

The generic identity of *Labeo quathlambae* Barnard (Pisces, Cyprinidae)

by

P. H. GREENWOOD (British Museum [Natural History])

and

R. A. JUBB (Albany Museum, Grahamstown)

INTRODUCTION

In 1938, K. H. Barnard described, as *Labeo quathlambae*, a new and unusual species of cyprinid fish from a high altitude stream on the Drakensberg Mountains of Natal. It is clear from the original description that Barnard was uncertain about the generic identity of his new species, which seemed to combine characteristics of both *Labeo* and *Barbus*. His decision to include the species in the genus *Labeo* was based largely on its possessing very small scales (thus, in Barnard's opinion relating it to *Labeo umbratus* [A. Smith] and *L. steiningi* G. and T.), and the presence of tubercles on the head in specimens of both sexes.

Recently, the junior author re-examined the type series, and concluded that the taxon *quathlambae* could not be included in the genus *Labeo* for several reasons. Some of the distinguishing characters he noted are the short gut (less than body length), the biserial pharyngeal dentition, and the unspecialized nature of the mouth and lips. After preliminary discussions between us on possible generic relationships, a few specimens were sent to the senior author who undertook to make a detailed osteological study of the species as part of our attempt to ascertain its relationships.

"*Labeo*" *quathlambae* is of considerable interest on several counts. Not only does it differ from all other African Cyprinidae (and resemble certain Eurasian and American cyprinids), but it is probably extinct. Even in 1938 there were strong indications that the population was declining in number. The first specimens sent to Dr. Barnard, taken from the Umkomazana River (altitude *ca* 5,000 feet), a tributary of the Umkomaas, were collected by the then acting Superintendent of Trout Hatcheries who reported that the species used to be common until the introduction of trout, *Salmo trutta*, some years previously; after that time it had become almost extinct. At Dr. Barnard's suggestion a further search for specimens was made, and produced only one additional fish from the same locality; however, later over fifty specimens were caught. Since 1938 no other specimens have ever been collected, despite deliberate attempts to do so in the type locality and other similar streams.

TAXONOMY

Because, at least superficially, "*Labeo*" *quathlambae* resembles certain species of *Labeo*, and is even more like some *Barbus* species, a detailed comparison was first made with these two genera. Some of the major differences are discussed below.

"*Labeo*" *quathlambae* differs from African and Asian species of *Labeo* in the following characters:

- (i) Lips not markedly thickened, and not forming a sucker-like disc around the mouth; upper lip not overhung by the frenum, from which it is separated by a distinct groove.

- (ii) Dorsal fin origin slightly behind the vertical through the insertion of the pelvic fins (in *Labeo*, the dorsal fin origin is always clearly in advance of the pelvics).
- (iii) No enlarged pelvic axillary scale developed; chest scaleless.
- (iv) Pharyngeal teeth in two rows only, and of a very characteristic shape. In *Labeo*, the pharyngeal teeth have crowns which are expansive (in relation to the slender necks) but laterally compressed and obliquely truncated so as to present an almost flat occlusal surface, with little space between the individual teeth of the three rows. In contrast, the teeth of "*L.*" *quathlambae* have strongly recurved crowns with expanded and concave (i.e. spoon-shaped) occlusal surfaces terminating in prominent, conical, curved and posteriorly directed tips; the teeth are widely spaced, and the crowns do not present a pavement-like occlusal surface (see figs. 13 and 14).
- (v) The dentary has a more prominent and higher coronoid process, and a longer, more gently curved and less massive precoronoid arm than is found in *Labeo* (see figs. 8 and 9). Mandibular shape in *Labeo* is very characteristic, and is not found in any other African cyprinid genus except in a few species currently referred to the disputable genus *Varicorhinus*. Associated with these differences in mandibular shape, the symplectic in "*L.*" *quathlambae* is noticeably longer than in *Labeo* species.
- (vi) There are only four circumorbital bones in "*L.*" *quathlambae* (five in *Labeo*).
- (vii) The gut is shorter than the body (in *Labeo* species, the gut is from 14 to 21 times as long as the standard length [Matthes, 1963]).

In its general facies, "*Labeo*" *quathlambae* is rather more like a species of *Barbus*, but it is nevertheless readily differentiated by these characters:

- (i) No *Barbus* species of the group with radiately striate scales has such small scales, and no species of this or any other group has a naked chest. The latter character should, however, be treated with caution since it may, to a certain extent, be environmentally determined (see Berg, 1949, on a clinal variation in chest squamation shown by populations of the gudgeon *Gobio gobio* in eastern Europe). An enlarged pelvic axillary scale is always present in *Barbus*.
- (ii) The biserial pharyngeal dentition and the shape of the pharyngeal teeth in "*L.*" *quathlambae*. Although tooth form in *Barbus* shows greater variation than in *Labeo*, we have not found the "*L.*" *quathlambae* dental form in any of the several European, Asian or African *Barbus* species we examined, or which have been figured in the literature (see especially, Chu, 1935). Also, in *Barbus* the pharyngeal dentition is more markedly heterodont than in "*L.*" *quathlambae*. In passing, it should be noted that several *Barbus* species have a diet like that of "*L.*" *quathlambae* (i.e. insectivorous).
- (iii) At least in relation to the African *Barbus* species with radiately striate scales, "*L.*" *quathlambae* has a higher vertebral count (39, cf. 29–33 [Daget, 1954, 1962 and 1965, and personal observations]). Vertebral counts as high as those of "*L.*" *quathlambae* are, however, found in some *Barbus* species referable to the group with parallel striae in the scales. By no means all small *Barbus* species have been checked for vertebral numbers, but counts within the range 29–33 are so common in those which have been examined that it seems reasonable to consider these figures as indicative of the modal range.

Most *Barbus* species so far described (see Daget, 1962 and 1965) or examined by us, with respect to the circumorbital bones have five bones in this series; "*L.*" *quathlambae* has four, as do *Barbus cadenati*, *B. apogonostomus* and *B. niokoloensis* alone amongst the described *Barbus* species (Daget, 1962).

From what has been said above, it is clear that the taxon *quathlambae* cannot be included in the genus *Labeo* which, despite its wide geographical distribution and high number of species, is readily and trenchantly definable on the basis of jaw and mouth morphology, and the nature of its pharyngeal dentition. Even the more heterogeneous characteristics of the less readily definable genus *Barbus* do not allow the inclusion of *quathlambae* as a constituent species. Likewise, jaw and mouth structure, the small scales, and the pharyngeal dentition of *quathlambae* effectively exclude the species from any other African cyprinid genus; if anything, *quathlambae* is more closely related to *Labeo* and *Barbus* than to these other genera.

There is, of course, the possibility that "*L.*" *quathlambae* might be an introduced species, a suspicion reinforced by its superficial resemblance to certain North American cyprinids (especially species of *Coxesius*). However, the shape of the pharyngeal teeth, the markedly emarginate anterior tip of the cleithrum (see Regan, 1911), and numerous small details of morphology at the "species character" level seem to rule out any such possibility as far as American cyprinids are concerned. Similarly, *quathlambae* cannot be identified with any European or Asian cyprinid genus, and we must conclude that "*Labeo*" *quathlambae* represents a unique, undescribed and endemic African genus.

Oreodaimon gen. nov.

