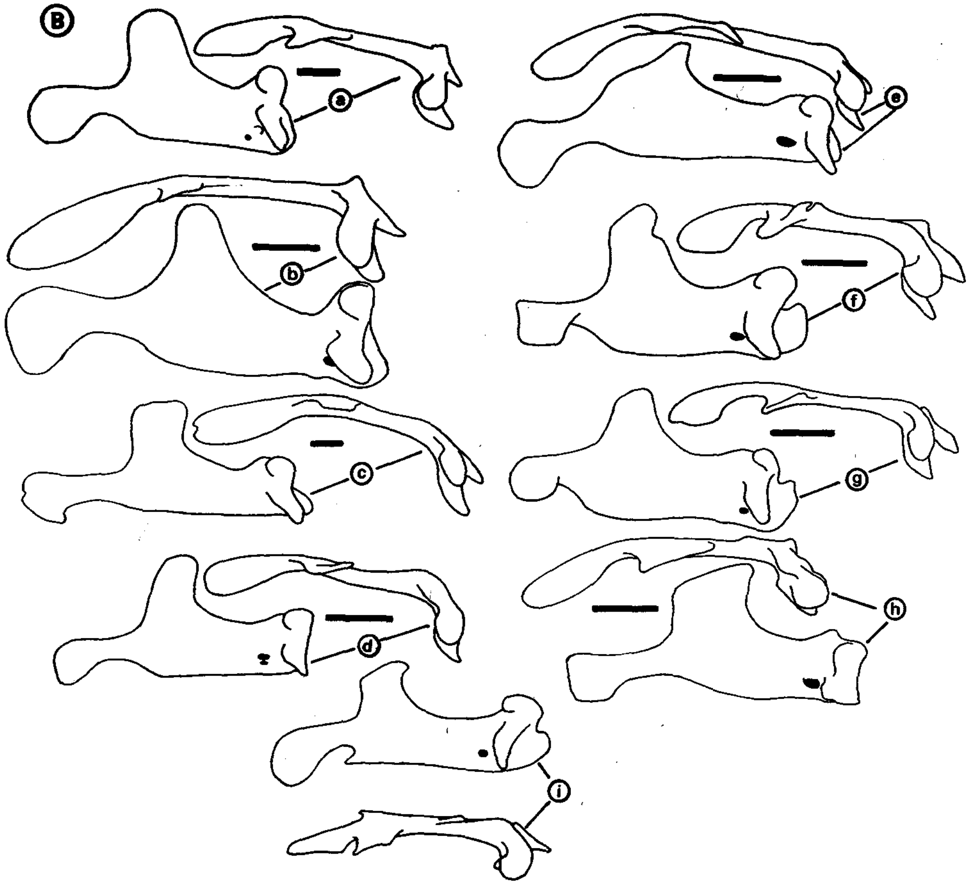


Fig 5.12b Examples of maxillae of Barbus species (medial and dorsal views).
a) B.holubi, b) B.serra, c) B.mattozi, d) B.trimaculatus,
e) B.eutaenia, f) B.unitaeniatus, g) B.radiatus, h) B.motebensis,
i) B.hospes. Scale bar = 1 mm.

The reduction of the flange and sensory canal is incomplete on the jaws of B.burchelli and B.burgi. This is the least derived condition and is plesiomorphic within the lineage. The complete loss of the canal and flange in the other flexible-rayed species is synapomorphic and, as mentioned under the preopercle section above, the character may be recorded as a reduction of the preopercular canal from the tip of the anterior limb of the preopercle.

Apart from this character the rather short dentary of B.phlegethon is unique among the redfins and is considered to be autapomorphic.

Upper Jaws. The most obvious differences in the upper jaw bones of the southern African Barbus species was in the various proportions of the bones (Fig. 5.12). Mahnert & Gery (1977) recorded similar findings for the upper jaws of several African Barbus species, and reported that differences in proportion occurred between apparently closely related species. The premaxilla and maxilla of southern African Barbus species have been assessed according to their shape into three categories, viz. "short and deep", "long and slender" and "intermediate". Although this is an arbitrary assessment and the categories are not always clear-cut it provides a useful way in which to gauge the upper jaw proportions in the redfins.

In general it has been found that the large Barbus with parallel striated scales have relatively short and deep upper jaw bones and the smaller Barbus with radiately striated scales have relatively long and slender upper jaw bones (Table 5.5). Barbus kimberleyensis, a large predator belonging to the first group has slender jaw bones. A few diverse smaller species of the latter group have shorter and deeper jaw bones. These few species include B.afrovernayi, a species with a small terminal mouth, B.trevelyani and B.unitaeniatus with inferior mouths.

The proportions of the upper jaw bones in the redfin Barbus species relates to the position and the size of the mouth. The serrated-rayed species have large terminal mouths and their premaxillae and maxillae are relatively long and slender. The flexible-rayed redfins and O.quathlambae have smaller sub-terminal or inferior mouths and the jaw bones are relatively short and deep. This is unusual for small southern African

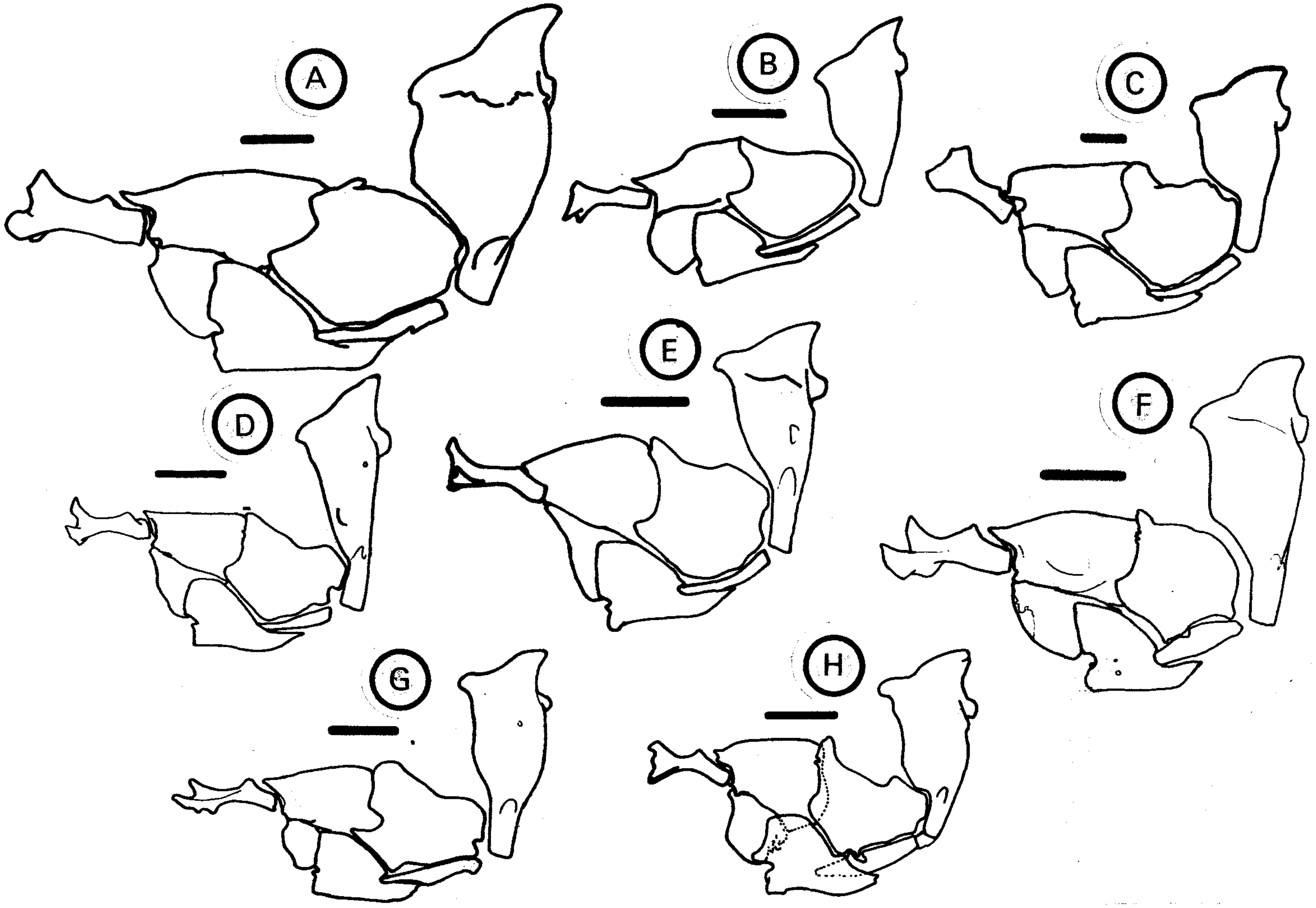


Fig 5.13 Examples of suspensoria of *Barbus* species (left side, lateral view). a) *B.holubi*, b) *B.serra*, c) *B.mattozi*, d) *B.trimaculatus*, e) *B.eutaenia*, f) *B.unitaeniatus*, g) *B.radiatus*, h) *B.motebensis*. Scale bar = 2 mm.

TABLE 5.6

A summary of plesiomorph and apomorph character states of the redfin Barbus species and O.quathlambae.

Symbols: 0 indicates plesiomorphic state; the numbers 1,2 etc indicate form and sequence of apomorphic states. The letters a,b,c indicate the character is apomorph but not synapomorph. A negative sign indicates the primitive state occurs within a morphocline.

	Character	B.afer	B.asper	B.burchelli	B.burgi	B.calidus	B.erubescens	B.phlegethon	B.tenuis	O.quathlambae
1	Red fins	1	1	1	1	1	1	1	1	1
2	Barbels	2	2	0	1	0	0	3	3	3
3	Scale radii	1	1	0	0	1	2	1	3	1
4	Scale size	0	1	0	0	0	0	0	0	2
5	Pelvic axil scale	1	1	1	1	0	0	1	1	1
6	Breast scales	1	2	1	1	0	0	1	1	3
7	Unbranched dorsal	0	0	0	0	1	2	0	0	0
8	Branched dorsal rays	1/0?	1/0?	1/0?	1/0?	1/0?	0/1?	1/0?	1/0?	1/0?
9	Branched anal rays	0	0	0	0	1	2	0	0	0
10	Tubercles	3	3	2	1	0	0	4a	4b	4c
11	Pharyngeal teeth no.	0	0	0	0	0	0	2	3	4
12	Pharyngeal teeth form	1	1	1	1	0	0	1	2	3
13	Intestine	1	1	1	1	0	0	1	2	3
14	Vertebrae	1	1	1	1	2	2	1	1	3
15	Predorsal vertebrae	1	1	1	0	2	1	1	1	3
16	Preanal	0	0	0	0	1	1	0	0	1
17	Supraneurals	1	1	1	1	0	0	1	1	1
18	Intramuscular bones	1	1	1	1	0	0	1	1	1
19	Frontal-supraethmoid	1	1	1	1	0	0	1	1	1
20	Ossification-supraethmoid	0	0	0	0	0	0	0	1	1
21	Pterosphenoids	0	0	0	0	1	1	0	0	0
22	Exoccipital flange	2	2	1	1	0	0	2	2	3
23	Neurocranium shape	0	0	0	0	0	0	-1	+1	0
24	Supraorbitals	0	0	0	0	0	0	0	1	1
25	Lachrymal	1	1	1	1	0	0	1	1	1
26	Dermosphenotic	0	0	0	-1	0	0	0	1	2
27	Suprapreopercle	1	1	1	1	0	0	1	1	1
28	Opercle (shape)	0	0	0	0	0	0	0	1	1
29	Maxillae & premaxillae	1	1	1	1	0	0	1	1	1
30	Dentary	2	2	1	1	0	0	2	2	2
31	Metapteryoid	1	1	1	1	0	0	1	2	2

Barbus with radiately striated scales and is tentatively considered synapomorphic for the flexible-rayed redfins and O.quathlambae.

Suspensorium. B.calidus and B.erubescens have a metapterygoid with the dorsal edge concave in profile. This is the usual condition in radiately striated, scaled southern African Barbus species (Table 5.5 & Fig. 5.13). Howes (1978) found this to be the more common state in a wide range of cyprinid genera. Although not entirely unique, a convex profile shown by the flexible-rayed redfins and O.quathlambae possibly represents a synapomorphy.

In the flexible-rayed redfins the dorsal edge of the metapteryoid is divided into two portions by a small notch. The division is usually small except in B.tenuis and O.quathlambae where the notch is deep and the lamellae formed are large (Fig. 4.26). The development of this deep notch is synapomorphous for these two species.

Discussion and conclusions

A summary of the above analysis is given in Table 5.6 . It is evident from this summary that the redfins sensu lato share only two possible apomorphic characters - the red fin-colour and similarity in certain vertebral counts. There are more apomorphic characters shared by the flexible-rayed group of species. These suggest that the redfins, as dealt with in this study, are in fact diphyletic, the two lineages being the flexible-rayed and serrated-rayed groups. Furthermore, the apomorphic characters which O.quathlambae has in common with the other flexible-rayed redfins confirms the close relationship of these species originally suggested by Skelton (1976).

Barbus calidus and Barbus erubescens are very similar in most respects and their relationship is confirmed by a few synapomorphies; an increased number of branched anal fin rays, the relatively high total number of vertebrae, the high number of pre-anal vertebrae, and united pterosphenoids. The relatively few obvious (or at least recognised) synapomorphies do not do justice to the many similarities between the two species which may provide further synapomorphies but which cannot be demonstrated at present.

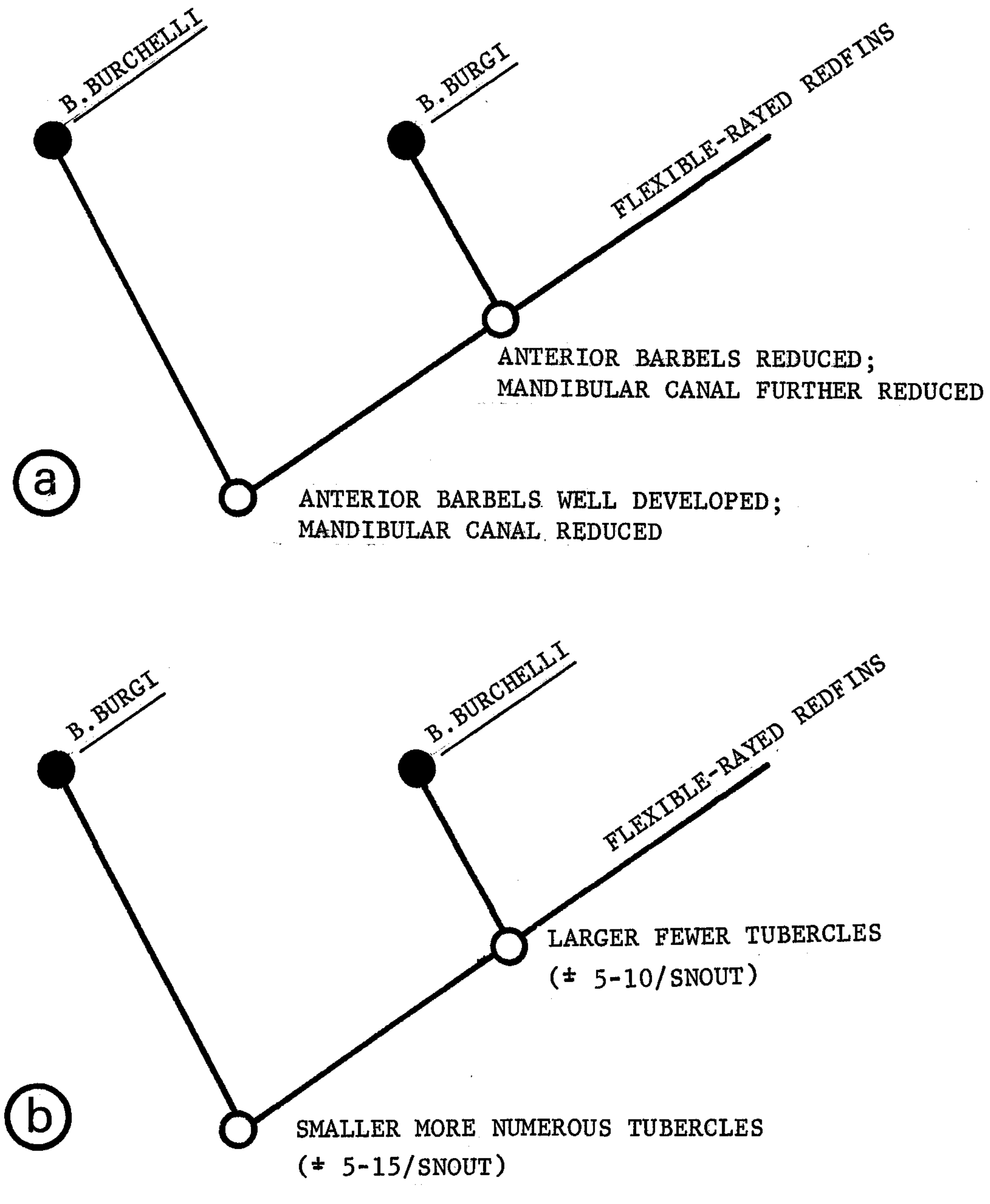


Fig. 5.14 Alternative phylogeny of *B.burchelli*, *B.burgi* and other flexible-rayed redfin species. Alternatives (a) and (b) based on synapomorphies as indicated on diagram.

With only two species to consider, the question of which is more primitive (stasigenetic) and which derived (anagenetic) is almost superfluous. B.erubescens does seem to be more derived in its diagnostic features: the loss of a strong, bony, serrated, dorsal fin ray, the addition of a branched anal and branched dorsal fin ray, and the loss of a pharyngeal tooth. The question of outgroup relationships of this group will be considered after attention has been given to the interrelationships of the flexible-rayed species.

The synapomorphies which confirm the monophyly of the flexible-rayed redfin lineage (including O.quathlambae) are as follows: the development of large, conical tubercles arranged in a specific pattern, the form of the pharyngeal teeth, the reduction or loss of the mandibular sensory canal, the absence of pelvic axillary scales, and the reduction of the breast scales. There are also less striking synapomorphic characters and considerable general similarity of form, which altogether form an impressive body of evidence for monophyly. There is little doubt that this is a most distinct group of African cyprinids. On these considerations it appears likely that the red fin-colour in the two groups represents convergence and not a shared derived character. However, the red fin-colour may still be synapomorphous for each lineage.

Within the flexible-rayed redfins several character transformations permit the reconstruction of the phylogeny of the species. The most primitive flexible-rayed redfin species is either B.burgi or B.burchelli. These two species are plesiomorphic in all the characters which are synapomorphic for the lineage. While the barbels suggest that B.burchelli is the plesiomorph sister species to the other species in the lineage, the tubercles and the number of predorsal vertebrae indicate that B.burgi should occupy this position (Fig. 5.14a, b). B.burgi and B.burchelli do not share any derived characters which are not also shared with other flexible-rayed redfins i.e. the two species are not themselves sister-species.

Acceptance of one or the other of the relationships as suggested in Figure 5.14 will necessitate at least some re-interpretation of character states. If B.burchelli is the plesiomorph sister-species the smaller and more numerous tubercles on the head of B.burgi are secondarily derived from the state in B.burchelli. On the other hand, if B.burgi is the plesiomorph sister species it means that either the better developed barbels of B.burchelli are derived or the shorter barbels of B.burgi are derived independantly of those of other flexible-rayed redfin species. The canal on the angulo-articular bone is present in certain B.burgi populations and therefore cannot be considered a reliable character for comparison with B.burchelli.

Winterbottom (1974) points out that characters of reduction or loss merit less weight than characters of gain in phylogenetic analysis, presumably because it is easier to lose a structure in evolution than to develop a new one. The evolutionary development of large tubercles in the redfin species is considered to be a particularly outstanding feature of the lineage because of the rare occurrence of similar structures in African Barbus species. Furthermore the recognised plasticity of cyprinid barbels tends to decrease their value compared with that of tubercles. From the available evidence it is therefore concluded that B.burgi is the plesiomorph sister species of the other flexible-rayed redfins.

The relative increase in size and reduction in the number of head tubercles in B.burchelli is the only synapomorphy which suggests that B.burchelli shares a more recent common ancestor with the other redfin species in the lineage rather than B.burgi. The very close similarity between B.burgi and B.burchelli, which led previous authors to consider that the two species were closely related (Barnard, 1943; Jubb, 1965) suggests that the dichotomy separating B.burchelli from the other redfins occurred relatively close in time to the initial dichotomy separating B.burgi from the lineage.

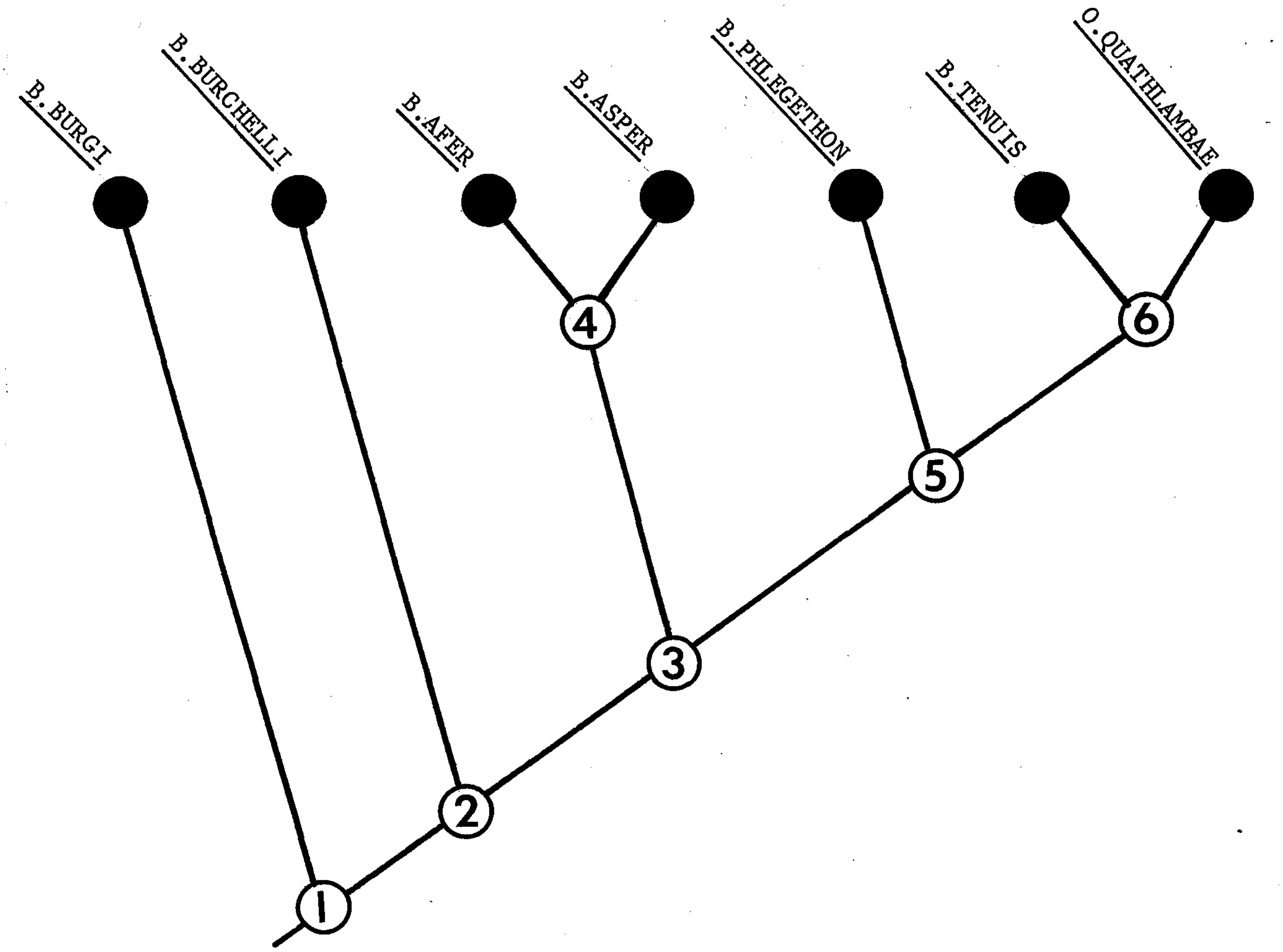
Several synapomorphies indicate the monophyly of B.asper, B.afer, B.phlegethon, B.tenuis and O.quathlambae. These are the loss of the anterior pair of barbels, the loss of the mandibular sensory canal, a slight increase in the number of scale radii, further reduction in the number of head tubercles, and the development of a more pointed flange on the exoccipital. Of these the most reliable characters are probably the loss of the mandibular sensory canal and the decrease in the number and increase in size of head tubercles.

B.afer and *B.asper* are morphologically extremely close and are generally conservative with regard to the primitive facies of *B.burgi* and *B.burchelli*. In spite of the close similarity between *B.afer* and *B.asper* it has not been possible to find a clear synapomorphy which would confirm their close relationship. The differences between the two species (Chapter 3) lie in the size of the scales, the length of the intestine and the pattern of pigmentation. In all of these characters *B.asper* is the more unusual of the two and probably represents the more derived species. The habitat preferences of *B.asper* are also unusual for a redfin species and it may be expected that the species is derived in terms of its physiological tolerances. The small scales of *B.asper* are apomorphic but probably not (as explained below) synapomorphic with the small scales of *O.quathlambae*.

B.phlegethon is a relatively unusual flexible-rayed redfin and has several autapomorphic characteristics such as the small mouth, narrow head, reduction of head tubercles and sexual dimorphism. The species shares two derived characters with *B.tenuis* and *O.quathlambae*: the loss of a tooth on the outer row of each arch (*B.tenuis* and *O.quathlambae* lack both the outer row teeth) and the reduction in size (length) of the barbels. These are both characters of reduction and in the case of the barbels admittedly rather weak but in the absence of evidence to the contrary, they do provide synapomorphies which establishes the relationship.

Skelton (1976) suggested that the relationships of *O.quathlambae* probably lie closest to *B.tenuis*. This relationship is fully endorsed by the following synapomorphies: pharyngeal teeth in two rows, the shape of the pharyngeal teeth, the similarity in development of a spur on the exoccipital bones, relatively short alimentary tract, the prominent notch on the dorsal edge of the metapterygoid, reduced ossification in the anterior region of the neurocranium, vestigial supraorbital bones, low and relatively long operculars and hyomandibulars, increased lack of ossification of the epipleurals, and narrow infraorbitals with dermosphenotic reduced (*B.tenuis*) or presumably absent (*O.quathlambae*).

Barbus tenuis has relatively large scales compared with *B.asper*. If *B.tenuis* is the sister species of *O.quathlambae* the small scales of the latter must have been independantly derived, as are those of *B.asper*.



5.15. Phylogeny of the flexible-rayed redfin Barbus species as concluded in this study.

A cladogram for the flexible-rayed redfins reflecting the above assessments of the characters of the group is given in Fig. 5.15.

Out-group relationships

The out-group relationships of the redfins have always been problematical because the redfins are rather distinctive species and not, at a specific level, obviously similar to other southern African Barbus species. The introduction of Hennigian methodology offers a more satisfactory approach to the problem of the relatives of these species because the relationships can be established by considering synapomorphies and not general similarity.

Serrated-rayed redfins

The serrated-rayed redfins are characterised by the following synopomorphies: red fins, a serrated, unbranched dorsal fin ray, six or seven branched anal fin rays, dorsal fin placed posterior to the pelvic fin base, high average vertebral counts, high predorsal fin vertebral counts.

There are two possible candidates for relationship with B.calidus and B.erubescens on the basis of red fin colour; B.argenteus from the Incomati and Pongola rivers in the eastern Transvaal (a good photograph is given in Pienaar, 1978); and B.gurneyi from the coastal rivers in Natal (Tugela to Umtamvuma). B.argenteus is a cool water species (Gaigher, 1969) with a serrated, unbranched dorsal fin ray and is very similar to B.calidus and B.erubescens in form (including osteology). There are at least two noteworthy differences between B.argenteus and the redfin species - the dorsal fin of B.argenteus originates over or slightly ahead of the pelvic fin (Table 5.5) and the tubercles on the pectoral fin are conical and occur in bands (Table 5.2). Apart from orange or reddish fins B.gurneyi has little similarity with the serrated-rayed redfins but may be related to the flexible-rayed redfins (see below).

A serrated, unbranched dorsal fin ray is not unique in cyprinids or Barbus species. The Barbus species in southern Africa with this character are diverse in form, and it would be difficult to claim monoplyly on the strength of this single character. The form of the serrated, unbranched ray itself differs between the species. In B.hospes, for example, the proximal serrations turn apically (Barnard, 1943) and in *B.trevelyani* the serrations are extremely weak (Jubb, 1965, 1967) and are undetectable in certain specimens. Because of the derived nature of the serrated dorsal fin unbranched ray it seems most probable that near relatives of serrated-rayed species would themselves have serrated unbranched dorsal fin rays.

B.andrewi is the only *Barbus* species in southern Africa apart from *B.calidus* and *B.erubescens* which regularly has six branched anal fin rays. Skelton (1976) suggested that on this basis the species may be interrelated. However *B.andrewi* bears greater similarity in all respects except the number of branched anal fin rays to *B.serra* from the Olifants River System. *B.serra* has five branched anal fin rays. *B.andrewi* and *B.serra* have several probable synapomorphies including the shape of the lachrymal bone and a long, narrow snout. The evidence clearly suggests that the two species are most closely related. If this is so then any relationship between the serrated-rayed redfins and *B.andrewi* on the basis of branched anal fin rays would either require that the five branched anal fin rays of *B.serra* is a derived character or the entire repertoire of similarities and suggested synapomorphies of *B.serra* and *B.andrewi* are due to convergence or parallelism. Both of these alternatives are considered unlikely and it appears more probable that the six branched anal fin rays were independently derived in either group.

The types of several Moroccan *Barbus* species with six branched anal fin rays have been examined in the British Museum but there is no evidence to support any relationship between them and the serrated-rayed redfins. Banister & Clark (1977) described two *Barbus* species from the Arabian Peninsula with six branched anal fin rays. Again, based on the descriptions of these species there is little indication of any relationship with the southern African species with six branched anal fin rays.

The posterior displacement of the dorsal fin is a characteristic of only two smaller *Barbus* species with a serrated, unbranched dorsal fin ray and radiately striated scales, *B.hospes* and *B.trevelyani*. This is correlated in both species with an above average number of predorsal vertebrae (Table 5.4 D). *B.hospes* is exceptional in the number of predorsal vertebrae (13-15) which is clearly autapomorphic for that species. Both *B.hospes* and *B.trevelyani* have seven branched dorsal fin rays, a possible synapomorphy with *B.calidus*, and both have scattered erupted tubercles on the head and scale surfaces (Fig. 5.1). *B.hospes* has bands of conical tubercles on the pectoral fins, but *B.trevelyani*, similar to *B.calidus* and *B.erubescens*, has a single row of erupted pectoral fin tubercles (Fig. 5.2). *B.hospes* is the only smaller *Barbus* species with a serrated, unbranched dorsal fin ray apart from *B.calidus* and *B.erubescens* in which the pterosphenoids meet.

The evidence for a relationship of *B.hospes* with the serrated-rayed redfins is tenuous. *B.hospes* is however a highly specialized species. This is evident not only from the predorsal vertebrae and placement of the dorsal fin but in several other striking autapomorphies. The pelvic fins are attached to the body by a membrane, the scales are small and thin, and there is a large orbitosphenoid-lateral ethmoid fenestrum not found in other *Barbus* species. The Weberian neural crest of *B.hospes* is large and expanded anteriorly. These specializations might mask other synapomorphies with the serrated-rayed redfins and the possibility of a relationship between them cannot be ruled out.

B.trevelyani also has several outstanding autapomorphic characters (e.g. the infraorbital bones, Fig. 5.8) which tend to obscure its relationships. For the present it is not possible to do more than suggest that the relationships of the species may, on the evidence mentioned above, be close to the serrated-rayed redfins.

Apart from *B.argenteus*, *B.trevelyani* and *B.hospes* I am unable to find substantial support that any other southern African *Barbus* is closely related to *B.calidus* or *B.erubescens*. It is possible to select similarities in different characters which may indicate relationship but it cannot at present be shown that the similarities are synapomorphies. Even with the above three species the similarities are not correlated to the extent that one or two likely cladograms can be presented without a complex re-evaluation of characters. It is best under these circumstances to refrain from presenting a formal scheme of relationships for these species.

Flexible-rayed redfins

It has been shown that there are several synapomorphies which establish the monophyly of the flexible-rayed redfins. It is reasonable to expect that close relatives of the flexible-rayed redfins will have morphological features which approach the synapomorphies of the flexible-rayed redfin species. A brief resumé of the plesiomorph state of the flexible-rayed redfin synapomorphies should provide the clues for the morphological framework expected of close relatives. The more primitive flexible-rayed redfins are medium sized fishes with moderately sized scales. The mouth is sub-terminal or inferior and sickle-shaped. Sexual dimorphism is characteristic and tubercles are prominent on males. Apart from the red fin markings, pigment patterns are generally conservative and variable. Irregular predorsal scales, reduced breast scales and the absence of pelvic axillary scales are characteristic. The numbers of branched rays in the dorsal fin (seven) and anal fin (five) are conservative characters. The intestine is involuted and moderately long, and the pharyngeal teeth have obliquely truncated crowns. There are an above average number of total vertebrae and predorsal vertebrae and there is a trend of reduction in the intramuscular bones and the supraneurals. The mandibular sensory canal is reduced and the preopercular canal is not connected to the lateral commissure.

There is no evidence to suggest that the flexible-rayed redfin species are derived from any of the serrated-rayed *Barbus* species. Furthermore, no grounds can be found for considering the following small *Barbus* species with a flexible unbranched dorsal fin ray closely related to the flexible-rayed redfins: *B.annectens*, *B.barnardi*, *B.bellcrossi*, *B.bifrenatus*, *B.fasciolatus*, *B.haasianus*, *B.lineomaculatus*, *B.macrotaenia*, *B.neefi*, *B.pallidus*, *B.puellus*, *B.radiatus*, *B.thamalakanensis*, *B.toppini*, *B.viviparus*. The majority of the above species are small (adults less than about 60 mm SL) with distinct pigment patterns and have tropical distributions. They generally have fewer than 34 vertebrae, and the dorsal fin originates over or before the pelvic fin base. Small conical tubercles are present in several of the species on the head and in bands on the pectoral fins. In most the tubercles are lightly scattered on top of the head. In *B.barnardi* the tubercles are concentrated in a band around the snout. Erupted tubercles have not been found in any of the small *Barbus* with radiately striated scales and a flexible unbranched dorsal fin ray.

With the exclusion of the above species the choice of possible relatives is narrowed to *B.treurensis*, *B.unitaeniatus*, *B.anoplus*, *B.motebensis* and *B.gurneyi*. *B.treurensis* is restricted to a single tributary of the

Limpopo River system. The species differs in most respects from the redfins and no pertinent similarities suggestive of synapomorphies have been found. *B.unitaeniatus* is a widespread species with an essentially tropical distribution extending as far south as the Pongolo River system in northern Natal. The species does have a sub-terminal mouth and embedded breast scales which are similar to the flexible-rayed redfins. Very small conical tubercles occur on the head and there are bands of tubercles on the pectoral fins. The species has above average vertebral counts (Table 5.4) but differs notably from the redfins in having fewer predorsal vertebrae (9 or 10). The dorsal fin origin is before the origin of the pelvic fins. In other respects *B.unitaeniatus* shows no pertinent similarities with the flexible-rayed redfins.

