

ON THE CYPRINID FISH *BARBUS ALLUAUDI*
PELLEGRIN : A POSSIBLE INTERGENERIC HYBRID
FROM AFRICA

STUDIES ON AFRICAN CYPRINIDAE
PART I

BY
KEITH EDWARD BANISTER



Pp. 261-290; 1 *Plate*, 29 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY

Vol. 24 No. 5

LONDON : 1972

THE BULLETIN OF THE BRITISH MUSEUM
(NATURAL HISTORY), *instituted in 1949, is
issued in five series corresponding to the Departments
of the Museum, and an Historical series.*

*Parts will appear at irregular intervals as they become
ready. Volumes will contain about three or four
hundred pages, and will not necessarily be completed
within one calendar year.*

*In 1965 a separate supplementary series of longer
papers was instituted, numbered serially for each
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*This paper is Vol. 24, No. 5 of the Zoological series.
The abbreviated titles of periodicals cited follow those
of the World List of Scientific Periodicals.*

*World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).*

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 29 December, 1972

Price £1.45

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STUDIES ON AFRICAN CYPRINIDAE PART I

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INTRODUCTION

WHILE identifying the fishes collected in the Mubuku and Sibwe rivers, Uganda (fig. 1) by Dr. I. G. Dunn of the Royal Society—International Biological Programme African Freshwater Research Team, Lake George, Uganda, I came across two specimens referable to *Barbus alluaudi* Pellegrin 1909. These two specimens were morphologically intermediate between the other cyprinid species collected, *Barbus somereni* Boulenger 1911 and *Varicorhinus ruwenzorii* (Pellegrin) 1909. The two specimens were collected upstream of the road bridge over the Mubuku river near Kasese, Uganda. More specimens were necessary before a full investigation could be pursued and these were obtained by Mr. Paul Ready and Mr. T. Slade of the Imperial College, London University, expedition to the Ruwenzori mountain range in 1971; they collected in the Mubuku and Sibwe rivers and obtained a further eight specimens of *Barbus alluaudi* from the Dunn locality and another specimen from the Sibwe river. The eight *Barbus alluaudi* were caught with 142 *Varicorhinus ruwenzorii* within a 30 yards stretch of river upstream from the road bridge.

Between these two events I had examined the types of *B. alluaudi* which were kindly loaned to me by Madame M. L. Bauchot of the Paris Museum. These two specimens were collected in the Wimi river (=Ruimi river) which is on the eastern flank of the Ruwenzori Mountain range (fig. 1).*

Hybrids between the genera *Barbus* and *Varicorhinus* have been reported before (Steinitz and Ben Tuvia, 1957, from Israel; although Karaman, 1969, has now placed *Varicorhinus damascinus* in the genus *Capoeta*). Demetrashvili (1963) noted

*The Wimi river does not appear on any modern maps. I have, however, been able to establish that it is an old name for the Ruimi river thanks to the detailed description of the expedition of Prince Luigi by Filippi (1908).

a hybrid between *Cyprinus carpio* L. and *Varicorhinus capoeta* Berg (*Capoeta capoeta* fide Karaman *op. cit.*) from the Khramsk reservoir, Georgia, U.S.S.R.

Slastenenko (1957) in his list of natural fish hybrids of the world does not list any hybrids between the genera *Varicorhinus* and *Barbus*.

In this paper I intend to offer evidence to support my hypothesis that specimens referred to the nominal species *Barbus alluaudi* are hybrids between *Barbus somereni* and *Varicorhinus ruwenzorii*.

It would seem that our knowledge of African freshwater fishes has only recently reached the stage at which hybrids can be determined. Hubbs (1955) predicted the presence of hybrids in African fishes and suggested that they may have been misidentified as distinct and rare species. Hybrids have been described for *Tilapia* (see bibliography in Elder, Garrod and Whitehead 1971) but *Tilapia* has long been cultivated in ponds and special emphasis has been placed on its systematics because of its commercial importance. Jubb (1967: 119) mentions a fish taken from a dammed stretch of river at Roodewal farm, Piet Retief district, South Africa

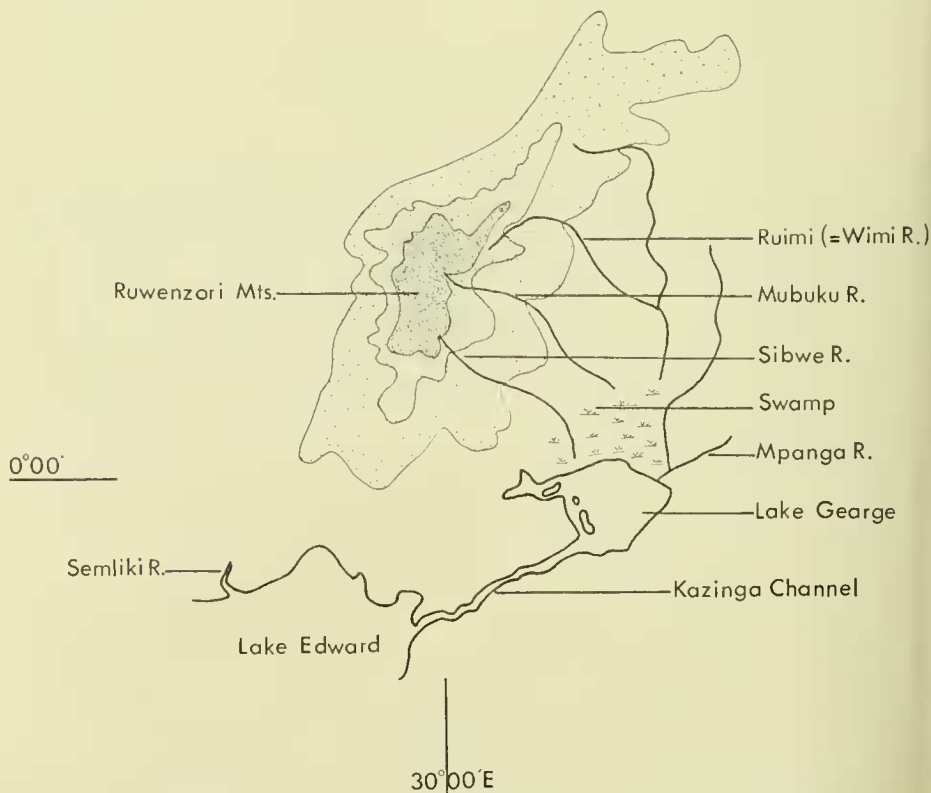


FIG. 1. A sketch map of the Ruwenzori region showing the rivers mentioned in the text.