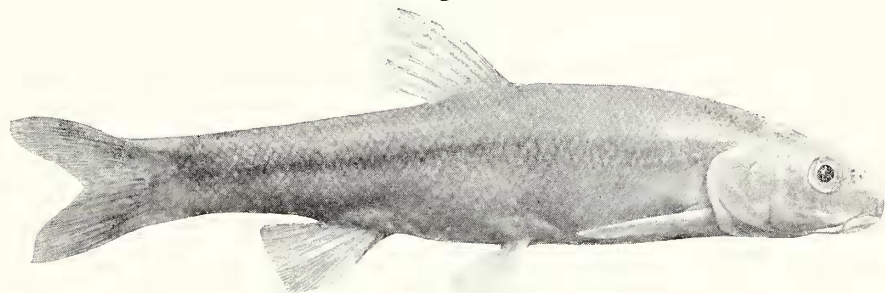


Fig. 1. *Oreodaimon quathlambae*; lateral view. S.L. 83 mm. S.A.M. 19018. Housed in Albany Museum.



Lateral view of head



Ventral view of head

Type species: Labeo quathlambae Barnard, 1938, *Ann. Natal Mus.*, 8 (3): 525–528; one text figure.

Mouth subterminal, crescentic. Lips smooth on their inner aspects, not enlarged and not forming a sucker-like disc around the mouth opening. Lower lip free laterally but fused with underlying tissue medially; upper lip separated from the frenum by a distinct groove. Upper jaw protrusile. A single (posterior) pair of maxillary barbels. Scales small but imbricate, radii present in the basal, lateral and apical fields, the latter radiately arranged; scales absent on the chest (the area between the isthmus and the pectoral fin bases). Dorsal fin origin slightly posterior to the vertical through the insertion of the pelvic fins; no enlarged pelvic axillary scale. Pseudobranchiae present. Pharyngeal bones with two rows of teeth (3, 4–4, 3), the teeth with strongly curved, broad and concave crowns which terminate in prominent, conical and recurved tips. Dentary with a prominent coronoid process, and a long, slender precoronoid arm. Weberian apparatus complete, the second and third vertebral centra fused, the first centrum not anteroposteriorly compressed. Cleithrum with deeply emarginate anterior tip. Vertebrae (including the four incorporated in the Weberian apparatus, and the ural centrum) 20 + 19 in the two specimens examined. Swimbladder large (extending throughout the abdominal cavity), transversely constricted, the posterior part about $1\frac{1}{2}$ times as long as the anterior portion. Gut short, about 0.7 times standard length.

The name *Oreodaimon* is derived from the Greek ὄρεο—a mountain, and δαίμων—a spirit, in allusion to the species' habitat and its probable extinction.

Oreodaimon quathlambae (Barnard), comb. nov.

OSTEOLOGY

In order to compare *O. quathlambae* with other cyprinid genera, and also in an attempt to assess its probable subfamilial relationships, certain osteological characters were studied. In many respects it is still too early to make full taxonomic use of osteological characters within the Cyprinidae because so few species have been studied from this point of view. Thus, it seemed worthwhile to give at least a brief description of skeletal features in *O. quathlambae*, if only to provide some data for another cyprinid genus and species. Two small specimens (ca. 40 mm. S.L.) were cleared and stained with alizarin; the figures and descriptions are based mainly on these specimens. The pharyngeal bones and certain other features were also examined, by dissection, on a larger fish (83 mm. S.L.).

In the descriptions that follow, bone nomenclature is essentially that used by Weitzman (1962).

Neurocranium (figs. 2–4): There is nothing outstanding about the general morphology of the neurocranium. In its overall proportions and appearance it resembles closely the neurocranium described for several cyprinid species (see Ramaswami, 1955 a and b; Harrington, 1955), and is very similar to that of *Barbus kerstenii* Peters (personal observations).

Olfactory region. The *nasals* are short, narrow and tubular bones.

The *supraethmoid* (figs. 2 and 4) is completely fused with the underlying ethmoid; posteriorly it articulates with the frontals through a deep, interdigitating suture. Its dorsal surface is deeply but broadly grooved; the indentation is more circumscribed and 'V' shaped anteriorly.

The *ethmoid* (figs. 2–4) is broad-based, but except along its transverse anterior margin (which is deeply notched) and for a short distance anterolaterally, the bone does not extend to the margin of the underlying *vomer*, which thus forms a narrow lateral platform around the ethmoid. Anteriorly and anterolaterally the ethmoid base slightly overreaches the vomer.

2mm

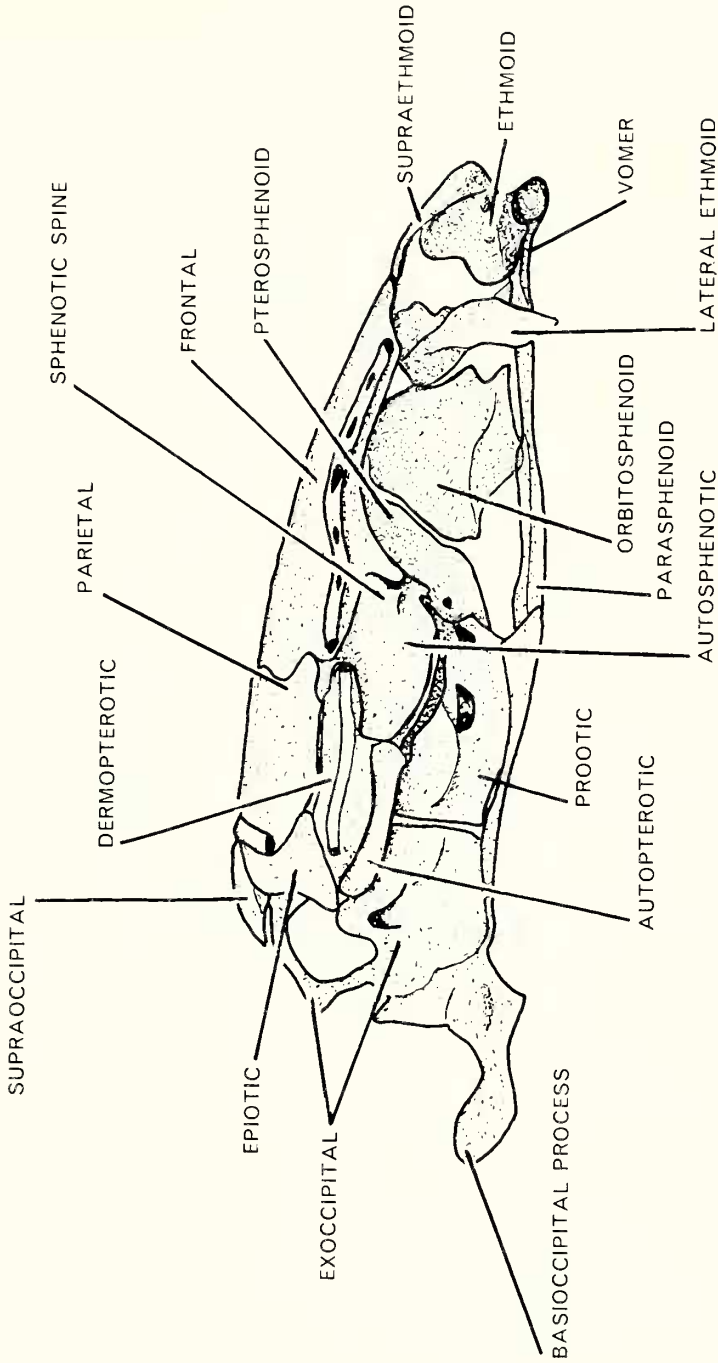


Fig. 2. *O. quathlambae*; neurocranium, right lateral view.