Of all the *Barbus* species in southern Africa *B.anoplus*, *B.motebensis* and *B.gurneyi* are in most respects similar to the flexible-rayed redfins. Some of the characters of these species are derived and are interpreted as synapomorphic with redfin characters. The three species are all medium sized southern African endemics with flexible, unbranched dorsal fin rays and seven branched dorsal fin rays. All three species show sexual dimorphism,and the males of *B.gurneyi* and *B.motebensis* develop relatively large conical tubercles on the head (Table 5.2, Fig. 5.3). The males of *B.anoplus* were supposed not to have head tubercles (Jubb, 1967) but populations have been found with tubercled males. This has led Gaigher (1976) to suggest the species is synonymous with *B.motebensis*. In contrast with the redfins, the head tubercles of *B.gurneyi* and *B.motebensis* do not differ in size and occur on the cheeks below and behind the orbits, on the rami of the lower jaw as well as on the snout and on top of the head. In essence this may be interpreted to represent a plesiomorphic character state relative to the tubercles of the flexible-rayed redfins.

The breeding males of *B.anoplus* and *B.motebensis* are golden yellow and those of *B.gurneyi* a golden bronze with orange-red fins, especially the caudal fin (Crass, 1964; Jubb, 1967; pers.obs.). Preserved specimens of these species have a thin lateral stripe from behind the head to the base of the caudal fin ending in a small but distinct spot. This pattern is generalized and similar to several of the flexible-rayed redfin species.

None of the species have a large triangular pelvic axillary scale and to a certain extent the breast scales are reduced in size and embedded. The mouth is small or moderate and terminal or slightly subterminal with variably one or two pairs of barbels. The pharyngeal teeth are slender and have recurved terminal cusps which is similar to most *Barbus* species examined (Fig. 5.5). The intestine is short and S-flexured. The teeth and intestine could also be regarded as plesiomorphic to the redfin character states.

The cephalic lateral line system of *B.anoplus*, *B.motebensis* and *B.gurneyi* is similar to the flexible-rayed redfins except that the mandibular canal is not reduced. The osteology is also generally similar and several features are suggestive of synapomorphy. The frontals do not overlap the supraethmoids; intercalars are absent or vestigial; the dorsal edge of the metapterygoids is more or less concave, and is divided by a notch into two lamellae. The supraneurals are small or vestigial especially in certain specimens of *B.anoplus*, and the epineurals before the dorsal fin are poorly ossified.

In conclusion there appears to be a reasonable body of evidence to suggest that *B.anoplus*, *B.motebensis* and *B.gurneyi* are the nearest relatives of the flexible-rayed redfins. This relationship is supported in terms of several likely synapomorphies, which includes the development of large tubercles, aspects of aquamation, reduction of ossification of the epineurals, reduction in size of the supraneurals and the shape of the metapterygoid. A broad,general morphological similarity enhances the evidence for close relationship.

Classification

There are a number of ways in which organisms may be classified. Here it is considered essential that living organisms interrelated by common ancestry are as far as possible classified in a manner which reflects their relationships (Hennig, 1966; Crowson, 1970; Nelson, 1971, 1972a, 1973, 1974; Brundin, 1972; Cracraft, 1974). The manner in which this may be done has been discussed by the above authors. A classification based on phylogeny takes the form of a hierarchy with successive sub-ordination of taxa according to their recency of common ancestors.

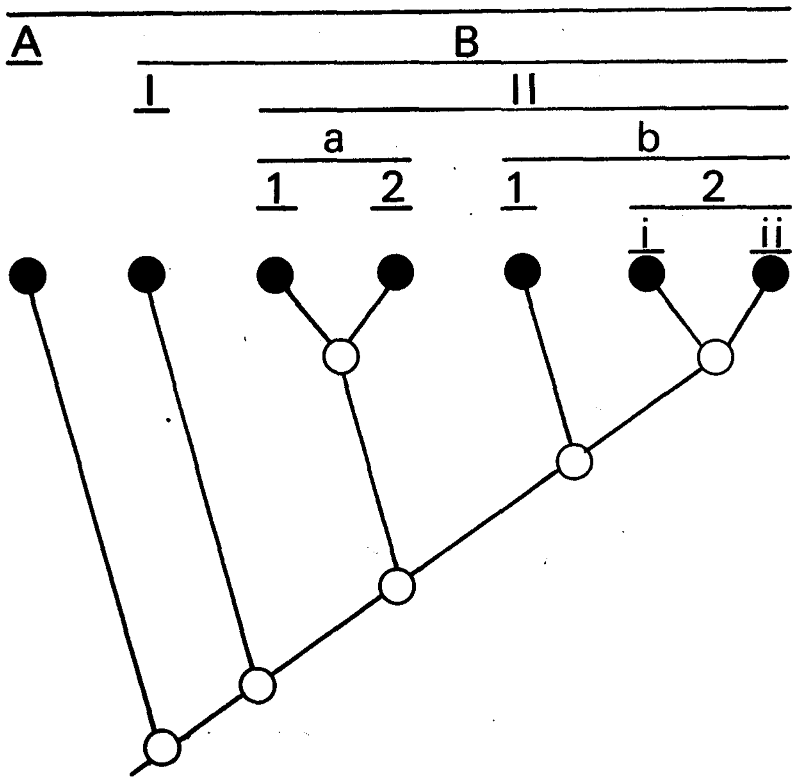


Fig. 5.16 Diagram illustrating hierarchy of flexible-rayed redfin sister groups. Overhead bars unite successive species sharing a common ancestor. Sister groups are indicated by matched pairs of symbols, e.g. A, and B.

The intrageneric relationships of *Barbus* species are not well understood at present. Consequently the classification of the species in taxonomic works has been either based on categories defined by certain key characters (e.g. Boulenger, 1911; Jubb, 1967) or the species have been simply listed alphabetically (e.g. Bell-Cross, 1976). Insofar as the former represents an attempt to group the species according to some concept of relationship, it is preferable to the latter which entirely fails to do this.

In the most recent account dealing with the red-fin *Barbus* species Jubb (1967) organised the southern African *Barbus* according to the following categories:

A. Species with parallel striated scales.
B. Species with radiately striated scales
    i) large species (adults >150 mm SL)
    ii) small species (adults <150 mm SL)

Within the B.ii) category the species were gathered informally according to the form of the last unbranched dorsal fin ray viz., non-serrated and bony, non-serrated and flexible, and serrated and bony. The redfin species were therefore divided and *B.calidus* was included among the species with a serrated and bony last unbranched dorsal fin ray whereas the flexible-rayed redfins were included with *Barbus*, the species with a flexible last unbranched dorsal fin ray. At that stage the relationships and generic status of *Oreodaimon quathlambae* were still being questioned and the species was not included under any particular genus.

With the relationships of the redfins now reasonably established the re-classification of the species can be considered. The two lineages should be divided and the species ranked subordinately according to their relationships. In the serrated-rayed lineage *B.calidus* and *B.erubescens* are sister species and require equal rank. A suitable hierarchy reflecting the relationships of the flexible-rayed redfins is:

A) *B.burgi*
B) (I) *B.burchelli*
    (II) (a) 1. *B.afer*; 2. *B.asper*
        (b) 1. *B.phlegethon*
            2. i. *B.tenuis*; ii. *O.quathlambae*

This hierarchy is explained diagrammatically in Figure 5.16.

The next stage in the classification of the redfin lineages poses the problem of at what taxonomic level each should be accommodated in the existing classification. The genus Barbus is so large that it is completely unwieldly as far as formal classification is concerned. Although several subgenera have been proposed over the years, few of these are applied in practice or have gained widespread support. Successful subdivision of Barbus depends on several factors, not the least of which is the strength of the characters used to circumscribe a group of species. It is because the characters were weak that early attempts to subdivide the genus failed. Those subgenera which have been accepted or even at a later stage elevated to generic rank are based on relatively smaller groups of species which are characterised by substantial characters (synapomorphies). Thus the subgenus Enteromius is accepted by most systematists and is based on the synapomorphy of prominent pit-lines on the head (Greenwood, 1962, 1963, 1970). Clypeobarbus was originally described as a subgenus of Barbus by Fowler (1936) and has since been raised to full generic rank (Poll, 1976). The characteristic features of Clypeobarbus include enlarged mid-lateral scales and distinctive large, conical tubercles on the head and lips of the specimens. These characters are clearly synapomorphies and fully justify, in the opinion of this author, full generic status.

The use of sub-genera and "species groups" was advocated by Rosen & Bailey (1963) as a general solution to the problem of large genera. In North America the sub-genus has been widely employed in the classification of large and unwieldly cyprinid genera such as Notropis and Hybopsis. In the 1950's there was a distinct trend toward the employment of large comprehensive genera (Bailey, 1959) but this trend has since been reversed and there is a more realistic tendency to recognise natural units as full genera (Jenkins & Lachner, 1971).

It has not been possible to recognise any particular trend in African cyprinid systematics. This is probably because of the diverse stage of exploration of the fauna in the various territories. In most cases systematic studies are directed not at particular groups but rather at regional accounts of entire faunas. The African cyprinids are gathered into a few very large genera (e.g. Barbus, Labeo etc.) and several smaller more unique genera (e.g. Coptostomabarbus, Raddabarbus, Clypeobarbus etc.).

The widespread distribution of certain species and the large genera does not encourage the use of sub-genera in the socio-political context of Africa. Such sub-divisions would soon be lost or have little influence beyond the region of the included species, and so far pan-African revisions are not the order of the day.

Any difference between the generic and the sub-generic category is an arbitrary matter. Mayr (1969) defined the genus as a taxonomic category containing a single species or a monophyletic group of species which is separated from other taxa of the same rank by a decided gap. The phrases "of the same rank" and "by a decided gap" are clearly the stumbling blocks in the case of large genera such as Barbus because natural sub-units tend to be engulfed in the larger whole purely on the gradistic grounds of general similarities of the organisms.

The emergence of the cladist philosophy and the greater appreciation that classification should reflect phylogenetic relationships offers a real solution to the problem of large genera. There are indications that this approach is likely to gain momentum and become a major force in African ichthyology in the future. An example of the movement in this direction is given by Greenwood (1979) who has provided the beginnings of a phyletic classification of the problematical cichlid genus, Haplochromis.

Both of the redfin lineages are evidently monophyletic. The flexible-rayed species are, relative to all other Barbus species, unique and morphologically distinct. It is entirely in the interests of comparative biology to recognise this relationship and the distinction of the species in formal classification. This is best done at the generic level, which embodies both the concepts of relationship and distinctiveness (Bolin, 1947; Mayr, 1969).

The serrated-rayed redfins, although quite evidently monotypic, do not have the same degree of uniqueness that the flexible-rayed species have. The synapomorphies of these two species are also found in other "Barbus" species and their very close similarity to these makes it difficult to define the group in terms of synapomorphies. At present it must suffice to recognise the relationship of the serrated-rayed redfins informally, pending more detailed investigation of other Barbus species. This would leave the way clear for future changes in classification where necessary.

In conclusion it is therefore proposed that the flexible-rayed redfins (including O.quathlambae) are placed in a new genus and the serrated-rayed redfins are recognised as a distinct "species group" within Barbus.

There is an available name which must be used for the flexible-rayed redfins - A. Smith's Pseudobarbus. Pseudobarbus was described as a sub-genus of Barbus and included two species, B.burchelli and B.pallidus in the original publication. The reasons given for the naming of the sub-genus was not that the two species had anything particularly striking, but that they were the first two minnow-like forms described from southern Africa, and Smith was unsure whether or not they were con-generic with Barbus. The sub-genus was poorly described by modern standards but, inter alia, included the criterion of "the intestinal canal long and contorted". This suggests that Smith based Pseudobarbus on B.burchelli and not B.pallidus because the latter does not have a "long and contorted" intestine. B.burchelli was recorded as the type species of Pseudobarbus by Jordan (1919). Although Jordan considered it to be the type species by original designation this is not strictly true (Smith, 1841 included both B.burchelli and B.pallidus in Pseudobarbus without qualification). B.burchelli is, however, validly the type species by subsequent designation by Jordan (1919).

The original definition of Pseudobarbus given by Smith (1841) is as follows: "Mouth opening forwards, lips thin and cartilagenous; intermaxillary bones extensible; nostrils double; four cirri, two from upper lip and one from each angle of mouth; lateral line consists of a series of slender tubes; dorsal fin short and commencing directly over base of ventral fins, intestinal canal long and contorted". This definition is inadequate and does not characterize the flexible-rayed redfin group. A new diagnosis which excludes Barbus pallidus, is given below.

Genus Pseudobarbus Smith (1841) Stat.nov.

Type Species: Pseudobarbus burchelli (by subsequent designation, Jordan, 1919). Moderate sized (50 mm > SL < 150 mm) fusiform or terete cyprinid fishes; snout rounded; mouth usually subterminal or inferior, crescentic or sickle-shaped; lips moderately developed; pharyngeal teeth in two or three series, 0-2,3,4 or 5 - 5 or 4,3,0-2; crowns variable with an obliquely moderate to well worn grinding surface or with latero-terminal recurved tips. Alimentary canal variable, from a simple, single flexure with length subequal to SL to multiple involutions with length up to 3.5 times the SL; peritoneum pigmented. One or two pairs of well developed or short circumoral barbels; scales moderately large to very small, radiately striated, radii present in all scale fields; scales on nape irregular, often reduced and crowded, breast scales reduced and imbedded, no enlarged triangular pelvic axillary scale. Trunk lateral line straight, interrupted or complete, running along middle of caudal peduncle; supraorbital sensory canals without median branches; preoperculo-mandibular canal reduced or absent on the mandible, not connected to postocular commissure. Adults with distinctive bright red patches on the basal half and adjacent axillary area of paired and median fins; melanophore pigmentation variable. Prominent conical tubercles on the head, margins of scales and fins of breeding males, tubercle buds develop on head of large females. Dorsal and anal fins with three or four flexible unbranched fin rays and invariably 7 and 5 branched fin rays respectively; gill rakers 5-10 on ceratobranchial of first arch, short and thick-set. Total vertebrae from 33 to 40; supraneural bones absent or vestigial; frontals not overlapping lamellae of supraethmoid; intercalars reduced or absent; exoccipitals with or without posterior flange; supraorbitals vestigial or short and accommodated in a recess on the supraorbital shelf; infraorbitals usually 5 or 4, lachrymal with low dorsal peak, upper jaws relatively short and deep; urohyal with horizontal flange tapered posteriorly. Pectoral fins sexually dimorphic, pectoral girdle stout in males, less so in females; intramuscular bones weakly ossified anterior to the dorsal fin.

The following species are included in the genus: (full synonymy for each is given in Chapter 3).

Pseudobarbus afer (Peters, 1864	Comb.nov.
Pseudobarbus asper (Boulenger, 1911	Comb.nov.
Pseudobarbus burchelli Smith, 1841	
Pseudobarbus burgi (Boulenger, 1911)	Comb.nov.
Pseudobarbus phlegethon (Barnard, 1938)	Comb.nov.
Pseudobarbus tenuis (Barnard, 1938)	Comb.nov.
Pseudobarbus quathlambae (Barnard, 1938)	Comb.nov.

The internal classification of *Pseudobarbus* requires no formal subdivision. The reasons for this are that the major phenotypic dichotomy of the species is between *P.quathlambae* and *P.tenuis* but this is merely the most recent phylogenetic dichotomy of the lineage. If *P.quathlambae* is given formal infrageneric recognition then in order to preserve the hierarchy presented above it would be necessary to give each preceding sister group at least the same recognition. The informal solution is therefore considered to be more desirable.

CHAPTER 6

DISTRIBUTION AND ZOOGEOGRAPHY OF THE REDFIN MINNOWS

One of the outstanding features of the southern African ichthyofauna is the relative paucity of species from the south coastal drainages. Traditionally these few species, including the redfins, have been regarded as the terminal products of one or other former "invasion" from the north (Boulenger, 1905a; Barnard, 1943; Darlington, 1957; Farquharson, 1962; Jubb, 1964a;1965, 1967; Jubb & Farquharson, 1965; Gabie,1965; Gaigher & Pott, 1973; Bowmaker *et al.*, 1978). The only accepted exception to the above explanation is *Galaxias zebratus*. Two theories explaining the presence of this species have been suggested: either it has reached Africa via oceanic dispersal (McDowell, 1973), or it is a Gondwana relict (Barnard, 1943; Rosen, 1974).

The dominance of the freshwater fish fauna in southern Africa by cyprinids increases progressively at higher latitudes (Bowmaker *et al.*, 1978). In addition to *Pseudobarbus* species other cyprinids in the southern coastal drainage (Chapter 2) fall into two genera, *Barbus* and *Labeo*. Both of these are widespread throughout Africa and beyond to Europe (*Barbus*) and Asia (*Barbus* and *Labeo*). Until now the interrelationships of the redfins with other *Barbus* species have not been known and the significance of their distribution at the southern tip of Africa has been swamped within the generalizations of pan-African *Barbus* distribution. The purpose of this chapter is fourfold viz., to consider recent advances in biogeographic theory, to review the previous explanations of redfin and other south-coastal and southern African fish distributions, to consider redfin distribution data in detail, and to provide alternative explanations for the distribution of the redfin minnows.

THEORETICAL ASPECTS

Explanations of biogeography are grouped into two classes depending on whether they are based on dispersal or vicariance (Platnich & Nelson, 1978). Dispersalist explanations seek to account for modern distributions of monophyletic lineages on the basis of localized evolution and subsequent extension of geographic range across isolating barriers. Vicariance explanations incorporate the concept of geographic fragmentation of a monophyletic lineage without the need of involving dispersal in the first instance (Croizat *et al.*, 1974). The essential difference between the two concepts is one of timing of isolating barriers. Dispersalist explanations involve the range extension of an ancestral species across pre-existing barriers which subsequently disrupts gene flow. Vicariance explanations suggest that isolating barriers develop subsequent to the dispersal of an ancestral species of the lineage (Platnich & Nelson, 1978).

The distribution of most animal groups involves both vicariance and dispersal (*sensu* Platnich, 1976). It has been shown that neither a vicariant nor dispersalist explanation has an *a priori* claim for any particular group of organisms (Ball, 1976; Platnich & Nelson, 1978). Nelson (1973) found it necessary to reconsider a previous attempt to formalize biogeographic rules (Nelson, 1969c) because they were based on the *a priori* assumption of dispersal being involved in the distribution of a monophyletic lineage. As shown by Croizat *et al.* (1974) and Rosen (1976) the evidence which shows that dispersal has occurred in the history of a lineage is sympatry of related species. Nelson (1974) suggests that the closest estimate to a distribution of an ancestral species is the sum of the present day distributions of species in the lineage.

Croizat *et al.* (1974) have developed a method of historical biogeography which involves the comparison of distribution patterns of monophyletic groups of organisms. If individual patterns (tracks) conform to describe a generalized pattern it is suggested that a common explanation should be sought for the pattern by correlation with the known geological or geographical history of the area. Rosen (1976) used the method to excellent advantage in explaining general distribution patterns in the Caribbean area.

The initial ideas of Croizat *et al.* (1974) have been developed further by Platnich & Nelson (1978) and Rosen (1978). These authors suggest that provided an allopatric speciation model is accepted, a known phylogenetic relationship between monophyletic organisms (cladogram) can be translated into a relationship of geographic areas (area cladogram). They propose that these area cladograms be compared and general area relationships exposed. The causal explanations for such general area relationships are then resolved by the evidence of geological or geographical history.

Certain qualifications are required for the method to be valid. Test groups for a generalized pattern must have three or more taxa in the total area of an original group and the test groups must have endemic taxa in each of the area subdivisions of the original group (Platnich & Nelson, 1978). Rosen (1978) shows that statistical methods can be applied to verify the hypotheses provided the above qualifications are met and that sound cladistic methods are used to derive the cladograms. The higher the degree of congruence between the biological cladograms and the area cladograms the higher will be the confidence levels of the hypotheses.

Geographic and geomorphological events are necessarily the independant variables on which the biological events are dependant. This does not mean that every biological pattern has an equivalent geographic pattern because there is a possibility of chance dispersal. Dispersalist explanations depend on chance processes and consequently cannot be falsified. On the other hand vicariance explanations may be falsified in theory if all biological patterns in a particular area do not conform to the established or known geographical history.

Clearly then it is one matter to establish a biogeographic hypothesis for a particular group of organisms and another to verify that hypothesis. Both Platnich & Nelson's (1978) and Rosen's (1978) carefully analysed methods imply, in their own words: "that the only way to deal objectively with causal explanations of biotic distribution is to work with general patterns and the historical events that can be correlated with them". They accordingly reject biogeographic analyses not meeting these criteria.

These theories and methods are still new and relatively few groups have been analysed in detail according to Hennig's (1966) cladistic principles. This is particularly true in southern Africa where the geomorphological and geographical history of the subcontinent is also still far from clearly understood or settled (Corbett, 1979). It is not possible at the present time to meet the strict demands presented by Platnich & Nelson (1978), and this study of the redfin minnows can only suggest possible explanations for their distribution. These may or may not stand the test of time, but unlike Platnick & Nelson (1978) I do not consider such exercises as unjustified, provided one works within the limits of the available data.

HISTORICAL REVIEW OF SOUTHERN AFRICAN FRESHWATER FISH ZOOGEOGRAPHY

It was not until late last century and the early years of this century that the freshwater fish species of southern Africa were known sufficiently well for a synthesis of distribution patterns to be contemplated. Thus the earliest views of any consequence were those expressed by Weber (1897) and Boulenger (1905 a).

Weber (1897) divided the subcontinent into four regions, a savannah region, an Erica or Protea region, a Karroo region and the Kalahari region. Although few freshwater fish species were yet known or their distributions accurately plotted he specifically associated Galaxias zebratus with the Erica or Protea region of the south-west Cape.

Boulenger (1905 a) considered the distribution of African freshwater fishes as a whole. He presented several important ideas with regard to the southern African fauna which have become somewhat entrenched legacies. The first of these was that, apart from Galaxias in the south-west Cape, he regarded the southern African forms as "comparatively recent immigrants from the north". The cyprinids were considered to have entered Africa from the north-east. Boulenger also made the point that the south-west Cape derived a "special character" from the presence of Galaxias and Sandelia (=Anabas).

In addition Boulenger (1905a) is noted for the fact that he placed importance on the physiological capabilities of continental fishes with regard to their distribution potential. This idea was further developed by Myers (1938, 1949) and has become a cornerstone of most continental fish biogeography (Darlington, 1957; Rosen, 1974; Roberts, 1975).

The concept of a north-east gateway for the cyprinids to Africa was given impetus by Regan (1922) who suggested that south-east Asia and India was the centre of evolution of the Cypriniformes. The latter concept was readily accepted by zoogeographers (e.g. Nichols, 1930; de Beaufort, 1951; Darlington, 1957), and is still in force (Bowmaker et al., 1978), as is the idea of a north-east entrance to Africa (Lowe-McConnell, 1975). North-west African Barbus species are more closely related to the European Barbus species and are regarded as reaching Africa from Europe (Roberts, 1975).

From the turn of the century up until the late 1950's knowledge of the freshwater fishes of southern Africa increased through the works of Boulenger (1911-1915), Gilchrist & Thompson (1913-1917), Barnard (1938 a & b, 1943, 1948), Groenewald (1958) and others. There was however no attempt at an overall zoogeographical synthesis on the fauna. In the case of K.H. Barnard this is rather surprising as he was in fact a very good zoogeographer (e.g. Barnard 1927; 1936) with a sound grasp of both the concepts of dispersal and vicariance! There is however good reason why he did not write much on this subject, as there was, in his view, insufficient knowledge of the fish fauna and the interrelationships of the species (Barnard, 1943).

Barnard's (1943) contribution to the fish biogeography of the southern coastal drainage was nevertheless considerable. He placed most of the species on firm taxonomic footing and recorded their distributions with far greater accuracy than had been done before. He pointed to pertinent relationships and their zoogeographical importance e.g. the links between the fauna of the Orange River system and that of the southern coastal drainage. With a first hand knowledge of the drainage of the region he was frequently able to provide sound explanations of individual species distribution on a local scale. Barnard was well versed in the geomorphological literature and pointed to many pertinent river captures and other geomorphological aspects of significance to the distribution of the freshwater fishes of the southern and southwestern Cape.

After the Second World War a new generation of scientists turned their attention to the freshwater fishes and their distribution in southern Africa. In the British colonies of Northern and Southern Rhodesia and Nyasaland R.A. Jubb began publishing on the freshwater fishes. There was also for the first time an organized body of scientists (Joint Fisheries Research Organization) involved in fish and fisheries research in these colonies. Rapid advances were made in regard to the knowledge of the species present and their distributions in this region which is a vital link to the southern fauna (Jackson 1961 a, b).

Research and knowledge of the fish fauna in South Africa itself was also making strides. In the Cape, the Transvaal and Natal the provincial authorities established research orientated organizations involved with fisheries development (primarily sport fisheries) in these provinces. The research conducted by these bodies naturally furthered the knowledge of the indigenous fishes and their distributions (e.g. Crass, 1964). By the early 1960's the time was ripe for the long awaited synthesis on the fish distribution of the sub-continent.

Jackson (1961 a) provided an annotated checklist of the fishes of Zambia (Northern Rhodesia) which are to a large degree those of the Upper Zambezi River system. In conjunction with Jubb (1961), Jackson (op.cit.) showed that many species of the upper Zambezi region were also found in the tropical or subtropical eastern Transvaal and Mozambique "lowveld" regions. There was also a rapid subtraction of these forms in the northern Natal coastal region (Zululand), especially to the south of the Pongolo (Maputo) River system (Crass, 1962, 1964, 1966; Bruton, 1979). Clear faunal similarities between the Upper Zambezi and Zambian Congo (Zaïre) River systems (Bell-Cross, 1965, 1968) ensured that the long proposed "northern origins" of the ichthyofauna of southern Africa received undisputed scientific respect.

Farquharson (1962) discussed cyprinid distribution in southern Africa. The cyprinids are a major component of the freshwater fish fauna increasing from 32-33% of the fauna of the Zambezi River System to 73-76% in the Orange River and south coastal drainages (Bowmaker et al., 1978). In retrospect Farquharson's study was of importance for it laid down the foundation for the current understanding of the freshwater fish distribution in the sub-continent. From the patterns of distribution of "taxonomically related" groups Farquharson (op.cit.) concluded that there had been a succession of cyprinid invasions from the tropics. The representatives of earlier invasions penetrated furthest south where they have had refuge from displacement by subsequent invaders (such displacement occurred in the rivers to the north of the south coastal drainage).

Jubb (1964) and Jubb & Farquharson (1965) considered the zoogeography of the fishes of the Orange and south coastal drainages. Their general thesis was an extension of Farquharson's (1962) "Waves of invasion" idea. The Orange River was considered a "stepping stone" for fishes dispersing from the tropics (Upper Zambezi region) southwards to the coastal drainage. Two separate "invasions" were suggested: a mid-Pliocene invasion which probably included the redfin species and all other south coastal species; and secondly a mid-Pleistocene invasion. The earlier mid-Pliocene invasion also provided elements of the Natal and Transvaal faunas via headwater exchange of the Orange-Vaal system with the more vigorously eroding rivers of these regions.

Jubb (1965, 1967) presented a general analysis of the Cape, and the southern African freshwater fishes. The distribution of each species was given in broad outline and the fauna of the larger rivers of the region analysed independently. These otherwise valuable works however provided little in the way of zoogeographical synthesis.

From literature sources Gabie (1965) provided a synthesis of the fish distribution in southern Africa. With the exception of Galaxias zebratus the fauna was considered to have been derived from central African sources via drainage links of the larger river systems. Two main routes were proposed - one via the Okavango-Ngami basin to the Limpopo and Orange River systems and the other via the Zambezi River system to the eastern coastal region. South coastal fishes were derived from links with the Orange River system. Gabie (1965) concluded by recognising three zoogeographical regions - a tropical region including the Cunene and Zambezi Rivers, a transitional region as far south as the Pongolo River, and a south temperate region to the south of the Pongolo.

The distribution of fishes in Natal was considered by Crass (1962, 1964, 1966). Two invasion routes were suggested to account for the derivation of the fish fauna of this region. The major route of tropical species came southwards from the Zambezi system along the Mozambique coastal plain. The alternative route which accounted for a relatively small proportion of the province's fish fauna was by headwater exchange of Natal rivers with those of the inland drainage (Orange-Vaal). There is a marked subtraction of tropical species in north-eastern Natal (Maputaland) which has been discussed in connection with the derivation of the fish fauna of Lake Sibaya by Bruton (1979). Bruton (op.cit.) supports the thesis that many species of this region are derived from central African stocks which have dispersed southwards via the Zambezi River system and the Mozambique coastal plain. The marked subtraction of species in this region is probably due to a phasing out of tropical conditions which is correlated with the reduction in width of the coastal plain (Stuckenberg, 1969; Bruton, 1979).

A synthesis of the major patterns of fish distribution in southern Africa was given by Gaigher & Pott (1973). These authors considered four major faunal exchanges to have occurred: a mid-Pliocene exchange between the Okavango-Upper Zambezi region and the Orange River system (the southern coastal and other endemic southern African species were derived from this invasion); a late Pliocene exchange between the Upper Zambezi-Okavango region and the Limpopo drainage with further dispersal of some of these species into Natal; an east coastal exchange (Lower Limpopo-Lower Zambezi) probably during the Pleistocene, and an exchange between the Orange and Limpopo River systems.

In conjunction with Jubb (1964) and Jubb & Farquharson (1965), Gaigher & Pott (1973) have provided the basis of the currently accepted explanation of the historical ichthyogeography of southern Africa. The explanation is clearly dispersalist but it is nevertheless based on the recognition of general ichthyological associations and patterns of distribution (or coincident "tracks" of Croizat et al., 1974). Furthermore, these tracks are explained without recourse to individual dispersals but as distinct pulses of ichthyofaunal exchange correlated as far as possible with palaeogeography (former drainage connections etc.). The components of the pattern or track are therefore considered as modern representatives of a distinct former biota.

Roberts (1975) discussed the pan-African distribution of freshwater fishes. Ten "ichthyofaunal provinces" were recognised, two of which (Zambezi and Cape of Good Hope) largely concern the southern African fauna. The Zambezi province included the hydrographic basins of the Zambezi itself as well as the Cunene, Ovambo, Okavango, Limpopo and eastern coastal rivers from the Zambezi to the Maputo (or Pongolo). The Cape faunal

Province included all drainages to the south of the Limpopo and Pongolo systems. Roberts (1975) more or less summarizes the known distribution of these regions without adding to any general hypothesis as regards their historical biogeography.

Bell-Cross (1965, 1968, 1972) and Bowmaker _et al_. (1978) demonstrate that the Zambezi River system is likely to have derived its fish fauna from at least two sources. The fishes of the Upper Zambezi are similar in composition to the tributaries of the Kasai-Zaïre system. The respective Zaïre tributaries are considered to have been the major sources of the respective divisions of the Zambezi fauna. Bell-Cross (1975) suggests that a possible route of invasion of the Middle and Lower Zambezi from the Lualaba may have been via Lake Tanganyika to the East Coast and thence southward to the Zambezi. Bowmaker _et al_. (1978) propose a more direct alternative route via a "Proto-Luangwa" River although the connections between the Zambezi and the Zaïre System are not disputed.

The most detailed and recent zoogeographical synthesis on southern African freshwater fishes is given by Bowmaker _et al_. (1978). These authors consider the many factors both ecological and historical which explain the patterns of distribution of the fauna. In essence they accept a Gondwana origin for the cichlids, characins and siluroids, as well as the galaxiids. The cyprinids are suggested to have colonized Africa from Asia although other shared genera between these continents do not, in their view, simplify the thesis and the possibility of a complex exchange via north-east Africa and the Middle East is entertained.

Apart from _Galaxias_, Bowmaker _et al_. (1978) consider that the primary freshwater fishes of southern Africa colonized the subcontinent in a series of faunal invasions along the lines proposed by Gaigher & Pott (1973). The "endemic" fauna is restricted to the region south of but including the Limpopo-Orange drainage. Endemicity is confined not only to species but includes phyletically interrelated species groups e.g. the redfins, the two _Sandelia_ species and the large parallel striated scaled _Barbus_ species. A distinct gap or disjunction occurs between these groups and groups considered to be their nearest relatives in tropical Africa. For this reason these species are considered the earliest post-Gondwana invaders of the sub-continent, and their time of arrival was placed in the mid-Pliocene.

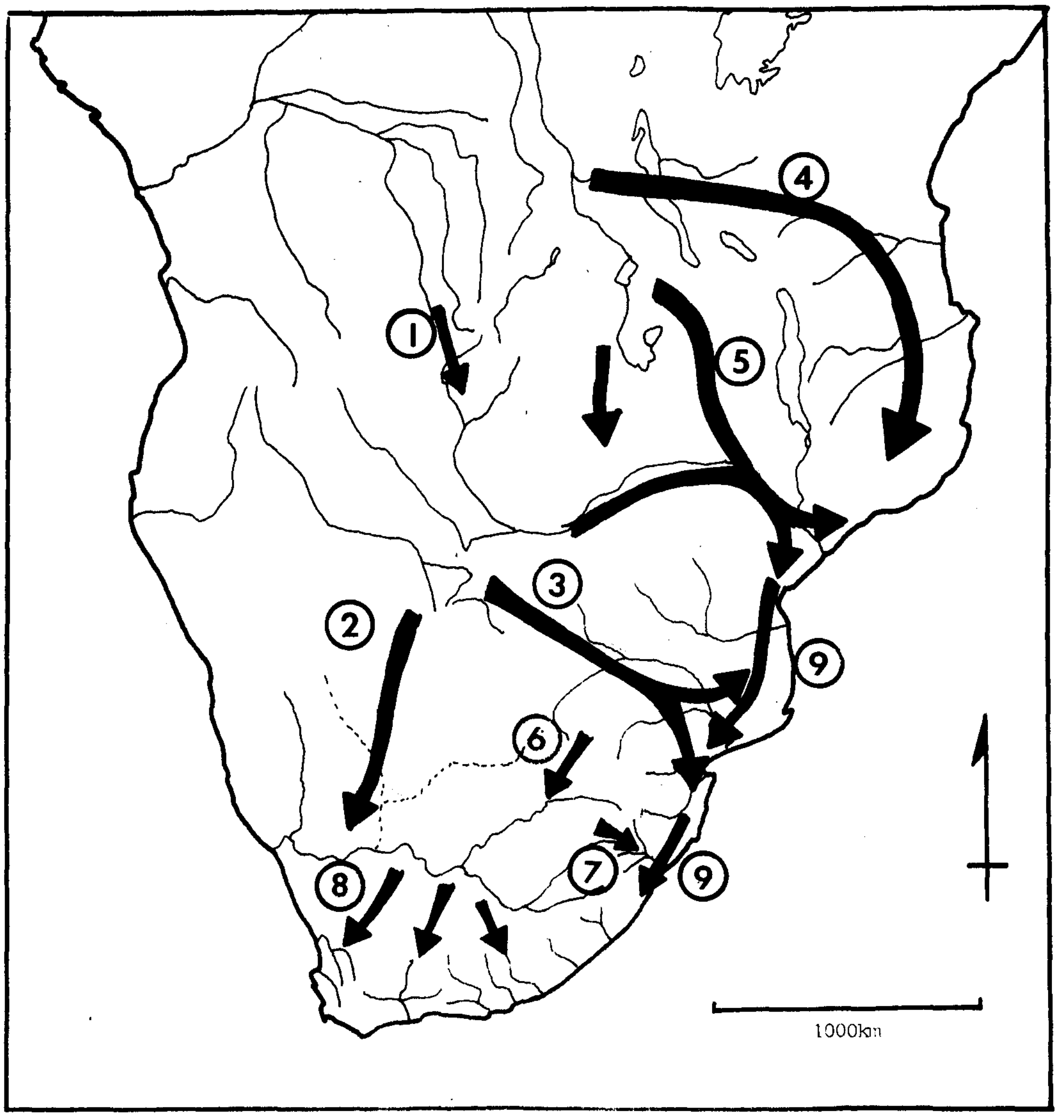


Fig. 6.1 Current explanation of historical biogeography of freshwater fishes in southern Africa as based on a theory of "invasions". after Bowmaker et al. (1978). 1. Zaïre-Upper Zambezi, Zaïre-Kafue interchange, 2. Mid-Pliocene invasion of Orange from Upper Zambezi region. 3. Upper Zambezi-Okavango to Limpopo link (late Pliocene). 4. Invasion from Zaïre via Malagarassi River and the east coast. 5. Zaïre-Luangwa-Middle Zambezi-east coast invasion route. 6. Faunal interchange between Limpopo River and Orange River systems by river capture. 7. Interchange between Limpopo and south-east coastal rivers by river-capture. 8. Invasion of south-coastal rivers from Orange River system by river-capture. 9. East coastal invasion from tropic regions.