(Maputo system), which he thought was a natural hybrid between *Varicorhinus nelspruitensis* Gilchrist and Thompson and *Barbus polylepis* Boulenger. I have not been able to examine this fish, but Jubb was of the opinion that hybridisation occurred as a result of the alteration of the environment; however, further specimens (Jubb, 1968) led Jubb to the conclusion that it was a natural variety of *B. polylepis*.

It may be noted that African *Barbus* and *Varicorhinus* have been, to some extent, problem genera. Groenewald (1958) demonstrated that in certain circumstances *Barbus* can achieve a '*Varicorhinus*'-like appearance, especially of the mouth.

It is not my intention in this paper to define the generic limits of either genus, but work is in progress on this problem and it is here implied that *Barbus somereni* and *Varicorhinus ruwenzorii* rightly belong in separate genera.

MATERIALS AND METHODS

A total of 63 specimens of *Varicorhinus ruwenzorii*, including the types, were examined. Two of these specimens were prepared by the alizarin technique and used in the osteological descriptions. Fifty one *Barbus somereni*, including the holotype, were examined and two were prepared by the alizarin technique.

One specimen of *Barbus alluaudi* BM(NH) No. 1971.1.5 : 135 was first partially dissected to study the jaw muscles and ligaments and then prepared by the alizarin method.

The standard length (S.L.) was taken as the distance from the end of the snout to the end of the hypural bones. This distance was measured with dial calipers. The eye diameter (I) was measured as the horizontal distance across the eye. In long-preserved specimens the tissues around the eye had shrunk and exposed more of the orbit so that, in this paper, the eye diameter was only measured on specimens sufficiently fresh for there to be no noticeable wrinkling or shrinking of the tissues around the eye. The eye diameter ratio in long preserved specimens was the same in *Barbus somereni* as in *Varicorhinus ruwenzorii*, the differences were only noticeable in the fresh material. The mouth width (M.W.) is the greatest width of the lower jaw. The head length (H) is the horizontal distance from the anterior margin of the snout to the posterior extremity of the operculum. The interorbital width (I.O.) is the least distance across the bony part of the interorbital space. The dorsal fin 'spine' (D.Sp.)—the last unbranched ray—was measured from its base to the proximal articulation which is almost always at the base of the flexible tip of the ray. Where measurements were repeatable and different on both sides of the specimen, the larger one was accepted unless the structure measured showed signs of gross abnormality.

Sections were cut of the testes of a *Barbus somereni* and of a *Barbus alluaudi*; some were stained with haemalum and eosin, whilst others were stained with Feulgen and light green in an attempt to show the presence of D.N.A.

Radiographs were taken of all three species. The vertebral counts include all the vertebrae from the first to P.U.₂ of Rosen and Greenwood (1970). This includes the four vertebrae involved in the Weberian mechanism and excludes all after and including P.U.₂—the vertebra which supports the parhypural. The abbreviations

used in the text and not mentioned above are Ab = anterior barbel; Pb = posterior barbel; N = the number of specimens considered.

THE PUTATIVE PARENT SPECIES

An interesting feature shared by the putative parent species and by *B. alluaudi* is the colour pattern. This is a deep olive-brown on the back which changes sharply into an ochreous yellow on the flanks and then fades on the belly. The dark olive of the back, however, is continued on to the lower lobe of the caudal fin. The upper lobe of the caudal fin and the dorsal fin are pale brown.

Specimens that have been stored in alcohol for a long time become uniformly brown.

A small specimen of *Varicorhinus ruwenzorii* (less than 40 mm S.L. and not included in the data) has a colour pattern consisting of a grey back, a dark lateral stripe ending in a dark spot on the caudal peduncle, and pale flanks and belly. There is just a trace of dark pigment on the caudal fin.

Barbus somereni Boulenger 1911

Plate 1a

HOLOTYPE. A fish of 172 mm S.L. BM(NH) 1911.7.26 : 1 from the Sibwe River, Ruwenzori mountains, Uganda.

There is no significant difference between certain morphometric ratios in *Barbus somereni* and in *Varicorhinus ruwenzorii*, so the only data discussed are those in which there is a noticeable difference.

The size range of the 51 specimens examined was from 66 to 279 mm S.L. The specimens came from the Sibwe river, Mubuku river, Tokwe river, Kirimia river and Ruimi river.

TABLE I

	N	\bar{x}	Range	S	Se
H	51	25.9	21.6-28.8	1.4	0.2
I	22	5.15	4.3- 6.6	0.7	0.14
M.W.	51	7.5	6.3- 9.2	0.8	0.14
Ab.	51	7.8	5.6- 9.6	1.0	0.1
Pb.	51	7.8	6.3-11.6	1.2	0.2
D.Sp.	51	13.8	8.7-21.2	2.9	0.4

All measurements are expressed as percentages of the standard length.

The mouth (fig. 2) is subterminal and horseshoe shaped. The anterior margin of the lower jaw is curved, the lips are soft, continuous and not usually enlarged. The isthmus extends a long way forward and the muscles are covered only by a thin layer of tissue below the skin.

The barbels are long and fleshy. The snout is gently curved and does not noticeably overhang the mouth. The eyes are usually visible in ventral view. The dorsal

fin has its origin in advance of the pelvic fins. It has four unbranched rays, the last one of which is ossified into a smooth spine. There are nine or ten branched rays.

The anal fin has three or four unbranched rays. The first ray, in the fishes with four rays, is extremely small and hidden below the skin so that it is only visible in radiographs or alizarin transparencies. The scales of *Barbus somereni* bear striae which do not conform neatly to either of the three divisions described by Boulenger (1911a). The striae on the exposed part of the scale vary between typically parallel and typically radiate; the number modally is about 18. In each case the fifth scale from the row above the lateral line has been examined. The buried portion of the scale has about the same number of striae but they are disposed more radially (fig. 3).

The number of scales in the lateral line varies from 26 to 34: 26 (f.1); 27 (f.2); 28 (f.3); 29 (f.5); 30 (f.11); 31 (f.12); 32 (f.7); 33 (f.7); 34 (f.1). This is expressed graphically in fig. 22.