The vertical lamina of the ethmoid has a roughly kidney-shaped outline, the hilum facing posteriorly. In contact with the ethmoid and vomer anterolaterally are the large *preethmoids* (figs. 2-4). No "second preethmoids" (*sensu* Ramaswami) are visible in the alizarin preparations, but superficial dissection of an untreated specimen (83 mm. S.L.) revealed a large

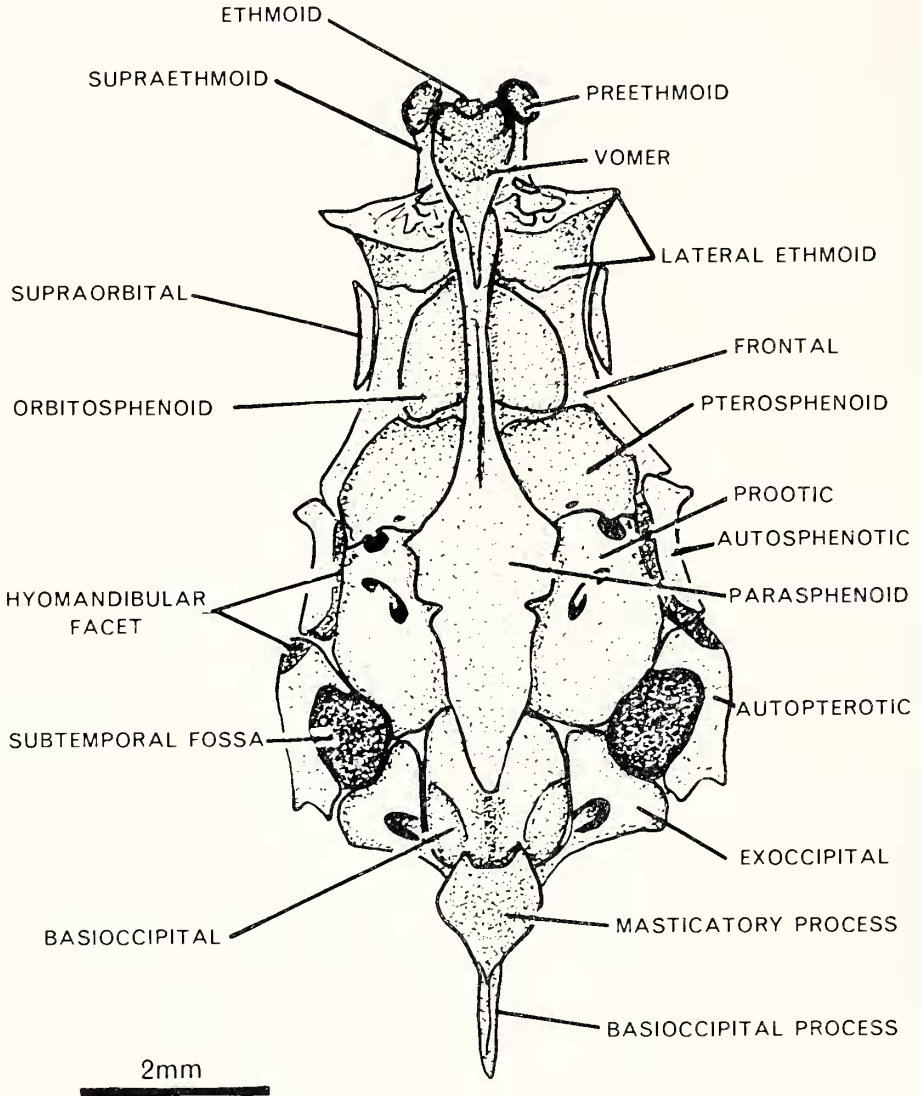


Fig. 3. *O. quathlambae*; neurocranium, ventral view.

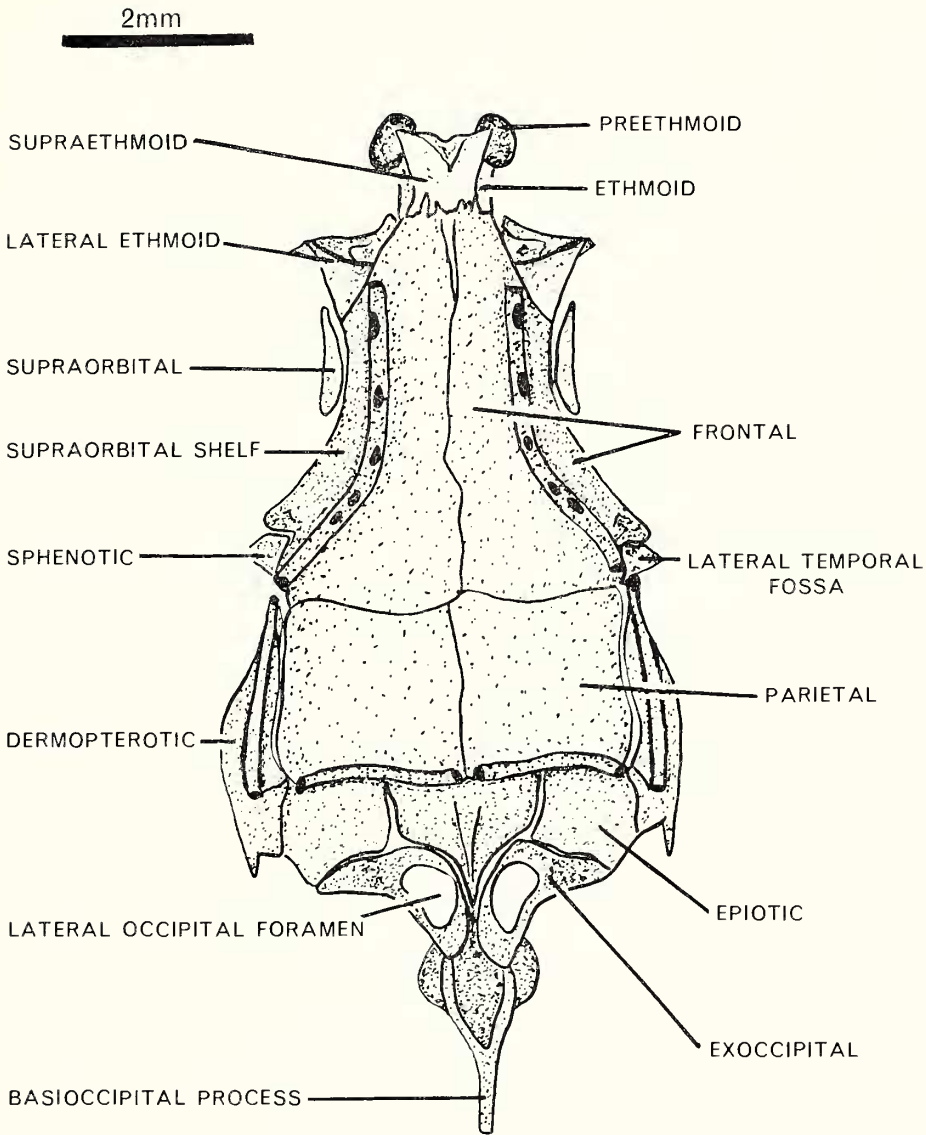


Fig. 4. *O. quathlambae*; neurocranium, dorsal view.

cartilaginous pad interposed between each preethmoid and the head of the maxilla and the palatine of each side. This cartilage seems to correspond with Ramaswami's second preethmoid, and is about the same relative size as the cartilage so labelled in his figures of *Gnathopogon*

elongatus and *Gobiobotia pappenheimi* (Ramaswami, 1955a). Unpublished and uncompleted studies (Greenwood and Meldrum) suggest that in many cyprinids the second preethmoid is a sesamoid cartilage (or ossification) developed in a ligament running from the palatine to the kinethmoid (rostral bone). Unfortunately, the necessary deep dissection could not be made on the large specimen of *O. quathlambae*, but from the superficial one carried out, the cartilage seemed to be a more discrete body than the meniscus developed in the palato-kinethmoid ligament of similar-sized specimens of *Barbus paludinosus*.