A late-Pliocene invasion is suggested to explain a distinct Upper Zambezi-Limpopo faunal connection and all subsequent colonisations are considered to have occurred during the Pleistocene. A summary of these invasions is given in Figure 6.1.

Based on current knowledge fish distribution in southern Africa has received reasonable explanation. There are nevertheless a number of outstanding problems such as the isolated distribution of certain species and the large disjunctions between related groups which have not received adequate explanation (e.g. the nearest known relatives of *Gephyroglanis* species from the Orange and Olifants Rivers are found in the Zaïre River). In addition many of the explanations are based on relationships which are established purely on grounds of general similarity and are therefore not always expected to be valid. Many of the problems concern the older endemic fauna which have vague interrelationships and isolated distributions. The current explanations (except in the case of *Galaxias*) are based on the assumption of a central African centre of origin and subsequent southward dispersal into southern Africa. Alternative theories based on vicariance have not been generally entertained.

DISTRIBUTION OF REDFIN SPECIES

The distribution of the redfin species based on recorded localities (Appendix 1) is given in Figures 6.2-6.4. The distribution of each species may be summarized as follows:

B.calidus (Fig. 6.2)	Cedarberg tributaries of the Olifants River system excluding the Twee River.
B.erubescens (Fig. 6.2)	Twee River of the Olifants River system, above a barrier waterfall 15 m high.
P.afer (Fig. 6.3)	Coastal rivers to the east of the Gourits River system up to the Sundays River system. No records are available for rivers between the Little Brak River and the Karatara River, but there appears to be no reason why the species should not be present there. Also there are no records from the smaller rivers of the Tsitsikamma coastal plain (i.e. those which have not deeply dissected the plain) or the Van Stadens River to the east of the Gamtoos River system.

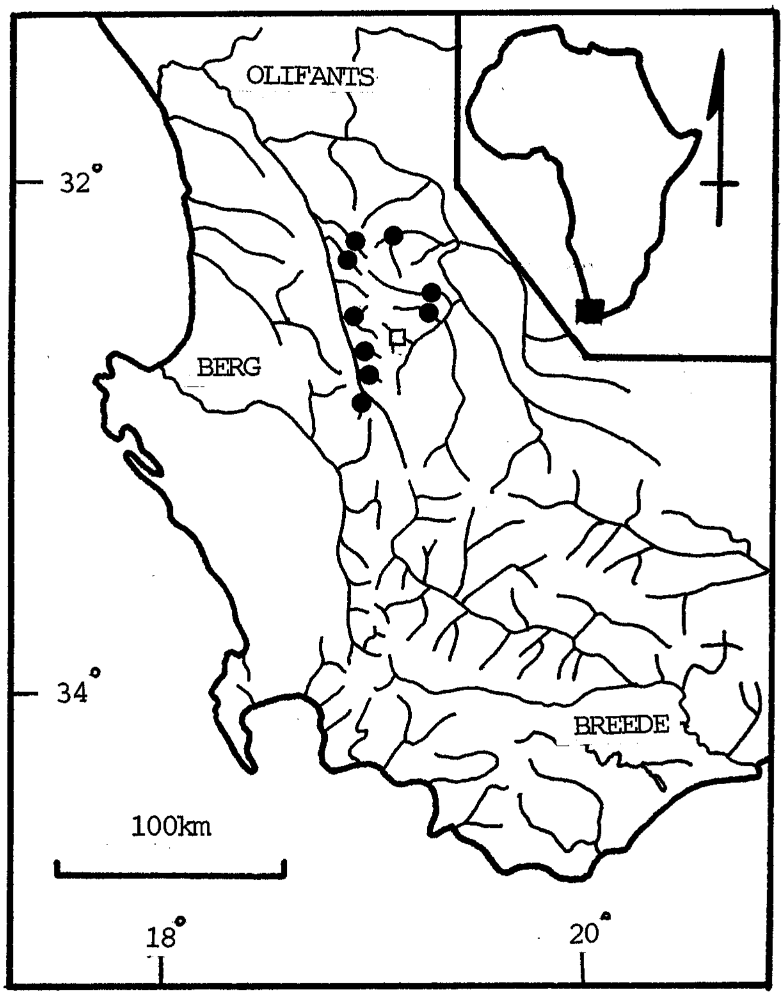


Fig. 6.2 Distribution of B. calidus and B. erubescens in the Olifants River system based on Museum records (Appendix 1). Each site may include several collection records. (● - B. calidus, □ - B. erubescens.

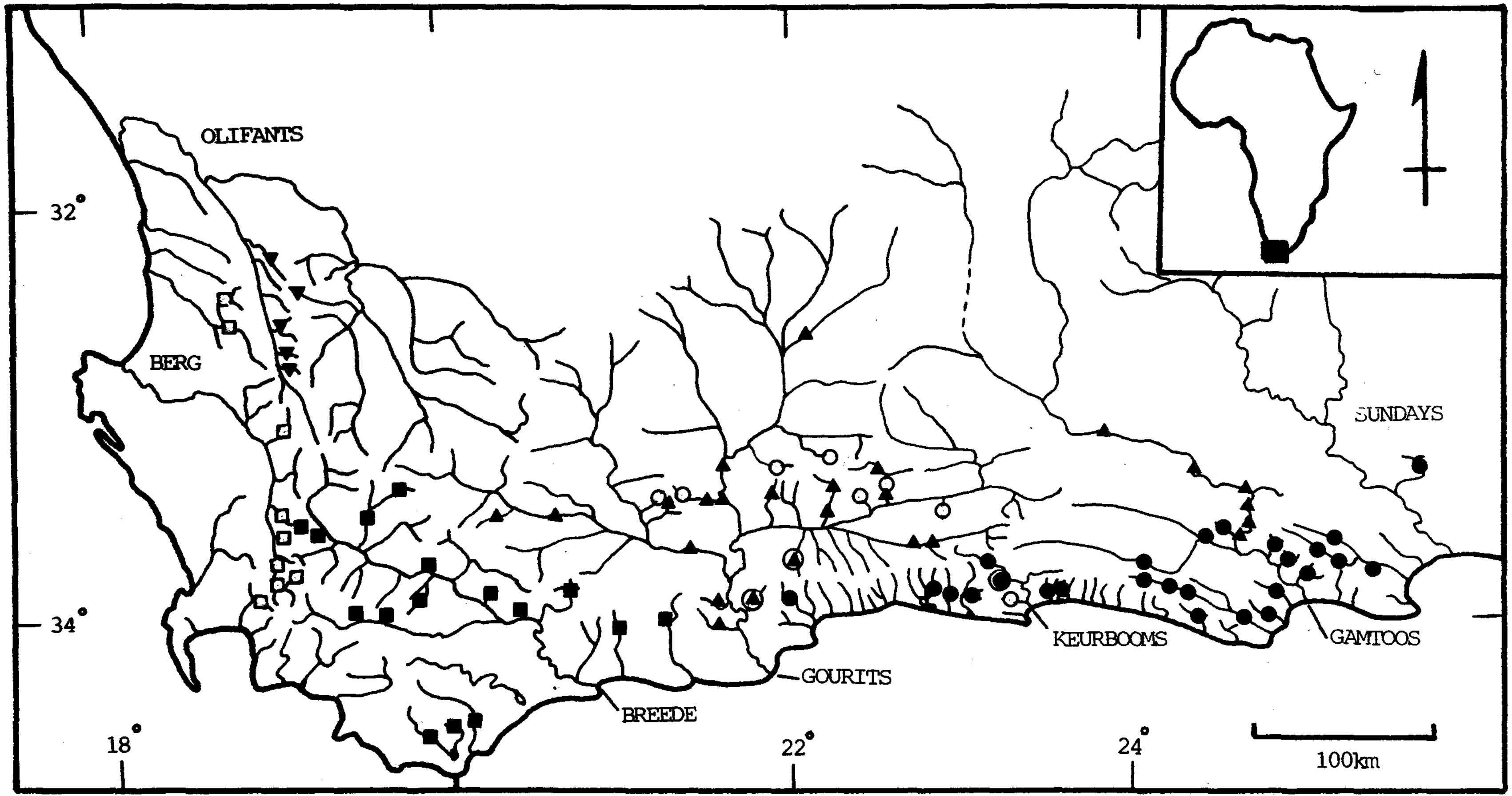
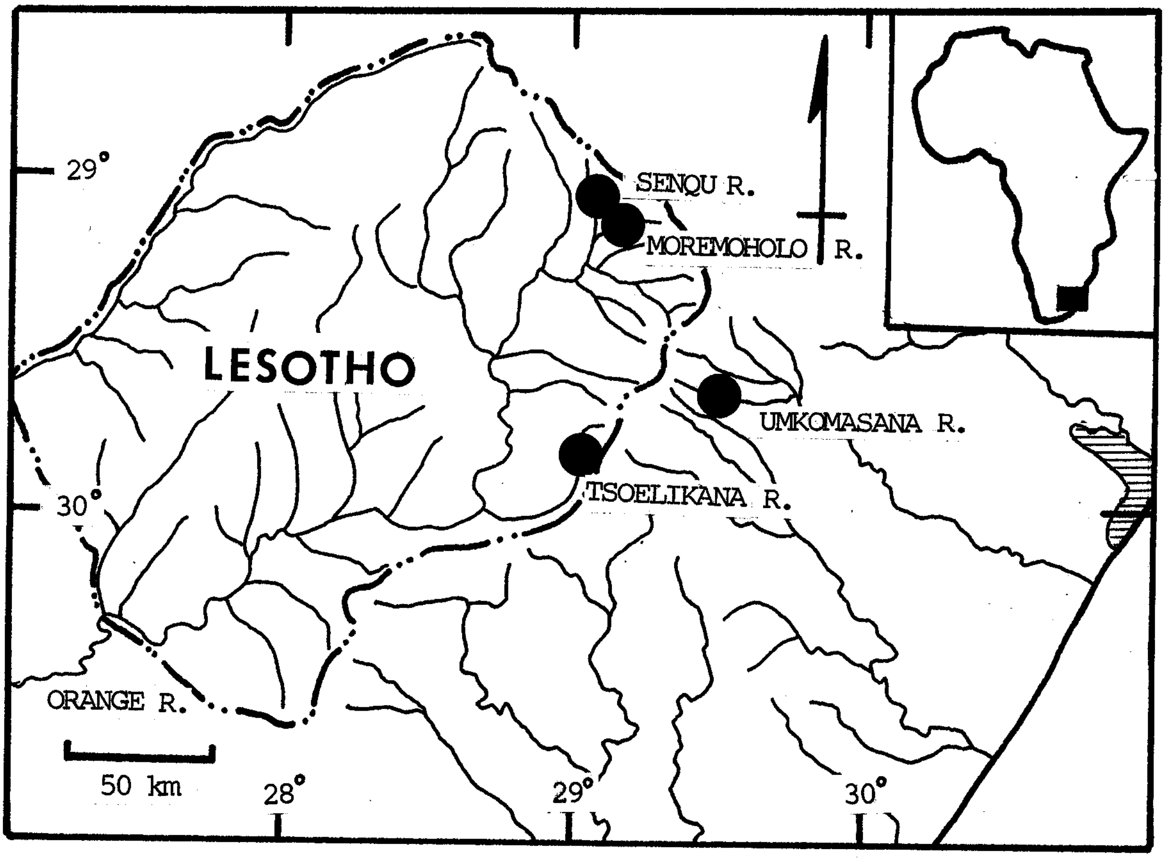


Fig. 6. 3 Distribution of *Pseudobarbus* species in the south coastal drainage basin based on Museum records (Appendix 1). Each site may include several collection records. □ - *P.burgi*; ▼ - *P.phlegethon*; ■ - *P.burchelli*; ▲ - *P.asper*; ○ - *P.tenuis*; ● - *P.afer*.


SENQU R.
MOREMOHOLO R.
LESOTHO
UMKOMASANA R.
TSOELIKANA R.
ORANGE R.
50 km
29°
30°
28°
29°
30°

P.asper (Fig. 6.3)	Tributaries of the Gourits River system and the Groot River Gamtoos system to within the Groot River gorge.
P.burchelli (Fig. 6.3)	Tributaries of the Breede River system as well as the Kaffirkuils River and Duivenhoks River to the east and the Kars, Sout and Nieuwejaars Rivers to the west.
P.burgi (Fig. 6.3)	Tributaries of the Berg River system, the Verlorevlei River to the north and, in former times, the Eerste River to the south.
P.phlegethon (Fig. 6.3)	Tributaries of the Olifants River within the Clanwilliam Valley, also the Driehoek River in the Cedarberg.
P.quathlambae (Fig.6.4)	Known from three tributaries of the Orange River in the Drakensberg mountains (Rondorf, 1976). The type locality is recorded as the Umkomazana River in Natal but the species is believed to be extinct there at present. Natal Parks Board officials suggest the type locality is recorded in error (Geddes-Page, 1977; Crass, in litt. 4/08/77). The evidence is equivocal and in the absence of proof to the contrary the Umkomazana River is accepted as the valid type locality.
P.tenuis	Mountain tributaries of the Gourits River system and the Keurbooms River system.

AN EXPLANATION OF REDFIN DISTRIBUTION

Freshwater fish distribution in southern Africa has until now usually been explained in terms of these organisms without comparison with the distribution of other organisms in the sub-continent. The explanation which has been given to the redfin species is simple - they are derived from a mid-Pliocene invasion via the Orange River from more northern sources.

The case for considering general patterns of distribution in the interpretation of animal and plant distributions has been most forcefully presented by Croizat *et al.* (1974). In this attempt to explain the distribution of the redfins a less formal but nevertheless similar approach will be taken. There are fortunately several fairly recent studies on various southern African faunal and floral groups which provide reasonable distribution maps and biogeographic accounts of the particular organisms concerned. This has facilitated the search for generalised distribution patterns and comparative distributions have been gleaned entirely from the literature.

The explanation which follows is divided into sections starting with a brief comparison of other pertinent freshwater fish distributions in southern Africa. This is followed by a consideration of the distribution of certain other organisms which suggest that the redfins might belong to a generalised distribution track. A brief account of certain palaeogeographical factors in the history of the region is then given, and finally an interpretation of redfin biogeography is provided.

Comparative distribution of primary freshwater fishes in the south coastal drainage

The following primary freshwater fishes (excluding redfins) occur naturally in the south coastal drainage: *Galaxias zebratus*, *Barbus capensis capensis*, *Barbus serra*, *Barbus andrewi*, *Barbus anoplus*, *Barbus pallidus*, *Barbus trevelyani*, *Labeo seeberi*, *Labeo umbratus*, *Gephyroglanis gilli*, *Sandelia capensis* and *Sandelia bainsii*. With the exception of *B.trevelyani* and *S.bainsii* all these species are coincident to a greater or lesser extent with redfin species.

B.capensis, *B.serra*, *L.seeberi*, *G.gilli* occur only in the Olifants River system. *B.capensis*, *L.seeberi* and *G.gilli* have close relatives in the Orange River system (*B.holubi*, *B.kimberleyensis*, *L.umbratus*, *L.capensis* *G.sclateri* respectively). *B.serra* is related to *B.andrewi* from the Berg and Breede River systems (Fig. 6.6).

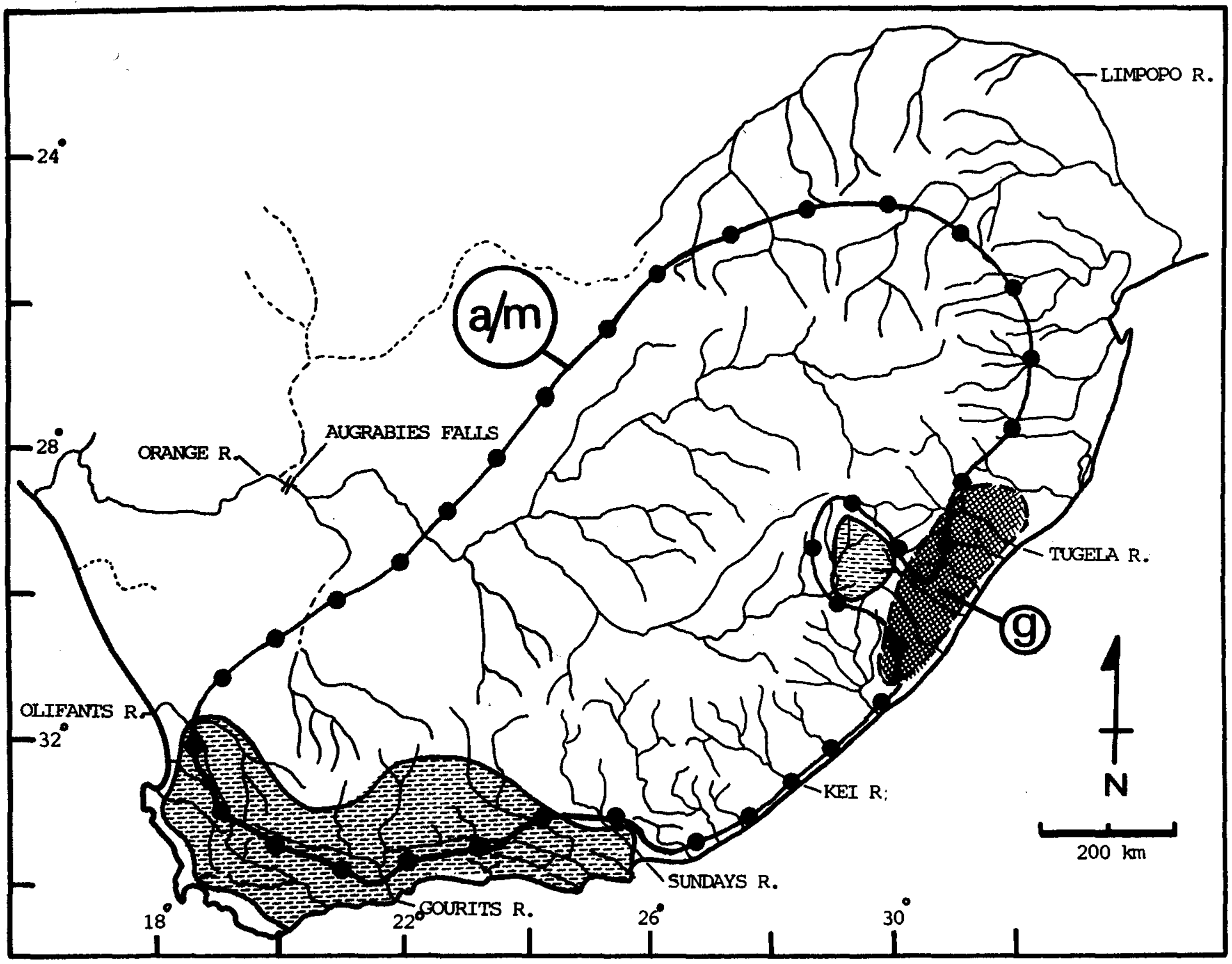


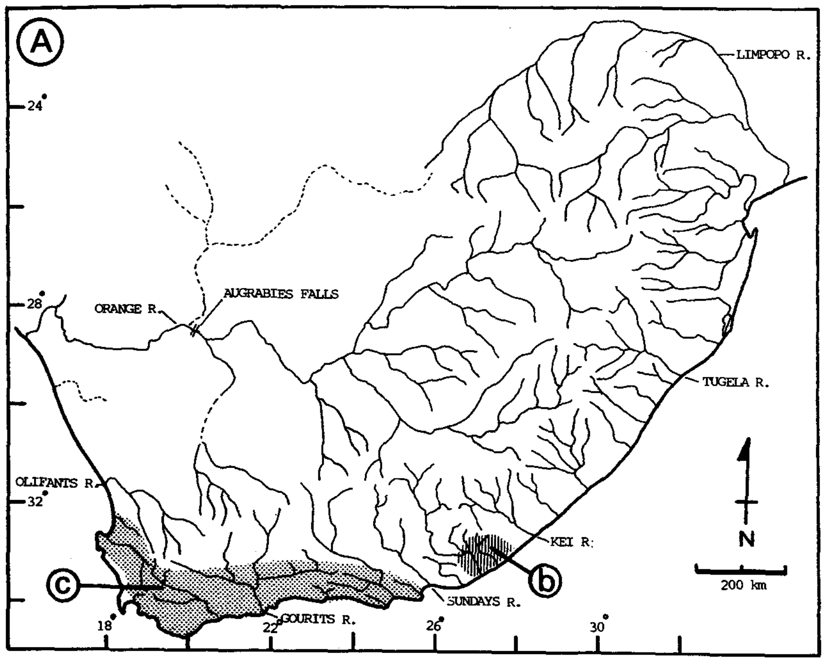
Fig. 6.5 The range of distribution of Pseudobarbus species (horizontal dashes), B.anoplus and B.motebensis (A/M, range bounded by chained line), B.gurneyi (g, crosshatching).

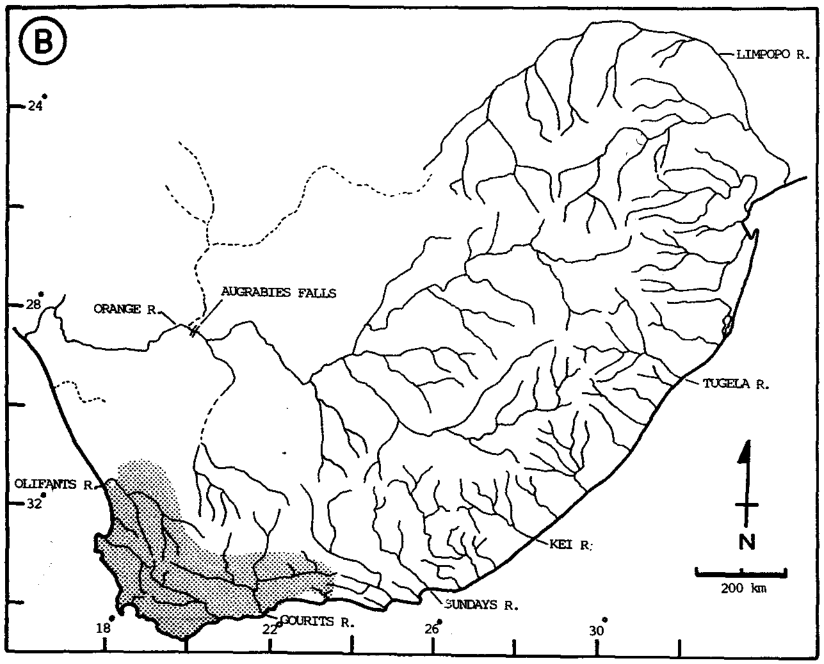
Gephyroglanis gilli is the most southern naturally distributed catfish species in Africa. Since *G.gilli* and *G.sclateri* share the apomorphic loss of the interhyal (Petrick, 1973) they are probably sister species. Their generic status is open to question (Roberts, 1975) but it is still remarkable that they appear to have no obvious relatives in the Limpopo, Okavango, Zambezi or Cunene Rivers.

Only two species, *B.anoplus* and *Labeo umbratus* are not endemic to the south coastal drainage. Both of these occur only in those south coastal rivers with tributaries extending beyond the fold mountain belt to the Great Escarpment. *Barbus anoplus* is the single most widespread species south of the Limpopo River system (Fig. 6.5). The extent of its distribution is all the more remarkable when considered together with its probable relatives, the *Pseudobarbus* group, *B.motebensis* and *B.gurneyi* (Fig. 6.5). Because of the relationship of these species with the *Pseudobarbus* species details of their distribution are given below.

Barbus anoplus occurs in the Orange-Vaal River system and also in certain south and south eastern coastal rivers - the Clanwilliam Olifants (the only non-endemic species in that system); the Gourits River system (its type locality); the Gamtoos system (recently discovered in a tributary of the Groot River - Albany Museum records); the Sundays River system and coastal rivers to the east of this as far north as the Umtamvuma River in Natal (Fig. 6.5). It is also found in the Illovo, Umgeni, northern tributaries of the Tugela, the Umfolozi and Pongolo Rivers in Natal (Crass 1964, 1966); the Incomati River system and certain tributaries of the Limpopo River system (Gaigher 1969, 1976; Gaigher & Pott, 1972). In the Orange River system *B.anoplus* does not occur below Aughrabies Falls nor in the high altitude tributaries in Lesotho (Jubb, 1967). In lower latitudes i.e. in Natal and the Transvaal the species is restricted to higher altitudes (above 915 m), but in the Cape, especially in the southern and eastern Cape the species occurs at lower altitudes (below 500 m, Gaigher 1973, 1976; Crass, 1964). An isolated population occurs in the Kuiseb River (South West Africa, Gaigher, 1976).

In contrast to the widespread distribution of *B.anoplus*, *B.motebensis* only occurs in southern tributaries of the Limpopo River system (Jubb 1967, 1968; Gaigher 1973, 1976).





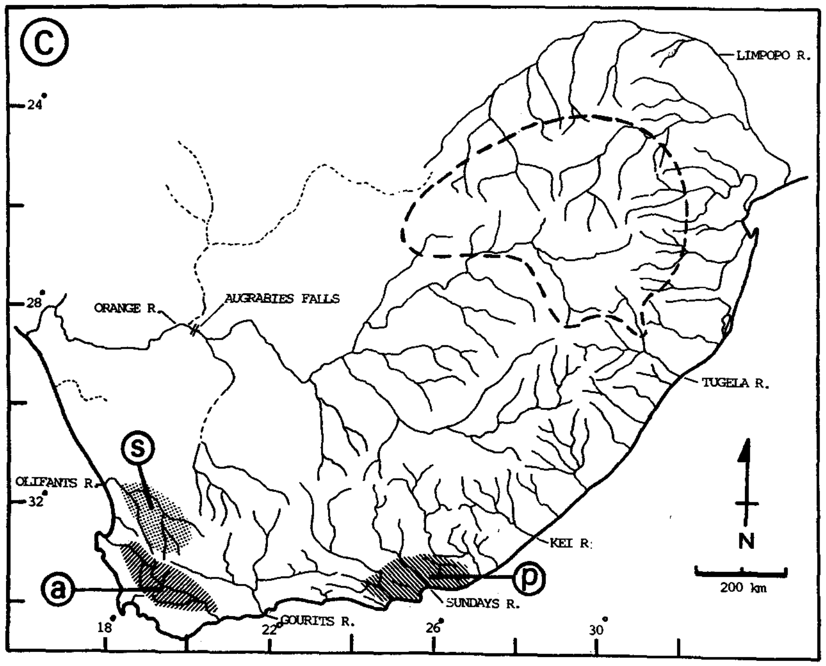


Fig. 6.6 Range of distribution of (A) Sandelia capensis (c, dotted region) and S.bainsii (b, vertical lines); (B) Galaxias zebratus; (C) B.serra (s, dotted region); B.andrewi (a, right slanted lines); B.pallidus (p., left slanted lines and also region bounded by a dashed line in the Transvaal and Natal).

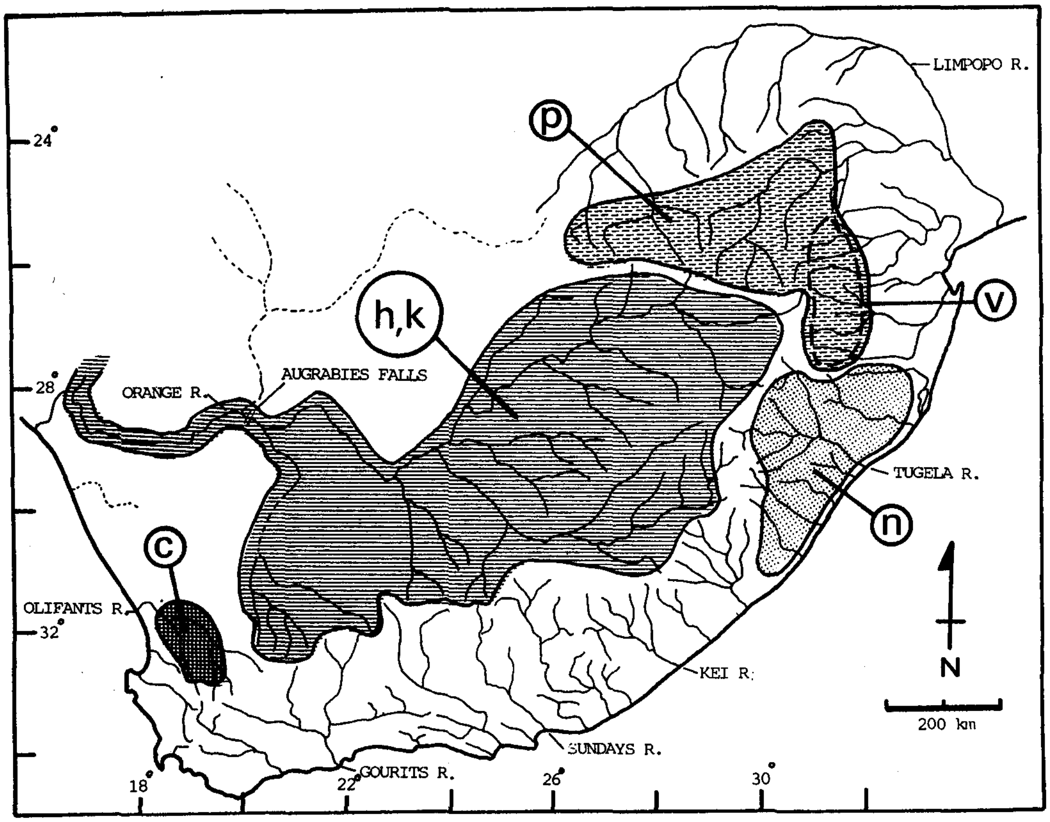


Fig. 6.7 Range of distribution of certain large Barbus species with parallel striated scales: Barbus capensis (c, crosshatching); B.holubi and B.kimberleyensis (h, k, horizontal lines); B.polylepis (p, horizontal dashes); B.natalensis (n, dots); Varicorhinus nelspruitensis (v, dashed line within B.polylepis range).

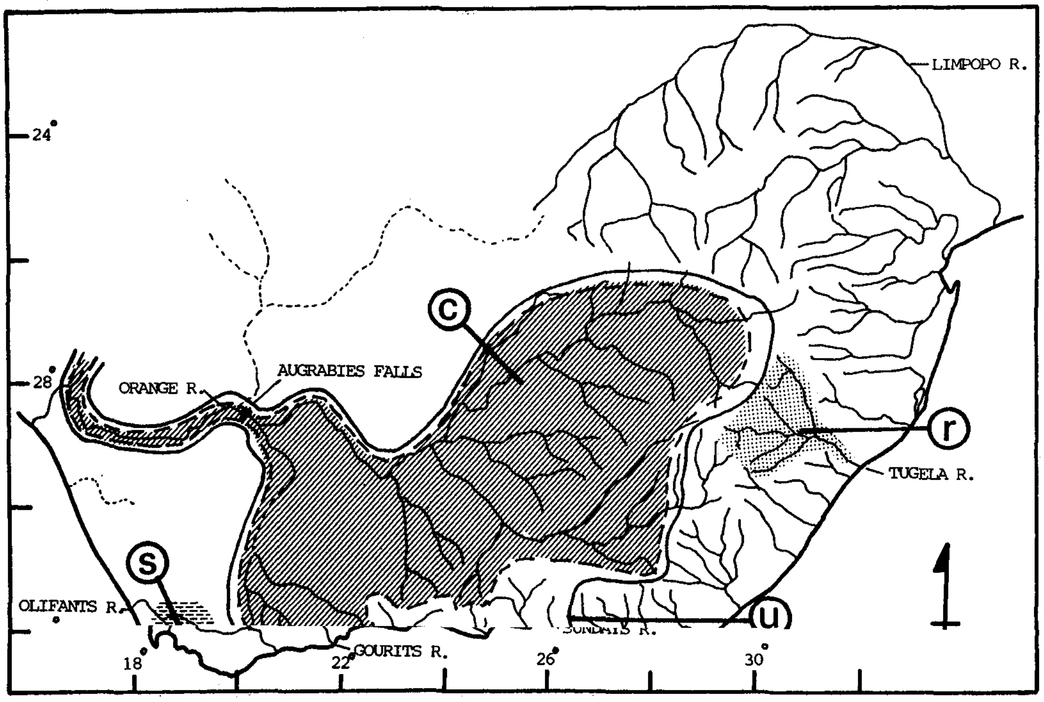


Fig. 6.8 Range of distribution of certain Labeo species in southern Africa: Labeo seeberi (s, horizontal dashes); L.capensis (c, right slanted lines); L.umbratus (u, within unbroken line); L.rubropunctatus (r, dots).

Barbus gurneyi has a localized distribution in Natal from the Umtamvuma River in the south to the Umhlatuzi River (Lake St Lucia System) in the north (Crass, 1964, 1966). Crass (1964) records that the species is particularly common up to an altitude of 1 150 m.

The small *Barbus pallidus* has an interesting distribution in the eastern part of the Cape fold belt from the Gamtoos River in the west through to the Kowie River in the east (Fig. 6.6). The Kowie River drains hills of Witteberg group formations and represent the easternmost outcrops of the Cape Supergroup. Elsewhere *B.pallidus* is found in northern tributaries of the Vaal River, as well as the Limpopo, Pongolo and Tugela River systems (Crass, 1964; Gaigher & Pott, 1972).

Labeo umbratus is a widespread species in the Orange River system and in south coastal rivers including the Gourits, Gamtoos, Sundays, Bushmans, Great Fish, Keiskamma and Buffalo Rivers (Fig. 6.8). The distribution pattern of the endemic *Labeo* species (Fig. 6.8) is similar to that of the large yellowfish (large *Barbus* with parallel striated scales) (Fig. 6.7).