There are twelve scales around the caudal peduncle; $5\frac{1}{2}$ (sometimes $4\frac{1}{2}$, rarely $6\frac{1}{2}$) between the mid-dorsal line and the lateral line and $4\frac{1}{2}$ - $6\frac{1}{2}$ (very rarely $7\frac{1}{2}$) between the lateral line and the mid-ventral line. Two and a half to $3\frac{1}{2}$ (modally 3) scale rows are present between the lateral line and the base of the pelvic fin.

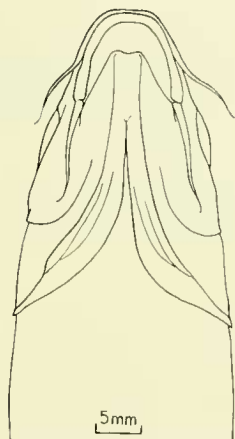


FIG. 2. The underside of the head of *Barbus somereni*.

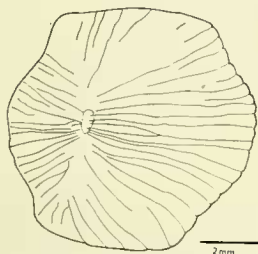


FIG. 3. A scale from the shoulder of *Barbus somereni* showing the position of the striae.

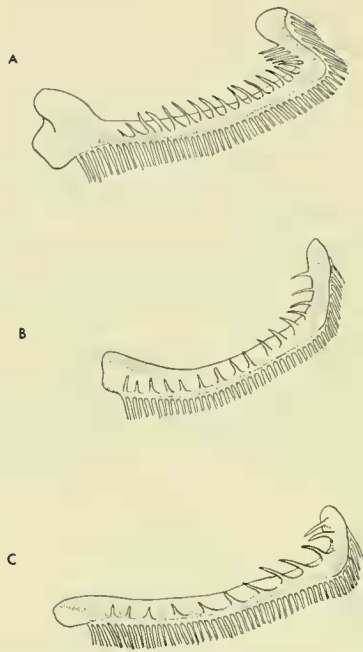


FIG. 4. Lateral aspects of the first gill arch in (a) *Varicorhinus ruwenzorii*, (b) *Barbus alluaudi*, (c) *Barbus somereni*.

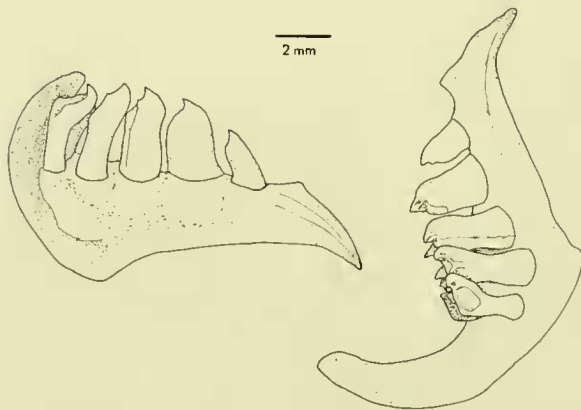


FIG. 5. The left pharyngeal bone of a *Barbus somereni* of 170 mm S.L.

The gill rakers on the first gill arch (fig. 4C) number modally $10 + 2$ within the range $8 + 2$ and $11 + 2$. They are strong and slightly hooked. The second tooth in the inner pharyngeal row of a specimen 170 mm S.L. shows no significant molarisation. The first tooth is stout, about $\frac{2}{3}$ of the length of the second tooth and angled towards it. Teeth three to five become progressively more recurved with hooked crowns (fig. 5). The teeth of the second and third rows are smaller versions of the third, fourth and fifth teeth of the inner row.

The pharyngeal bone is broad, the anterior process (*sensu* Matthes, 1963) bears a sharp longitudinal ridge on the occlusal face of the bone and a moderately well defined lateral flange is present. The bone in a specimen of 170 mm S.L. measured 16 mm in a direct line from the extremity of the ascending process to the end of the anterior process. The vertebrae in ten specimens examined numbered 37 (f.3); 38 (f.6); 39 (f.1). The 37 vertebrae comprise 20 abdominal + 17 caudal (f.2) or 21 + 16 (f.1), the 38 comprise 19 + 19 (f.1); 20 + 18 (f.1) or 21 + 17 (f.4), the 39 comprise 18 + 21.

Suspensorium and jaws

An exploded diagram of the suspensorium is shown in fig. 6.

The dentary is long with a large based coronoid process. The rami of the lower jaw (fig. 7) smoothly taper rostrad and gently curve in towards their symphysis. The dotted line in fig. 7 represents the outer limit of the lower lip.

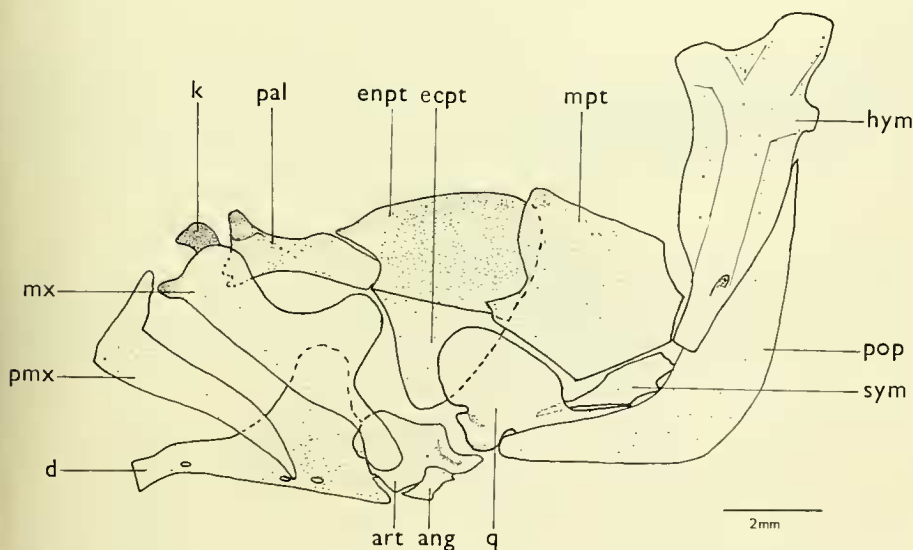


FIG. 6. A diagram of a partially disarticulated suspensorium of *B. someveni*. ang = angular; art = articular; d = dentary; ecpt = ectopterygoid; enpt = endopterygoid; hym = hyomandibula; mpt = metapterygoid; mx = maxilla; pal = palatine; pmx = premaxilla; pop = preoperculum; q = quadrate; sym = symplectic; k = kinethmoid.