Since, in the material available, it is impossible to distinguish between the prefrontal and lateral ethmoid ossifications the bone forming the anterior orbital margin will be referred to as the *lateral ethmoid*. The lateral ethmoids of each side meet medially only at their bases, and are easily separated. Their anteromedial tips closely approach the ethmoid lamina but are not in contact with it. Posteriorly, contact between the lateral ethmoids and the orbitosphenoids is restricted to a small area on the dorsal third of the anterior margin of each orbitosphenoid. There is no distinct, tunnel-like *anterior myodome*; the eye muscles insert into a concavity on the medial aspect of each lateral ethmoid. No facet for articulation with the entopterygoid is discernible on the ventral aspect of the lateral ethmoid (as has been described in some, but not all, cyprinids studied by Ramaswami, 1955a and b).

The *orbitosphenoids* (figs. 2 and 3) are paired and easily separated. Ventromedially, a small area of the orbitosphenoids meets a dorsal projection from the parasphenoid, but the greater part of the ventral orbitosphenoid margin is free from the parasphenoid. Spatial relations between the lateral ethmoids and the orbitosphenoids are described above.

Otic region (figs. 2-4). The *prootic* (figs. 2 and 3) is distended by a prominent bulla acoustica utricularis; dorsally this bone carries a large part of the facet for the hyomandibular head. The *autosphenotic* carries the equivalent lateral component of the hyomandibular facet (see also page 28); anteriorly there is a moderately well-developed sphenotic spine which meets the downwardly curved supraorbital shelf of the parietal; the two bones contribute to a shallow, rather poorly defined lateral temporal fossa (fig. 4).

The *auto-* and *dermopterotic* (figs. 2-4) cannot be separated. A narrow, anteriorly directed laminar projection surrounding the temporal lateral line tubule, and which overlaps the posterior part of the autosphenotic, seems to correspond to the bone called supratemporal-intertemporal-membranopterotic by Harrington (1955). Although this bone cannot be separated from the underlying pterotic, it has a distinct outline around the ventral side of the tubule and dorsoposteriorly to it; in fact, it gives the impression of being plastered onto the pterotic and fused with it (figs. 2 and 4). Laterally the pterotic is distended by the underlying horizontal semicircular canal, which forms a prominent ridge.

No *intercalar* (opisthotic) could be located in either of the specimens examined.

The *exoccipital* (figs. 2-4) is perforated by a large lateral occipital foramen, and by the relatively large vagus foramen. It is greatly swollen by a prominent bulge formed around the junction of the horizontal and posterior vertical semicircular canals. This eminence is only slightly smaller than that formed over the bulla acoustica utricularis in the prootic. Ventrally, the exoccipital is distended by part of the bulla acoustica lagenaris. A shallow *posttemporal fossa* lies medial to the semicircular canal junction in the exoccipital; the smaller, dorsal part of this fossa lies in the epiotic.

The *basioccipital* is distended posterolaterally on each side by the ventral portion of the bulla acoustica lagenaris, but otherwise its ventral face is flat. The posterior pharyngeal process of the basioccipital is a moderately stout structure carrying a broad, roughly cardiform masticatory process.

The *subtemporal fossae* are deep pits (fig. 3).

The *parasphenoid* and *epiotics* show no outstanding characteristics.

Roofing and associated bones (figs. 2 and 4). The *frontals* are approximately triangular in outline, with the hypotenuse gently concave above the orbits. The two frontals overlap in the midline along a broad, sinuous zone of contact; the overlap is irregular, with the left frontal superimposed along parts of the suture, the right in other parts. The dorsal contour of the frontals is slightly convex except for a relatively broad and flat shelf above each orbit; this shelf curves downwards rather sharply over the posterior third of the orbit. The supraorbital lateral line canal runs parallel with the lateral outline of each frontal, along the junction between the supraorbital shelf and the main body of the bone, and extends to its posteroventral margin. There is an appreciable gap between the supraorbital and temporal canals at their junction. In one specimen, on the right side only, the two canals lie at different horizontal levels.

The *supraorbitals* are narrow, and occupy only a small part of the supraorbital indentations of the frontals.

The *parietals* are large, rectangular and almost square bones, with the supratemporal cross-commisure of the lateral line running along their posterior margins; the canals are firmly fused with the parietals, and no distinct median extrascapular bones could be distinguished. Each supratemporal canal ends laterally at the posterior angle of the parietal; that is, it is not continued beyond the body of the parietal as in certain cyprinids, e.g. *Notropis cornutus* (Harrington, *op. cit.*).

Posteriorly, the supraoccipital crest juts out and forms a stem to the shield-shaped *supraoccipital*. This crest is low and fairly broad; on either side of it lies a broad but shallow concavity in the otherwise convex surface of the supraoccipital. The concavities extend forward almost to the anterior margin of the bone.

The *extrascapular* (supratemporal) is a broad, bluntly triradiate bone carrying the Y-shaped, but very unequally armed, supratemporal canal. It is loosely applied to the epiotic and pterotic bones, and partially overlaps the dorsal part of the posttemporal. The *posttemporal* itself (fig. 5) has a stout head through which runs the lateral line canal, and a slender, deeply grooved vertical limb which is closely applied to the dorsoposterior aspect of the supracleithrum. The ventromedial aspect of the posttemporal head is flattened, and is firmly bound to the epiotic by a broad, stout ligament.

Circumorbital and opercular series. There are only four *circumorbital bones*; all are thin and not greatly expanded. The first (lachrymal) is the broadest in the series, the third is the longest. The fourth bone, presumably the *dermosphenotic*, is flimsy, thin and poorly ossified. Although there is a distinct suture between this ossicle and the stouter third one, the canal passes uninterrupted from the latter bone onto the dermosphenotic (fig. 6). The dorsoposterior margin of the dermosphenotic fits into the gap between the dermopterotic and the frontal (see page 24); thus the openings of the temporal, supraorbital and infraorbital lateral line canals are brought into approximate juxtaposition, but there is still an appreciable gap between their respective openings.

Little need be said about the *opercular series* except to note that there is no "supra-preopercular" sensory canal developed in the anterodorsal angle of the operculum. This canal has been described in several other cyprinids (see Ramaswami, *op. cit.*). Neither could we locate, with certainty, any of the foramina for the ramus opercularis superficialis VII which Harrington (*op. cit.*) described in *Notropis cornutus*. However, there is a vertical tubular canal lying just behind the thickened anterior margin of the operculum; the upper opening of this canal is mesial, and is situated immediately below the socket which received the opercular boss of the hyomandibula. This tube may correspond to a similarly situated canal in *N. cornutus*; in that species the tube carries a lower branch of the ramus to supply sense organs on the ventral and antroventral aspects of the operculum (Harrington, *op. cit.*).

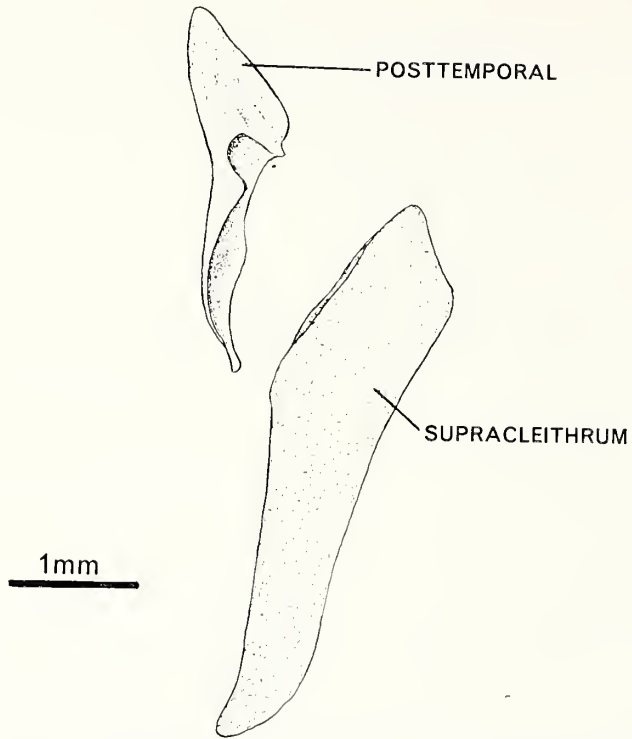


Fig. 5. Right posttemporal and supracleithrum of *O. quathlambae* in lateral view (from a specimen 83 mm. S.L.)