Galaxias zebratus is widespread in all the rivers between the Olifants in the west and the Kaaimans River in the east (Fig. 6.6). It has also been found in the Keurbooms River system which is separated by several rivers from the Kaaimans. Barnard (1943) and Rosen (1975) consider this species to be a Gondwana relict whereas McDowell (1973) suggests it has reached Africa via oceanic dispersal.

The anabantid genus *Sandelia* is conspicuous by its absence from the Olifants River system (Fig. 6.6). There are also no relatives in the Orange River system. There are only two species. *S.capensis* has a widespread distribution from the Coega River to the east of the Swartkops along the coastal rivers until the Verlorevlei River situated to the north of the Berg River. It is absent from rivers on the Cape Peninsula except the streams on the north-east side (Liesbeek and Diep Rivers, Barnard, 1943). *Sandelia bainsii* is separated from the range of *S.capensis* by a gap and is found in rivers to the east of the fold belt region i.e. from the Kowie River to the Buffalo and Nahoon Rivers near East London. The distribution of this species is to a large extent coincident with that of *B.trevelyani* (given in Fig. 6.11).

There appear to be several different patterns evident from these distributions. No single group extends over the complete range of the *Pseudobarbus* species. *P.quathlambae* in the Drakensberg is an exceptional isolate of any south coastal species or species group. The distribution of *Sandelia capensis* is the nearest approach to the distribution of *Pseudobarbus* in the south coastal drainage but the absence of the species from the Olifants River system is certainly problematical. After *S.capensis* the distribution of *Galaxias zebratus* approaches that of *Pseudobarbus*. The occurrence of this species in the Keurbooms River system is remarkably coincident with the presence of *P.tenuis*. It suggests that there has been at least one common episode in the biogeographic history of the two species.

B.anoplus and *Labeo umbratus* have an extremely similar pattern of distribution in the fold belt region. They are the only two species found in only the larger rivers draining from the Great Escarpment. As pointed out by Jubb (1964) and Jubb & Farquharson (1965) the most logical explanation for this is that their distribution is derived by way of headwater exchange with southern tributaries of the Orange River.

Other recognisable patterns of distribution are all associated with the Olifants River system. The distribution of *B.andrewi* and *B.serra* is unusual among these patterns as the track extends from the Olifants to south-coastal rivers (Berg and Breede) and not to the Orange River as in the case of the majority of Olifants River species. The distributions of *B.capensis*, *B.anoplus*, *Labeo seeberi*, *Gephyroglanis gilli* in the Olifants and related species in the Orange clearly points to a generalized track which is only partially coincident with the *Pseudobarbus* track. If the relationships of *B.calidus* and *B.erubescens* lie with *B.hospes* from the Lower Orange River it could be coincident with the Olifants-Orange generalized track. There is also a link in the *Pseudobarbus* distribution track between the Olifants River (*P.phlegethon*) and the Orange (*P.quathlambae*).

The case for a generalized track

It is evident from several literature sources that the distribution of the redfin species is coincident with a distinctive pattern of distribution of other organisms. The following comparisons are

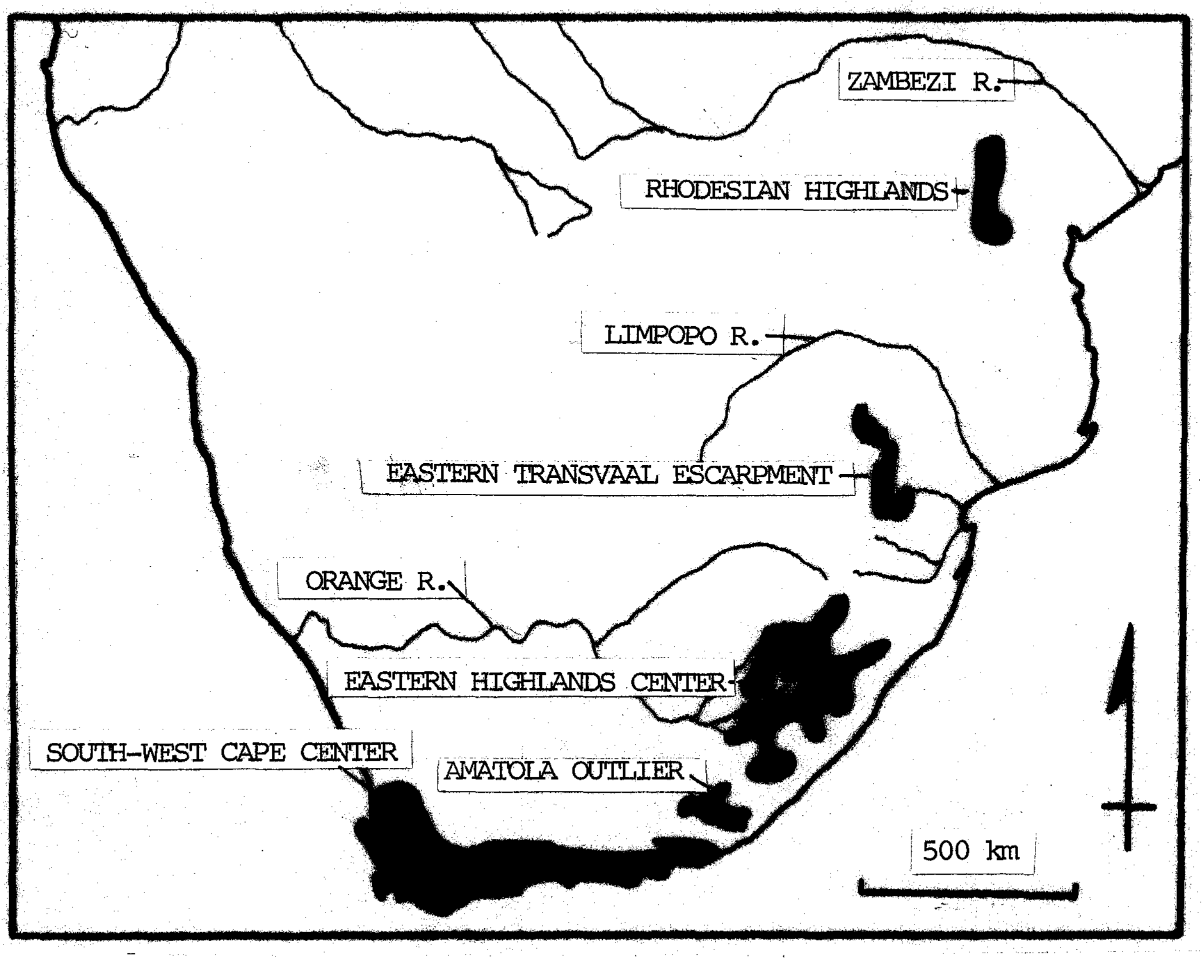


Fig. 6.9 The montane palaeogenic invertebrate distribution track in southern Africa. After Stuckenberg (1962).

considered bearing in mind that they may not be valid in every case because relationships and classification of the organisms has not necessarily been established according to Hennigian methods. Distributions may or may not be accurate but I am not in a position to comment on this.

The clearest evidence of a generalized distribution track involving the *Pseudobarbus* species comes from the work of Stuckenberg (1962). Stuckenberg (*op.cit.*) compared the known distribution of diverse palaeogenic invertebrate groups in southern Africa. He found that there was a remarkable pattern (shown in Fig. 6.9) which includes the southern and south-west Cape region within the fold mountain belts, an eastern outlier around the Amatola mountains, an eastern highlands centre concentrated on the Drakensberg mountains, an eastern Transvaal escarpment centre and to a lesser extent a centre in the eastern highlands of Zimbabwe-Rhodesia.

The taxa studied by Stuckenberg (1962) included several dipteran genera and families, the coleopteran genus *Colophon*, several megalopteran genera and two onychophoran. Bowden (1978) mentions that species of Chironomidae may be added to the list. There are many coleopteran species endemic to the Cape fold belt region, and Endrödy-Younga (1978) described a pattern within this region (including an eastern extension line) which agrees with the distribution pattern described by Stuckenberg (1962).

Harrison & Agnew (1962) describe a distinctive invertebrate fauna associated with the acid streams of the fold mountains. Later Harrison (1965) divided the riverine invertebrates in southern Africa into two groups, an "old element" distributed more or less according to Stuckenberg's (1962) pattern and a comparatively recent group more tolerant of higher temperatures. The second group included a pan-Ethiopian element of which a few stenothermal montane species were also distributed in the Cape fold belt-eastern highlands distribution pattern.

A number of vertebrate groups, particularly the amphibians and reptiles, follow the Cape fold belt-eastern highlands distribution pattern (FitzSimons, 1962; Poynton, 1964; Greig & Burdett, 1976; Poynton & Broadley, 1978). Amphibian taxa include species of *Xenopus*, *Bufo*, *Breviceps*, *Cacosternum*, *Arthroleptella*, *Hyperolius* and *Heleophryne*. Reptile taxa include *Psammobates geometricus* and *Homopus areolatus*,

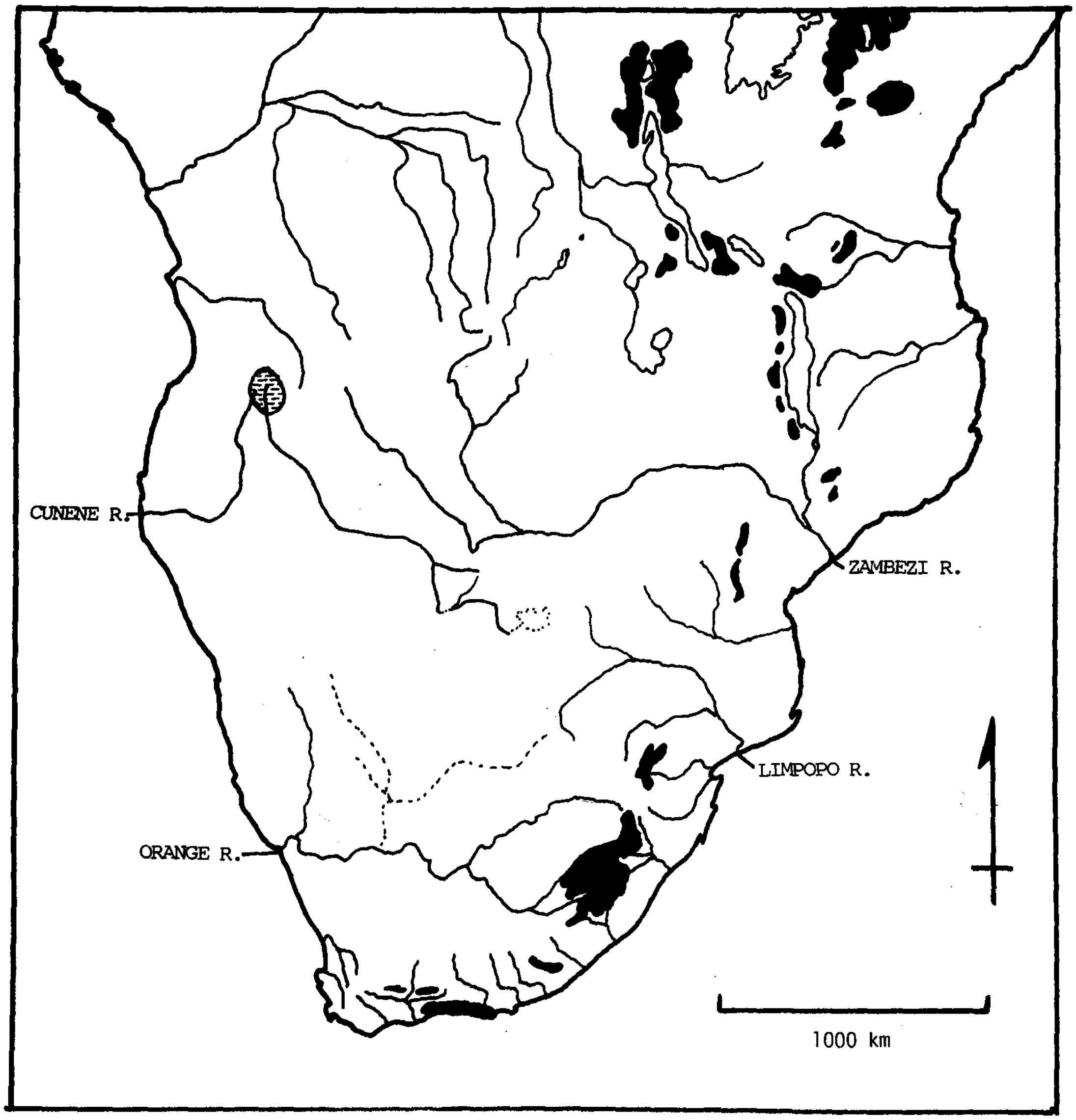


Fig. 6.10 Distribution of Afro-montane vegetation in Africa south of the equator showing an archipelago type of pattern. After White (1978).

Lamphrophis species, *Typhlops* and *Leptotyphlops* species, *Lycodonomorphus*, *Duberria lutrix*, *Psammophylax* species, *Elaps lacteus* and *Hemachatus haemachatus*.

A small endemic "Cape" avifauna also coincides with this pattern and includes the following species: *Promerops cafer*, *P.gurneyi*, *Nectarinea violacea*, *Bradypterus victorini*, *Serinus tottus*, *S.leucopterus*, *Pycnonotus capensis* and *Chaetops frenatus* (Roberts, 1978; Winterbottom, 1978).

There are mammal species too which fall within this distribution track. Included here are *Crocidura flavescens* (Meester, 1962); *Tatera afra* *Praemys verrauxi*, *Acomys subspinosus* (Davis, 1962). Other endemic mammals to the southern or south-western Cape are the Cape dune-molerat (*Bathyergus suillus*), the extinct Bloubok (*Hippotragus leucophaeus*) and the Bontebok (*Damaliscus dorcas dorcas*) (Bigalke, 1978).

The concept of a Cape fold belt-eastern highlands distribution pattern is further strengthened by including plant distribution. Three vegetation types occur in the fold belt region (Acocks, 1975), the Capensis flora (Taylor, 1978), the Karroo vegetation (Werger, 1978) and a montane forest vegetation (White, 1978). The Karroo vegetation represents interdigitated intrusions of the more widespread Karroo vegetation to the north of the fold belt region and occurs mainly in the lower altitude rainshadow regions of the fold belt. The Capensis flora is renowned for the abundance of species of predominantly three kinds, restioid, ericoid and proteoid (Taylor, 1978). Many members of this Capensis flora show a characteristic distribution pattern in Africa mainly on mountains. In southern Africa this pattern conforms with the centres in Stuckenberg's (1962) palaeoendemic distribution track (Wild, 1968; Taylor, 1978). The distribution of Afromontane vegetation "conforms" in a similar way to this distribution track, and White (1978) refers to the pattern as the Afromontane archipelago (Fig. 6.10).

Palaeogeology and Palaeogeography

The separation of the African plate during the Jurassic and early Cretaceous involved the rifting off of Antarctica and South America and later Madagascar and India. At the beginning of this rifting Africa was situated approximately 30° further south than it is at the present time (Owen, 1976). Following the break up of Gondwanaland Africa drifted gradually northward to reach the present latitudes at which it was found by the late Oligocene (Axelrod & Raven, 1978).

As a result of recent researches on southern African geomorphology established theories are being questioned and the science is in a state of flux. King (1963) provides a universal scheme of landscape genesis which is summarized again in King (1978). This model has however proved unsatisfactory and has been rejected in recent years. Corbett (1979) critically reviews the various theories and provides alternative explanations. Truswell (1977) gives a recent account of the geological evolution of South Africa.

King's model is based on a series of cycles of uplift and denudation which are identified with reference to various land surfaces. The earliest of these is the Gondwana cycle which, it is claimed, is still present as relic patches in the Drakensberg mountains and also the Windhoek and Benguela highlands in South West Africa. The second land surface represents a remnant of the post-Gondwana or early Cretaceous denudation cycle and is also found in Lesotho in high altitude situations as well as at a few isolated localities elsewhere in southern Africa. There followed a long period of tectonic quiescence until Miocene times which resulted in the formation of the great African plateau, essentially the open savannah plains of Africa. During the early Miocene there were widespread regions of uplift initiating a further erosion cycle. This lasted until Pliocene times when there was a further period of uplift, rejuvenating rivers and forming large basins by scarp retreat. By end-Tertiary times the geomorphological aspect of southern Africa was to a large extent similar to what it is at present. At the beginning of the Quaternary period tectonic upheavals raised interior plateaus and disrupted drainage patterns. Rivers were again rejuvenated so that large, steep gorges were incised by several e.g. Victoria Falls, Ruacana on the Cunene and Aughrabies on the Orange.

An alternative theory has been proposed by De Swardt & Bennett (1974) and developed further by Corbett (1979). De Swardt & Bennett propose that if Gondwanaland broke up as a result of rifting this would possibly occur initially in analogous fashion to the East African rift system. Crustal upwarping results in subsidence of the "graben" floor which results in a gentle slope of the land surface away from the rift shoulders and a steeper slope towards the graben. Thus soon after Gondwana break-up the southern African continental margin had an elevated rift shoulder with gentle interior, and steep coastal slopes. The coastal erosion cycle initiated as a result of this would be more active and retreat from the coast, capturing more and more of the inland drainage. By continued retreat the scarp has migrated to its present position - the great escarpment.

The inland drainage system which developed at the time of the Gondwana break-up had headwaters on the landward side of the gently sloping rift shoulders. The major rivers of Africa pass through relatively narrow gaps in the great escarpment. De Swardt & Bennett (1974) suggest they only became major rivers as a result of selected capture by headward erosion of coastal rivers through the great escarpment.

Corbett (1979) concludes that there are three erosion cycles operating in southern Africa. The first two represent the coastal and inland drainages initiated at the time of Gondwana break-up with the inland cycle initially operating to a higher base level than the coastal cycle. The subsequent capture of inland drainage by headward incision of coastal rivers gave the inland drainage a new base-level (the sea). Corbett (op.cit.) suggests that the rivers which have captured inland drainage did so due to an advantage they gained from relief which existed in certain areas and also to their drainage of structurally weak zones developed during the break-up of Gondwanaland.

The third erosional cycle was caused by a major eustatic drop in sea-level during Plio-Pleistocene times. Corbett (op.cit.) attributes the nick points on the major rivers (e.g. Aughrabies Falls, Victoria Falls) as a result of this event.

Drainage evolution in the southern Cape has evidently been complicated by the Cape fold mountains which today occur between the coast and the great escarpment. These appear to be by-passed residuals (Corbett, 1979) and the initial drainage is expected to have been within the strike valleys, i.e. primarily east-west (du Toit, 1926). Later these were transformed into north-south drainages by penetration of the mountains by certain tributaries. The spectacular gorges which divide the mountain chains have long interested geomorphologists and they are variously regarded as either superimposed features (e.g. Rogers, 1903) or subsequent features (Haughton, et al.1937; Lenz, 1957). The general opinion on the age of the rivers of this southern Cape region is that they are ancient, dating back to the initial isolation of the subcontinent (Lenz, 1957). Some of the short coastal rivers have cut deep gorges in the coastal plain which dates from Tertiary times (Toerien, 1976), suggesting that these rivers date at least from that time.

The history of the inland drainages is complex and not well understood. Corbett (1979) suggests the initial post-Gondwana inland drainage operated to a Kalahari basin base level. On account of the direction of drainage lines,the early drainage of the Luangwa, Kafue and Upper Zambezi was possibly toward the Kalahari basin (Wellington, 1954). The initial drainage of inland systems has evidently been altered by the subsequent capture of the inland drainage by coastal systems. The upper Zambezi-Okavango drainage was probably connected in former times to the Limpopo drainage (du Toit, 1926). The Orange and Limpopo Rivers have also been interconnected in historic times (Wellington, 1958). Given that there has been continuous scarp retreat since the break-up of Gondwana (Corbett, 1979) the catchment of the Orange River system must have extended further coastwards in the east, and southwards to the fold belt, in the south (Wellington, 1958). There is evidence that a northern tributary, the Molopo was once a large river and also that the present south-western tributaries of the Limpopo tapped the source of the Molopo drainage.

The present day drainage lines of the Orange River system bear testimony to the complex evolutionary history of the system. The freshwater fish fauna suggest strongly a former interconnection between the Orange and the Olifants River systems. The direction of drainage lines, if extended as in Howell & Boulier (1963) (Fig. 6.13), would meet the Olifants River. This hypothesis suggests that the middle and upper Orange have been captured by the lower Orange. It is interesting to note that the occurrence of alluvial diamonds as far south as the mouth of the Olifants River possibly provides geological support for this connection.

Consideration of palaeoclimate is also an important factor in explaining the present distribution of organisms. van Zinderen Bakker (1976) considers that modern climatic regimes originated in the Tertiary after the circum-Antarctic oceanic current system had developed and Africa had reached more-or-less its present global position (i.e. in the late Oligocene). Palaeoclimate reconstructions are still matters of calculated guess-work but it is generally agreed that there has been much climatic fluctuation, at least in the late Tertiary and the Quaternary (Livingstone, 1975; van Zinderen-Bakker, 1978).

Coetzee (1978) working on pollen zones from cores in western and south-western Cape suggested the following climatological sequence in the region: a tropical climate existed in the early Tertiary (Palaeocene and early Eocene), followed by a steady lowering of temperature to sub-tropical and temperate climes during the Eocene (60-40 MY). During the Oligocene (40-25 MY) the temperature oscillated at these levels; warm, humid climates prevailed in early Miocene followed by intense cooling in mid-Miocene and a reversal to warmer climes during the late Miocene. The Pliocene was colder and drier and Quaternary climates have fluctuated between cooler-wetter climates to warmer and drier climates than at present.

Sea-level fluctuations are of local importance in the distribution of the redfins. Major transgressions occurred during Tertiary times and were instrumental in the formation of the prominent coastal plain at the southern arc of fold mountains (Butzer & Helgren, 1972; Toerien, 1976). During the Pliocene there was a major eustatic drop in sea level (De Swardt & Bennett, 1974; Corbett, 1979). Pleistocene sea level fluctuations are reported by Davies (1971), Dingle & Rogers (1972), Birch *et al.*, (1978), and others.

Discussion and Conclusions

When Stuckenberg (1962) described the distribution track of the montane palaeogenic invertebrates in southern Africa he was careful not to include non-palaeogenic (i.e. post-Gondwana) elements. Balinsky (1962) stated that the "temperate" fauna in southern Africa "is nothing else but the relict of the Gondwana fauna" (p.308).

If the distribution track described for these organisms is restricted to palaeogenic elements it would mean that the redfins, which are cyprinids of post-Gondwana age, are excluded. There is however an overwhelming body of evidence to show that the distribution track which is so clearly described includes both palaeogenic and post-Gondwanoid elements. The present distribution track is therefore clearly derived from a series of former biotas welded together by the geological and geographical history of the region.

The evidence for the above conclusion comes from a number of sources covering several different groups of organisms. The Capensis flora includes both the older Gondwana elements and evidently younger elements (Taylor, 1978; Axelrod & Raven, 1978). Galaxias zebratus is the only likely Gondwana form among the freshwater fishes included in this track. Within the Amphibia the genus Heleophryne (Leptodactylidae) has Gondwanoid distribution. Other amphibian genera involved in a "Cape" pattern of distribution are mainly African. The freshwater invertebrates of this distribution include both palaeogenic and Ethiopian forms (Harrison, 1965), and the Coleoptera include both Gondwana and post-Gondwana stock (Endrödy-Younga, 1978).

Linking the distribution of the redfin species to this generalized track opens an entirely new perspective on their biogeography. Various explanations for the distribution of the other Cape faunal and floral elements have been suggested. Taylor's (1978) view of the evolution and biogeography of the Capensis flora is instructive. The flora then became an old Gondwanoid flora when it was isolated with the rifting of the mega-continent. In the southern half this flora was adapted to temperate conditions as the continent was at least 15^{o} further south than it is at present. With northward drift the warmer and wetter climates encroached further south and eliminated this flora in many areas. The flora then became more and more restricted to the south and higher lying regions where temperate conditions still prevailed. With the cyclic fluctuations of the climate since Miocene times (van Zinderen-Bakker, 1976; Coetzee, 1978) it is envisioned that the flora extended and contracted its range leaving relicts on the cooler and moister higher altitude regions with each retreat. Although the origins of the Capensis flora are possibly ancient this history together with the varied topography in the south west Cape suggests that the characteristically speciose nature of the flora itself may be recent.

The distribution of the Afromontane flora (White, 1978) is also intimately associated with the distribution track suggested by Stuckenberg (1962). The history of this flora has been explained by Wild (1968) in similar terms to the Capensis flora above. Wild suggests the Afromontane flora was continuously distributed in former times but became disrupted on dissection of the landscape and with changing climatic conditions. These former connections probably extend to beyond Quaternary times on account of the fact that climatic fluctuations during this period (Quaternary) were probably not sufficient to allow a bridging of the Limpopo Valley. Wild suggests the connections as being of Palaeocene or Eocene times when the landscape was apparently not extensively dissected. Again the present distribution of the flora is not considered a reflection of extensive plant migrations but rather represents the relicts of a former continuous distribution.

Stuckenberg (1962) regarded the characteristic pattern of distribution of the montane palaeogenic invertebrates as a relict of an ancient distribution. Endrödy-Younga (1978) gives a similar explanation for the distribution of certain beetles as Taylor (1978) did for the Capensis flora, that with the northward drift of the continent the temperate region and its associated fauna became restricted to favourable localities provided by high relief and higher latitudes.

A similar explanation can be given to the distribution of the redfin groups. In the case of these fishes it is necessary to make certain qualifications because their past distribution is as dependant on drainage lines and connections between these drainages as it is today. Thus increasing restriction due to changing climates (whether as a result of northward drift of the continent or global climatic shifts or even more localized changes in climate is immaterial) can only occur if the rivers provide a suitable refuge or have connection with rivers providing refuge.

There is no evidence to suggest that B.calidus or B.erubescens ever had close relatives in any other rivers of the fold belt region other than the Olifants River system. There is little doubt that the other fold belt rivers where Pseudobarbus species occur have provided suitable refuge in which a B.calidus-like ancestor or relative could have survived. It is simpler to suggest that the necessary drainage connections did not exist at the right time in the history of the group.

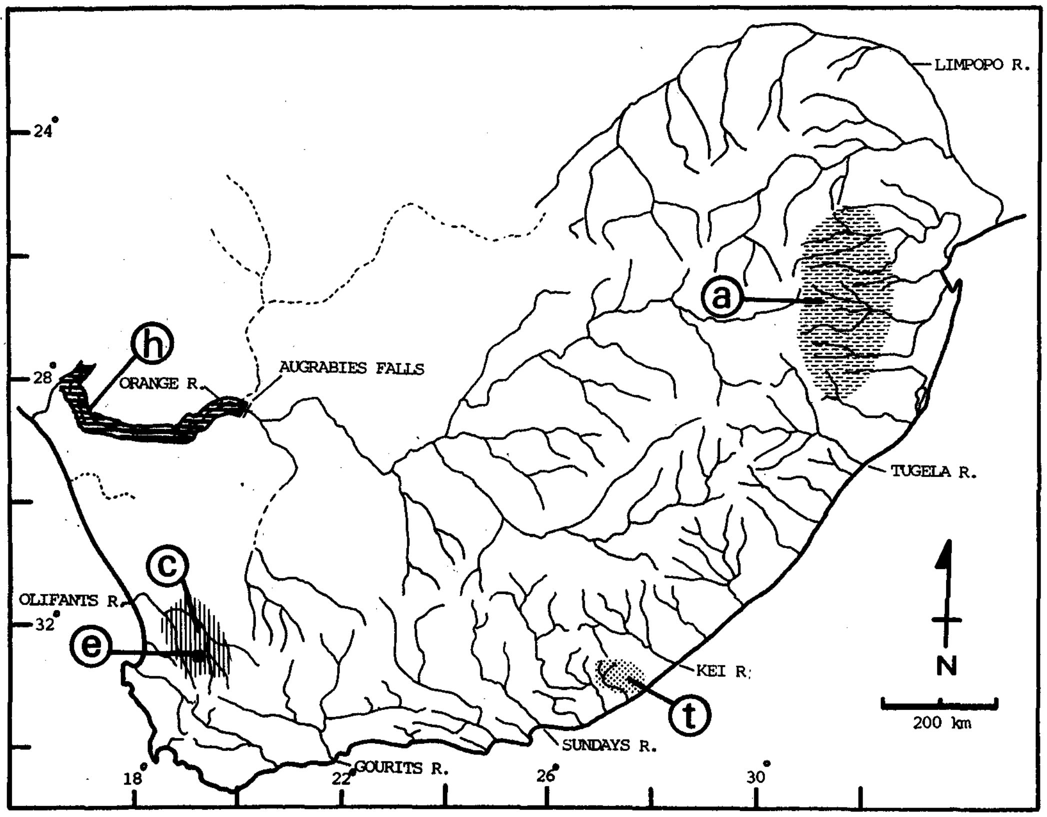


Fig. 6.11 Range of distribution of Barbus calidus (c, vertical lines); B.erubescens (e, black square); B.hospes (heavy horizontal lines); B.trevelyani (t, dots); B.argenteus (a, horizontal dashes); (B.argenteus also occurs in Angolan rivers - Jubb 1967).

In the phylogenetic section it has been stressed that the out-group relationships of *B.calidus* and *B.erubescens* are not yet settled. Nevertheless the most likely candidates for relatives are the species *B.hospes*, *B.trevelyani* and *B.argenteus*. Although there is a danger of circular reasoning it is notable that these species are distributed in a pattern which conforms with the Cape fold belt - African montane archipelago distribution track (Fig. 6.11).

The distribution of *B.trevelyani* and *B.argenteus* conforms acceptably with this track (Fig. 6.11). The Keiskamma and Buffalo Rivers in which *B.trevelyani* is found (Gaigher, 1976) drain the Amatola Mountains. This region was included by Stuckenberg (1962) as an outlier in the palaeogenic invertebrate distribution track. *B.argenteus* is found in the highveld tributaries of the Incomati and Pongolo Rivers (Gaigher & Pott, 1972) which conforms with the Transvaal Drakensberg part of the distribution track. *B.argenteus* also occurs in Angola (Jubb, 1967) and there is a species in Malawi (*B.choloensis*) which is close to *B.argenteus* in form. Both these localities conform to "islands" in the archipelago distribution track where there are Capensis and Afromontane floral elements (Taylor, 1978; White,1978).

Barbus hospes is endemic to the lower Orange River (Fig. 6.11) which at first does not appear connected with the Cape fold belt - montane archipelago distribution track. However it appears that there is a definite faunal link between the Namaqualand region through which the lower Orange flows and the fold belt region. There is evidence from diverse groups to support the concept of this extension of the track. The distribution of the land snail genus *Trigonephrus* includes Namaqualand and the southern and south-west Cape (van Bruggen, 1978). Endrödy-Younga (1978) describes a Cape fold belt coleopteran distribution which has a western extension to the north-west Cape and the Namib region. The distribution of amphibian species e.g. *Breviceps* spp. match this distribution track (Poynton, 1964). The distribution of *Rana grayi* given by Poynton (1962, 1964) is also remarkably similar. Provided allowance is made for the fact that terrestrial forms are not as restricted as aquatic ones then the distribution of several other reptile and bird species can certainly be invoked as support (Greig & Burdett, 1976; Roberts, 1978).

These distributions are usually explained in terms of past climatic fluctuations. According to van Zinderen-Bakker (1976) and Coetzee (1978) cooler winter rainfall conditions have in past times extended as far north as 24°S in southern Africa. The fossil fauna of Arrisdrift on the Orange River, of Miocene age, indicates an environment of relatively high rainfall and luxurient vegetation (Corvinus, 1978; Hendey, 1978). But Coetzee (1978) has also shown that tropical environments extended as far south as the Cape Flats in the past. During such periods it is envisioned that terrestrial faunas and floras may have extended their distribution ranges to include the fold belt region and Namaqualand. A change to dry climates evidently caused the extinction of many forms, except those which have adapted or survived in refuges. The mainstream Orange River, which depends on its water from the regions of greater precipitation in the east, appears to be a refuge. In addition to *B.hospes* two other freshwater fish species, each with tropical connections, also occur there (*B.trimaculatus*, and *Engraulicypris brevianalis*).

Although theoretically a link between the Lower Orange and the Olifants system may be suggested, there is as far as is known no published geomorphological support for this.

Within the Olifants River system the allopatric distribution and sister relationship of *B.calidus* and *B.erubescens* fit a vicariance model perfectly. It would be extremely useful if the formation of the barrier waterfall (Skelton, 1976) could be dated as this would provide a reasonable guide to rates of evolution of these species.

Compared with other freshwater fishes in the Cape Ichthyofaunal province *Pseudobarbus* present several outstanding features. The first of these is that there are seven species in the group - the largest non-cichlid monophyletic lineage in southern Africa. Secondly, the distribution of the species is with the exception of *P.quathlambae* confined to, but more or less extended over a geographically distinct region - the fold mountain drainages. Thirdly, the distribution of the species are, with one exception, entirely complementary and allopatric. The exception is *P.tenuis* which is found sympatrically with *P.asper* and *P.afer* in the Gourits and Keurbooms Rivers respectively.

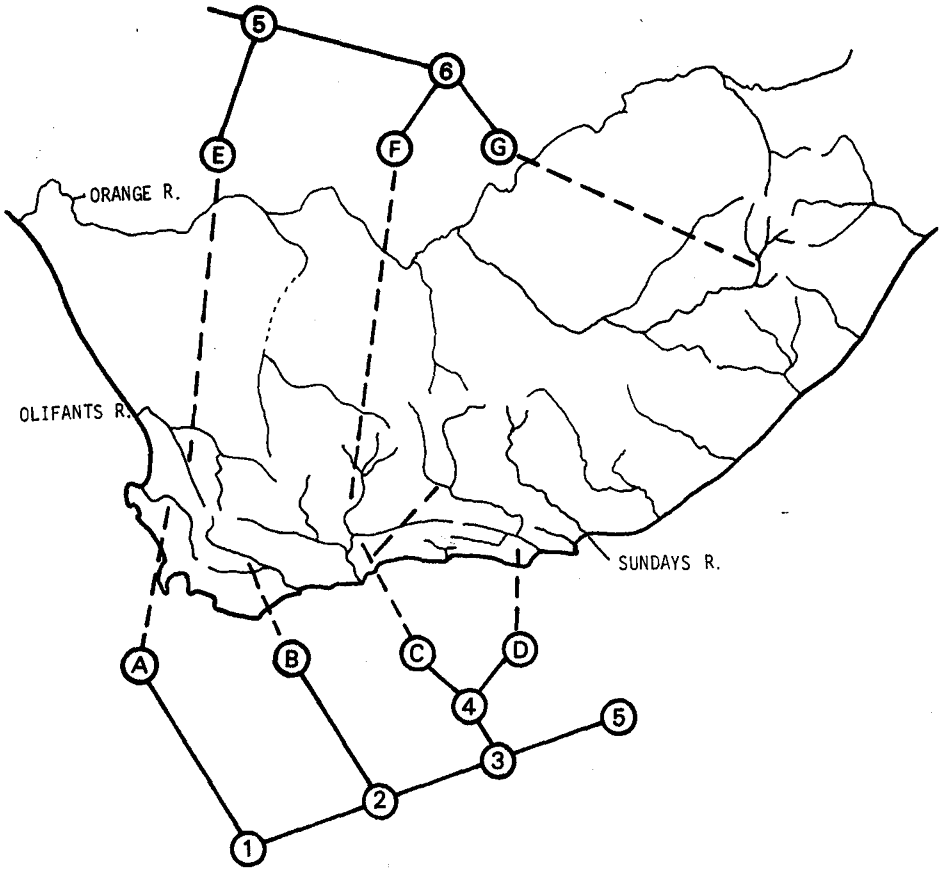


Fig. 6.12 The phylogeny of the <u>Pseudobarbus</u> species in relation to their distribution. A - <u>P.burgi</u>, B - <u>P.burchelli</u>, C - <u>P.asper</u>, D - <u>P.afer</u>, E - <u>P.phlegethon</u>, F - <u>P.tenuis</u>, and G - <u>P.quathlambae</u>.