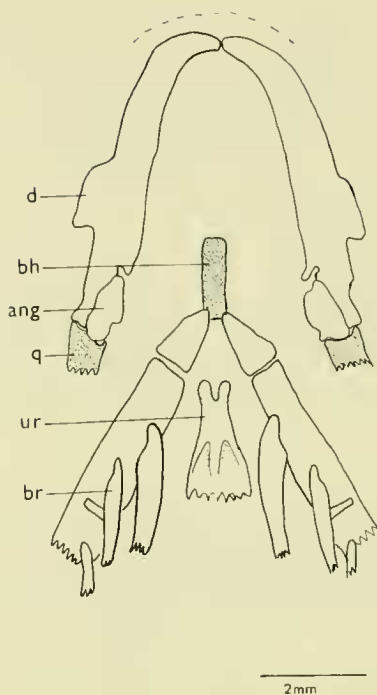


FIG. 7. Ventral aspect of the head and hyoid region of an alizarined specimen of *B. somereni*. Key as in fig. 6 except, br = branchiostegal ray; bh = basihyal; ur = urohyal. The dotted line indicates the edge of the lower lip.

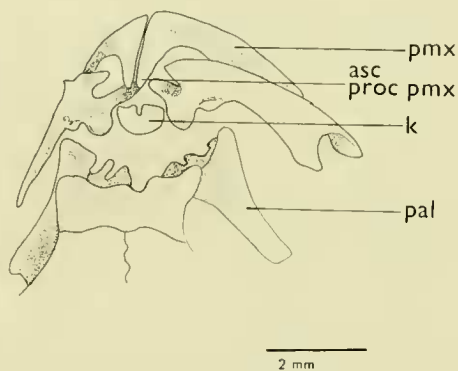


FIG. 8. Dorso-lateral view of the upper jaws and ethmoid region of *B. somereni*. asc = ascending process of premaxilla.

The premaxilla (figs 6 & 8) has an ascending process approximately as long as the labial part of the premaxilla is deep.

Visceral cavity

The colour of the peritoneum in preserved specimens varies from light grey to dark grey. Matthes (1963) comments that the peritoneum is darker in herbivorous fishes than in carnivorous fishes. Steinitz and Ben Tuvia (1957) have noted that the peritoneum is black in *Varicorhinus damascinus* C. and V. but lighter in *Barbus longiceps* C. and V. and intimate that this character is not of any value in the problem under investigation, because of its variability. The cause of the variability is unknown but may reflect the *in vivo* state or may be the result of post mortem changes.

The alimentary tract of five specimens was measured with the following results: 200 mm S.L.—gut length 700 mm; 178 mm S.L.—gut length 570 mm; 168 mm S.L.—gut length 400 mm; 160 mm S.L.—gut length 350 mm; 160 mm S.L.—gut length 300 mm. This gives an overall gut to standard length ratio of from 1.9 to 3.5. All these specimens came from the Sibwe river. The gut length was only measured to the nearest 10 mm as in some specimens decay had started before fixation became effective and the gut had to be reconstructed, hence precise measurements would be meaningless.

Habitat

Little is known of the habitat of *B. somereni*. Greenwood (1966) states that it is found in streams up to an altitude of 5,500 feet. The Imperial College expedition noted that in the River Sibwe *B. somereni* would be found in stretches of fast, deep, smooth water without boulders. The food seemed mostly to be insects.

Varicorhinus ruwenzorii (Pellegrin) 1909

Plate 1(b)

Varicorhinus ruwenzorii was described by Pellegrin as *Capoeta* (*Pterocapoeta*) *ruwenzorii* from three specimens from the Wimi river; Paris Museum Nos. 09-583, 09-584, 09-585 of standard lengths 67, 70 and 65 mm respectively.

The size range of the specimens examined was from 57-231 mm S.L.

TABLE 2

	N	\bar{x}	Range	S	Se
H	63	21.87	19.2-30.2	1.54	0.33
I	32	3.9	2.8-4.85	0.55	0.09
M.W.	63	9.07	7.5-10.2	1.02	0.22
Ab.	63	—	—	—	—
Pb.	63	—	—	—	—
D.Sp.	63	7.6	5.9-11.4	1.75	0.38

All measurements are expressed as a percentage of the standard length.

The anterior barbel is invariably absent. The posterior barbel is usually present as a small protuberance, too small to measure, at the corner of the mouth.

The mouth is wide and ventral. The anterior margin of the lower jaw is nearly straight in fishes of over 60 mm S.L. (fig. 9) and its horny covering is visible. In a specimen of 40 mm S.L. the lower jaw is more rounded anteriorly and lacks the horny edge.

The isthmus is short and the anterior gular surface has a smooth, padded appearance due to the presence of fatty deposits between the skin and the muscles. The snout is fleshy and overhangs the mouth, forming a rostral flap (Matthes, 1963). There is a well marked rostral groove in front of the upper jaw. The eye is small and not visible from below. The dorsal fin has its origin in front of the pelvic fin. There are four unbranched rays, the last one is weaker than in *Barbus somereni*, thinner and with persistent articulations throughout the distal two-thirds. There are nine or ten branched rays. The anal fin has three unbranched and five branched rays.

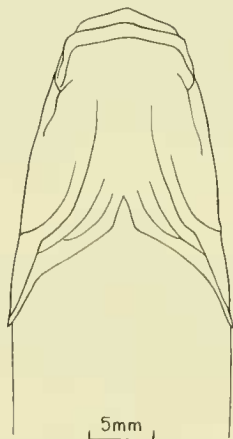


FIG. 9. Ventral view of the head of *Varicorhinus ruwenzorii*.

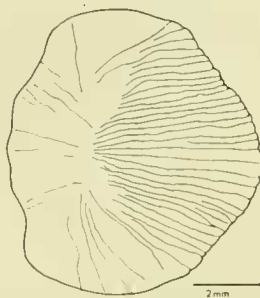


FIG. 10. A scale from the shoulder of *Varicorhinus ruwenzorii* showing the position of the striae.

The scales (fig. 10) have many more striae on the exposed part of the scale than in *Barbus somereni*. The fifth scale from the row above the lateral line has 34 striae on the posterior part of the scale but only a few incomplete striae on the anterior part.