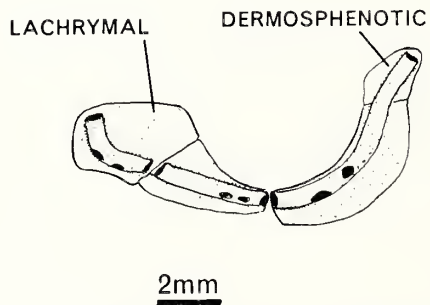


Fig. 6. Left circumorbital bones of *O. quathlambae* (from a specimen 83 mm. S.L.).

Oromandibular region. Jaws (figs. 7-9). Each *premaxilla* (fig. 7A) is a relatively deep bone, with a short but well-defined, rather slender ascending (rostral) process aligned perpendicularly to the long arm of the bone. This type of premaxilla is found in many *Barbus* species, and is quite unlike that in *Labeo* (see Ramaswami, 1955b). The premaxillae curve medially to form a loose symphysis with each other in the midline.

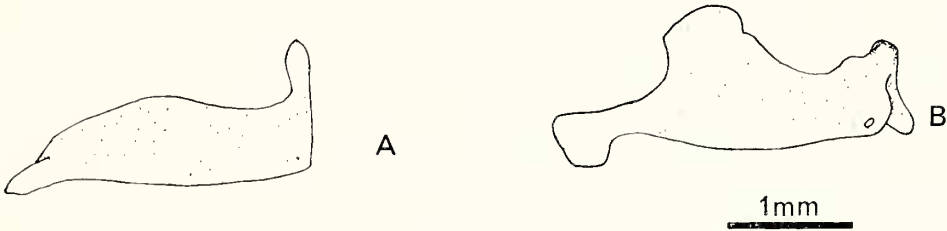


Fig. 7 A. Right premaxilla (lateral view) of *O. quathlambae*.
 B. Right maxilla (lateral view) of *O. quathlambae*.

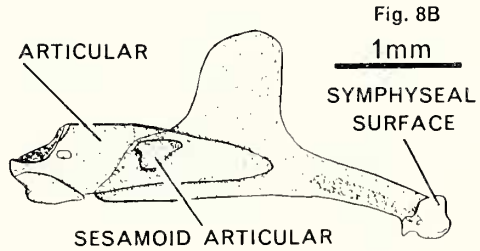
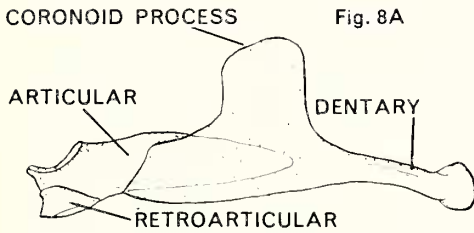


Fig. 8 A. [Right] lower jaw (in lateral view) of *O. quathlambae*.
 B. Left lower jaw (medial aspect) of *O. quathlambae*.

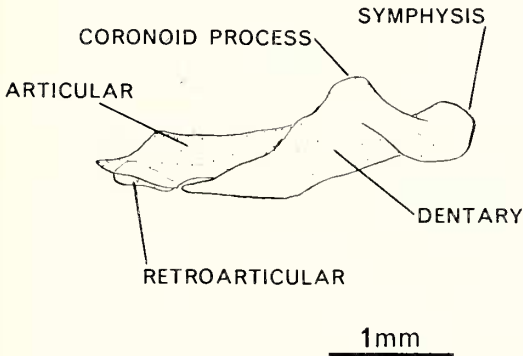


Fig. 9. Right lower jaw of *Labeo niloticus*, viewed slightly dorso-laterally.

Also *Barbus*-like is the *maxilla* (fig. 7B), which has a moderately developed, medially directed rostral process, and a small but distinct anterodorsal boss for articulating with the preethmoid. At about the middle of the maxilla, the dorsal margin is drawn up into a long-based and prominent process; posteroventrally there is a small flange which slips mesially under a short posterior prolongation of the premaxilla.

Each ramus of the *lower jaw* (fig. 8) has a typical complement of four bones. The *dentary* has a high, fairly broad-based coronoid process, and a slender, subcylindrical, mesially curved precoronoid arm which is slightly expanded dorsoventrally at the symphyseal face. The dorsal surface of the precoronoid arm is somewhat flattened and slightly overhangs the anterior face of the underlying bone. There is, apparently, no trace of a mandibular lateral line canal on the dentary, and nor are any mandibular pores visible on the lower jaw of an entire fish. This condition seems to be unique, but should be investigated further before a definite conclusion can be reached; regrettably the material at our disposal is not suitable for the detailed dissection and histological examination which would be necessary to check this point.

The *articular* is a long, substantial bone, notched dorsoposteriorly by the articulatory surface for the head of the quadrate. Almost mirroring this notch is a ventral excavation in which the *retroarticular* (angular) lies. The *sesamoid articular* lies on the medial face of the articular at about its midpoint and a little below its dorsal margin.

The lower jaw of *O. quathlambae* is quite unlike that in *Labeo*, as a comparison of figures 8A and 9 will show (see also Ramaswami, 1955b, fig. 16, page 221, and page 19). It does not, however, differ greatly from the lower jaw in the several *Barbus* species we have studied.

Part of the *suspensorium* is illustrated in figure 10, and requires no comment except to note that the symplectic is relatively longer than in *Labeo*.

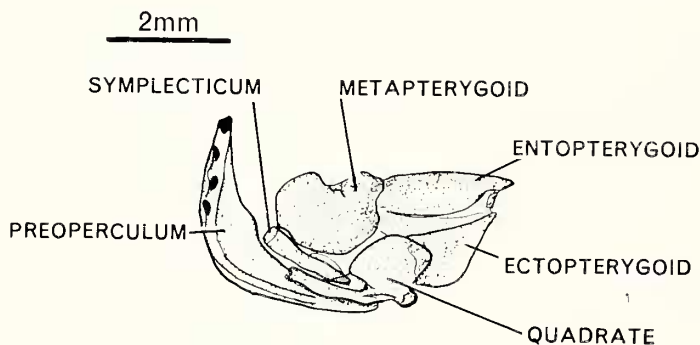


Fig. 10. Part of the right suspensorium of *O. quathlambae*, in lateral view.

Hyoid arch. The hyoid arch shows no outstanding characteristics; the *epi- and ceratohyals* are moderately stout and short bones, and the *hypohyals* are double. The *urohyal* is illustrated in figure 11. The *branchiostegal* rays are slender, elongate and gently curved bones.

The *hyomandibula* is short and broad, with two ill-defined heads; its articulatory facet on the neurocranium is formed principally by grooves along the junction of the prootic and autosphenotic bones (fig. 3), but posteriorly there is a small area contributed by the autoptero-otic, and anteriorly a minute facet on the pterosphenoid.