There is another outstanding feature about the distribution of the Pseudobarbus species (Fig. 6.5). If this is plotted with the distribution of the suggested sister-group of the lineage (B.anoplus/B.motebensis and B.gurneyi) there is an almost perfect jigsaw pattern of distribution presented covering most of the subcontinent south of the Limpopo River. There are a few rivers in the fold mountain drainage where there is sympatry between B.anoplus and Pseudobarbus species but, as mentioned above, this may be explained by relatively recent dispersal of B.anoplus from southern tributaries of the Orange River.

The remarkable allopatric distribution of the Pseudobarbus species can be largely explained by vicariance of a widespread ancestral species. Possibly the most difficult aspect to be explained concerns the disjunct distribution of P.quathlambae and its closer relationship with P.tenuis in the Gourits and P.phlegethon in the Olifants River (Fig. 6.12).

There is an early phase in the distribution of Pseudobarbus, the origin and "arrival" of the ancestral species in the sub-continent, about which there is little information and on which very little comment can be made at present. Zoogeographers generally have suggested that the cyprinids arose in south-east Asia during either the late Mesozoic or early Tertiary times. From here they are to have spread, entering Africa in the north-east (and north-west) relatively late in the Tertiary (Miocene?) (Darlington, 1957; Lowe-McConnell, 1975; van Couvering, 1977; Bowmaker et al., 1978). This dispersalist explanation of cyprinid distribution has not yet been seriously questioned. There are however a number of related fish groups besides cyprinids shared between Africa, and southern and south-east Asia suggesting the presence of a generalized track. This in turn suggests there may be a vicariance - continental drift explanation involving the Indian plate. Banister & Clark (1977) suggest that a possible reason for the absence of small Barbus from Arabia is that they originated in Africa itself and the African species are not necessarily monophyletic with Asian species.

Since the Pseudobarbus lineage has been linked to the Cape fold belt - montane archipelago distribution track it is suggested that the common ancestor to the lineage evolved or became established during a time when temperature conditions were widespread over southern Africa. This was possibly before the continent had reached present latitudes, possibly during late Eocene to Oligocene times (45-25 MY) when climates were known to have been cooler. During the early Tertiary warm waters prevailed in the Antarctic and southern Africa probably experienced tropical climates (Coetzee, 1978). Tropical climates prevailed again during the early Miocene. A second possible period is during the late Miocene to Pliocene when a further period of cooling was experienced. This latter period is more in accordance with the suggested entry of cyprinids into Africa during the early Miocene (van Couvering, 1977).

The common ancestor probably achieved a widespread distribution in the proto-upper Orange and rivers of the fold belt region. Having attained this primitive widespread distribution the history of the Pseudobarbus species is most simply explained by vicariance and a few episodes of dispersal. This is necessary in the case of P.tenuis which is sympatric with other species.

The earlier episodes of vicariance of the Pseudobarbus species (numbers 1-3 in Fig. 6.12) would have occurred on the isolation of the Berg River, the Breede River and the rivers to the east of the Breede. The dispersal of a common ancestor throughout the rivers of the fold belt region probably occurred primarily via river capture processes. It is possible to suggest that the early vicariance of P.burgi was effected by the capture of the upper part of the Breede River by the Little Berg tributary of the Berg River system. Barnard (1936) described this capture as a "primary" capture suggesting that it occurred relatively early in the drainage history of the region.

The continued interconnection of the Breede and Gourits River systems was possibly realised by the "secondary" captures recorded by Barnard (1936) namely those via Mitchell's Pass, Waaikloof, Tradouw Pass and Garcia's Pass. These connections have therefore possibly ensured the more recent common ancestry of P.burchelli and P.afer-P.asper. The vicariance of P.burchelli occurred with the isolation of the Breede River system. The isolation of the Breede has been maintained during periods of lowered sea levels (Dingle & Rogers, 1972).

The dichotomy between P.asper and P.afer is less easy to pinpoint because of the widespread distribution of P.afer. Nevertheless the dichotomy appears to be between the coastal rivers and the larger inland drainages of the Gourits and Gamtoos River systems. The distribution of P.afer into many of the coastal rivers must have occurred via interconnections made

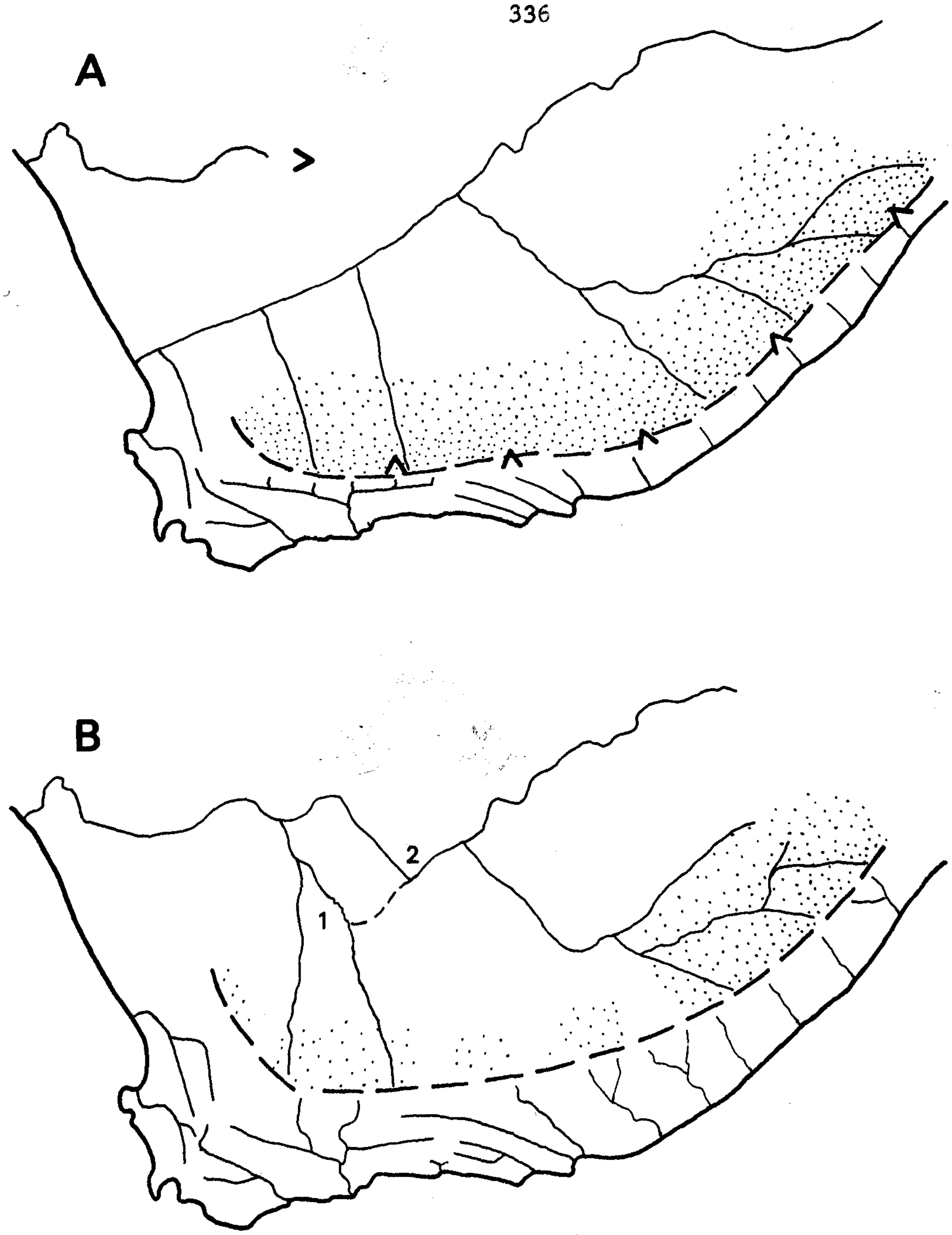


Fig. 6.13 Hypothetical evolution of part of the Orange River system explaining the phylogeny and present day distribution of P.phlegethon, P.tenuis and P.quathlambae. Stippled area denotes high altitude regions. A. Possible early drainage pattern with Orange reaching the sea via present day Olifants River system. Lower Orange River possibly relied on Molopo River for its existence and is actively eroding towards the east. Proto-Orange tributaries extend further towards continental margins than at present. Coastal rivers are shorter and actively eroding causing the retreat of the Great capture possibly occurred in two [illegible] respectively. Coastal rivers have increased their catchment areas at the expense of Orange tributaries. The higher regions at the periphery of the Orange basin are eroded and have become fragmented. Continuation of the erosion process causes progress toward the present day drainage pattern as illustrated for example in Figure 6.12.

during lower sea-levels because the majority of these rivers do not penetrate the watershed of the coastal mountain chains.

An offshore and onland geological and geophysical study made by Birch *et al*. (1978) provides a model suggesting a way in which the coastal rivers may have intercommunicated during periods of lowered sea levels. The superficial sediments of the eastern Agulhas bank (i.e. the offshore region between the Breede and Gamtoos Rivers) are predominantly drowned sand dunes (Dingle & Rogers, 1972). The regions between the major river valleys (Gourits, Gamtoos) was relatively poorly drained with meandering rivers facilitating transverse drainage patterns and interconnection of rivers.

It has been shown in Chapter 3 that *P.asper* was probably present in the Groot River tributary of the Gamtoos system before its capture. There was evidently some connection between the drainage of the Gourits and the Groot River of the Gamtoos system in the past for at the present time there are several regions of extremely low divides between the two. It is possible that both drainage captures and sheet flooding during periods of high rainfall have provided interconnections between the systems in such regions.

Under present conditions the relationship between the phylogeny and distribution of the remaining three *Pseudobarbus* species, *P.phlegethon*, *P.tenuis* and *P.quathlambae* is at first glance difficult to conceive (Fig. 6.3). However, by proposing a relatively simple hypothetical but entirely feasible drainage history (Fig. 6.13), a logical explanation can be given. It has already been suggested that the Orange River system formerly linked with the Olifants River system. The former drainage line may be suggested to extend from the right angle bend in the Orange River at Prieska across the level country around Verneukpan as in Figure 6.13A. At this time the tributaries of the proto-Orange would have extended further South toward the fold belt and coastal region (du Toit, 1933; Wellington, 1958). The land toward the outer margin of the proto-Orange basin is expected to have been of relatively high altitude due to the thickness of Karroo sediments and the upwarping from the earlier rifting. On the coastward side of the escarpment the rivers were by Oligocene-Miocene times well established and actively eroding the scarp face. In the south the fold mountain belts were reasonably exposed and the drainage directed primarily sub-parallel to the coast within the strike valleys of the mountains. The common ancestor to *P.phlegethon*, *P.tenuis* and *P.quathlambae* was evidently widespread in the proto-Orange at this stage.

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The vicariance of P.phlegethon (and possibly several other Olifants River species), would have occurred with the capture of the middle Orange by the headward erosion of the lower-Orange (Fig. 6.13B). It is possible that the capture of upper-Orange occurred in two stages which would explain the modern drainage lines of southern tributaries. The first would possibly have been a capture via the Hartebeest River in the Verneukpan region (Fig. 6.13B number 1) and later a possible capture via the main Orange River at the Prieska bend (Fig. 6.13B number 2).

According to this model P.tenuis therefore evolved in the proto-Orange River system and not the Gourits where it occurs at present. The vicariance between P.tenuis and P.quathlambae is likely to have been effected within the proto-Orange system itself. With continued erosion the Orange basin became more and more dissected. The great thickness of Karoo sediments in the east with the resistant Stormberg lava cap ensured the prolonged survival of a high altitude block (the Drakensberg) in this region. It is possible that the vicariance of P.tenuis and P.quathlambae was caused by isolation of headwater regions by unfavourable downstream conditions such as warmer temperatures or different physico-chemical river conditions. Further the southern Orange tributaries and the more rapidly eroding larger rivers to the east of the fold belt region (Sundays River, Great Fish River, Kei River) had begun to dissect the higher altitude regions into pockets. These pockets have remained as refuge areas in the generalized distribution track described above for the temperate fauna (Stuckenberg, 1962).

Rivers of the fold mountain drainage had by this time penetrated through the northern fold arc and were eroding the southern scarp flanks. P.tenuis was probably translocated from the Orange to the Gourits by river capture concomitant with the scarp retreat. With continued erosion the headwaters of the southern tributaries of the Orange have retreated further and further from the coast and during dry climes probably ceased to exist for long periods. At the present time these drainages are extremely intermittent and do not provide suitable conditions for a fluviatile species such as P.tenuis to survive. An extinction of P.tenuis in the Orange is thus proposed. Its presence in mountain streams of the Gourits is seen to represent a relict survival in suitable habitats provided in the fold mountain catchments.

This theory also explains the sympatry of the species with P.asper. The presence of P.tenuis in the Keurbooms River can also be explained by dispersal via river capture. The Keurbooms River is the only river of the coastal portion between the mouth of the Gourits and the Tsitsikamma coastal plain which has penetrated the Outeniqua-Tsitsikamma mountain divide. In so doing it must have tapped drainages which formerly flowed into the Kammanassie River of the Gourits River system. The selective dispersal of P.tenuis and not P.asper into the Keurbooms is explained by reason of habitat differences of these two species - P.tenuis a mountain tributary species and P.asper is a mainstream form. The coincident distribution of Galaxias zebratus in the Keurbooms River provides a further measure of support for this theory.

The isolation and restricted distribution of P.quathlambae in the Drakensberg occurred in conjunction with the evolution of the Orange River system. The Stormberg lava capped Drakensberg represent an erosional remnant of formerly more widespread and thick full sequence of Karroo sediments. Wellington (1958) has pointed out that the present thickness of the lava strata must be considerably less than in the past. Consequently it is expected that altitudes were also far greater than at present. Wellington (op.cit.) estimates a removal of at least 2 000 m of lava by weathering and erosion. Although this figure is probably a gross over-estimation the concept is in agreement with recent ideas (De Swardt & Bennett, 1974; Corbett, 1979) that the present land surface is not a preserved remnant of the Gondwana or early post-Gondwana land surface as proposed by King (1978).

It is reasonable to suggest that P.quathlambae has become highly adapted (Greenwood & Jubb, 1967) in response to higher altitudes and probably more extreme environments in the past than occur at present.

The presence of P.quathlambae in the Umkomazana River in Natal is logically explained by headwater capture of Orange River tributaries. The relatively low altitude of these localities suggests probably a sub-optimum environment for the species. Barnard (1938a) notes that the original specimens were submitted with a note from the collectors that they were common in Drakensberg streams before the introduction of trout. The species appear to be extinct today in Natal waters although it survives in the Tsoelikana

River in the presence of trout. Gephard (1978) has suggested that the difference between survival and extinction in these two situations is probably a reflection of difference in an optimum environment for this specialized species.

In conclusion it is believed that the distribution of the redfin minnows is intimately interrelated with the historical development of the region. The span of time which the species have been in the region appears to be considerable. There are geological clues which could in future be used to provide a more accurate dating of the group, and the redfins may then be instrumental in revising the time scale of cyprinids in Africa.

The distribution of the redfin species is explained above using both the concepts of dispersal and vicariance. Vicariance is seen to be the primary factor in the distribution of the species, dispersal a secondary factor. The most problematical questions which remain concern the initial or ancestral distributions of the two redfin groups. Just how widespread the ancestral redfin _Barbus_ and _Pseudobarbus_ species were in Africa will be extremely difficult to answer without further knowledge of relationships within and beyond southern Africa. The chance discovery of fossil relatives could also provide some answers to the questions of space and time of redfin origins.

CHAPTER 7

GENERAL DISCUSSION WITH SPECULATION ON ASPECTS OF REDFIN EVOLUTION

Ultimately one looks towards the broader implications of a study such as this on the redfin minnows. The solutions to the special taxonomic problems of cyprinids requires a firm foundation of the morphological characters of the fishes. The study has provided the redfin species with such a foundation and the results have bearing in the light of developing trends on the broad front of systematics and especially the systematics of the cyprinids. This discussion will consider these implications especially with regard to future studies on the redfins and other African cyprinids, especially the small Barbus. Other points including preliminary speculation on redfin evolution and a conservation note will be presented.

Future implications of the redfin study

It is a natural consequence of detailed study that as answers for questions are provided new questions arise. At the outset this study attempted to answer several basic questions on the redfins - how many species are there? What phylogenetic relationship do they have? What is their relationship with other Barbus species? How is their geographical distribution explained. To a greater or lesser extent answers to these questions have been provided.

The taxonomic questions were approached in the light of recent approaches on similar groups of fishes elsewhere. For example revisions of the genus Nocomis (Lachner & Jenkins, 1967, 1971a & b; Lachner & Wiley, 1971; Jenkins & Lachner, 1971) emphasised the need for a thorough analysis of morphometric and meristic values over a complete range of each taxon and also stressed the desirability of investigating particular character complexes in depth. The lack of such knowledge on African cyprinids and the redfins was emphasised by the identification problems these species present to both the field worker and the taxonomist. This stressed the need to make such a study on the redfins as a basis for understanding cyprinid characters and their variation. The study has produced ample rewards in the case of the redfin species. Without the initial attention to detail the later sections of the study dealing with phylogenetic relationships and biogeography would have been severely hampered.

Although the results of the redfin study might be useful for comparison with other small *Barbus* species in southern Africa each problem should ideally be judged on its own merits. Redfin variability is possibly higher than most small *Barbus*-like cyprinids in Africa. This opinion is based on factors which pertain to the redfins and which is unusual in the African context. These are (a) their geographical location and (b) what appears to be a low ecological saturation with regard to other fishes in redfin inhabited waters. Nikolsky (1976) has shown that fishes at higher latitudes have in general a greater range of variability and also that variability of characters in fishes is inversely proportional to the diversity of the fish fauna.

The depauperate nature of the south coastal drainage in Africa is well known (Jubb, 1965; Bowmaker *et al.*, 1978). Most rivers in the region have at most four or five indigenous fish species. The Clanwilliam Olifants is exceptional with nine species. *P.quathlambae* is the sole indigenous fish inhabitant of the localities where it is known to occur at present. The successful introduction of several fish species to south coastal rivers through man made agency provides circumstantial support to the concept of the low degree of saturation of these environments.

It would require a similar extensive morphometric and meristic analysis of the characters of many other small *Barbus* species to effectively gauge the comparative variability of the redfin characters. Based on the species accounts in Jubb (1967) however it is notable that e.g. caudal peduncle scale rows of many small *Barbus* species have more narrow limits of variation. A single count often identifies a species. Comparison of variability of characters in small *Barbus* species from different situations would make an interesting and useful investigation. This knowledge would be extremely valuable when making taxonomic decisions on these frequently problematical cyprinids.

The major change brought about in redfin taxonomy is the direct result of the interpretation of the phylogeny of the species. The status of most of the species was endorsed in the initial taxonomic study and there was no formal designation of any subspecific categories. These decisions are in agreement with the concept that the measurable intraspecific variation in these cyprinids is primarily a reflection of plastic phenotypes responding to variable environmental conditions. For these riverine cyprinids it is of distinct advantage to be adaptable to a fluctuating and variable environment. In the absence of genetic evidence it is considered weak practice to apply formal taxonomic labels to populations which differ in characters which elsewhere have been shown to change in response to physical or chemical environmental parameters.

It should be stressed that this study has had to rely excessively on available literature for the evaluation of character differences and variation. The necessity to determine the effect of variable environmental parameters on a wide spectrum of taxonomic characters is clearly an important field of future research on the redfins and other African fishes. Such studies must be conducted both in the field and under experimental conditions.

Problems such as that presented by *P.afer* and *P.asper* would be better understood if there was available information from experiments which determine the effect of physico-chemical parameters on characters such as scale size or body proportions. It would also be extremely useful to physico-chemical tolerances of the species and to relate this to the field situation. The study by Hofmeyr (1966) illustrates the potential value there is in information of this kind.

Redfin taxonomy would benefit particularly on studies designed to determine factors influencing the length and coiling of the gut or the function of the tubercles. These could be corroborated with field observations.

Field studies, at least as far as systematic questions are concerned should concentrate on breeding behaviour, feeding regimes and ecological interactions in relation to the annual cycles of the environment. It would be useful to study growth under natural conditions. For example preliminary observations suggest that the relatively small size of *P.phlegethon* is due to a shorter life cycle and earlier maturation of the species relative to other *Pseudobarbus*. It is desirable to know the habitat preferences of the species and this would be particularly useful to the taxonomy of *P.afer* and *P.asper*.

The application of Hennigian philosophy to the redfin study realized a number of definitive results which would have been different if any other approach had been used. Firstly the decision to recognise the generic status of *Pseudobarbus* is made in the light of the clear monophyly of the group. The incorporation of *P.quathlambae* in this genus is a logical consequence of the relationships of the species. Nevertheless the species is as distinctive as it ever was when it fully justified generic ranking (Greenwood & Jubb, 1967).

The decision to include *P.quathlambae* with *Pseudobarbus* will possibly meet with resistance from the non-systematic orientated biological fraternity to whom it is advantageous to refer to the distinctness of the species. There is undoubtedly an innate human resistance to taxonomic change, at least when it involves well known species. This fact was recognised by Ribbink (1975) when, in spite of considerable biological evidence supporting the formal recognition of an isolated population of *Pseudocrenilabrus philander* as a distinct species, he declined to do so. There was and still is much "consumer resistance" among field biologists, fisheries scientists and others, to accepting the decision by Trewavas (1973) to divide "*Tilapia*" into *Tilapia* and *Sarotherodon*.

This is made note of because it constitutes a real problem with several groups of African freshwater fishes when a Hennigian philosophy is adopted for their systematic study. Greenwood (1979) divided the large cichlid genus *Haplochromis* into several genera on the basis of shared derived characters. There has not been sufficient time for his ideas to enter general circulation to assess reaction, and it is almost certain that it will be some time before the new generic names become well known and generally used. It is however important that general acceptance is forthcoming, because classifications based on cladistic philosophy are made with the sole criterion of the close relationships of taxa as evidenced by shared derived characters. Relationships between organisms forms the basis of the concept of comparative biology (Nelson, 1970) and is vital for the practical implementation of scientific biological knowledge.

In this light the redfin study makes certain clear implications for future studies on the genus *Barbus*. Provided the problems of parallelism and convergence can be overcome - and this is possible if sufficient attention is given to the details of characters (e.g. the pharyngeal teeth of

P.quathlambae) - natural subunits of the "genus" can be recognized on the basis of shared derived characters. These natural groups can then be safely separated from the whole and gradually a complete picture built up. Cladistics therefore offers a logical solution to the problem of large and unwieldly genera so common in the cyprinids.

Although the problem has not arisen with this particular study, the question of applying the biological species concept in studies based on Hennigian concepts has recently been discussed by Rosen (1978, 1979) and Bremer & Wanntorp (1979). These authors have concluded that the two concepts are incompatible. Because it is likely that Hennigian methods will be applied to future Barbus studies it is desirable to examine these developments further.

Rosen's (1978) argument is basically that if an allopatric speciation model is accepted (it appears to apply in all cases of redfin speciation) it will most often be the case that sister species are allopatric in distribution. This being so they will generally not satisfy the biological species criterion of non-interbreeding sympatric units. Furthermore this criterion applies only to living representatives of related species and does not account for the possibility of extinctions of intermediate relatives. For these reasons the biological species does not satisfy the demands on the species unit in Hennigian studies.

Wiley (1978) has reconsidered the evolutionary species concept and defines a species as a single lineage of ancestral-descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. This definition caters more for the requirements of cladistic philosophy. If an interbreeding criterion is not required Rosen (1978) suggests that the number of populations to be included in the lineage need only be determined on the basis of shared derived characters. According to this view and for practical purposes a "species" is merely a unit of taxonomic convenience applied to a population or assemblage of populations in which no taxonomic divergence is detected (Rosen op.cit.).

Rosen (1979) extends this idea that species are merely units of taxonomic convenience by arguing the fact that reproductive incompatibility is a plesiomorphic character within any monotypic lineage (i.e. the lineage is derived from a single species). A "species" in cladistic analysis cannot therefore be considered on the basis of reproductive compatibility (a cornerstone of the biological species concept) because such compatibility will be a plesiomorph character not yielding information on relationships. Rosen (1979) concludes that the "species" is, at least for the purposes of cladistic analysis,"the smallest aggregation of individuals with specifiable geographical integrity that can be defined by any current set of analytical techniques" (:277). According to this criterion the subspecies category, by virtue of its definition (vide Mayr, 1963, 1969) is redundant.

Bremer & Wanntorp (1979) have also exposed incongruities between the biological species concept and Hennigian phylogenetics. The incompatibility exists in that cladistics considers the sequence of geographical isolation of populations which is not necessarily the same sequence as the development of reproductive barriers between isolated populations. The latter development represents the completion of speciation according to the biological species concept. Bremer & Wanntorp (op.cit.) advocate the adoption of Wiley's (1978) evolutionary species concept.

The above alterations in species concept would not seriously effect redfin taxonomy at the present time because the species are all, as far as I can determine, the "smallest" aggregation of individuals which are defined by the set of morphological criteria which were employed. This statement is necessarily qualified by the fact that there are some redfin species populations which do differ from other populations, but there is no evidence yet that such differences are genotypic.

If redfin taxonomy is not likely to be effected much by these philosophical developments the same cannot be said for other African fish groups including many cyprinids. The polytypic nature of many species is frequently recognised. Each such recognizable subunit could in future become a full "species" according to the above criteria. In order to prevent an unnecessary "explosive" phase of taxonomy it will become increasingly important to consider carefully the taxonomic weight of the characters employed.

As demonstrated in the redfins many traditional characters in cyprinids are weak indicators of phylogeny and are required to be used with caution.

These characters are of limited value in Hennigian analysis. In many cases these characters are suitable for descriptive purposes only. Most southern African freshwater fish species are adequately described. If there are to be relatively rapid advances in determining relationships of the species research should concentrate on qualitative character analysis - such as provided by osteology - which are likely to provide adequate synapomorphies. At present such characters are barely explored. The good results which can be expected by such investigations are readily demonstrated in the success this study achieved in determining the relationships of P.quathlambae.

Speculation on the evolution of the redfins

With a knowledge of the morphology, phylogeny and ideas on the biogeography of the redfins it is possible to present tentative thoughts on their evolution. Naturally there are major limitations in the presentation of these ideas because of the lack of knowledge on important aspects other than morphology when considering the evolution of the species. Not only is the environment poorly known but almost nothing is known about redfin biology and ecology. One has only a few impressions based on handling numerous specimens and on casual observations during collecting activities.

It is nevertheless important that what ideas there are, are presented because in this way a start can be made on defining the gaps in our knowledge and possibly guide the ways of filling these gaps.

There is no known fossil record from which we can get any ideas of early morphology of the redfins. We have only the endpoints of the evolutionary process. By considering those characters which are probably plesiomorphic some idea of the nature of the postulated ancestor can be established.

Considering first the Pseudobarbus lineage a moderate size, fusiform shape and sexual dimorphism are entrenched characters of the species. A barbelled inferior mouth as well as the tendency for the plesiomorph species to have elongated involuted guts suggest that all the above were characteristic of the hypothesized ancestor. A tendency to reduce the supraneural bones and anterior intramuscular bones was also established early in the history of the group.

These characters suggest the ancestral species was probably similar to P.burgi, P.burchelli and P.afer. The environment under which the species existed was probably not unlike the rivers of the fold belt region at the present time. These rivers are ancient (Chapter 6) and the geology of the region has exerted much the same influence on the physical and chemical nature of the rivers since the postulated early origin of the redfins presumably during the Mio-Pliocene. There have undoubtedly been considerable climatic fluctuations over the period of evolution of the group (van Zinderen Bakker, 1976; Coetzee, 1978). It is impossible to select any divergent extreme from present day conditions which might have had a greater evolutionary impact on the majority of the species. To a certain extent it does appear that the evolution of P.tenuis and P.quathlambae was probably determined during more extreme conditions than at present (see below).

According to the biogeographical hypothesis presented in Chapter 6, the speciation of the group is due to geographical vicariance. The rivers in which P.burgi, P.burchelli and P.afer occur are reasonably characteristic and similar in physico-chemical parameters (Harrison & Agnew, 1962). The invertebrate fauna of the rivers is also similar (Harrison & Agnew, op.cit.) and there are no great differences in cohabiting freshwater fishes. It is more than likely therefore that what evolutionary change there has been in these more plesiomorph species has been the result of a long history of isolation rather than any major change in the environment, biotic or abiotic.

Trophic adaptations, sexual dimorphism including prominent tubercles, squamation characteristics and skeletal reduction form the more obvious particularities of Pseudobarbus. These morphological features provide a few clues as to what the guiding factors in the initial evolution of the lineage appear to have been. There is little evidence of any external biotic pressure being a major force.

Sexual dimorphism and prominent tubercles may have evolved entirely in response to intraspecific pressures. Wiley & Collette (1970) and Collette (1977) list several possible functions for tubercles similar to those found in Pseudobarbus species. These include the three primary functions of maintaining body contact between sexes during spawning (scale and fin tubercles?), defence of nests or territories, and stimulation of females in breeding (head tubercles?). The development, form and distribution of the tubercles on the fish suggest that these functions probably fit the role of the tubercles in the more plesiomorph Pseudobarbus species. They could quite possibly have developed to satisfy intraspecific and physical environmental demands (clear flowing water?).

A protrusile inferior mouth, scraping pharyngeal teeth and an intestine which is variably elongated indicates that the species are primarily geared for benthic omnivorous feeding. Presumably this represents a general adaptation for the maximum exploitation of available food resources.

Reduction in scale size occurs in various fishes in response to different pressures. Fast swimming oceanic fishes or fishes which exist in strong current environments reduce friction by developing small scales or losing them entirely. Species which require enhanced flexibility usually also have small scales (e.g. anguilliforms mastacembelids). Benthic species or species which make frequent contact with the substrate also frequently have small scales - at least ventrally. The reduced breast scales of the Pseudobarbus group correlates with the inferior mouth and the suggested basic benthic feeding habits of the species. The reduction of the pelvic axillary scale also correlates with this habit as it has been found that this scale is reduced in many species living at or near the bottom (Norman, 1975).

The reason for the evolutionary reduction of supraneural and intramuscular bones in Pseudobarbus is not well understood. This may be a response to particular locomotory demands or even possibly reduction through absence of a sustaining selection pressure. A chemical impoverishment is a notable characteristic of the acid waters of the Cape fold belt (Bond, 1946; Harrison & Elsworth, 1958; Harrison & Agnew, 1962). The aquatic medium itself forms a major source of mineral ions, especially calcium, in fishes (Simmons, 1971). Reduction of ossification in Pseudobarbus may therefore be a response of physiological expediency possibly in the absence of strong functional demands on these structures.

The evolution of more divergent species in the later phylogeny of the lineage appears at least partly explained by known factors of the particular environments in which these species occur. P.asper inhabits larger tributaries of the Gourits and Gamtoos River systems which differ markedly physically and chemically, from mountain tributaries of these systems.

The most outstanding feature of the species are the relatively small scales.

In freshwater fishes an increase in salinity tends to retard the rate of embryological development. This in turn tends to increase meristic characters (Barlow, 1961; Fowler, 1970). The small scales of P.asper may be a physiological evolutionary response to an environment which relative to other Pseudobarbus environments, has greater mineral and ionic concentrations.

The most notable features of P.phlegethon relative to other Pseudobarbus species are small size and reduction in sexual dimorphism and tubercles. Other distinguishing characters include a narrow profile, a small mouth and adult pigmentation. The outstanding feature of the Olifants River system (where P.phlegethon occurs) in relation to other rivers of the fold belt region is the high number of endemic fish species (Jubb, 1965; Bowmaker, et al., 1978). It is to be expected that this would mean a quite different ecological situation operating for much of the evolutionary time span of P.phlegethon (the fact that there are several endemic species in the Olifants indicates that the forms have probably been present there for a relatively long time).

In what way might these cohabiting species influence the evolution of P.phlegethon? If sexual dimorphism and large tubercles indicate specialized territorially orientated breeding behaviour in the more primitive Pseudobarbus species, it could be that such behaviour was selected against in P.phlegethon by interference (predation?) from cohabiting species. Smaller size, narrow profiles and disruptive pigment patterns of P.phlegethon could be adaptations facilitating avoidance of or refuge from cohabiting species.

P.tenuis and P.quathlambae are relatively specialized species. P.tenuis has a slender profile suggesting it has adapted to moving water (Hubbs, 1940, 1941). In streams where there is sufficient current for a fish species to be adapted in the manner in which P.tenuis is, there is usually very little organic sediment. A bottom feeding species is likely to exploit benthic organisms. The unusual degree of specialization of the pharyngeal teeth of P.tenuis and O.quathlambae indicates that there has been a strong selection pressure on these structures, and it would seem that the pressure was exerted by the food source itself.

According to the hypothesis of the biogeography of the redfins given in Chapter 6, P.tenuis probably evolved in a proto-Orange River system and later dispersed to the Gourits River system where it has had refuge. It has been collected in sites which suggest that the present day environment in Gourits tributaries is not the optimum under which the main facies of the species evolved. These sites consisted of slow flowing pools with marginal vegetation and deep bottom sediments. The gut contents of individuals from these localities consisted of filamentous algae and diatoms.

P.tenuis and P.asper are both found in the Gourits River system. Both species have opposing character traits in the lineage, and to a greater extent, different habitat preferences. It is possible therefore that these morphological characters and habitat preferences of each species may have been reinforced through character displacement. This possibility would have to be investigated extensively in the field before it could be verified. It would, however, be difficult to find a suitable location at which to conduct a study because there are few, if any, which are unaffected by human activity.

The specializations of P.quathlambae are clearly supralimital as regards the Barbus level of organization (Greenwood & Jubb, 1967). These specializations point to adaptations for the high altitude mountain environment where the species occurs. There is firm evidence that the environment in the Drakensberg has been considerably more extreme than at present, especially in respect of colder climates (Harper, 1969; Fitzpatrick, 1978). This factor must be considered when explaining the evolution of P.quathlambae. Physical environmental parameters such as temperature, current and substrate appear to dominate the evolutionary directions taken by this species. Various explanations for characters such as small scales and pharyngeal teeth have been given elsewhere in this study. As in the case of P.tenuis the trophic specializations of P.quathlambae appear likely to have evolved in response to the favourable food resource (benthic and allochthonous invertebrates).