There are from 38 to 44 scales in the lateral line; 38 (f.3); 39 (f.18); 40 (f.17); 41 (f.17); 42 (f.5); 43 (f.2); 44 (f.1). This is expressed graphically in fig. 22. There are from 12 to 15 scales around the caudal peduncle, 12 (f.33); 13 (f.16); 14 (f.10); 15 (f.1). There are $6\frac{1}{2}$ (rarely $5\frac{1}{2}$) scale rows from the mid-dorsal line to the lateral line, and from $7\frac{1}{2}$ to $10\frac{1}{2}$ scale rows between the lateral line and the mid-ventral line. The size of the scale rows on the ventral surface varies considerably and in some cases the scales are very reduced. Four scale rows (rarely $3\frac{1}{2}$ or $4\frac{1}{2}$) are present between the lateral line and the base of the pelvic fin.

The gill rakers on the first gill arch (fig. 4A) range from 16-18 + 4 in number and are long and fine.

The pharyngeal bones (fig. 11) are very much shorter than in equal sized specimens of *Barbus somereni*; the bones illustrated, from a specimen of 166 mm S.L. (*c.f.* *Barbus somereni* of 170 mm S.L.) measured only 9.7 mm from tip to tip (see page 269), less than $\frac{2}{3}$ of the measurement in *Barbus somereni*.

All the specimens examined had four teeth in the inner row. The teeth tend to be longer and thinner than their counterparts in *Barbus somereni* but are of the same general pattern. The teeth are more crowded in *V. ruwenzorii* than in *B. somereni*. There is hardly any lateral flange in the former species. The other differences in shape can be seen by comparing figs 5 and 11.

The vertebral number is 38 (f.1); 39 (f.6) and 40 (f.3) in the ten specimens radiographed. The 38 vertebrae comprise 18 abdominal + 20 caudal, the 39 comprise

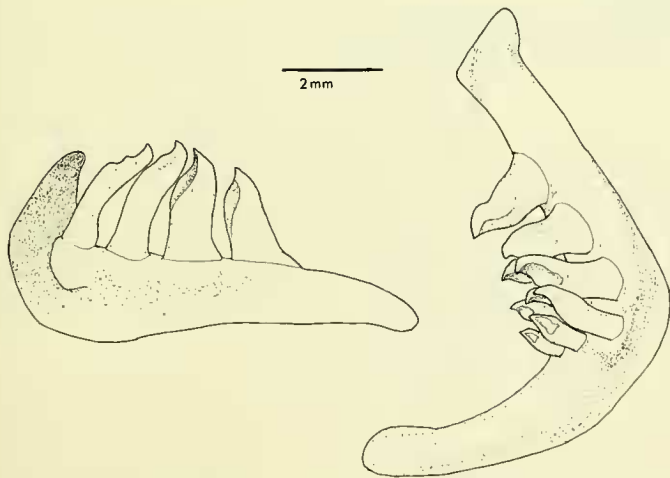


FIG. 11. The left pharyngeal bone of a specimen of *V. ruwenzorii* of 166 mm S.L. Compare with fig. 5.

19 + 20 (f.1) or 20 + 19 (f.5) and the 40 vertebrae comprise 20 + 20 (f.2) and 21 + 19 (f.1).

Suspensorium

A diagram of a slightly disarticulated suspensorium is given in fig. 12. The symplectic and preopercular are shorter than in *B. somereni*; generally the bones are thicker and more robust.

The rami of the lower jaw (fig. 13) are very much stouter than in *B. somereni* and anteriorly bend sharply, almost at a right angle, towards the symphysis. The dotted line in fig. 13 represents the anterior extent of the horny edge of the lower jaw. The second branchiostegal ray in fig. 13 is not in its life position but as a result of maceration is on its side and therefore appears thicker than in its normal position.

The premaxilla in *V. ruwenzorii* is much stouter than in *B. somereni* and lacks the ascending process (fig. 14). The maxilla is of the same fundamental shape in both species and its articulations are similar.

Visceral cavity

The peritoneum varies from black to grey, the range is such that its value as a taxonomic character is small. *Varicorhinus ruwenzorii* appears to feed largely on diatoms. The gut length in three specimens was measured with the following

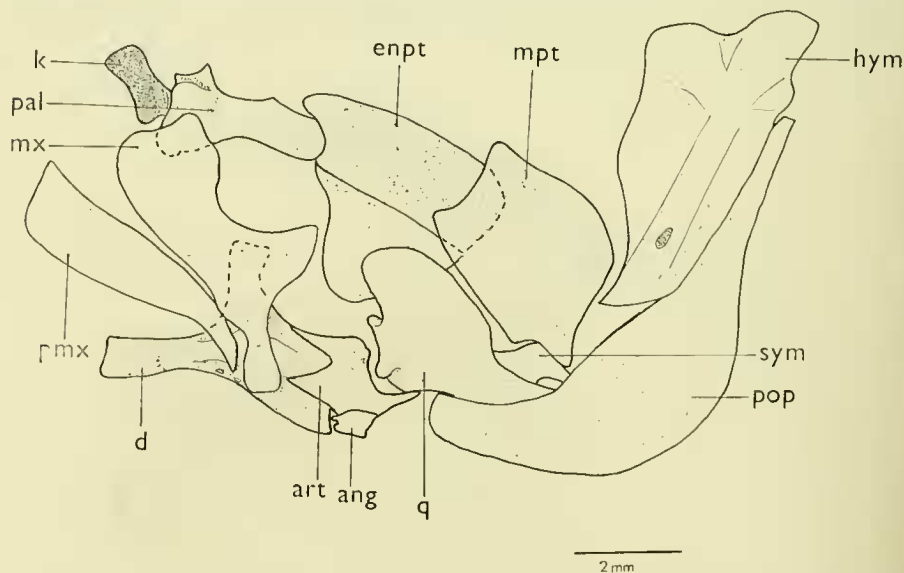


FIG. 12. A diagram of a partially disarticulated suspensorium of *V. ruwenzorii*. Key as in fig. 6.

results; S.L. 157 mm—gut length 580 mm; S.L. 160 mm—gut length 740 mm; S.L. 162 mm—gut length 635 mm. This gives a gut/standard length ratio of from $3\frac{1}{2}$ to $4\frac{1}{2}$.