Branchial skeleton and pharyngeal bones (figs. 12-14). The branchial skeleton is essentially as described for other cyprinids (Ramaswami, 1955 a and b; Harrington, 1955). The *ceratobranchials* are fairly stout, but the *epibranchials* are slender. Gill rakers on the ceratobranchials of all four gill-bearing arches are short and acutely conical; there are two rows of 6-8 rakers on each arch. The first *pharyngobranchial* is reniform, and pharyngobranchials two and three are fused into a large, broad, trianguloid plate. The pharyngobranchials of each side are contiguous, the two fused elements slightly overlapping the first along the dorsal side of its posteromedial angle. An unossified third pair of pharyngobranchials has been described in some cyprinids (see Harrington, *op. cit.*), and are probably present in *O. quathlambae*. The alizarin technique does not stain cartilage, but probing with a needle in the gap between the fourth epibranchial and the fused second and third pharyngobranchials indicates that the tissue is more resilient than would be expected if it was only connective tissue and muscle.

The first two pairs of *hypobranchial* bones are short, dumpy and somewhat compressed rods, but the third pair are more slender and have long, curved ventromedially directed processes. There are three median *basibranchials*; the dumbbell-shaped, and cylindrical second and third elements are subequal in length, the spatulate first basibranchial about half their length.

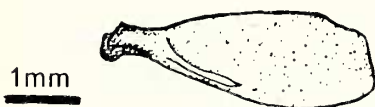


Fig. 11. Urohyal of *O. quathlambae* in left lateral view.

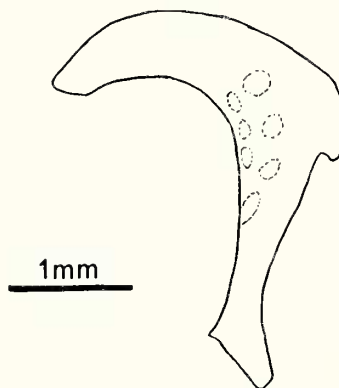


Fig. 12. Outline of right pharyngeal bone from a specimen of *O. quathlambae* 40 mm. S.L. The bone is laid flat on its lateral aspect. Alveoli of the teeth are indicated by broken lines.

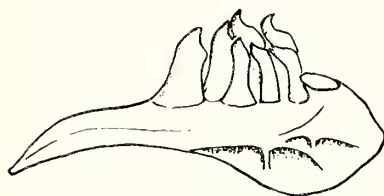


Fig. 13. Left pharyngeal bone and teeth of *O. quathlambae*, dorsal aspect, from a specimen of 83 mm. S.L.



Fig. 14. Left pharyngeal bone and teeth of *O. quathlambae* (83 mm. specimen), viewed somewhat dorso-medially (two positions) to show crown shape in teeth; about $18 \times$ N.S.



The *pharyngeal bones* (figs. 12 and 13) are distinctly falcate, with a prominent anterior angle which is produced slightly in an anterolateral direction; the posterior angle is so smoothly incorporated into the curve of the posterior limb that it is not discernible. Each bone is about 3.3 times as long as broad; the anterior limb is slightly shorter than the posterior one (nomenclature and reference points after Chu, 1935). The pitted surface is moderately broad; in the smaller specimens it extends almost to the tip of the posterior limb, but only to about halfway between the posterior tooth and the tip of the posterior arm in the larger fish. In specimens of all sizes, the pits extend to the level of the anterior angle.

The pharyngeal teeth (figs. 13 and 14) are arranged in two rows, the outer with three teeth, the inner with four. Teeth of the inner row have relatively stout necks, subcylindrical in cross-section; the crowns are expanded and slightly broader than the necks, and are inclined anteriorly at an appreciable angle to the posterior margin of the neck. In cross-section, the crowns are concave above, giving a spoon-like occlusal surface; their tips, however, are conical, produced and strongly curved posteriorly. The two anterior teeth in this row are coarser than the posterior pair, and have their crowns less obliquely inclined.

Outer row teeth resemble those of the inner row but are smaller and more slender; the posterior tooth in this row has its crown inclined almost at right angles to the posterior margin of the neck.

Comparison of the pharyngeal bones and teeth from the smaller specimens (*ca* 40 mm. S.L.) with those from the large fish (83 mm. S.L.) do not indicate any appreciable difference in bone shape or tooth form.

Although we have not been able to examine the pharyngeal teeth in every species of African *Barbus*, the sample we did study indicates relatively little intrageneric variation in tooth form. The most pronounced differences seem to be associated with an increased "molarization" of the crowns (especially of the anterior teeth in the principal row) in certain species. The chief types of tooth morphology in *Barbus* are illustrated by Matthes (1963; plate VII). On these basic types are superimposed slight differences in crown form, but in some species spoon-shaped, obliquely curved crowns approaching the *O. quathlambae*-type are seen in teeth of all rows (this is especially so in *B. treurenensis*). We have not encountered a pharyngeal dentition of the *O. quathlambae*-type in any of the Asian or European *Barbus* species we have studied, nor have we seen it illustrated. Likewise the pharyngeal teeth of other cyprinid genera in Africa do not approach the *O. quathlambae*-type (except that in some the dentition is biserial). Comparisons made with representative species of several North American, Asiatic and European genera also serve to emphasise the uniqueness of the pharyngeal dentition in *O. quathlambae* (and, incidentally, the relative uniformity of tooth shape in the leuciscine genera, and some groups of the Gobioninae).

Weberian apparatus (figs. 15 and 16). The apparatus is carried on two discrete (the first and fourth) and two fused centra (the second and third). The centrum of the first vertebra is almost the same length as that of the fourth. Its lateral processes are relatively short and slender; when viewed from above each process has a weakly sigmoid outline, and is directed ventrally. The lateral processes of the fused vertebrae are much longer and stouter; the process of each side arises near the anteroventral border of the centrum. Basally, the process is curved anteriorly and somewhat ventrally, but it then bends sharply upwards and backwards. A pair of stout, ventrally directed ribs are associated with the fourth vertebra; medially from each rib there is a long but broad-based os suspensorium. The ossa suspensoria are closely apposed in the midline but do not contact. Compared with the fourth ribs in the *Labeo* species examined, those of *O. quathlambae* are very slender and narrow-based. Slender fourth ribs are apparently also characteristic of *Barbus* species, particularly in those with adults attaining only a small size. In some species with large adults (e.g. *B. tanensis* and *B. altianalis*) the ribs are stout, but are still relatively more slender than in *Labeo* species, irrespective of the adult size.

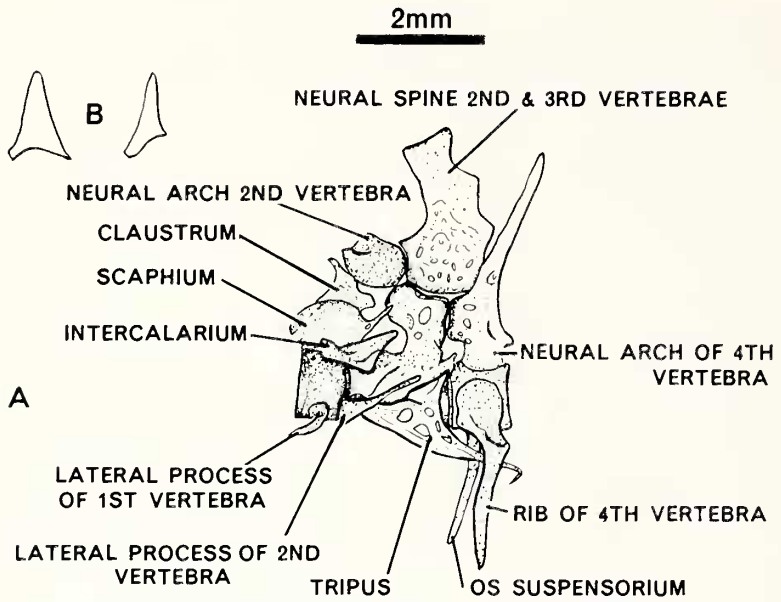


Fig. 15. Weberian apparatus of *O. quathlambae*.
 A. Entire apparatus in left lateral view (40 mm. specimen).
 B. Left intercalaria from two specimens (both ca 40 mm. S.L.) to show variation in outline.