Gephard (1978) considers certain aspects of the evolution of P.quathlambae and emphasises its adaptation to high altitude situations. An interesting point raised by Gephard (op.cit.) concerns the competitive ability of the species. P.quathlambae is known from three localities in only one of which it is known to survive in the presence of trout (Tsoelikana River). This locality is the one in which another indigenous species (Barbus holubi) is found during spawning runs. Gephard suggests this population may therefore be more equipped than others to withstand predation.

This idea has a certain amount of merit (see conservation note below) and possibly highlights a factor which appears conspicuous by its absence (or low profile at most) in the evolution of the Pseudobarbus - namely a low interspecific competitive factor. The possible significance of this on taxonomic characters has been mentioned earlier in this discussion and now as then it would be interesting to know more about this aspect. It certainly suggests that the Pseudobarbus species would make interesting comparative subjects for an evolutionary study especially as so little is known about the evolution of Africa's cyprinids and other riverine fishes.

Factors in the evolution of B.calidus and B.erubescens are more difficult to make on account of the difficulty in interpreting plesiomorph and derived characters of the species. Field and aquarium observations indicate both the species are active mid-water swimmers feeding probably by sight from the water column or water surface. Both species are usually encountered in large open river stretches or in clear deep pools with a through water flow. The morphological adaptations of both species but more especially B.calidus, are towards active swimming habits (Chapter 3).

Mode of life was probably firmly established before the vicariance of the species. Subsequent to this vicariance the selection forces appear to have maintained or enforced the morphological characters related to swimming of B.calidus to a greater extent than those of B.erubescens. Thus B.calidus has a narrower caudal peduncle, more falcate fins and a dorsal fin more posterior than B.erubescens. The serrations on the dorsal spine are either defensive or possibly related to functional actions of the fin during locomotion. In either case the strong spine of B.calidus agrees with other circumstantial factors (if defensive B.calidus co-exists with at least six or seven other fish species and B.erubescens with only one much smaller species Galaxias zebratus; if the spines serve as a fin support for more stringent swimming actions the morphological characters mentioned above are all positively correlated).

The most obvious differences between the environments of the two species at the present time appears to be the absence of cohabiting fish species with B.erubescens (Skelton, 1974b). It seems reasonable to suggest that these cohabiting species or lack thereof have played an important rôle in the evolution of B.calidus and B.erubescens. Further speculation is not justified but it would make an interesting comparative study for the student of evolution.

A note on conservation

One of the prime reasons for initially undertaking this study of the redfins was a concern over their conservation. The following few thoughts are presented in the belief that this study can contribute to the conservation of these fishes. Indeed this is vital if there is to be a future for the numerous fields of enquiry which remain. The redfins may not be commercially or economically important. I trust however, that this study has exposed the scientific interest of and, by intimate link with the evolution of the sub-continent, their great aesthetic value for man. If a reason be required for their conservation it is this, that they are so much part of this environment that to lose them would be a mark only of the lack of concern or respect we have for it.

An assessment of the conservation status of the redfin species was given by Skelton (1977). P.phlegethon and P.quathlambae were considered endangered, P.erubescens as vulnerable and the other species as rare. This assessment is due to be reviewed in the near future in the light of additional information which has come to hand. In the case of P.asper and P.afer this will necessarily include the taxonomic changes made in this study.

The redfins are threatened for one basic, perhaps self evident reason, viz. adverse ecological changes brought about through man's agency. The actual factors involved can be grouped into several classes, a few of which are of major importance in the case of the redfins.

Physical exploitation of water resources is a major factor effecting the existence of indigenous fishes. Due to ever increasing populations it appears that there is little which can be expected by way of future improvement of the situation. In one respect however, something could be done. Agricultural exploitation of the rivers and water resources in the fold belt region tends to operate via numerous weirs and diversions by individual land owners on each and every stream or river. There are naturally many larger irrigation schemes but these probably do not effect redfin populations to the extent that the former class do. These smaller diversions frequently destroy the entire downstream environment (by total water abstraction). They also more often than not limit upstream habitat for the fishes and are frequently made inhospitable by the introduction of exotic predators.

Effective conservation will only be possible with a rewriting of the water laws so that the state has a say in the manner of water exploitation by the riparian landowners. At present these laws do not even consider that the waters of South Africa's rivers even have fishes in them.

Introduction of exotic predator species has been a second major factor in the decline of the redfin species. The influence of introduced exotics appears to have been particularly severe in the case of the redfins and this probably relates to the low level of competition evident in their evolution. Communities which have evolved in the absence of specialized predators are unlikely to be equipped with the necessary mechanisms to withstand such predation. This has been demonstrated on several occasions (e.g. McDowell, 1968; Smith, 1978) and it is highly likely that the principle pertains to the redfins including P.quathlambae (Gephard, 1978).

Gephard (1978) considers that the demise of P.quathlambae is the inevitable fate of this specialized species in its diminishing habitat. This may be so but it would be a tragedy if through man's selfish folly, this demise is hastened any more than it has been already. Whereas it is extremely difficult to implement conservation measures with regard to man's overall usage of water resources it is within the bounds of conservation authorities to enact only sound measures with regard to the introduction of destructive exotic organisms.

Although this study of the redfins has advanced our systematic knowledge of the species it has also exposed many gaps. This exposure is hopefully timely. The science of systematics is making rapid advances in many spheres. The taxonomy of freshwater fishes in southern Africa is sufficiently advanced to be standing at a crossroads where it may join what promises to be a rewarding highway. The redfin study has, it is hoped, indicated something of what this highway offers.

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APPENDIX 1

Material examined of redfin Barbus and Pseudobarbus species. (Note: a few SAM records not seen, but presumably valid and recorded for distribution plots).

Abbreviations. AM/P: Albany Museum (fish collection); BMNH: British Museum (Natural History); MACT: Muséé d'Afrique Centrale, Tervuren; NM: Natal Museum; RUSI: J.L.B. Smith Institute of Ichthyology, Rhodes University.

Collectors (only the first in case of several): KHB - Dr Keppel Barnard; RAJ - Dr Rex Jubb; PHS - P.H. Skelton; CWT - Mr C. Thorne; ST - Mr S. Thorne.

Ditto refers to previous mentioned sample.

BARBUS CALIDUS

Lectotype: SAM 18605 (Jan Diessels R. , KHB, 1936)

Paralectotypes: SAM 18605 (ditto) ; SAM 18606 (TRA-TRA River 32° 17'S, 19° 14'E, KHB, 1936); 18756 (Olifants R., KHB, 11 April 1937); 19002 (KHB, 16-18 April 1938); SAM 22499 (Boontjies R., 32° 36'S, 19° 04'E; KHB, Nov. 1936) ; SAM 215-216 (Olifants R., C.L. Leipoldt, 30 Nov. 1897); SAM 2012-2915 (Clanwilliam, R.M. Lightfoot).

Olifants River System: SAM 22478 (KHB, April 1949); AM/P 728 (Thee R. K. van Rensburg, Feb 1964) ; AM/P 885 (K. van Rensburg, 1965) ; AM/P 1371 (Rondegat R., F.L. Farquharson, April 1967) ; AM/P 1393 (Keerom K. van Rensburg, Jan. 1964) ; AM/P 1581 (Tra-Tra R., R. Louw, Nov. 1968) ; AM/P 1644 (Noordhoeks R., F.L. Farquharson, April 1967) ; AM/P 1797 (Rondegat R., PHS, Sept 1972) ; AM/P 1818 (Thee R., D. Heard, Sept 1972) ; AM/P 1844 (Tra-Tra R., PHS, Jan 1973) ; AM/P 1850 (Jan Diessels R., PHS, Jan. 1973) ; AM/P 1855 (Matjies R., PHS, Jan. 1973) ; AM/P 1857 (Breekkrans R., PHS, Jan. 1973) ; AM/P 1862 (Noordhoeks R., PHS, Feb. 1973) ; AM/P 1869 (Thee R., PHS, Feb. 1973) ; AM/P 1871 (Ratels R., PHS, Feb. 1973) ; AM/P 1883 (Rondegat R., D. Heard, Nov. 1972) ; AM/P 2050 (Matjies R., PHS, Oct. 1973) ; AM/P 2051 (Noordhoeks R., PHS, Oct. 1973) ; AM/P 2052 (Tra-Tra R., PHS, Oct. 1973).

BARBUS ERUBESCENS

Holotype and Paratypes: as in appendix 3.

Olifants River System: AM/P 1388 (Twee R., F.L. Farquharson, April 1967) AM/P 1799 (Middeldeur R., PHS, Sept. 1972) ; AM/P 1866 (Middeldeur R., PHS, Feb. 1973) ; AM/P 1867 (Twee R., PHS, Feb. 1973) ; AM/P 1881 (Middeldeur R., D. Heard, Nov. 1972) ; AM/P 1882 (Middeldeur R., K. van Rensburg, Mar. 1964) ; AM/P 2043; 2044; 2045; 2046; 2047; 2049; 3710; (Twee R., PHS, Oct. 1973) ; AM/P 2048 (Suurvlei R., PHS, Oct. 1973) ; AM/P 7348 (Middeldeur R., I. Gaigher, Nov. 1977) ; AM/P 7442, (Twee R., PHS, Oct. 1973)

PSEUDOBARBUS AFER

Sundays River System: AM/P 455, (Wit R., RAJ, April 1959) ; AM/P 586 (Wit R., RAJ. 1960) ; AM/P 755 (Wit R., RAJ, April 1959) ; AM/P 1188 (Wit R., B. Donnelly, Feb. 1965) ; AM/P 3843 (Wit R., PHS, Dec. 1976) ; AM/P 7465 (Wit R., PHS, Dec. 1977)

Swartkops River System: SAM 18592 (Swartkops R., C.L. Biden 1935) ; SAM 19208 (Groendal R., CWT Oct. 1938) ; SAM 19212 (Brak R., CWT, Oct. 1938) ; SAM 22330 (Swartkops R., Arendse) ; SAM 22334 (Swartkops R.) ; AM/P 675 (Elands R., RAJ. 1963.) ; AM/P 745 (Elands R., RAJ. Feb. 1964) ; AM/P 2524 (Elands R., PHS, Sept. 1974) ; AM/P 3786 (Bulk R., D. Heard, Oct. 1976).

Baakens River: SAM 10654 (P.E. Museum, pre-1913) ; AM/P 776 (D. Bickill, Jan. 1964) ; AM/P 1810 (PHS, Nov. 1972) ;

Maitlands River: AM/P 5835 (A. Bok, Jan. 1978)

Gamtoos River System: SAM 19216 (Loerie R., CWT Oct. 1938) ; SAM 19319 (Patensie, CWT Oct. 1938) ; SAM 19496 (Baviaanskloof R., KHB April 1939) ; AM/P 473 (Baviaanskloof R.,) ; AM/P 676 (Loerie R., F.L. Farquharson, 1964) ; AM/P 712 (Moordenaars R., RAJ Feb. 1978) ; AM/P 1374; 1375; 1376; 1389; 1390; 1413 (Couga Dam, F.L. Farquharson, July, 1967) ; AM/P 1402; 1412; (Wit R., F.L. Farquharson, July 1967) ; AM/P 1415; 1416 (Loerie Dam, F.L. Farquharson, July 1967) ; AM/P 1562; 1563; (Hankey, C.M. Gaigher, Oct. 1970) ; AM/P 1741 (Wit R., PHS, June 1972) ; AM/P 1742; AM/P 1803 (Bukkraal R., PHS June 1972) ; AM/P 1751 (Kleinberg R., H. Hofmeyer, Nov. 1964) ; AM/P 1921 (Wit R., PHS April 1973) ; AM/P 2533 (Hankey, B. Donnelly Aug. 1966) ; AM/P 3789 (Hankey, D. Heard, Oct 1976) ; AM/P 3792 (Diepkloof R., D. Heard, Oct. 1976) ; AM/P 5841 (Wit R., J. Hoffman, Mar. 1977) ; AM/P 7465 (Wit R.)

Kabeljous River: SAM 19321 (CWT, Nov, 1938) ; AM/P 3805 (Kranzplaas, D.Heard, Oct. 1976) ; AM/P 3807 (Musgund, D. Heard, Oct. 1976).

Seekoei River: SAM 19323 (CWT, Nov. 1938)

Kromme River: SAM 19325 (Geelhoutboom R., CWT, Nov. 1938) ; SAM 19326, 19330 (CWT, Nov. 1938) ; AM/P 230 (Assegaaibos, RAJ, Feb. 1958) ; AM/P 1739 (Assegaaibos, PHS, June 1972) ; AM/P 1801 ditto, Sept. 1972) ; AM/P 2082 (ditto, Dec. 1973) ; AM/P 2651 (ditto Jan. 1975) ; AM/P 3103 (ditto, ex aquarium Aug. 1975) ; AM/P 3460 (ditto, Oct. 1975) ; AM/P 3810 (Assegaaibos, D. Heard, Oct. 1976) ; AM/P 3811 (Melkhoutkraal, D. Heard, Oct. 1976) ; AM/P 3812 (Witels R., D. Heard, Oct. 1976) ; AM/P 3813 (Damsekloof R., D. Heard, Oct. 1976) ; AM/P 3815 (Eerstedrif R., D. Heard, Oct. 1976) ; RUSI 304, (Holotype Barbus Senticeps ; Assegaaibos, 38 57'S, 24 20'E, J.L.B. Smith).

Tsitsikamma River: AM/P 3568 (Sarnia, PHS, Oct. 1975) ; AM/P 3816 ; 3817; (Palmiet R., D. Heard, Oct. 1976) ;

Bloukrans River: AM/P 1707; 1742 (PHS, April 1972) ; AM/P 2652 (ditto, Jan 1975) ; AM/P 2654 (Vark R., PHS, Jan. 1975) ; RUSI 75-120 (J.L.B. Smith, Mar. 1965).

Groot River: (Nature's Valley) ; AM/P 1706 (PHS, April 1972) ; AM/P 2656 (Ditto, Jan. 1975) ; AM/P 3456 (ditto, Oct. 1975)

Keurbooms River System: SAM 19334 (Edmonton, CWT, Nov. 1938) ; SAM 19335 (Paardekop, CWT, Nov. 1938) ; AM 19337 (CWT, Nov. 1938) ; SAM 22333 ; AM/P 1784 (Diep R., PHS, Sept. 1972) ; AM/P 1789 (De Vlug, PHS Sept. 1972), AM/P 3461 (Diep R., PHS, Oct. 1975) ; AM/P 3823 (Diep R., D. Heard, Oct. 1976) ; AM/P 3826 (Boegoes-kraal, D. Heard, Oct. 1976) ;

Knysna River: AM/P 113 (Gouna R., RAJ,) ; AM/P 152 (R.A. Jubb Feb, 1958) ; AM/P 1790 (Grootkop R., PHS, Sept. 1972)

Goukamma River: SAM 19338 (Homtini R., CWT, Nov. 1938) ; AM/P 100 (Homtini R., RAJ, Nov. 1957) ; AM/P 110 (Homtini R., RAJ,) ; AM/P 584 (Homtini R., RAJ, 1958);

Karatara River: SAM 19196 (Ruigte Vlei, CWT, Oct. 1938) ; SAM 19343 (Ruigte Vlei, CWT, Nov. 1938) ; AM/P 1793 (PHS, Oct. 1972).

Klein Brak River: SAM 19345 (Haalkraal, CWT, Nov. 1938)

PSEUDOBARBUS ASPER

BMNH 1909.12.8:10. Holotype (Groot R., Gamtoos System, South African Museum)

BMNH 1909.12.8.6-9 Paratypes (Le Roux R., Gourits System, South African Museum)

Gamtoos River System: (Groot River) SAM 19205 (Fullarton, Groot R., CWT Oct. 1938) ; SAM 19206 (Steytlerville, CWT Oct, 1938) ; AM/P 1744 (PHS June, 1972) ; AM/P 1745 (Steytlerville, PHS, June 1972) ; AM/P 3060 (Sandfort west, PHS, July 1975) ; AM/P 3064, (Groot River Poort, PHS July, 1975) ; AM/P 3065 (Bucklands, PHS, July 1975); AM/P 3066 (Weymouth PHS, July 1975); AM/P 3456 (Wit R., 1st Drift, PHS, Oct. 1975) ; AM/P 3458 (Wit R., Armansvriend, PHS Oct. 1975) ; AM/P (Goedehoop, D. Heard, Oct. 1976) ;

Gourits River System: SAM (10664 (Le Roux R.,) ; SAM 10673 (Grobbelaars R.,) ; SAM 14284 (Leeus R., S.H. Haughton, 1916) ; SAM 18954 (Grobbelaars R., KHB, Oct. 1937) ; SAM 18957 (Langtouw R., KHB, Oct. 1937) SAM 18959 (Zanddrift, KHB Oct. 1937) ; SAM 18951 (Rossel R., KHB, Oct. 1937) ; SAM 18952 (Meiringspoort, KHB, Oct. 1937) ; SAM 18962 (Buffels R., KHB, Oct. 1937) SAM 18965 (Touws R., KHB, Oct. 1937) ; SAM 18941 (Buffalo R., KHB, Oct. 1937) ; SAM 19497 (Doorn R., KHB, April 1939) ; SAM 18990 (Weiders R., KHB, Feb. 1938) ; SAM 18991 (Walsch R., KHB, Feb. 1938) ; SAM 18949 (Gamka Poort, KHB, Oct.1937). SAM 18956 (Moeras R., KHB, Oct. 1937) ; AM/P 42 (Meiringspoort, RAJ, Nov. 1960) ; AM/P 376 (ditto, Oct. 1960) ; AM/P 607 (ditto, Oct. 1961) ; AM/P 1695 ; 1696 ; (Jan Muller Bridge, PHS, April 1972) ; AM/P 1699 (Van Wyksdorp, PHS, April, 1972) AM/P 1703 (Gamka R., PHS, April, 1972) ; AM/P 1786 ; 1787 ; 1788 ; (Meiringspoort PHS, Sept. 1972) ; AM/P 1943 ; 1945 (Meiringspoort, PHS, April 1973) ; AM/P 1956 (Olifants R., R.E. Stobbs, Sept. 1972) ; AM/P 2661 (Diep R., PHS, Jan. 1975) ; AM/P 2663 (Rusoord, PHS, Jan. 1975) ; AM/P 2668 (Kruis R., PHS, Jan. 1975) ; AM/P 4279 (Jan Muller Bridge, M. Currey, Mar. 1977) ; AM/P 4281 (Van Wyks Dorp, M. Currey, Mar. 1977) ; AM/P 4289 (Meiringspoort, M. Currey, Mar. 1977) ; AM/P 6561 (Kamanassie R., ST, Aug. 1978) ; AM/P 6033 (Nels R., ST, Aug. 1978) AM/P 6045 ; 6052 (Olifants R., ST, Aug. 1978), AM/P 6055 (De Rust, ST, Aug. 1978) ; AM/P 6058 ; 6059 (Groot R., ST, Aug. 1978) ; AM/P 6062 ; 6065 ; 6066 ; 6068 ; 6070 ; 6072, (Meiringspoort, ST, Aug. 1978) ; AM/P 6078 (Kamanassie R., ST, Aug. 1978) ; AM/P 6085 (Grobbelaars R., ST, Aug. 1978) ; AM/P 6099 (Olifants R., ST, Aug. 1978) ; AM/P 6103 (Gourits R., ST, Aug. 1978) ; AM/P 6107 ; 6112 (Groot R., ST, Aug. 1978) ; AM/P 6115 (Touws R., ST, Aug. 1978) ; AM/P 6118 (Groot R., ST, Aug. 1978) ; AM/P 6123 (Gamka, ST, Aug. 1978) ; AM/P 6128 (Brak R., ST, Aug, 1978) ; AM/P 6131 ; 6133 (Jan Muller Bridge, ST, Aug. 1978) ; AM/P 6136 (Weiders R., ST, Aug. 1978) ; AM/P 6561 (Kamanassie R., ST, Aug. 1978) ; RUSI 75-139 (Kamanassie R.).

PSEUDOBARBUS BURCHELLI

Neotype: AM/P 7223 A (Trib. Tradouw R., 33° 56'50"S, 20° 42'39"E S. Thorne, 13 Dec. 1978).

Breede River System: SAM 4693 (Robertson, L. Keet) ; SAM 17621 (Wit R., Baineskloof, E.F. Steer) ; SAM 17422 (Tradouw R., KHB, Oct. 1925) ; SAM 18731 (Genadendal, KHB, Jan. 1937) ; SAM 18750 (Wit R., Baineskloof, L. Boonstra, Mar. 1937) ; SAM 18751 (Slanghoek R., KHB, Mar 1937) ; SAM 18937 (R. Sonderend, H.G. Wood, Sept. 1937) ; SAM 18987 (Buffeljags R., KHB., Feb. 1938) ; SAM 22279 (Hex R., A.C. Harrison) AM/P 482 (Wit R., (Baineskloof, RAJ, Nov. 1960) ; AM/P 1411 (Wit R., Baineskloof, F.L. Farquharson April 1967) ; AM/P 1566 (Keisers R., K. van Rensburg, Dec. 1967) ; AM/P 1791 (Keisers R., PHS,Oct. 1972) ; AM/P 2031 (Tradouw R., R.E. Stobbs, 1973) AM/P 2077 (Kabous R., PHS, Dec. 1973) ; AM/P 2079 (Klipplaas R., PHS, Dec. 1973) ; AM/P 3463 ; 3465 (Wit R., Baineskloof, PHS, Oct. 1975) ; AM/P 3840 (Spreeudrifspruit R., I.Gaigher, Nov. 1976) AM/P 4972 (Keisers R., C. Stewart, Sept. 1977) ; AM/P 5475 (Kogmanskloof R., C. Stewart, Nov. 1977) ; AM/P 5911 ; 5912 ; 5913 ; 5914 ; 5915 (Keisers R., W.C.N. Esterhuizen, 1977-1978) ; AM/P 6028 (Helderstroom T., S.J. McVeigh, June 1978) ; AM/P 7205 ; 7220 (Wit R., Baineskloof, ST, Feb. 1979) ; AM/P 7223 (Tradouw R., ST, Dec. 1978) ; AM/P 7224 (Slang R., ST, Dec. 1978) ; AM/P 7443 (Breede R. PHS) ; AM/P 7444 (Spreeudrifspruit R., PHS, Nov. 1976) ;

Kaffirkuils River: SAM 18988 (Vette R., KHB, Feb. 1938) ; AM/P 7393 (Kruis R., ST, Dec. 1978)

Duivenhoks River: SAM 19345 (KHB, Oct. 1938) ; AM/P 3472 (PHS, Oct. 1975) ; AM/P 6138 (ST, Aug. 1978) ; AM/P 7227 (ST, Dec. 1978).

Kars River: SAM 18979 (KHB, Dec. 1937)

Grashoek River: SAM 18978 (KHB, Dec. 1937)

Nieuwejaars River: SAM 18981 (KHB, Dec. 1937)

PSEUDOBARBUS BURGI

Holotype: BMNH: 1901 -2.11 : 14-16 (taken to be number 14) (Berg River, Paarl division, Mr Brown)

Paratypes: BMNH 1901 -2.11 : (14) 15-16

(Note: type material was selected from SAM 4696)

Berg River System: SAM (4696 (Paarl, Mr Brown) ; SAM 18094 (Groot Drakenstein, A.C. Harrison, 1930) ; SAM 18608 (Lemiet R., KHB 1936) SAM 18747 (Groot Drakenstein, KHB, Feb. 1937) ; SAM 19027 (Bushmans R., KHB, Sept. 1938) ; SAM 18935 (Twenty four R., KHB, Aug. 1937) ; AM/P 1578 ; 1579 (Krom R., C.M. Gaigher, Feb. 1971) ; AM/P 2076 (Krom R., PHS, Dec. 1973) AM/P 4041 (Wemmershoek, PHS, June. 1977) ; AM/P 6144 ; 6148 (Franschoek R., ST, Nov. 1978) ; AM/P 6153 ; 6156 (Wemmershoek, ST, Nov. 1978) ; AM/P 6170 (Wemmers R., ST, Nov. 1978) ; AM/P 7211 (Boesmans R., ST, Feb. 1979).

Eerste River: SAM 4695 (Peringuey) ; SAM 5090 (Dr Kruger) ; SAM 22746 (Stellenbosch Dam, A.C. Harrison).

Verlorevlei River: AM/P 1874 (Berg Valley Stream, PHS, Feb. 1973) ; AM/P 1875 (Kruis R., PHS, Feb. 1973) ;

PSEUDOBARBUS PHLEGETHON

Syntypes: SAM 18767 (25 specimens Boontjies R., Olifants River System, 32° 36'S, 19° 04'E, KHB April 1937) ; SAM 19003 (29 specimens ditto, April 1938) ; SAM 22484 (?).

Olifants River System: SAM 22479 (Thee R., KHB, April (1949?)) ; SAM 22483 (KHB, Feb. 1939) ; AM/P 722 (Thee R., K. van Rensburg, Jan, 1964) AM/P 1394 (Keerom, K. van Rensburg, Jan. 1964) ; AM/P 1399 Noordhoeks R., F.L. Farquharson, April 1967) ; AM/P 1820 ; 1821 ; (Thee R., D. Heard, Sept. 1972) ; AM/P 1852 (Jan Diessels R., PHS, Jan. 1973) ; AM/P 1863 (Noordhoeks R., PHS, Feb. 1973) ; AM/P 1868 (Thee R., PHS, Feb. 1973) ; AM/P 1880 (Noordhoeks R., K. van Rensburg, Mar. 1965) ; AM/P 2053 (Noordhoeks R., PHS, Oct. 1973) ; AM/P 2054 (Driehoek R., PHS, Oct. 1973) AM/P 7366 (Driehoek R., PHS, Dec. 1978).

PSEUDOBARBUS QUATHLAMBAE

Lectotype: SAM 19019 (Umkomazana River, near Himeville, Natal, A.M. Copland, S.Vaughn, Aug. 1937.

Paralectotypes: SAM 19018 (ditto) ; NM 1416 (ditto).

Orange River System: AM/P 1540 ; 3477 (Tsoelikana R., A. Tedder, Nov. 1970) ; AM/P 1877 ; 3476 ; 3478 (Tsoelikana R., A. Tedder, April 1972) ; AM/P 1823 ; 1824 (Tsoelikana R., PHS, Jan. 1973) ; AM/P 3473 (Tsoelikana R., PHS, Oct, 1975) ; AM/P 3474 (Tsoelikana R., D. Rondorf, Nov. 1974) ; AM/P 3475 (ditto, Jan, 1975) ; AM/P 3479 (Moremoholo R., D. Rondorf, July 1975) ;

AM/P 3480 (Senqu R., D. Rondorf, Aug. 1975).

PSEUDOBARBUS TENUIS

Lectotype: SAM 18953 (Nels River (?) between De Rust and Rust-en-Vrede, 33° 28'S., 22° 27'E, KHB, 24 Oct. 1937.)

Paralectotypes: SAM 18953 (313 specimens, ditto per lectotype) SAM 18946 (220 specimens, Seven Weeks Poort, 33° 25'S, 21° 24'E, KHB, Oct. 1937) ; SAM 18969 (specimens Grobbelaars R., 33° 26'S, 22° 15'E, KHB 24 Oct, 1937) ; SAM 18970 (Langtouw R., 34° 01'S, 21° 45'E, KHB, 26 Oct. 1937) SAM 18970 (Langtouw R., 34° 01'S, , 21° 45'E, KHB, 26 Oct, 1937) ; SAM 10667 (3 specimens Le Roux R., 33° 25'S, 22° 15'E.)

BMNH 1938-2.28 : 7-8 (tributary Olifants R., KHB)

Gourits River System: SAM 19535 (Waterval, Kamanassie, KHB, Jan, 1940) ; SAM 22332 (Moeras R.,) ; AM/P 608 (Meiringspoort, RAJ, Oct. 1961) ; AM/P 1569 (Meiringspoort, C.M. Gaigher, Nov. 1970) ; AM/P 1587 (Waterkloof R., C.M. Gaigher, May 1971) ; AM/P 1935 (Wilge R., PHS, April 1973) ; AM/P 2081 (Wilge R., PHS, Dec. 1973) ; AM/P 2664 (Rusoord, PHS, Jan. 1975) AM/P 2666 (Waterkloof R., xx, PHS, Jan. 1975 ; AM/P 2667 (Kruis R., PHS, Jan 1975) ; AM/P 2945 (Meiringspoort, RAJ, Nov. 1960) ; AM/P 2946 (Meiringspoort, RAJ, Oct. 1960) ; AM/P 3455 (Wilge R., PHS, Oct. 1975) ; AM/P 4288 (Meiringspoort, M. Currey, Mar. 1977) ; SAM 4809 (Bo-Buffelskloof R., S. Rudd, April 1977) ; AM/P 4920 (Seven-weeks-poort, R. Boycott, Jan. 1977) ; AM/P 6030 (Kruis R., ST., Aug. 1978) ; AM/P 6031 ; 6032 ; 6036 ; 6038 (Nels R., Gamka, ST. Aug. 1978) ; AM/P 6060 (Groot R., ST. Aug. 1978) ; AM 6063 ; 6064; 6067 ; 6071 (Meiringspoort, ST., Aug. 1978) ; AM/P 6079 ; 6080 ; 6083 ; 6084 (Grobbelaars R., ST., Aug. 1978) ; AM/P 6081 ; 6082 Le Roux R., ST. Aug. 1978) ; AM/P 6121 (Seven-weeks-poort, ST. Aug. 1978) AM/P 6161 (Jan Muller Bridge, ST. Aug. 1978).

x Waterkloof R. 33° 20'S, 21° 50'E; xx Waterkloof R., 33° 17'S, 22° 15'E

Keurbooms River: AM/P 2944 (Diep R., PHS, Sept. 1972) ; AM/P 3462 (Diep R., PHS, Oct. 1975) ; AM/P 3822 (Bitou R., D. Heard, Oct 1976) ; AM/P 3824 (Diep R., D. Heard, Oct. 1976) ; AM/P 3825, (Voogste R., D. Heard, Oct. 1976) ;

APPENDIX 2

Osteological material examined. Entries recorded as: museum no., no. of specimens, locality. The collector, date of collection and river system of redfin material are given in appendix 1. Abbreviations as in appendix 1.

A. Redfin Material

BARBUS CALIDUS

AM/P 1371, 3 (Rondegat R.) ; AM/P 1871, 6 (Rattels R.) ; AM/P 1844, 1 (Tra-Tra R.) ; AM/P 7441, 5 (Tra-Tra R.)

BARBUS ERUBESCENS

AM/P 2044. 4 (Twee R.) ; AM/P 2074, 2 (Suurvlei R.) ; AM/P 1388, 2 (Twee R.) ; AM/P 7442, 9 (Twee R.) ;

PSEUDOBARBUS AFER

AM/P 609, 3 (Wit R. Sundays) ; AM/P 676, 2 (Loerie R., Gamtoos) ; AM/P 745, 1 (Swartkops R.) ; AM/P 1376, 5 (Couga Dam) ; AM/P 1739, 1 (Kromme R.) ; AM/P 1790, 4 (Knysna R.) ; AM/P 2652, 1 (Bloukrans R.) ; AM/P 2654, 3 (Bloukrans R.) ; AM/P 2656, 4 (Groot R.) ; AM/P 3807, 3 (Kabeljous R.) ; AM/P 3815, 4 (Kromme R.) ; AM/P 3826, 8 (Keurbooms R.) AM/P 7465, 8 (Wit R. Sundays).

PSEUDOBARBUS ASPER

AM/P 376, 2 (Gourits R.) ; AM/P 1696, 58 (Gourits R.) ; AM/P 3060, 5 (Groot R., Gamtoos) ;

PSEUDOBARBUS BURCHELLI

AM/P 1566, 3 (Keisers R,) ; AM/P 3463, 2 (Wit R.) ; AM/P 7443, 6 (Breede R.) ; AM/P 7444, 8 (Spreeudrifspruit).

PSEUDOBARBUS BURGI

AM/P 1578, 1 (Kromme R.) ; AM/P 1874, 3 (Verlorevlei R.) ; AM/P 1875, 4 (Verlorevlei R.); AM/P 2076, (Kromme R.) ; AM/P 4041, 1 (Wemmershoek Dam).

PSEUDOBARBUS PHLEGETHON

AM/P 722, 2 (Thee R.) ; AM/P 1863, 14 (Noordhoeks R.).

PSEUDOBARBUS TENUIS

AM/P 1935, 1 (Wilge R.) ; AM/P 2659, 3 (Keurbooms R,) ; AM/P 2667 3 (Kruis R.) ; AM/P 2944, 2 (Keurbooms R,) ; AM/P 7456, 1 (Gourits R System).

PSEUDOBARBUS QUATHLAMBAE

All material from Tsoelikana R. ; AM/P 1877, 1 ; AM/P 3474, 1 ; AM/P 3476, 1 ; AM/P 3479, 1.

B. Other Cyprinids

BARBUS AFROHAMILTONI

AM/P 4408, 2 (Nsimbi Pan, Pongola R. floodplain, H.Kok, Dec. 1976).

BARBUS AFROVERNAYI

AM/P 3313, 3 (Zambezi, B.v.d. Waal, Aug. 1975).

BARBUS ANDREWI

SAM 18936, 2 (Riviersonderend,

BARBUS ANNECTENS

AM/P 4410. 3 (Nsimbi Pan, Pongolo R. floodplain, H. Kok, Dec. 1976).

BARBUS ANOPLUS

AM/P 838, 2 (Limpopo, Tvl. P.f.1., 1965) ; AM/P 361, 2 (Fish, R.A. Jubb, Apr. 1962) ; AM/P 585, 4 (Upper Caledon - Orange, R.A. Jubb, Feb. 1965) ; AM/P 901, 2 (Selons - Olifants - Limpopo, Tvl. P.F.I.) ; AM/P 1697, 3 (Groot-Gouritz, PHS, Apr. 1972) ; AM/P 1802, 2 (Kowie R., PHS, Aug. 1972) ; AM/P 1806, 2 (Orange, A.A. Marais, July 1972) ; AM/P 2061, 2 (Breekrans - Groot- Doring - Olifants, Oct. 1973) ; AM/P 2707, 3 (Little Caledon - Orange, PHS, Oct. 1974) 1, (Molteno, Orange, P.Coetzee.)

BARBUS ARGENTEUS

AM/P 904, 2 (Umtitje - Incomati, Tvl. P.F.I., 1965) ; AM/P 5553, 2 (Pongola - Maputo, R. Mc. C. Pott, June 1967).

BARBUS BARBUS

AM/P 7445, 2, (Tinis R., Roumania, P. Banarescu, Oct. 1964).

BARBUS BARNARDI

AM/P 1500, 1 (Okavango Swamps, I. Gaigher, Apr. 1959) ; AM/P 1320, 2 (Luombe R. Congo, G. Bell-Cross, Apr. 1970).

BARBUS BREVIPINNIS

AM/P 905, 2 (Sabie-Incomati. P.F.I., 1966).

BARBUS CAMPTACANTHUS

AM/P 3101, 1 (Olonou, Ceele Miane, Cameroun, Mus. Roy. Afr. Cent. Terv. Sept. 1971).

BARBUS CAPENSIS

AM/P 1370, 3 (Noordhoek - Olifants, F. Farquharson, Apr. 1967).