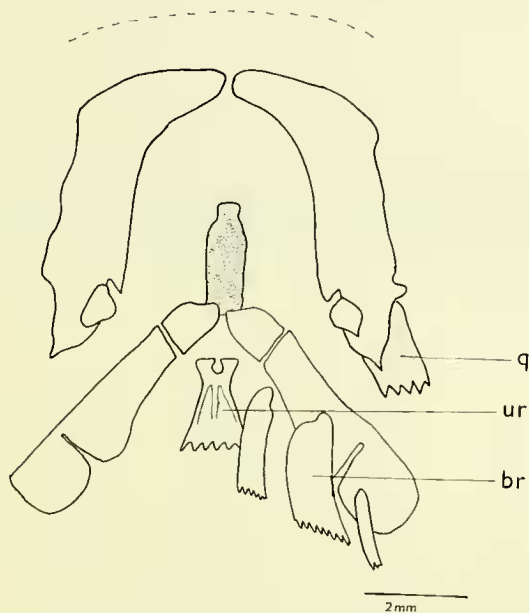


FIG. 13. The lower jaw and hyoid region of *V. ruwenzorii*. Key as in fig. 7.

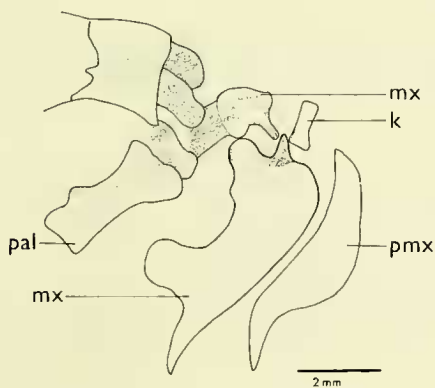


FIG. 14. Dorso-lateral view of the upper jaws and ethmoid region of *V. ruwenzorii*. Key as in fig. 6.

Habitat

Varicorhinus ruwenzorii was most frequently encountered by the Imperial College expedition in stretches of fast turbulent broken water with many boulders behind which the fishes sheltered.

Barbus alluaudi Pellegrin 1909

Plate 1(c)

Barbus alluaudi was based on two small fishes from the Wimi (=Ruimi) river; Paris Museum Nos. 09-586 and 09-587 of S.L. 67 and 58 mm respectively. The size range of the 13 specimens examined is from 58 mm to 198 mm S.L. The nine specimens collected by the Imperial College expedition are in the 168 mm to 198 mm S.L. range. The two specimens collected by Dr. I. G. Dunn are of 67 mm and 106 mm S.L.

TABLE 3

	N	\bar{x}	Range	S	Se
H	13	23.1	21.1-27.6	2.03	0.56
I	10	4.14	3.8- 5.0	0.33	0.1
M.W.	13	7.50	6.9- 8.1	0.42	0.13
Ab.	11	2.25	+ - 3.0	0.60	0.18
Pb.	13	3.05	2.7- 4.7	0.71	0.19
D.Sp.	12	10.27	8.5-13.8	2.05	0.85

All measurements are expressed as percentages of the standard length.

The mouth is ventral, its width modally about the same as in *B. somereni* but the lower jaw is not so long, nor is its anterior curvature so extreme. There is no horny covering, but the anterior edge of the lower jaw is firm and sharp. As can be seen in fig. 15, the development of the isthmus is intermediate between that of each of the putative parent species, and a certain amount of firm fatty tissue is present between the dentaries. A rostral flap is developed but is less marked than in *V. ruwenzorii*. The eyes are just visible in ventral view in some of the specimens and just hidden in others.

There are four barbels. In 09-587, a Paris Museum specimen of *B. alluaudi*, the anterior barbel is present only on one side; in other specimens the anterior barbels are present although they are about as small as the posterior barbels of *V. ruwenzorii*. The barbels are fleshy and clearly visible.

The dorsal fin has four unbranched rays. The last ray is ossified and intermediate in length and strength between this ray in the putative parent species. The number of branched rays varies from 8 to 10; 8 (f.1); 9 (f.9); 10 (f.3). The anal fin has three unbranched rays and five branched rays. The dorsal fin origin lies anterior to the pelvic fin origin.

The number of striae on the exposed part of the scales examined, and their distribution is intermediate between that of *B. somereni* and *V. ruwenzorii*; 26 striae

are present on the fifth scale of the row above the lateral line (fig. 16). The striae on the buried portion of the scale are radiately disposed and are stronger than in *V. ruwenzorii*. The lateral line has from 35 to 38 scales; 35 (f.4); 36 (f.5); 37 (f.6); 38 (f.1). Three specimens have different counts on either side. There are 12 (f.9) or 13 (f.4) scales around the caudal peduncle. There are $5\frac{1}{2}$ (f.4) or $6\frac{1}{2}$ (f.9) scale rows between the mid-dorsal line and the lateral line and $6\frac{1}{2}$ (f.2); $7\frac{1}{2}$ (f.6) or $8\frac{1}{2}$ (f.1) scales between the lateral line and the mid-ventral line. Between the lateral line and the base of the pelvic fin there are $3\frac{1}{2}$ (f.7) or 4 (f.6) scales.

The gill rakers number between $11 + 3$ and $14 + 3$ on the first gill arch (fig. 4B).

The pharyngeal bones (figs 17 and 18) are intermediate in size between those of *B. somereni* and *V. ruwenzorii*. The bone shown in fig. 17 from a specimen of 173 mm S.L. measures 14 mm from tip to tip (see p. 269). The degree of development of the lateral flange and the shape of the anterior process is intermediate between those of the putative parent species, as is the size of the bone in equal-sized fishes.

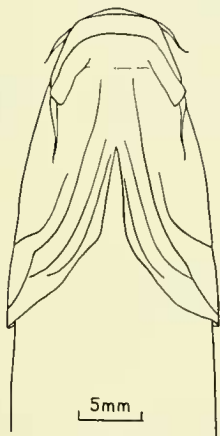


FIG. 15. Ventral view of the head of *Barbus allaudi*.

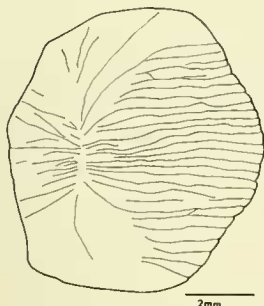


FIG. 16. A scale from the shoulder of *Barbus allaudi* showing the position of the striae.