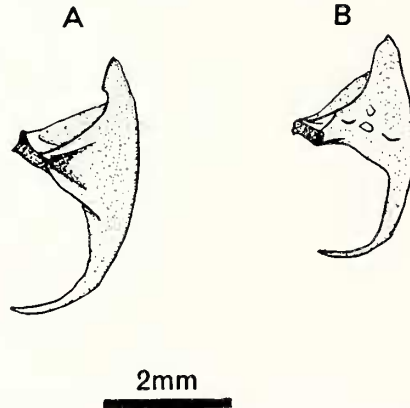


Fig. 16. Right tripus (dorsal aspect) of : A. *Labeo niloticus* B. *Oreodaimon quathlambae*.

Ossicles. The *claustrum* is a large slightly concavo-convex and trianguloid bone. A thickened lateral ridge, at a point about one third of the distance from the ventral margin, indicates the zone of contact between this bone and the scaphium.

The *scaphium* is roughly hemispherical, with a thin, backwardly directed spine arising from about the middle of its posterior margin. A stout, ventrally directed peg on the ventral margin articulates with a deep socket situated dorsolaterally on the first centrum.

The thin *intercalarium* is basically triangular in outline. In one specimen, the base of the triangle is broad, and the outline of the bone is proportionately broad. In the other fish, however, the base is short, and consequently the bone is narrow and spicule-like (see fig. 15B). The intercalarium articulates with a deep pit lying dorsolaterally on the anterior third of the fused centra. Compared with the intercalarium of *Labeo* (12 species examined) and *Barbus* (5 African and 2 Eurasian species), that of *O. quathlambae* is larger and coarser; also, in the *Labeo* and *Barbus* species it is clearly triradiate, with distinct but unequal arms. The same characteristics distinguish the intercalarium of *O. quathlambae* from that of *Saurogobio duerili*, *S. dabrayi* and *Gobiobotia pappetheini* as figured by Ramaswami (1955a). The intercalarium of *Gobio polytaenia* (Ramaswami, *op. cit.*) and *Gobio gobio* (personal observations) is relatively as long as that of *O. quathlambae*, but is more slender and rod-like, thus approaching the condition found in one of the *O. quathlambae* specimens. The closest resemblance to any other figured species is with the intercalarium of *Vimba vimba* and *Alburnoides bipunctatus* (see Chranilov, 1927).

The *tripus* is essentially like that described by Ramaswami (1955 a and b) for *Notropis cornutus* and *Pseudogobio esocinus*, and the tripus of all African *Barbus* species examined by us. Although basically like the tripus in *Labeo*, it differs somewhat in that the *Labeo* tripus has a deeper articular surface, and the limb connecting this face with the horizontal part of the bone is broader and is reinforced dorsally by two vertical ridges which converge at the articular head (see fig. 16). The tripus articulates with a shallow pit lying midlaterally on the posterior half of the fused vertebral centra.

Pectoral girdle (fig. 17). The various elements of this girdle show no outstanding characteristics. The cleithrum has a wide lateral shelf developed from the horizontal limb; the anterior tip of this shelf is deeply and obliquely emarginate. The wide vertical limb of the cleithrum is somewhat shorter than the horizontal limb. The single *postcleithrum* is a substantial, subcylindrical and rib-like bone which curves posteriorly and ventrally.

The club-shaped *supracleithrum* (fig. 5) is loosely bound, over its lower two-thirds, to the lateral face of the cleithrum; the upper third of the supracleithrum is thicker, and has an ill-defined facet on its posterior face. This facet lies in the deeply grooved anterior face of the posttemporal (see page 25).

DISCUSSION

Taken in concert, the biserial pharyngeal dentition, the peculiar crown-form of these teeth, the small scales (absent from the chest), and the unspecialized mouth of *O. quathlambae* provide a character complex which trenchantly separates this genus from all other African Cyprinidae. This high degree of distinctiveness immediately raises questions about the derivation of the genus, and its position within the family.

At the generic level, *Oreodaimon quathlambae* cannot be closely allied with such genera as *Barilius*, *Leptocypris*, *Engraulicypris*, *Chelaethiops* or *Coptostouabarbuis* (see, especially Matthes, *op. cit.*, for descriptions of jaw and pharyngeal structure in these fishes). Thus, one is left with *Barbus*, *Labeo*, *Varicorhinus*, *Garra*, *Prolabeo* and *Prolabeops* as possible relatives, if *O. quathlambae* evolved from a stem represented by other extant derivatives in Africa. Again, each of these genera is readily distinguished from *O. quathlambae* at the generic level, but the separation is less obvious at a suprageneric level. Two characters, the biserial pharyngeal teeth, and the crown form in these teeth, are probably the only ones which do not conform at

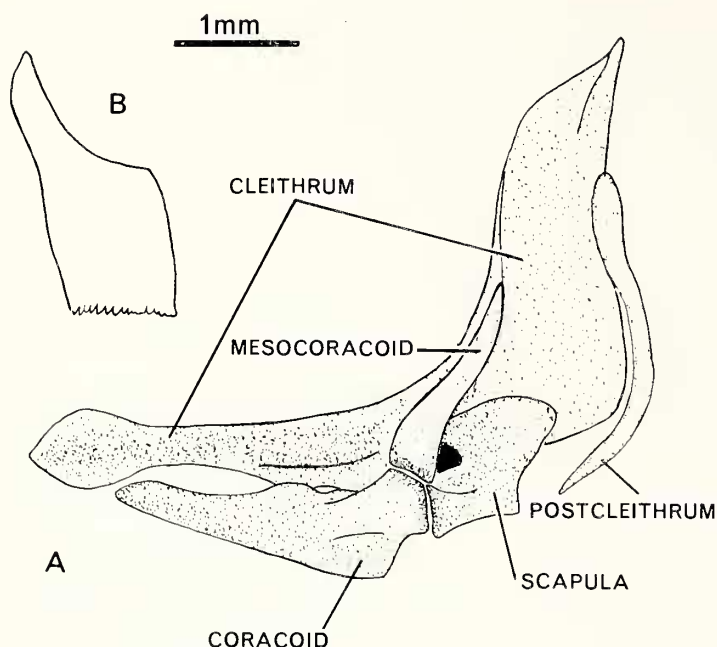


Fig. 17 A. Right pectoral girdle of *O. quathlambae*, medial aspect.
 B. Anterior tip of right cleithrum, viewed from above.

that level. The number of tooth rows seems to be of some phyletic significance, although the reasons for intragroup constancy in this character are not apparent. Take, for example, the genus *Barbus*. Here there are species showing every trophic specialization (except, possibly, exclusive vegetarianism), and these are, to a certain extent, reflected in the morphology of the pharyngeal teeth (Matthes, 1963; personal observations). But, the teeth are invariably triserial. In *Labeo* (an exclusively vegetarian species group), triserial teeth are also invariable. On the other hand, the tropically varied leuciscine genera of Eurasia and America have biserial or, rarely, uniserial pharyngeal teeth.