BARBUS EUTAENIA

AM/P 358, 2 (Gairezi (Lower Zambezi) RAJ, May 1958) ; AM/P 7446, 2 (Okavango, PHS, Sept. 1975).

BARBUS FASCIOLATUS

AM/P 7443, 3 ; AM/P 7448, 1 (Okavango, PHS, Sept. 1975).

BARBUS GURNEYI

AM/P 847, 2 (Upper Otimati Natal Parks Board, Apr. 1964) ; AM/P 7449, 2 (Kranskloof, M. Coke, Sept. 1977).

BARBUS HAASIANUS

AM/P 3156, 3 (Upper Zambezi, B.v.d. Waal, Sept. 1975).

BARBUS HOLUBI

AM/P 3638, 5 (Seekoei spruit, Orange, J. Cambray, July, 1975) ; AM/P 1483, 5 (Telle-Orange, Cape Dept. Nat. Cons. Sept. 1970).

BARBUS HOSPES

AM/P 1580, 1 (Orange, C.M. Gaigher, May 1971) ; AM/P 2066, 3 (Orange PHS, Oct. 1973).

BARBUS cf. KIMBERLEYENSIS

AM/P 7450, 2 (Hardap dam, I. Gaigher, Apr, 1975)

BARBUS LINEOMACULATUS

AM/P 1982, 4 (Sabie-Lundi, F. Junor, 1963) ; AM/P 2005, 3 (Lake Kariba, Middle Zambezi, PHS, Aug. 1973).

BARBUS MACROTAENIA

AM/P 7451, (Lower Zambezi area).

BARBUS MARAQUENSIS

AM/P 877, 3 (Pongola, Natal Parks Board, May 1964)

BARBUS MATTOZI

AM/P 4151, 2 (Trib. Tuli - Limpopo, B. Donnelly, Oct. 1974) ; AM/P 7452 1 (Limpopo R.).

BARBUS MERIDIANALIS PETENYI

AM/P 2190, 2 (N.E. Roumania, P. Banarescu, Nov. 1958).

BARBUS MOTEBENSIS

AM/P 842, 1 (Treur R. - Limpopo, Tvl. P.F.I. 1965) ; AM/P 6386, 3 (Limpopo, I. Gaigher, May 1968).

BARBUS MULTILINEATUS

AM/P 734, 2 (Lake Mweru, Zambia, J.F.R.O., Jan. 1960).

BARBUS NATALENSIS

AM/P 243, 3 (Umzimkulwana R., Sept. 1957)

BARBUS PALLIDUS

AM/P 849, 2 (Steelpoort - Limpopo, Tvl. P.F.I. 1965) ; AM/P 1404, 3 (Couga Dam - Gamtoos, F. Farquharson, July 1967) ; AM/P 1543, 2 (Bronkhorstspruit - Limpopo R., I. Gaigher June 1969) ; AM/P 1888, 4 (Kowie, PHS, March 1973).

BARBUS PALUDINOSUS

AM/P 278, 3 (Vaal R., RAJ, June 1961) ; AM/P 2671, 1 (Fish R. Orange,

I. Gaigher, Jan, 1975) ; AM/P 3588, 4 (Hardap Dam. Fish R. - Orange, I. Gaigher, Oct. 1974).

BARBUS POECHII

AM/P 946, 2 (Okavango, I. Gaigher, Apr. 1969).

BARBUS POLYLEPIS

AM/P 283, 3 (Hartebeestpoortdam - Limpopo. A.A. Groenewald, Sept. 1962).

BARBUS PUELLUS

AM/P 1195, 1 (Kabompo - Upper Zambezi, G. Bell-Cross, 1961).

BARBUS RADIATUS AURANTIAUIS

AM/P 3203 and 2410, 5 (Upper Zambezi, B.v.d. Waal, Sept. 1975, Nov. 1973).

BARBUS RADIATUS

AM/P 7454, 1 (Sabie-Sand, Incomati R., 1974; AM/P 7455, 2 (Okavango).

BARBUS SERRA

AM/P 1845 and 1856, 4 + 2 (Tra-Tra R. - Olifants, PHS, Jan. 1973).

BARBUS TANGANDENSIS

AM/P 594, 2 (Kabompo - Upper Zambezi, G. Bell-Cross, 1961).

BARBUS THAMALAKANENSIS

unaccessioned, 3 (Upper Zambezi, PHS, Sept. 1975)

BARBUS TOPPINI

AM/P 766, 1 (Incomati, Natal Parks Board, 1961) ; AM/P 3748, 10 (Olifants - Limpopo, I. Gaigher, June 1968).

BARBUS TREURENSIS

AM/P 4727, 1 (Limpopo, Tvl. P.F.I. 1970) ; AM/P 1536, 1 (Limpopo, Tvl. P.F.I.).

BARBUS TREVELYANI

AM/P 126, 1 (Buffalo R., RAJ, Mar. 1958) ; AM/P 2586, 3 (Keiskamma, I. Gaigher, Oct. 1972) ; AM/P 7458, 1 (Tyume R., Keiskamma R., System, AM/P 7459 (Tyume R., Keiskamma R. System).

BARBUS TRIMACULATUS

AM/P 810, 3 (Umshandige Dam, Limpopo R., RAJ, Apr. 1958) AM/P 550, 3 (Amanzimnyama, F. Farquharson, Sept. 1959) ; unaccessioned, 1 (Sand R. Incomati).

BARBUS UNITAENIATUS

AM/P 1243, 2 (Shangani, Mid. Zambezi, R.A. Jubb, July 1959,) ; AM/P 3577, 2 (Limpopo, Tvl. P.F.I., Sept. 1968) ; AM/P 7461, 1 (Pampoenpoort Dam, Rhodesia B. Donnelly Oct, 1975).

BARBUS VIVIPARUS

AM/P 395. 3 (Umzimkulwana, R.A. Jubb, Sept. 1957) ; AM/P 3242, 3 (Sangwali - Linyati, B.v.d. Waal, Sept. 1975).

BARILIUS ZAMBEZENSIS

AM/P 3766, 6 (Incomati , I. Gaigher, Apr. 1967).

ENGRAULICYPRIS BREVIANALIS

AM/P 1836, 2 (Orange, C. Gaigher, May 1971) ; AM/P 7462, 2.

LABEO ALTIVELIS

AM/P 75, 3 (Middle Zambezi, Bernard Carp Exped. July 1950) ; AM/P 36, 2 (Sabi-Lundi, Bernard Carp, Exped. June 1950).

LABEO CAPENSIS

AM/P 1384, 3 (Orange R) ; AM/P 1387, 3 (Orange R. C.M. Gaigher).

LABEO CYLINDRICUS

AM/P 44, 3 (Mtilkwe, R. R.A. Jubb, June 1958) ; AM/P 7463, 3 (Pongola)

LEUCASPEUS DELINEATUS

AM/P 2232, 2 (Inare, Bouhemia).

PHOXINUS PHOXINUS

AM/P 2244, 2 (Roumania, P. Banarescu, June 1962).

VARICORHINUS NASUTUS

AM/P 30, 1 (Gairezi R., Rhodesia, R.A. Jubb, May 1958).

VARICORHINUS PUNGWEENSIS

AM/P 1284, 1 (Pungwe R. D.C.H. Plowes, Sept. 1965).

APPENDIX 3

The
J. L. B. SMITH INSTITUTE OF
ICHTHYOLOGY

SPECIAL PUBLICATION
No. 13

A NEW *BARBUS* SPECIES (PISCES, CYPRINIDAE) FROM THE OLIFANTS RIVER SYSTEM, WESTERN CAPE PROVINCE, SOUTH AFRICA

BY
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30 August 1974

ABSTRACT

A new species of small *Barbus* is described from the Olifants River System, western Cape Province, South Africa. The new species is restricted to a single tributary complex of the river system and appears closely related to *B. calidus*. Diagnostic features include pharyngeal teeth formulae, colour pattern, and dorsal and anal fin ray characteristics.

A NEW *BARBUS* SPECIES (PISCES, CYPRINIDAE) FROM THE OLIFANTS RIVER SYSTEM, WESTERN CAPE PROVINCE, SOUTH AFRICA

by

P. H. SKELTON[1]

Barbus calidus Barnard, one of five freshwater fish species endemic to the Olifants River System, western Cape Province, South Africa, is exceptional for at least two reasons. It is the only "red fin"[2] *Barbus* species with a strong, serrated last unbranched ray in the dorsal fin, and it has six branched rays in the anal fin. Surveying the Olifants River system for the Cape Nature Conservation Department in 1964, Mr K.J. van Rensburg collected and submitted to the Albany Museum specimens which could be referred to *B. calidus* except that, on initial analysis, the last unbranched dorsal ray was not serrated. Further collecting has shown that the aberrant fish are geographically restricted to a single tributary complex of the river system. There is no eco-physical or eco-chemical evidence for causing the observed morphological differences and the species is here described as new.

All measurements were made with vernier calipers, usually with the aid of a Wild M5 stereoscopic microscope. Measurements and scale counts follow Hubbs and Lagler (1947:8 – 15) with the following exceptions:

(1) head length is taken from the anterior tip of the premaxillary symphysis (with the premaxilla retracted), or from the upper labial groove (in specimens with mouth extended), to the posterior edge of the operculum, excluding the opercular membrane;

(2) predorsal and postdorsal lengths are measured along the horizontal midline, from the vertical line through the anterior margin of the base of the dorsal fin;

(3) the first caudal vertebra is taken as the first to show closure of the haemal arch; and

(4) predorsal count is the number of (oblique) scale rows anterior to the dorsal fin.

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[1] Albany Museum, Grahamstown, 6140, Republic of South Africa.

[2] A group name given to several species of small *Barbus* inhabiting the southern and south-west Cape coastal rivers, characterized by having red patches on their fins.

The following two measurements are not defined by Hubbs and Lagler (1947); distance between pectoral and pelvic fins is taken along the ventral midline between the points opposite the posterior margins of the bases of the fins; the distance pelvic to anal fins is taken along the ventral midline from a point opposite the posterior margin of the bases of the pelvic fins to the anterior margin of the base of the anal fin. Vertebral counts include the Weberian apparatus as four and the ultimate ural centrum as one. Dorsal Pterygiophore Intercept (D.P.I.) and Anal Pterygiophore Intercept (A.P.I.) is the vertebral count up to and including that vertebra opposite or anterior to the spine of the respective first pterygiophore. Scale radii refer only to primary radii (i.e. reaching from or in the immediate vicinity of the focus to the margin of the scale); the number of radii for each fish is the mean of five scales from four different body regions, viz., anterior above and below the lateral line, posterior at the level of the anal fin above and below the lateral line. Scales showing a diffused focus were not used in radii counts.

Barbus erubescens new species. (figs. 1 – 3)
Twee River Redfin. (Twee Rivier Rooivlerk)

Holotype: Male 84 mm SL, AM/P 2424
Suurvlei River, Olifants River system, western Cape Province, South Africa, 32°38'56"S., 19°12'21"E., collected by P.H. Skelton and A. Coetzer, 8 December, 1973.

Paratypes: 39 Adult Males, 59.5 – 95 mm SL, collected with the holotype
21 AM/P 2425; 6 RUSI 74 – 268; 6 BM(NH) 1974.6.13:1 – 6; 6 MACT 192175 – 192180.

5 Juveniles, 30.5 – 35.6 mm SL, collected from the Twee River, Olifants River System, western Cape Province, South Africa, 32°41'52"S., 19°18'40"E. by P.H. Skelton, 10 October, 1973. 2 AM/P 2426; 1 RUSI. 74 – 266; 1 BM(NH) 1974.6.13:9; 1 MACT 192171.

5 Juveniles, 35 – 53.75 mm SL collected from the Twee River, Olifants River system, western Cape Province, South Africa, 32°41'35"S., 19°17'23"E., by P.H. Skelton, 6 October, 1973. 2 AM/P 2427; 1 RUSI 74 – 265; 1 BM (NH) 1974.6.13:10; 1 MACT 192172.

5 Females, 66.2 – 81 mm SL, collected from the Twee River, Olifants River system, western Cape Province, South Africa, 32°41'15"S., 19°16'47"E., by P.H. Skelton, 11 October, 1973. 2 AM/P 2428; 1 RUSI 74 – 267; 1 BM(NH) 1974.6.13:8; 1 MACT 192173.

5 Females, 67.5 – 77 mm SL collected from Middeldeur River Olifants River system, western Cape Province, South Africa, 32°40'34"S., 19°12'44"E., by P.H. Skelton and A. Coetzer, 8 December, 1973. 2 AM/P 2429; 1 RUSI 74 – 269; 1 BM(NH) 1974.6.13:7; 1 MACT 192174.

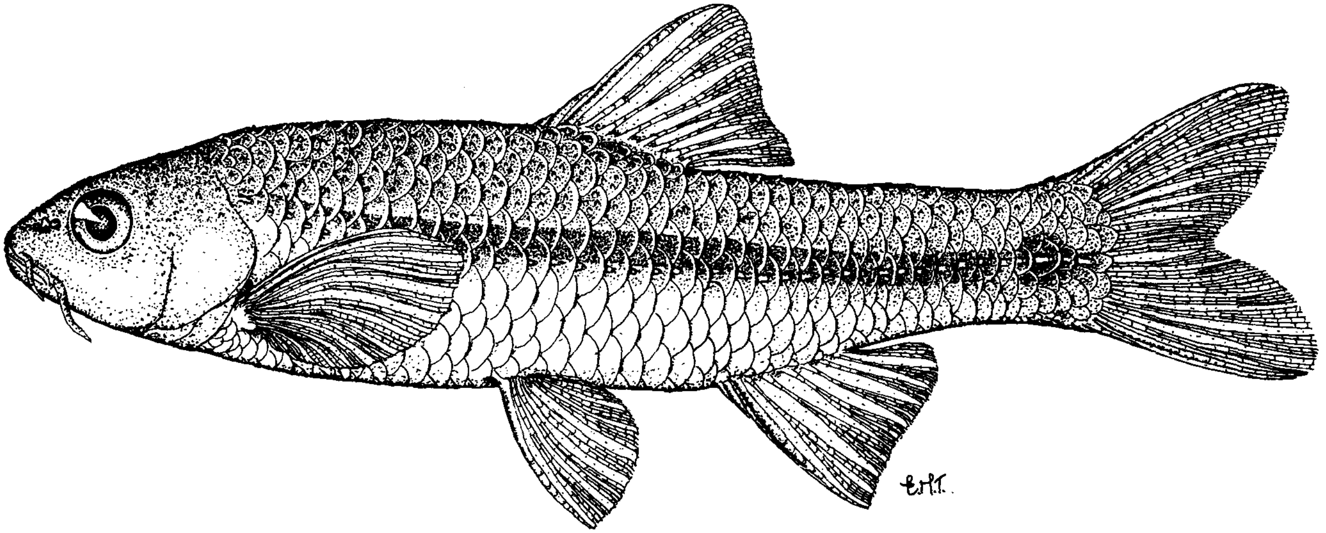

Fig. 1
BARBUS ERUBESCENS – HOLOTYPE

Diagnosis

Barbus erubescens is closely related to *B. calidus* Barnard, from which it differs in having the last unbranched dorsal ray with extremely weak or no serrations (*B. calidus* has strong serrations); eight branched rays in the dorsal fin (seven in *B. calidus*); more often seven and occasionally six or eight branched rays in the anal fin (usually six in *B. calidus*); an extra scale (four) between the lateral line and pelvic fins; one less pharyngeal tooth on the inner row of each lower pharyngeal bone (five in *B. calidus,* four in *B. erubescens*); typically one less vertebra (twelve) before the interception of the first dorsal pterygiophore; scales with about 13 primary radii (about 8 in *B. calidus*); the dorsal surface without spots or markings (*B. calidus* invariably with such markings); and breeding *B. erubescens* males develop an overall reddish hue (not observed in *B. calidus*).

Description

Based on the holotype (fig. 1) and 59 paratypes taken from the Twee, Middeldeur and Suurvlei Rivers, Olifants River system, western Cape Province, South Africa. Measurements and meristics are based on the holotype and 49 paratypes, pharyngeal teeth data and gillraker counts were obtained from ten other paratypes not included in the material used for meristic counts. Meristic values are given with the number of individuals in parenthesis with the symbol f.

A typical fusiform cyprinid fish with dorsal profile gently concave anteriorly from snout to dorsal fin and gently convex posteriorly from dorsal fin to the end of the caudal peduncle. The nape is sometimes prominent in adult specimens. The mouth is sub-terminal, the lips are thin and there are two pairs of well developed barbels. In adults the anterior barbel length equals the orbit diameter and the posterior barbel is about 1.3 times the orbit diameter.

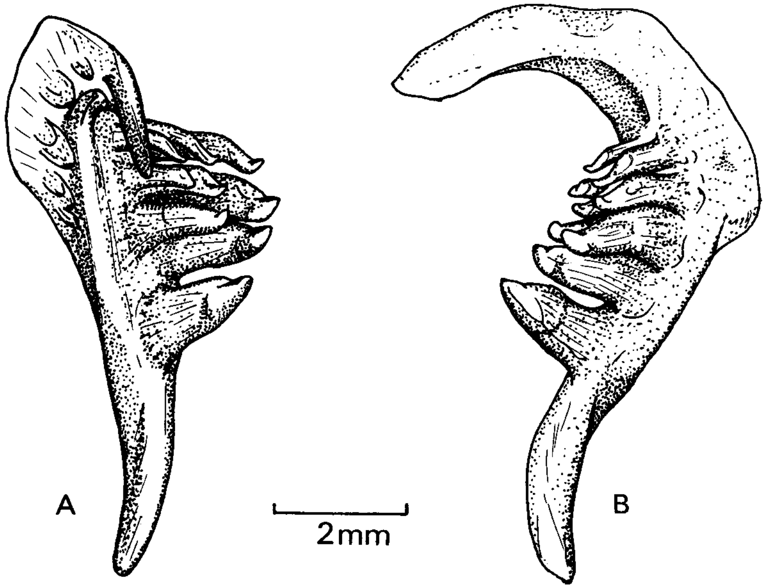

Fig. 2

Morphometric data as follows:

Measurement	x̄	S.D.	S.E.	Range
Standard length	68.54	17.83	2.52	30.5 – 95 mm

I. Proportional measurements as % standard length. (N = 50)

head length	27.46	1.11	0.16	25.56 – 31.15
predorsal length	52.83	1.2	0.17	50.3 – 55.56
postdorsal length	47.17	1.2	0.17	44.26 – 49.7
body depth	23.84	0.85	0.12	21.91 – 25.98
body width	16.42	0.91	0.13	14.43 – 18.28
pectoral – pelvic fins	23.4	0.93	0.13	21.36 – 25.16
pelvic – anal fins	18.17	1.43	0.20	15.15 – 21.19
caudal peduncle length	21.54	0.80	0.11	20.0 – 23.4
caudal peduncle depth	12.0	0.44	0.06	11.15 – 12.78
dorsal fin base	14.06	0.98	0.14	12.06 – 15.71
dorsal fin length	21.03	1.16	0.16	18.95 – 24.0
anal fin base	12.14	1.12	0.16	9.81 – 13.87
anal fin length	17.76	0.83	0.12	15.68 – 19.99
pectoral fin length	20.64	0.69	0.10	18.74 – 22.17
pelvic fin length	17.61	0.81	0.12	15.58 – 19.99

II. Proportional measurements continued; as % head length.

Measurement	x̄	S.D.	S.E.	Range
head depth	69.96	2.67	0.38	62.11 – 75.0
snout length	34.03	1.33	0.19	30.53 – 36.22
orbit diameter	26.20	2.49	0.35	22.17 – 32.35
post-orbit width	45.71	1.71	0.24	40.78 – 49.14
inter-orbit width	28.74	1.62	0.23	24.51 – 33.16

Scales radiately striated, with radii in both anterior and posterior fields of the scale; about 13 principal radii. Lateral line with modes of 37 (f23) and 38 (f19) and range 35 (f2), 36 (f1), 39 (f4), 40 (f1) scales; 5 (f17) or 6 (f33) scales between lateral line and pelvic fin; occasionally 3 (f6) or 5 (f1) but usually 4 (f43) scales between lateral line and pelvic fin; 4 (f47), occasionally 5 (f3) scales between lateral line and anal fin; 15 (f15), 16 (f24) or 17 (f10) scale rows around the caudal peduncle; and modally 15 (f20) or 16 (f20) [range 14 (f1), 17 (f8), 18 (f1)] predorsal scale rows.

Dorsal fin with iii (f31) or iv (f19) unbranched rays, the last unbranched ray flexible with no or, at most, few reduced serrations; 7 (f9) or 8 (f41) branched rays. The origin of the dorsal is slightly posterior to the origin of the pelvic fins. Anal fin (fig.3) not reaching caudal, with iii (f48) and occasionally iv (f2) unbranched rays; and 7 (f42) or occasionally 6 (f5) or 8 (f3) branched rays. Pectoral fins not reaching pelvics with 13 (f4), modally 14 (f30), 15 (f14) or 16 (f1) visible rays. Pelvic fins not reaching anal, with 7 (f6) and usually 8 (f44) visible rays.

Vertebral column with 37 (f29), 38 (f19), or 39 (f2) vertebrae; of which 18 (f15), 19 (f23), or 20 (f1) are precaudal and 18 (f15), 19 (f22) or 20 (f13) are caudal vertebrae. D.P.I. is 11 (f2), 12 (f37) or 13 (f11); A.P.I. is 20 (f3), 21 (f41) or 22 (f6). There are 6 (f25), 7 (f24) or 8 (f1) predorsal supraneural bones.

Gillrakers 2 or 3 + 6 - 9 on the anterior arch. Pharyngeal bones illustrated in fig. 2, each with three rows of teeth, formula 2,3,4, – 4,3,2. Teeth in outer rows small, the first (lying dorsal) recurved and hooked, the second blunt and obliquely conical at the tip. A similar trend is evident in each tooth row where the first teeth are slender with a recurved tip and the subsequent teeth are progressively blunter.

In ripe running males there are numerous small tubercles (approximately 0,2 mm in diameter and height), irregularly scattered on the dorsal surface of the head from the tip of the snout to the nape. These tubercles also occur laterally posterior to the orbit (on preopercle and opercle) petering out ventrally at the level of the ventral margin of the orbit. Tubercles are found on the scales dorsal to the lateral line from the nape to the tip of the caudal peduncle, especially anterior to the dorsal fin, where from 10 – 15 tubercles per scale have been recorded. Single open rows of tubercles occur on the rays of the dorsal and anal fins and dorsally on the rays of the paired fins. These latter tubercles appear to be less well developed than the body and head tubercles.

The following colour descriptions are derived from live aquarium specimens, preserved specimens, field notes and colour transparencies taken in the field. Sexual differences are restricted to intensity of pigmentation out of the breeding season; in ripe breeding condition only males have been observed with an overall reddish hue as described below.

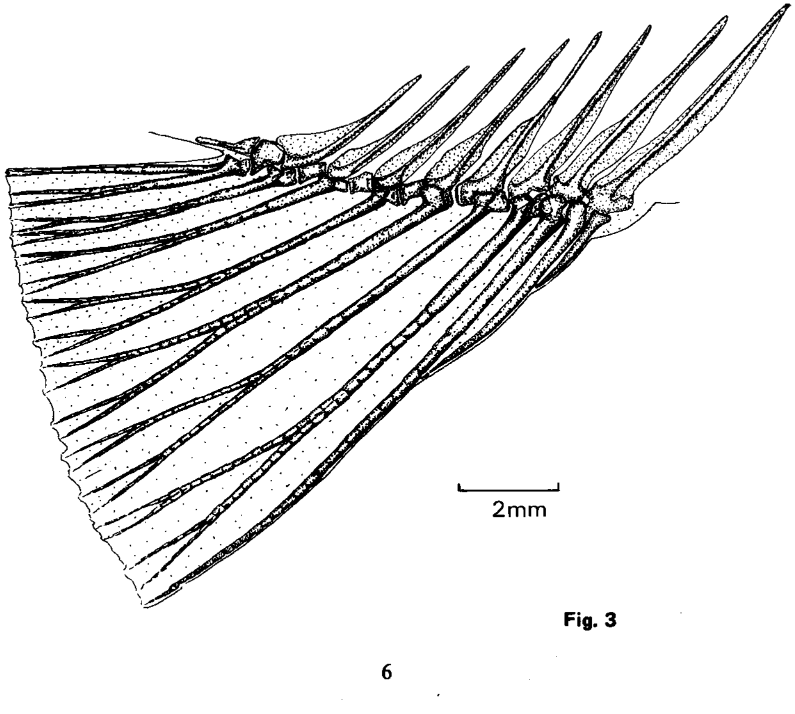

Fig. 3

In non-breeding condition members of this species are a pale brown to olive green dorsally (much faded in aquaria), the dorsal and ventral surfaces being without markings. A dark unbroken lateral band extends along the body from posterior to the head to the tip of the caudal peduncle. Tapering anteriorly the band runs immediately dorsal to the lateral line as far as a point opposite the anterior margin of the anal fin. It thereafter straddles the lateral line and ends, slightly expanded at the base of the caudal fin. The head is silvery, tinged greenish brown lateroventrally, olive greenish brown dorsally and metallic silvery gold over the operculum and suborbital area. The iris is golden shading to olive-golden peripherally, the pupil is black. The barbels are dark and often conspicuous. In adults the pectoral and pelvic fins are bright red basally, the colour extending onto the axils, the outer regions being hyaline. The anal and dorsal fins are less markedly red basally than the pectorals and pelvics. Distally the anal fin is hyaline, the dorsal and caudal fins have light brown rays with a transparent light brown membrane, fading distally.

In breeding condition the red fin-flashes become accentuated in both sexes although the males are more deeply pigmented. In addition the male assumes an overall reddish hue. The pectorals, pelvics and anal fins remain hyaline distally, the brown of the dorsal and caudal fins becomes suffused with red. The red suffusion affects the entire fish, particularly the posterior trunk region. The latero-ventral silvery gold of the head and body cavity underlies the reddish hue in those regions. The dark lateral band, although evident, is not accentuated.

In formalin fixed, n-propyl alcohol preserved specimens, the dorsal surface is uniformly pigmented without marks, the deeply pigmented lateral band tapers anteriorly and is usually unbroken. Laterally the scales are faintly outlined with melanophores, the dorsal and caudal fin rays are pigmented and the pectoral, pelvic and anal fin rays only slightly so basally.

Distribution and habitat

Barbus erubescens has been found only in the Twee River and its two source tributaries, the Middeldeur and Suurvlei Rivers. Downstream its distribution is limited by a vertical waterfall estimated to be about 12 metres high. This waterfall is found 800 metres upstream from the confluence of the Twee and Leeu Rivers, which combine to form the Groot River. This, in turn, joins the Doring before entering the Olifants mainstream. Immediately below the waterfall is a large and deep pool from which no small species have yet been collected, probably due to the presence of the exotic *Micropterus salmoides.* Extensive collecting throughout the Olifants River system indicates that *B. erubescens* is not found elsewhere where populations of indigenous fish, including *B. calidus,* exist (Gaigher, 1973; and pers. observ).

The Middeldeur is the major tributary of the Twee River, and rises sluggishly on an intermontane plateau at an altitude of about 880 metres. The highest point upstream where *B. erubescens* has been found is at the base of the fall line from this marshy plateau, at an altitude of about 770 metres. In the Suurvlei River a population was found some four and a half kilometres above the confluence with the Middeldeur and it is likely that the species exists for a further four to five kilometres upstream from this point.

Typically the Middeldeur, below the fall line, is from 10 to 15 metres wide and consists of pools broken by islands and interspersed with rocky runs. The river bed is sandy and rocky in nature. The Suurvlei, in contrast, is more sandy than rocky and from 3 to 7 metres wide. The Twee River is in effect an extension of the Middeldeur with a sandy rocky bed, well vegetated islands, cataracts, three substantial waterfalls (excluding the fall already mentioned) and several large and deep pools.

The water is invariably very clear although slightly peat stained; pH (October, 1973) 6.8 – 6.9; conductivity low (0.15 mg / ℓ NaCl). Temperature records kept by Mr E.J.A. Evans, a land owner on the Twee River, indicate that annual cycles fluctuate between 7.5°C and 27°C. Diurnal temperature fluctuation recorded during October, 1973, was between 2°C and 3°C.

Biology

Barbus erubescens is found in the pools and river channels singly or in aggregations of up to 30 or so individuals. Breeding occurs during the summer months and field observations indicate that congregation for this purpose in the pools probably occurs. A large school of the species netted in December, 1973, proved to be entirely ripe running males.

Etymology

The name *erubescens* is derived from Latin meaning "to become red" and refers to the colouration (of at least the males) during the breeding period.

Discussion

Barbus erubescens is the fifth endemic *Barbus* species in the Olifants River system. It is exceptional, however, in being the only fish species in the system that is apparently restricted to a single tributary complex. The only other fish species as yet found above the waterfall in the Twee, Middeldeur or Suurvlei Rivers is the small galaxiid, *Galaxias zebratus*. *B. erubescens* is interesting in another respect; it is (to the author's knowledge) the only African *Barbus* species to have a modal count of seven branched rays in the anal fin.

There is little doubt that the new species is closely related to *B. calidus* (fig.4). An interpopulation morphometric and meristic analysis of *B. calidus* was made to determine the geographic variation of that species. Several clear differences between the two species, as summarized in the diagnosis above, are recorded. In addition there are differences in the postorbital width (as percent head length, *B. calidus* 43.27, S.D. 2.0; *B. erubescens* 46.71, S.D. 1.5), and caudal peduncle depth (as percent SL, *B. calidus* 9.82, S.D. 0.5; *B. erubescens* 11.98, S.D. 0.5). A comparison of figures 1 and 4 indicates a difference in the orbit diameter of the two species. Allometric growth of the orbit diameter (Barnard 1943; and pers.obs.) complicates the analysis, but a mean from several populations of *B. calidus* of the orbit diameter as percentage head length (29.08, N = 180) does differ from the value for the type series of *B. erubescens* (26.2, N=50). Other trends in certain meristic characters are also evident, (e.g. caudal peduncle scale rows, pectoral fin rays) but these are not sufficiently marked to be diagnostic.

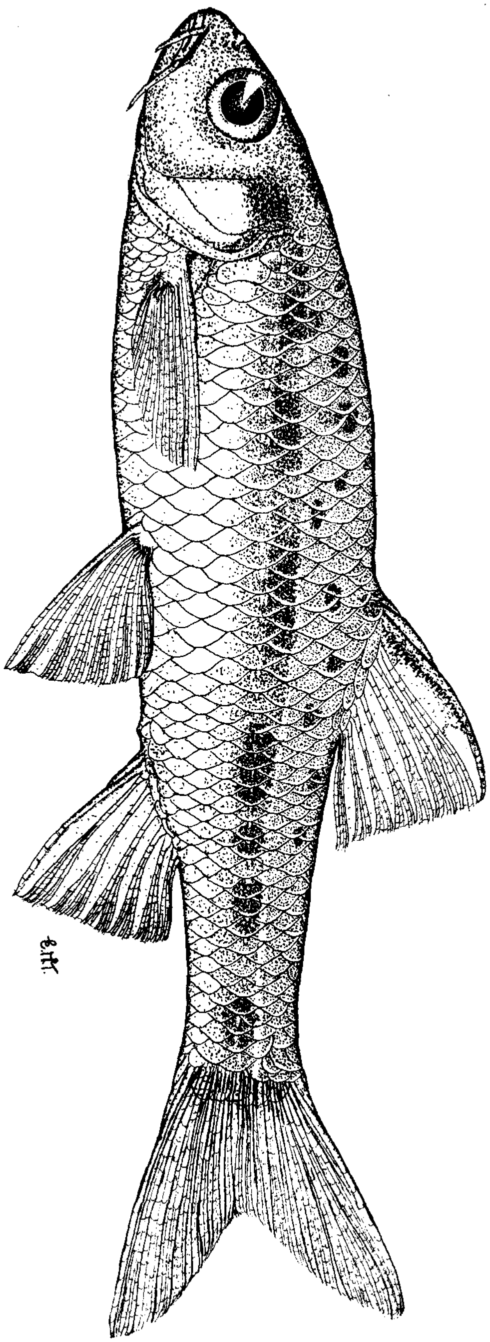

Fig. 4
BARBUS CALLIDUS

It is generally assumed that the "red fin" group of *Barbus* species are closely interrelated on account of the red fin colour character and geographical proximity. Barnard (1938, 1943) noted that *B. calidus* differed from all the other "red fin" species (*B. phlegethon, B. burgi, B. burchelli, B. tenuis, B. asper, B. afer)* in having a serrated last dorsal unbranched ray and six branched anal fin rays. Although the serrated unbranched dorsal ray character has been used extensively in *Barbus* classification, its phylogenetic significance is not altogether clear. Intra-specifically the character varies considerably in several species. Bell-Cross (1973) reported such variation in *B. eutaenia* from the Busi River in eastern Rhodesia and Mozambique, and Jubb (1967) mentions similar variation in *B. andrewi* and *B. trevelyani.* Such variation, *a priori,* might well be a result of differential environmental effects, as, for example, recorded by Greenwood (1964). However, as far as has been determined, the Twee River and its tributaries are not physically or chemically distinct from the rest of the Olifants River system. It will be difficult to determine to what extent, if any, bio-ecological differences (e.g. the lack of piscine predators and competitors) might be responsible for the above observed morphological differences.

The majority of African *Barbus* species have, as a rule, five branched rays in the anal fin. A few large species from Morocco, North Africa, have six anal branched rays (Boulenger 1911), as do *B. andrewi* and *B. calidus* from the south west Cape Province, South Africa (Barnard 1938). The North African species have affinities with European fishes (Banister 1973) and at present it is assumed that there is no close relationship between the large *B. andrewi* and the small *B. calidus.* Barnard (1943) illustrates a typical anal fin of *B. calidus* and indicates that there are exceptional individuals of that species with seven branched rays in the anal fin. In the present study it has been found that approximately 7% of *B. calidus* populations have seven branched rays, whereas up to 80% of *B. erubescens* populations are thus characterzied. The fact that there is a corresponding pterygiophore increase (fig. 3) shows that the increase is not merely due to a splitting of the last ray. There is no significant difference in relative basal length of the anal fins of the two species.

The most ventral pharyngeal tooth on the inner rows are vestigial in *B. calidus* and absent in *B. erubescens.* (fig. 2). The usual pharyngeal tooth formula for African *Barbus* species is 2,3,5, – 5,3,2, (Matthes 1963; Banister 1973) and it is reasonable to suppose that *B. erubescens* shows a derived condition. Studies have not, as yet, been carried out to investigate whether or not there is a corresponding food or feeding difference between the two species.

In the present study there is no evidence that the number of primary radii increases with age. Barnard (1943) found that for *B. calidus* the number of "striae" increases from 4 – 5 in juveniles to 12 – 14 in adults. Although he stated that "striae" meant "striae on exposed (posterior) field of scale (main striae, not short intercalaries)", it appears that Barnard has included what would here be regarded as secondary radii in his adult scale radii counts. *B. erubescens* is characterized by about 13 primary radii and for *B. calidus* a lower mean count of about eight primary radii is recorded.