The bone bears either 5 teeth in the inner row (fishes from the Mubuku and Sibwe rivers) or 4 teeth (the types from the Wimi river). When 5 teeth are present the first tooth in the inner row is smaller than it is in *B. somereni* (cf. fig. 5). The teeth otherwise resemble more closely those of *B. somereni* than they do those of *V. ruwenzorii*. The pharyngeal bones of the types of *B. alluaudi* (fig. 18) have only 4 teeth in the inner row. The shape of the teeth is more like that in *V. ruwenzorii* than in *B. somereni*.

The vertebrae were counted in eight specimens. There are modally slightly fewer vertebrae than in the samples from the putative parent species; 37 (f.2); 38 (f.5); 39 (f.1).

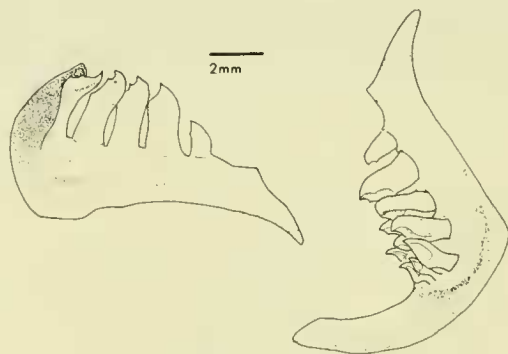


FIG. 17. Left pharyngeal bone from a specimen of *B. alluaudi* of 173 mm S.L. Compare with figs 5 and 11.

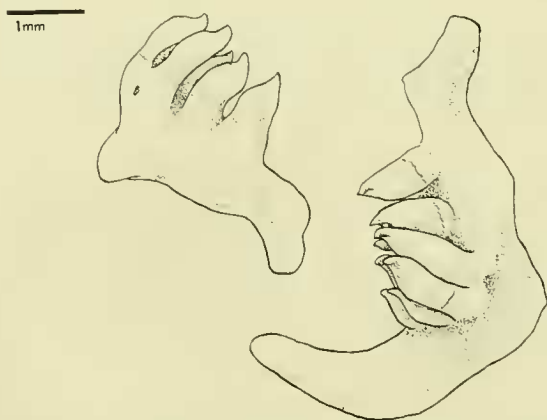


FIG. 18. Left pharyngeal bone from one of the types of *B. alluaudi*.

The 37 vertebrae comprise 18 abdominal + 19 caudal (f.1) or 19 + 18 (f.1); the 38 vertebrae comprise 18 + 20 (f.1); 19 + 19 (f.1); 20 + 18 (f.2) or 21 + 17 (f.1); the 39 vertebrae comprise 20 + 19 (f.1).

Suspensorium and jaws

A lateral view of a partially disarticulated suspensorium is shown in fig. 19. The symplectic resembles the *B. somereni* condition more than it does the *V. ruwenzorii* condition, whilst the reverse is true of the preoperculum. The quadrate is more compact than in either of the putative parent species.

The ascending process of the premaxilla (fig. 21) is intermediate in length between those of *V. ruwenzorii* and *B. somereni*. The slope at the anterior end of the ethmoid, the curvature of the rami of the lower jaw (fig. 20) and the extent of the lower lip development are also mixtures of the characters in the supposed parents. There is less fat between the rami of the lower jaw than in *V. ruwenzorii*.

Visceral cavity

The colour of the peritoneum varies considerably from light to dark grey. In any individual specimen the colour is not always uniform; dense black patches of melanin are sometimes present on a paler background.

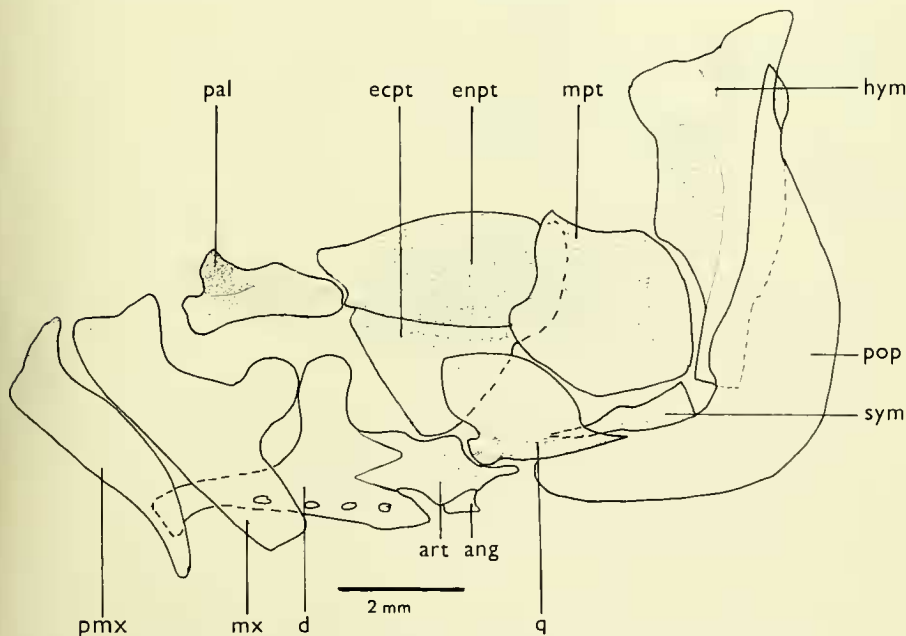


FIG. 19. A diagram of a partially disarticulated suspensorium of *B. alluaudi*. Key as in Fig. 6.

The gut lengths of two specimens were measured with the following results: S.L. 198 mm—gut length 490 mm; S.L. 175 mm—gut length 450 mm. This gives a gut/standard length ratio of about $2\frac{1}{2}$, a ratio below that of *V. ruwenzorii* but within the upper part of the range of *B. somereni*.

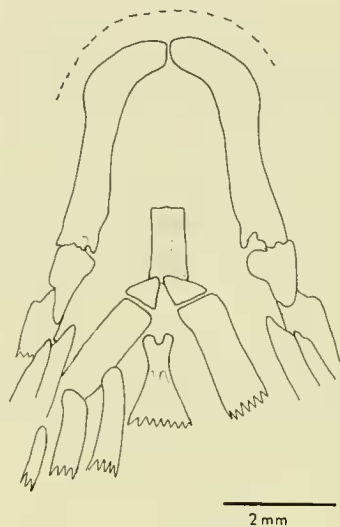


FIG. 20. The lower jaw and hyoid region of *B. alluaudi*.