Attempts to split the Cyprinidae on a subfamilial basis have not proved successful. Ramaswami (1955b), after investigating the cranial osteology of several genera, concluded that "... I have not been able to find a set of them [skull characters] as distinguishing each of the subfamilies of the Cyprinidae." Earlier, Regan (1911) reached virtually the same conclusions after examining, albeit somewhat more superficially, a greater variety of characters; however, Regan was able to indicate certain groups as being better defined than the others. Chu's (1935) studies on the scales and pharyngeal dentition of Chinese Cyprinidae suggest that these structures are also of little value in helping to define subfamilies, although in certain groups they may aid in the recognition of a modal group condition.

In part, the difficulties encountered in defining subfamilies are due to insufficient detailed knowledge about most character systems in this vast and varied family. This impediment must also affect any considerations we may make about the taxonomic position of *O. quathlambae*.

Nikolski (1954) used tooth row numbers, together with other characters (squamation, relative lengths of median fin bases, *etc.*) as criteria for recognising nine subfamilies of Soviet Cyprinidae. On Nikolski's scheme, *O. quathlambae* most closely approaches the subfamily Gobioninae, differing from other members principally in having such small scales. It also approaches his subfamily Barbinae, but differs in not having a triserial pharyngeal dentition. Although no obvious gobionines are present in Africa, the ill-defined position of *O. quathlambae* relative to the Gobioninae and Barbinae (*sensu* Nikolski, Cyprininae of others) warranted a close comparison of this species with true gobionines.

Ramaswami's (1955a) osteological studies immediately showed that several gobionine genera differ quite markedly from *O. quathlambae* in details of the neurocranial architecture, and in the Weberian apparatus. But, there is quite close correspondence in these characters between *O. quathlambae* and more generalized members of the subfamily (e.g. *Gobio* and *Gnathopogon* spp.). Parenthetically, it should be noted that these remarks also apply to generalized species of the Barbinae.

The chief differences between the basic gobionines and *O. quathlambae* lie in squamation and the shape of the pharyngeal teeth (but not in their serial arrangement). Crown shape in the species of *Gnathopogon* we examined (*G. polytaenia* and *G. elongatus*) differs considerably from that in *O. quathlambae*, and from that in the species of *Gobio* we studied (*G. gobio*, *G. uranoscopus*, *G. argentatus*, *G. nummifer* and *G. zoldatovi*). In turn, the teeth of *O. quathlambae* differ from those of the *Gobio* species, but to a less marked degree. However, none of the *Gobio* species shows a crown shape as near to that of *O. quathlambae* as some we observed in various African species of *Barbus* (e.g. the posterior teeth in *Barbus kerstenii* and *B. paludinosus* (both from east Africa), and particularly *B. gurneyi* and *B. birchelli* from South Africa).

Thus, to summarize, *Oreodaimon quathlambae* agrees with the Gobioninae in having a biserial pharyngeal dentition, but differs in the shape and number of the teeth, and in having very small scales. Small scales occur in various species of Barbinae (e.g. certain *Barbus* and *Labeo* species) and some species do have certain pharyngeal teeth which approach the *Oreodaimon*-type, although the total dental pattern (tooth shape, number and disposition) is dissimilar.

On this sort of evidence only the most tentative conclusions can be reached, but we believe (with that reservation) *O. quathlambae* to be nearer the Barbinae than the Gobioninae, and certainly nearer these than any other subfamily, except possibly the Leuciscinae. Affinity with the Leuciscinae was rejected on the grounds of *O. quathlambae* having an emarginate anterior tip to the cleithrum, and because of its pharyngeal tooth morphology (especially considering the relative constancy of tooth form in those North American leuciscines which *O. quathlambae* most resembles).

On zoogeographical grounds as well as on anatomical ones, *O. quathlambae* is probably a derivative of the Barbinae, and, for the moment it should be included in that group. The blurred phenetic affinities of *O. quathlambae* serve to emphasise the difficulties of producing biologically satisfactory subdivisions of the Cyprinidae.

If *O. quathlambae* is a member of the Barbinae, it must have evolved from a *Barbus* or *Barbus*-like ancestor. Other members of the subfamily are too specialized to be considered. No extant African *Barbus* species shows the sort of characteristics which might be indicative of the species-group from which *O. quathlambae* evolved, although in *B. treurenensis*, an endemic species isolated in a mountain stream in the north-eastern Transvaal, certain pharyngeal teeth have crowns very like those of the teeth of *O. quathlambae*. The very distinctive characters of *O. quathlambae* hint at a long isolation from the *Barbus* stem. Certain of these characters, such as the small scales, naked chest, flattened ventral profile and horizontally inserted pectoral fins, probably are adaptations to mountain stream habitats. What is surprising,

however, is the absence in Africa of other *Barbus* derivatives showing similar adaptations. For instance, *Barbus anoplus* occurs in mountain stream habitats, yet it retains all the characteristics of a typical *Barbus* species. This suggests that the *Barbus* 'bauplan' can be successful in the demanding environment of a mountain stream without undergoing any morphological adaptation. Perhaps the greater specializations (physiologically as well as anatomically) of *O. quathlambae* have contributed to its extinction.

NOTE ON THE TYPE LOCALITY

We are indebted to Mr. R. S. Crass of the Natal Parks, Game and Fish Preservation Board, for a detailed description of the type locality. The Umkomazana River rises at an altitude of about 9,000 feet some ten miles west-north-west of the area in which the collection of *O. quathlambae* was made. The upper valley leads to the Sani Pass over which a rough road enters Lesotho (Basutoland). The Drakensberg Escarpment is subject to periodic rain or snow throughout the year and the headstreams, rising near the crest, are torrential with numerous cascades and waterfalls. The headstreams of the Umkomazana unite to form the upper river which continues to flow down a steep narrow valley incised into the sandstones and shales of the Stormberg Series. The gradient of the valley for the last mile or so above where the fish were found is about 1 in 50, but the type locality, approximately 5,100 feet above sea level, is at a point where the valley opens out and becomes less steep. This part of the valley is on Beaufort Beds.

The stream bed consists of rounded boulders, stones and sand which shift readily in times of flood. When the river is low there are slowly flowing pools and flats, with riffles in between. There is a broad flood plain with sandy soil full of water-worn rocks, and the stream readily changes its course when in spate. Since early this century denudation of grass cover by grazing animals in the upper catchment area has tended to accentuate the severity of floods and scouring after heavy rain. Riparian vegetation consists of a sparse growth of grasses and sedges, with thickets of the shrub *Leucosidea sericea*. Aquatic vegetation is almost entirely absent. The mean width of the pools in the dry season is about 30 feet and the normal low flow is of the order of 15 cusecs.

Below the type locality of *O. quathlambae* the river has a gradient of 1 in 300 or 400 with an unstable stony bed for about a mile, until a dolerite sill causes a waterfall which is high enough to form a barrier to fish moving upstream. No specimens of *O. quathlambae* have ever been recorded from the river system below this waterfall, or the Umkomaas River into which it flows, and no other indigenous fishes, including the common large *Barbus*, *B. natalensis*, from above it.

Brown trout, *Salmo trutta*, were first introduced into the Upper Umkomazana River at some time between 1910 and 1920, the exact date not being known. Later, in 1926 and 1927, additional stockings of *S. trutta* and also of rainbow trout, *S. gairdneri* were made. The latter species did not become established but a breeding population of *S. trutta* has been maintained to this day. The trout are affected by both floods and droughts, numbers fluctuating from year to year due to the instability of the habitat.

Thus, early this century this unique and specialized species, *O. quathlambae*, which had survived in the sanctuary of the Upper Umkomazana River out of reach of other indigenous fishes, became faced with the presence of a large predator, *S. trutta*, a serious competitor for food, and a deteriorating habitat—all of which have no doubt contributed towards the disappearance of *O. quathlambae* from its type locality.

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