The restricted distribution of *B. erubescens* is significant especially when considered in the light of the absence of other fish species. *Galaxias zebratus* probably invaded the system at a very early stage via oceanic sources (McDowall 1973). It is possible that the *B. erubescens* / *B. calidus* ancestral stock arrived independently and before the other primary division freshwater fishes (*sensu* Myers 1938), including the "red fin" species *B. phlegethon.*

Below the first waterfall on the Twee River only large indigenous species (*Barbus serra, Barbus capensis, Labeo seeberi* and the exotic *Micropterus salmoides)* have been found. It is probable that this latter species has been largely responsible for the elimination of many of the smaller fish species, thus precluding the chance of locating a possible *B. erubescens* / *B. calidus* hybrid population. The nearest downstream population of *B. calidus* yet sampled (27.5 km river distance), in the Breekkrans River, shows characters typical for that species.

Acknowledgements

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Appendix 1

Abbreviation code for Institutions.
AM/P: Albany Museum, Grahamstown, Cape Province, South Africa.
B.M. (N.H.): British Museum (Natural History), London.
M.A.C.T.: Musée d'Afrique Centrale, Tervuren, Belgium.
RUSI : J.L.B. Smith Institute of Ichthyology, Rhodes University, Grahamstown, South Africa.

List of Figures

Figure 1 *Barbus erubescens* new species, Holotype, 84 mm SL.

Figure 2 *Barbus erubescens;* Right hand side pharyngeal bone and teeth from specimen of 95 mm SL.
A – Internal antero-lateral view
B – External postero-lateral view

Figure 3 *Barbus erubescens;* typical anal fin with basal radial and pterygiophore bones from specimen of 78 mm SL.

Figure 4 *Barbus calidus;* a specimen of 89 mm SL taken from the Rondegat River, Olifants River System, western Cape Province.

APPENDIX 4

Tables of

Morphometric measurements

TABLE 1

Standard length of measured specimens of redfin *Barbus* species.

SPECIES	N:	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	136.0	28.0	54.26	15.08	1.13
B. burgi	107	109.0	34.0	59.40	14.83	1.43
B. phlegethon	92	59.5	27.5	43.28	7.93	0.83
B. tenuis	96	80.0	30.0	54.27	9.79	1.00
B. afer	95	82.0	43.0	55.34	8.17	0.84
B. afer (*G.*)	50	73.0	50.0	56.85	4.73	0.67
B. asper	110	80.0	43.0	58.88	8.25	0.79
B. asper (*var.*)	144	104.0	48.0	61.08	10.90	0.91
O. quathlambae	32	102.0	46.0	82.44	11.72	2.07
B. calidus	275	82.0	22.5	51.52	11.64	0.70
B. erubescens	110	95.0	30.5	64.55	13.74	1.31

TABLE 2

Head length (% SL) of redfin Barbus species.

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	33.09	24.70	27.04	1.55	0.12
B. burgi	107	29.41	22.94	25.86	1.46	0.14
B. phlegethon	92	28.73	23.88	25.60	1.00	0.10
B. tenuis	96	30.00	24.64	26.69	1.15	0.12
B. afer	95	29.62	25.44	27.43	0.94	0.10
B. afer (G.)	50	29.11	25.24	26.84	1.01	0.14
B. asper	110	28.23	24.74	26.46	0.75	0.07
B. asper (var.)	142	30.36	25.91	28.56	0.90	0.08
O. quathlambae	32	27.12	22.74	24.76	1.15	0.20
B. calidus	238	30.00	24.59	27.23	1.07	0.69
B. erubescens	110	31.15	25.56	27.81	1.02	0.10

TABLE 3.

Head length (% SL) of B.asper, B.afer and B.asper (variant) samples.

SPECIES	N.	MAX.	MIN.	MEAN.	S.D.	S.E.
Sundays	30	28.2	25.4	26.8	.7	.1
Swartkops	30	28.9	25.6	27.6	.8	.1
Baakens	5	27.5	25.9	26.6	.7	.3
Couga	30	29.1	25.4	26.5	.8	.1
Wit	10	29.0	25.2	26.8	1.3	.4
Loerie	10	28.8	26.7	27.8	.7	.2
Krom	30	29.6	26.1	28.1	.9	.2
Bloukrans	30	29.1	25.9	27.8	.8	.2
Groot	30	30	27.7	28.7	.6	.1
Keurbooms	22	29.5	27.2	28.3	.7	.1
Knysna	30	30.4	28.2	29.2	.5	.1
Homtini	30	30.3	26.7	28.9	1.1	.2
Groot (Gamtoos)	30	27.4	25.2	26.4	.7	.1
Groot (Gourits)	30	27.9	25.6	26.3	.7	.1
Van Wyksdorp	20	28.2	25.4	26.7	.7	.2
Kammanassie	30	28.2	24.7	26.5	.9	.2

TABLE 4

Head depth (% HL) of redfin Barbus species and O.quathlambae

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	76.84	62.22	69.90	2.84	0.21
B. burgi	107	80.77	63.96	73.78	2.76	0.27
B. phlegethon	92	82.42	66.90	74.97	3.11	0.32
B. tenuis	96	71.20	61.11	65.86	2.47	0.25
B. afer	95	78.23	65.31	71.30	2.62	0.27
B. afer (G.)	50	76.19	66.22	70.90	2.68	0.38
B. asper	110	76.39	66.84	71.73	2.20	0.21
B. asper (var.)	142	79.44	62.10	71.88	3.06	0.26
O. quathlambae	32	69.35	59.91	64.34	2.30	0.41
B. calidus	238	76.67	60.87	68.24	3.09	0.20
B. erubescens	110	78.57	62.11	69.16	2.75	0.26

TABLE 5

Snout length (% HL) of redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	41.46	30.56	38.96	2.13	0.16
B. burgi	107	42.1	30.00	35.63	3.12	0.30
B. phlegethon	92	41.22	31.13	35.21	2.11	0.22
B. tenuis	96	42.42	30.66	34.98	1.89	0.19
B. afer	95	39.02	29.65	34.27	1.85	0.19
B. afer (*G.*)	50	37.35	28.57	33.68	1.68	0.24
B. asper	110	38.00	31.07	33.93	1.35	0.13
B. asper (*var.*)	142	41.82	30.99	35.82	2.26	0.19
O. quathlambae	32	39.29	33.33	36.80	1.66	0.29
B. calidus	237	40.0	28.1	34.4	2.0	0.13
B. erubescens	110	36.22	26.38	33.25	1.69	0.16

TABLE 6

Orbit diameter (% HL) of redfin Barbus species and O.quathlambae

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	36.73	17.78	28.51	3.24	0.24
B. burgi	107	37.50	22.27	29.06	3.35	0.32
B. phlegethon	92	36.26	25.34	30.22	2.19	0.23
B. tenuis	96	30.21	20.56	25.98	1.90	0.19
B. afer	95	30.37	21.70	26.71	1.78	0.18
B. afer (G.)	50	32.86	24.83	28.00	1.56	0.22
B. asper	110	28.67	22.00	26.03	1.36	0.13
B. asper (var.)	142	29.86	18.67	25.80	1.96	0.16
O. quathlambae	32	27.87	19.42	23.61	1.62	0.29
B. calidus	238	36.36	25.00	29.09	2.02	0.13
B. erubescens	110	32.35	22.17	26.73	1.96	0.19

TABLE 7

Postorbital length (% HL) of redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	50.74	38.51	45.19	1.88	0.14
B. burgi	107	53.02	38.71	47.09	2.38	0.23
B. phlegethon	92	57.14	43.14	46.35	1.99	0.21
B. tenuis	96	54.35	43.69	47.45	1.89	0.19
B. afer	95	51.16	42.22	46.36	1.66	0.17
B. afer (G.)	50	51.00	42.25	45.74	1.99	0.28
B. asper	110	52.11	37.80	46.97	2.05	0.20
B. asper (var.)	142	51.03	42.16	45.76	1.80	0.15
O. quathlambae	32	57.79	46.38	49.69	2.25	0.40
B. calidus	237	53.33	38.24	43.59	2.21	0.14
B. erubescens	110	50.00	40.78	45.97	1.56	0.15

TABLE 8

Interorbital length (% HL) of redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	36.51	24.07	30.57	2.39	0.18
B. burgi	107	40.00	27.78	33.46	2.19	0.21
B. phlegethon	92	38.82	27.18	32.79	2.42	0.25
B. tenuis	96	35.71	25.23	30.13	1.99	0.20
B. afer	95	33.02	25.17	29.13	1.54	0.16
B. afer (G.)	50	33.54	26.43	29.45	1.55	0.22
B. asper	110	35.15	25.45	31.21	2.36	0.22
B. asper (*var.*)	142	39.18	24.54	30.31	2.52	0.21
O. quathlambae	32	30.15	24.42	27.40	1.11	0.20
B. calidus	238	41.67	28.57	34.12	2.18	0.14
B. erubescens	110	37.93	24.51	31.88	3.34	0.31

TABLE 9

Predorsal length (% SL) of redfin Barbus species and O.quathlambae

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	55.15	48.87	51.25	1.18	0.09
B. burgi	107	53.75	44.64	48.89	2.17	0.21
B. phlegethon	92	55.17	49.02	52.38	1.16	0.12
B. tenuis	96	54.55	48.28	51.39	1.18	0.12
B. afer	95	55.00	49.30	51.85	1.00	0.10
B. afer (G.)	50	53.10	50.00	51.49	0.80	0.11
B. asper	110	54.55	47.83	51.04	1.42	0.14
B. asper (var.)	142	55.68	48.60	52.28	1.23	0.10
O. quathlambae	32	55.00	47.37	50.75	1.71	0.30
B. calidus	237	57.45	50.00	54.31	1.30	0.09
B. erubescens	110	55.74	50.30	53.12	1.10	0.10

TABLE 10

Postdorsal length (% SL) of redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	51.13	44.85	48.78	1.16	0.09
B. burgi	107	55.36	46.25	51.10	2.16	0.21
B. phlegethon	92	50.98	44.83	47.62	1.16	0.12
B. tenuis	96	51.72	45.45	48.61	1.18	0.12
B. afer	95	50.70	45.00	48.15	1.00	0.10
B. afer (G.)	50	50.00	46.90	48.49	0.82	0.12
B. asper	110	52.17	45.45	48.96	1.42	0.14
B. asper (var.)	142	50.94	44.32	47.66	1.21	0.10
O. quathlambae	32	52.63	45.00	49.25	1.71	0.30
B. calidus	280	50.00	42.55	45.69	1.30	0.09
B. erubescens	110	49.70	44.26	46.88	1.09	0.10

TABLE 11.

Head length (% SL) of B.burgi samples

SPECIES	N.	MAX.	MIN.	MEAN.	S.D.	S.E.
Great Drakenstein	30	27	23	25.2	.9	.2
Paarl (types)	2	24.6	23.3	24	.9	.7
Krom	30	26.1	22.9	24.8	.8	.2
Paarl	7	25.1	23.8	24.7	.6	.2
Eerste	7	27.8	26.1	26.8	.6	.2
Verlorevlei	30	29.4	26.	27.7	.8	.1

TABLE 12.

Predorsal length (% SL) of B.burgi samples

SPECIES	N.	MAX.	MIN.	MEAN.	S.D.	S.E.
Great Drakenstein	30	50	44.6	47.7	1.3	.2
Paarl (types)	2	47.2	44.3	46.8	.7	.5
Krom	30	49	45.4	47.5	1.0	.2
Paarl	7	50	46.4	47.8	1.4	.5
Eerste	7	53.8	48	50.8	2.4	.9
Verlorevlei	30	53.5	48.2	51.3	1.3	.2

TABLE 13

Length of the base of the dorsal fin (% SL) of each of the redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli ♀	98	15.56	11.18	13.22	0.71	0.07
B. burchelli ♂	76	15.17	12.00	13.59	0.90	0.10
B. burgi ♀	63	15.00	11.80	13.57	0.71	0.09
B. burgi ♂	42	15.44	11.70	13.81	0.91	0.14
B. phlegethon ♀	49	14.62	12.22	13.25	0.63	0.09
B. phlegethon ♂	31	14.91	10.91	13.44	0.93	0.17
B. tenuis ♀	66	14.29	11.03	12.63	0.75	0.09
B. tenuis ♂	30	14.04	11.19	12.56	0.68	0.12
B. afer ♀	66	14.20	11.01	12.79	0.64	0.08
B. afer ♂	29	14.43	11.04	13.10	0.78	0.15
B. afer (G.) ♀	25	14.59	11.92	13.29	0.64	0.13
B. afer (G.) ♂	25	15.10	12.79	13.89	0.61	0.12
B. asper ♀	69	14.75	11.26	12.98	0.77	0.09
B. asper ♂	41	15.70	12.24	13.55	0.73	0.11
B. asper (var.) ♀	71	15.26	11.94	13.44	0.72	0.09
B. asper (var.) ♂	71	15.77	12.27	13.98	0.68	0.08
O. quathlambae ♀	20	13.17	10.71	11.78	0.70	0.16
O. quathlambae ♂	12	13.45	10.54	12.04	0.86	0.25
B. calidus ♀	120	16.96	12.07	13.62	0.82	0.08
B. calidus ♂	102	15.63	12.22	13.79	0.72	0.07
B. erubescens ♀	44	15.26	12.07	13.82	0.79	0.12
B. erubescens ♂	56	15.62	12.06	14.00	0.83	0.11

TABLE 14

Length of the dorsal fin (% SL) of each sex of the redfin Barbus species and O.quathlambae

SPECIES		N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	♀	98	25.65	19.03	22.68	1.49	0.15
B. burchelli	♂	76	26.58	21.40	23.83	1.55	0.18
B. burgi	♀	63	27.65	16.06	23.89	2.53	0.32
B. burgi	♂	42	28.40	19.24	25.39	2.20	0.34
B. phlegethon	♀	49	27.14	19.15	23.30	1.71	0.24
B. phlegethon	♂	31	27.64	22.65	24.77	1.22	0.22
B. tenuis	♀	66	25.64	19.73	22.43	1.37	0.17
B. tenuis	♂	30	28.00	20.00	23.54	1.45	0.27
B. afer	♀	66	25.21	20.36	22.76	1.22	0.15
B. afer	♂	29	25.22	20.80	23.34	1.09	0.20
B. afer (G.)	♀	25	24.62	20.91	22.96	1.03	0.21
B. afer (G.)	♂	25	25.17	17.59	23.13	1.78	0.36
B. asper	♀	69	26.04	18.89	22.50	1.58	0.19
B. asper	♂	41	27.87	20.86	23.81	1.59	0.25
B. asper (var.)	♀	71	25.58	20.90	23.49	1.22	0.15
B. asper (var.)	♂	71	26.85	20.71	24.29	1.13	0.13
O. quathlambae	♀	20	20.85	17.68	19.35	1.01	0.23
O. quathlambae	♂	12	22.00	18.78	20.54	0.93	0.27
B. calidus	♀	120	26.04	18.33	22.02	1.52	0.14
B. calidus	♂	101	25.53	18.75	22.19	1.26	0.13
B. erubescens	♀	44	22.73	19.14	20.97	0.98	0.15
B. erubescens	♂	56	22.55	18.90	20.91	0.93	0.12

TABLE 15

Length of the pectoral fin (% SL) of each sex of the redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli ♀	98	23.50	18.61	21.05	1.10	0.11
B. burchelli ♂	76	25.00	19.60	22.67	1.52	0.17
B. burgi ♀	63	26.05	14.68	20.39	2.28	0.29
B. burgi ♂	42	26.44	18.10	23.05	1.87	0.29
B. phlegethon ♀	49	24.57	17.84	20.10	1.34	0.19
B. phlegethon ♂	31	25.26	19.64	22.16	1.18	0.21
B. tenuis ♀	66	23.00	16.72	20.19	1.39	0.17
B. tenuis ♂	30	24.29	20.00	22.64	1.12	0.20
B. afer ♀	66	23.04	17.59	20.21	1.23	0.15
B. afer ♂	29	23.96	18.67	22.37	1.08	0.20
B. afer (*G.*) ♀	25	22.95	16.10	20.12	1.63	0.33
B. afer (*G.*) ♂	25	25.47	18.03	21.90	1.80	0.36
B. asper ♀	69	22.77	17.03	19.98	1.43	0.17
B. asper ♂	41	26.09	19.47	22.98	1.65	0.26
B. asper (*var.*) ♀	71	23.54	18.81	21.63	1.06	0.13
B. asper (*var.*) ♂	71	26.07	20.51	23.82	1.15	0.14
O. quathlambae ♀	20	21.67	15.51	18.49	1.41	0.32
O. quathlambae ♂	12	21.30	17.26	19.36	1.35	0.39
B. calidus ♀	120	23.26	18.75	21.02	1.00	0.09
B. calidus ♂	102	23.40	18.63	21.34	1.05	0.11
B. erubescens ♀	44	22.17	18.33	20.54	0.74	0.11
B. erubescens ♂	56	22.46	18.74	20.63	0.77	0.10

TABLE 16

Distance between the pectoral and pelvic fins of each sex of the redfin Barbus species and O.quathlambae

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli ♀	98	27.63	22.05	25.16	1.07	0.11
B. burchelli ♂	76	27.29	21.10	23.86	1.68	0.19
B. burgi ♀	63	32.02	21.96	24.98	1.57	0.20
B. burgi ♂	42	27.39	16.51	24.36	1.84	0.28
B. phlegethon ♀	49	31.85	24.37	28.23	1.50	0.21
B. phlegethon ♂	31	29.02	23.33	26.14	1.42	0.26
B. tenuis ♀	66	28.46	22.74	25.67	1.22	0.15
B. tenuis ♂	30	26.91	22.41	24.54	1.16	0.21
B. afer ♀	66	27.02	21.72	24.44	1.06	0.13
B. afer ♂	29	25.00	20.93	23.17	1.16	0.22
B. afer (G.) ♀	25	27.62	23.33	25.14	0.98	0.20
B. afer (G.) ♂	25	25.88	22.09	24.02	0.83	0.17
B. asper ♀	69	29.84	22.45	25.69	1.47	0.18
B. asper ♂	41	27.42	21.06	24.03	1.26	0.20
B. asper (var.) ♀	71	28.20	21.57	24.85	1.41	0.17
B. asper (var.) ♂	71	26.67	19.68	23.59	1.59	0.19
O. quathlambae ♀	20	27.67	23.68	26.26	1.17	0.26
O. quathlambae ♂	12	26.07	22.98	24.32	0.83	0.24
B. calidus ♀	124	27.21	19.64	23.35	1.32	0.12
B. calidus ♂	103	26.56	18.75	23.17	1.31	0.13
B. erubescens ♀	44	26.54	21.58	23.93	1.89	0.18
B. erubescens ♂	56	25.89	21.30	23.51	1.01	0.13

TABLE 17

Length of the pelvic fin (% SL) of each sex of the redfin *Barbus* species and *O.quathlambae*

SPECIES		N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	♀	98	18.47	14.00	16.27	0.86	0.09
B. burchelli	♂	76	19.23	14.30	17.27	1.02	0.12
B. burgi	♀	63	20.41	13.39	17.49	1.33	0.17
B. burgi	♂	42	20.65	7.91	18.45	2.03	0.31
B. phlegethon	♀	49	18.08	15.70	16.87	0.67	0.10
B. phlegethon	♂	31	20.79	15.36	18.01	1.13	0.20
B. tenuis	♀	66	18.06	10.89	15.43	1.23	0.15
B. tenuis	♂	30	17.79	14.56	16.52	1.02	0.19
B. afer	♀	66	18.60	14.29	16.19	0.97	0.12
B. afer	♂	29	19.06	15.45	17.50	0.90	0.17
B. afer (*G.*)	♀	25	18.42	14.92	16.57	0.97	0.19
B. afer (*G.*)	♂	25	19.63	14.24	17.22	1.38	0.28
B. asper	♀	69	18.96	12.63	15.81	1.24	0.15
B. asper	♂	41	21.76	15.81	17.98	1.33	0.21
B. asper (*var.*)	♀	71	19.07	15.67	17.33	0.79	0.09
B. asper (*var.*)	♂	71	20.42	16.92	18.47	0.77	0.09
O. quathlambae	♀	20	15.85	12.76	14.79	0.93	0.21
O. quathlambae	♂	12	16.67	14.05	15.46	0.78	0.22
B. calidus	♀	120	19.79	16.00	18.08	0.82	0.08
B. calidus	♂	102	20.19	16.28	18.26	0.83	0.08
B. erubescens	♀	44	19.72	15.58	17.50	0.70	0.11
B. erubescens	♂	56	19.30	16.07	17.59	0.84	0.11

TABLE 18

Distance between the pelvic and anal fins of each sex of the redfin *Barbus* species and *O.quathlambae*

SPECIES		N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	♀	98	17.06	12.00	14.57	1.05	0.11
B. burchelli	♂	76	16.75	11.90	14.04	0.99	0.12
B. burgi	♀	63	21.12	13.38	15.93	1.13	0.14
B. burgi	♂	42	18.19	13.03	15.53	1.45	0.22
B. phlegethon	♀	49	17.84	12.07	15.08	1.39	0.20
B. phlegethon	♂	31	18.86	11.96	14.23	1.38	0.25
B. tenuis	♀	66	18.21	12.50	14.66	1.07	0.13
B. tenuis	♂	30	15.43	12.50	14.06	0.85	0.15
B. afer	♀	66	18.14	12.71	15.43	1.05	0.13
B. afer	♂	29	16.21	13.07	14.79	0.92	0.17
B. afer (*G.*)	♀	25	17.44	12.79	15.18	1.16	0.23
B. afer (*G.*)	♂	25	16.11	13.33	14.84	0.86	0.17
B. asper	♀	69	17.58	12.71	14.96	1.01	0.12
B. asper	♂	41	15.74	11.84	13.94	0.95	0.15
B. asper (*var.*)	♀	71	18.36	13.09	14.99	1.25	0.15
B. asper (*var.*)	♂	71	16.80	12.43	14.17	0.87	0.10
O. quathlambae	♀	20	17.50	13.25	15.14	1.29	0.29
O. quathlambae	♂	12	17.01	12.74	14.59	1.20	0.35
B. calidus	♀	124	22.97	15.00	18.65	1.37	0.12
B. calidus	♂	103	24.11	15.91	18.65	1.28	0.13
B. erubescens	♀	44	20.00	16.43	18.05	0.95	0.14
B. erubescens	♂	56	21.19	16.89	18.29	1.01	0.13

TABLE 19

Length of the base of the anal fin of each sex of the redfin *Barbus* species and *O.quathlambae*

SPECIES		N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	♀	98	13.45	8.46	10.55	0.77	0.08
B. burchelli	♂	76	12.50	7.10	10.90	0.93	0.11
B. burgi	♀	63	11.46	8.46	10.14	0.59	0.08
B. burgi	♂	42	12.35	9.11	10.60	0.76	0.12
B. phlegethon	♀	49	11.50	9.07	10.06	0.50	0.07
B. phlegethon	♂	31	12.09	9.29	10.31	0.62	0.11
B. tenuis	♀	66	12.86	8.79	10.44	0.77	0.09
B. tenuis	♂	30	11.93	8.21	10.24	0.91	0.17
B. afer	♀	66	11.56	8.95	10.18	0.61	0.08
B. afer	♂	29	11.85	9.53	10.65	0.65	0.12
B. afer (G.)	♀	25	11.85	9.49	10.84	0.62	0.12
B. afer (G.)	♂	25	12.22	10.09	11.21	0.55	0.11
B. asper	♀	69	11.38	8.53	10.03	0.58	0.07
B. asper	♂	41	13.27	8.93	10.48	0.88	0.14
B. asper (var.)	♀	71	12.28	9.80	10.78	0.55	0.07
B. asper (var.)	♂	71	12.00	9.84	11.18	0.50	0.06
O. quathlambae	♀	20	11.25	8.92	9.98	0.71	0.16
O. quathlambae	♂	12	12.05	9.54	10.48	0.85	0.25
B. calidus	♀	120	13.24	10.20	11.45	0.72	0.07
B. calidus	♂	102	13.89	9.09	11.81	0.90	0.09
B. erubescens	♀	44	13.24	10.53	11.68	0.54	0.08
B. erubescens	♂	56	13.87	10.71	12.27	0.82	0.11

TABLE 20

Length of the anal fin (% SL) of each sex of the redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli ♀	98	25.00	17.30	19.98	1.31	0.13
B. burchelli ♂	76	22.67	18.00	20.74	1.44	0.17
B. burgi ♀	63	23.06	14.04	19.50	1.89	0.24
B. burgi ♂	42	23.40	15.70	20.85	1.55	0.24
B. phlegethon ♀	49	23.06	17.04	20.84	1.24	0.18
B. phlegethon ♂	31	23.42	20.00	21.68	0.89	0.16
B. tenuis ♀	66	22.18	16.91	19.81	1.29	0.16
B. tenuis ♂	30	24.08	18.25	20.85	1.24	0.23
B. afer ♀	66	21.88	18.02	20.02	1.07	0.13
B. afer ♂	29	22.92	18.40	20.80	0.96	0.18
B. afer (*G.*) ♀	25	22.63	17.80	20.41	1.00	0.20
B. afer (*G.*) ♂	25	22.78	16.61	20.18	1.66	0.33
B. asper ♀	69	22.92	16.77	19.76	1.37	0.16
B. asper ♂	41	24.27	18.25	20.98	1.37	0.21
B. asper (*var.*) ♀	71	22.94	18.67	21.00	0.91	0.11
B. asper (*var.*) ♂	71	23.53	19.19	21.49	0.96	0.11
O. quathlambae ♀	20	18.50	15.10	17.20	0.94	0.21
O. quathlambae ♂	12	20.00	16.19	17.86	1.23	0.35
B. erubescens ♀	44	21.67	16.56	18.48	0.93	0.14
B. erubescens ♂	56	20.00	15.68	17.96	0.88	0.12

TABLE 21

The depth of the body (% SL) of each sex of the redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli ♀	98	29.34	22.75	25.44	1.34	0.14
B. burchelli ♂	76	29.00	22.90	25.56	1.78	0.20
B. burgi ♀	63	30.67	20.91	27.19	1.94	0.24
B. burgi ♂	42	31.96	23.97	27.83	1.97	0.30
B. phlegethon ♀	49	27.80	21.88	24.28	1.30	0.19
B. phlegethon ♂	31	27.33	21.36	24.32	1.00	0.18
B. tenuis ♀	66	26.76	18.81	22.64	1.23	0.15
B. tenuis ♂	30	24.00	19.53	21.75	1.09	0.20
B. afer ♀	66	27.76	22.50	24.86	1.29	0.16
B. afer ♂	29	28.33	23.46	25.64	1.31	0.24
B. afer (*G.*) ♀	25	28.46	24.44	26.39	1.25	0.25
B. afer (*G.*) ♂	25	30.00	24.73	27.63	1.47	0.29
B. asper ♀	69	28.96	23.47	26.29	1.35	0.16
B. asper ♂	41	29.54	21.52	26.55	1.67	0.26
B. asper (*var.*) ♀	71	30.60	23.06	26.50	1.54	0.18
B. asper (*var.*) ♂	71	29.29	24.14	26.98	0.93	0.11
O. quathlambae ♀	20	25.49	20.00	22.22	1.07	0.24
O. quathlambae ♂	12	22.98	20.00	21.53	0.86	0.25
B. calidus ♀	124	26.98	19.35	22.49	1.21	0.11
B. calidus ♂	103	25.86	20.00	22.86	1.28	0.13
B. erubescens ♂	56	25.41	20.18	23.38	1.00	0.13
B. erubescens ♀	44	26.47	21.15	23.82	1.18	0.18

TABLE 22

The width of the body (% SL) of each sex of the redfin Barbus species and O.quathlambae

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli ♀	98	21.75	13.70	16.71	1.52	0.15
B. burchelli ♂	76	20.82	13.80	16.84	1.88	0.22
B. burgi ♀	63	18.57	9.82	15.43	1.86	0.23
B. burgi ♂	42	17.65	11.35	14.97	1.48	0.23
B. phlegethon ♀	49	17.60	11.80	14.58	1.36	0.19
B. phlegethon ♂	31	16.52	12.05	14.31	1.13	0.20
B. tenuis ♀	66	18.65	13.64	16.71	1.12	0.14
B. tenuis ♂	30	20.36	13.33	16.19	1.64	0.30
B. afer ♀	66	20.18	13.96	16.40	1.45	0.18
B. afer ♂	29	19.83	11.86	16.89	1.76	0.33
B. afer (G.) ♀	25	17.63	13.82	16.10	1.05	0.21
B. afer (G.) ♂	25	18.81	11.53	16.64	1.55	0.31
B. asper ♀	69	19.67	13.33	16.79	1.81	0.22
B. asper ♂	41	20.00	10.87	16.43	2.02	0.32
B. asper (var.) ♀	71	20.48	15.21	17.41	1.22	0.14
B. asper (var.) ♂	71	19.71	15.20	17.91	0.92	0.11
O. quathlambae ♀	20	16.67	11.93	14.99	1.16	0.26
O. quathlambae ♂	12	15.71	13.10	14.09	0.85	0.24
B. calidus ♀	124	17.65	11.90	14.06	0.88	0.08
B. calidus ♂	103	18.46	11.94	14.34	1.28	0.13
B. erubescens ♀	44	18.28	12.50	15.46	1.27	0.19
B. erubescens ♂	56	17.92	12.04	15.59	1.34	0.18

TABLE 23

The length of the caudal peduncle (% SL) of each sex of the redfin Barbus species and O.quathlambae

SPECIES		N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	♀	98	27.23	21.32	24.55	1.18	0.12
B. burchelli	♂	76	28.00	22.47	25.32	1.33	0.14
B. burgi	♀	63	27.22	20.87	24.86	1.33	0.17
B. burgi	♂	42	27.69	22.10	25.02	1.45	0.22
B. phlegethon	♀	49	26.17	21.40	23.51	1.04	0.15
B. phlegethon	♂	31	26.90	22.44	24.61	1.08	0.19
B. tenuis	♀	66.	28.87	23.58	26.26	1.21	0.15
B. tenuis	♂	30	29.18	23.09	26.49	1.34	0.24
B. afer	♀	66	27.64	22.55	24.79	1.12	0.14
B. afer	♂	29	27.37	23.33	25.13	0.98	0.18
B. afer (G.)	♀	25	26.54	23.10	24.59	0.97	0.19
B. afer (G.)	♂	25	27.41	23.72	25.31	0.80	0.16
B. asper	♀	69	29.58	21.52	24.87	1.58	0.19
B. asper	♂	41	29.56	23.93	26.09	1.33	0.21
B. asper (var.)	♀	71	26.03	21.72	24.21	0.92	0.11
B. asper (var.)	♂	71	26.27	21.29	24.27	0.93	0.11
B. calidus	♀	124	24.14	17.46	20.51	1.19	0.11
B. calidus	♂	103	25.00	17.39	20.88	1.23	0.12
B. erubescens	♀	44	22.73	18.57	20.54	0.89	0.13
B. erubescens	♂	56	23.40	19.86	21.55	0.74	0.10

TABLE 24

The caudal peduncle length of _B_._asper_ samples. (% SL)

Locality	N	Max.	Min.	Mean	S.D.	S.E.
Groot (Gamtoos)	30	29.6	25.2	27.2	0.9	0.2
Groot (Gourits)	30	26.1	22.	24.3	0.9	0.2
Vanwyksdorp	20	28.0	23.2	25.72	1.2	0.2
Kammanassie	30	25.9	21.5	24.2	1.0	0.2

TABLE 25

The depth of the caudal peduncle (% SL) of each sex of the redfin *Barbus* species and *O.quathlambae*

SPECIES		N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	♀	98	13.93	10.90	12.04	0.64	0.06
B. burchelli	♂	76	14.60	11.50	12.63	0.57	0.07
B. burgi	♀	63	13.33	9.09	11.61	0.69	0.09
B. burgi	♂	42	13.23	10.39	12.00	0.68	0.11
B. phlegethon	♀	49	12.00	9.07	10.51	0.53	0.08
B. phlegethon	♂	31	12.00	10.41	11.23	0.40	0.07
B. tenuis	♀	64	14.00	10.56	12.08	0.67	0.08
B. tenuis	♂	30	13.67	10.70	12.29	0.59	0.11
B. afer	♀	66	13.20	10.85	11.88	0.50	0.06
B. afer	♂	29	14.21	10.49	12.41	0.76	0.14
B. afer (G.)	♀	25	13.69	10.47	12.61	0.70	0.14
B. afer (G.)	♂	25	14.71	12.54	13.76	0.52	0.10
B. asper	♀	69	12.41	9.64	11.31	0.58	0.07
B. asper	♂	41	13.23	11.23	12.18	0.49	0.08
B. asper (*var.*)	♀	71	13.64	10.33	12.04	0.73	0.09
B. asper (*var.*)	♂	71	14.71	11.64	12.74	0.61	0.07
O. quathlambae	♀	20	11.56	9.88	10.84	0.49	0.11
O. quathlambae	♂	12	12.06	10.66	11.33	0.44	0.13
B. calidus	♀	124	11.63	8.45	9.81	0.53	0.05
B. calidus	♂	103	11.61	8.65	10.05	0.59	0.06
B. erubescens	♀	44	12.69	10.45	11.57	0.52	0.08
B. erubescens	♂	56	12.78	10.34	11.80	0.54	0.07

TABLE 26.

The length of the anterior barbel (% orbit diameter) of certain redfin *Barbus* species.

SPECIES	N.	MAX.	MIN.	MEAN.	S.D.	S.E.
B.burchelli	179	115.	3.7	55.2	21.2	1.6
B.burgi	107	80.	27.8	18.7	13.	1.3
B.calidus	280	133.3	8.7	75.8	39.	2.3
B.erubescens	110	122.2	35.7	97.	16.3	1.6

TABLE 27

The length of the posterior barbel (% orbit diameter) of the redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	179	166.0	3.7	94.69	29.67	2.22
B. burgi	107	147.3	21.87	71.19	18.23	1.76
B. phlegethon	92	50.0	2.56	26.91	9.99	1.04
B. tenuis	96	100.0	20.00	68.13	17.38	1.77
B. afer	95	156.5	42.11	85.47	25.60	2.63
B. afer (G.)	50	127.3	39.53	73.81	20.35	2.88
B. asper	110	116.3	45.95	70.72	12.10	1.15
B. asper (var.)	142	169.6	68.29	107.55	17.98	1.51
O. quathlambae	32	80.7	34.15	56.25	9.15	1.62
B. calidus	280	157.1	41.67	107.83	20.33	1.22

TABLE 28

The number of scale radii in redfin *Barbus* species and *O.quathlambae*

SPECIES	N.	MAX.	MIN.	MEAN	S.D.	S.E.
B. burchelli	175	13.3	7.2	9.64	1.07	0.08
B. burgi	105	10.4	6.0	8.07	0.80	0.08
B. phlegethon	90	14.4	9.2	11.88	1.09	0.12
B. tenuis	96	19.5	11.0	14.41	1.90	0.19
B. afer	95	15.0	9.25	11.58	1.09	0.11
B. afer (G.)	50	15.4	9.6	12.85	1.50	0.21
B. asper	110	14.4	8.2	10.51	1.20	0.11
B. asper (*var.*)	142	16.6	9.0	12.47	1.37	0.12
O. quathlambae	30	13.3	8.4	10.21	1.02	0.19
B. calidus	192	12.2	5.8	8.92	1.26	0.09
B. erubescens	110	18.0	9.0	13.36	1.60	0.15