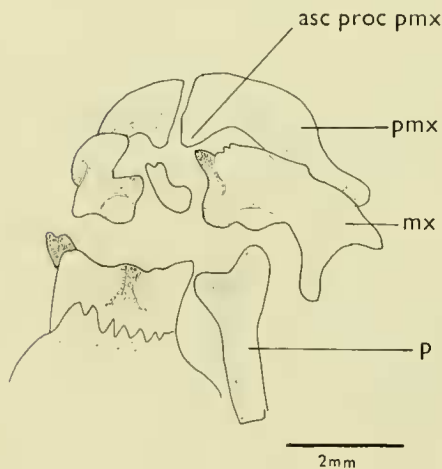


FIG. 21. Dorso-lateral view of the upper jaw and the ethmoid region of *B. alluaudi*. Key as in fig. 8.

Habitat

The Imperial College expedition specimens were caught in turbulent water about six feet deep in an area slightly sheltered from the main force of the stream. The bed of the river was largely composed of small stones.

DISCUSSION

It would seem from the differences between *Barbus somereni* and *Varicorhinus ruwenzorii* that there can be no doubt as to their specific integrity. It is most unlikely that the consistent differences in scale counts, dorsal spines and pharyngeal teeth could represent less than specific distinction, although the mouth form and its associated structures could, arguably, be the result of particular responses to the environment (Groenewald, 1958).

At the outset I must admit that all the evidence for the suggested hybridisation between these species is circumstantial. Breeding experiments would help to strengthen the hypothesis but these are, for the moment, impractical and I have had to rely heavily on the morphological intermediacy of the *B. alluaudi* specimens. The morphological intermediacy of aquarium bred hybrids has been noted before (e.g. Holčík and deWitt, 1962a, 1962b; Hubbs and Hubbs, 1932; Hubbs and Miller, 1952). The morphological intermediacy of hybrids in the wild has been described by Hubbs (1955).

I have used the Schultz and Schaefer technique (1936) for estimating the probability of morphological characters in the hybrids falling within the known range of variability for these characters in the putative parent species.

The absence of information on hybrids from African freshwaters can have at least two possible explanations. The study of African fish systematics lags behind that for North America and Europe. Secondly, there are many more species and species flocks in Africa than in the colder northern waters and this also makes the identification of hybrids more difficult.

Hubbs, Hubbs, and Johnson (1943) quote for the North American ostariophysans *Catostomus macrocheilus* and *C. syncheilus*, the proportion of hybrids to parent species collected from the same river system as respectively 6.4 and 4.2 per cent. Nelson (1968) gives a figure of approximately 7.0 per cent as the abundance of hybrids in the combined parental population for *Catostomus commersonii* and *C. macrocheilus*. Hubbs, Hubbs and Johnson (*op. cit.*) state that some hybrids are much rarer and perhaps one catostomid in a hundred on the average is an inter-specific hybrid in parent sympatric areas.

In the short stretch of the River Mubuku where the Dunn and Imperial College collection were made, *V. ruwenzorii* was the only putative parent species caught. The latter collectors found nine *B. alluaudi* specimens amongst 142 *Varicorhinus ruwenzorii*, a proportion of 6.4 per cent.

Barbus alluaudi is much rarer in the wild than either *Barbus somereni* or *Varicorhinus ruwenzorii* and it is known from only three localities. At one of the localities (the Mubuku river) its relative abundance is of the same order of magnitude as the relative abundance of the hybrid catostomids in North America. These facts,

coupled with the conspicuous morphological intermediacy between *B. somereni* and *V. ruwenzorii* possessed by *B. alluaudi* suggest that it is unlikely that *B. alluaudi* is a good species.

My arguments for the hybrid origin of *B. alluaudi* are similar to those of Hubbs and Miller (1952) for the hybrid origin of the catostomid *Xyrauchen uncomphagre*. Hubbs and Miller (*op. cit.*) rely on the infrequent occurrence of the nominal species in the wild, its association with the species whose characters it shares and the intermediacy of its characters between those of its associated, putative parent, species.

The possibility that *B. alluaudi* represents an extreme example of either parent species must now be considered. The techniques of Schultz and Schaeffer (1936) and of Hubbs, Hubbs and Johnson (1943) have been used here to evaluate the probability of a *B. alluaudi* character falling within the range of variation for that character in either of the putative parent species. The results are shown in Table 4.

TABLE 4

Character	N	\bar{x}	S	%R	%S	P
H						
<i>V. ruwenzorii</i>	63	21.87	1.54			0.1
<i>B. alluaudi</i>	13	23.10	2.03	69	31	
<i>B. somereni</i>	51	25.89	1.40			0.1
I						
<i>V. ruwenzorii</i>	32	3.93	0.55			.30
<i>B. alluaudi</i>	10	4.14	0.33	83	17	
<i>B. somereni</i>	22	5.15	0.68			.01
I.O.						
<i>V. ruwenzorii</i>	63	8.48	0.55			.04
<i>B. alluaudi</i>	13	8.13	0.51			
<i>B. somereni</i>	51	8.47	1.13			.33
M.W.						
<i>V. ruwenzorii</i>	63	9.07	1.02			.01
<i>B. alluaudi</i>	8	7.50	0.42	1	99	
<i>B. somereni</i>	51	7.48	0.84			.95
D.Sp.						
<i>V. ruwenzorii</i>	63	7.60	1.75			.01
<i>B. alluaudi</i>	8	10.27	2.05	57	43	
<i>B. somereni</i>	51	13.84	2.91			.01
Ab.						
<i>V. ruwenzorii</i>	63	—				
<i>B. alluaudi</i>	8	2.25	0.60			
<i>B. somereni</i>	51	7.83				.01
Pb.						
<i>V. ruwenzorii</i>	63					
<i>B. alluaudi</i>	8	3.05	0.71			
<i>B. somereni</i>	51	8.56	1.20			.01

For the characters H, I, M, W. and D.Sp. the mean for *B. alluaudi* lies between the means for the other two species. The per cent R refers to the percentage distance of this mean from the mean for *V. ruwenzorii* and per cent S refers to the percentage distance from the mean for *B. somereni*. Thus a per cent R of 50 indicates the *B. alluaudi* lies exactly halfway between the other two. The probability, P, refers to the probability of observing a mean equal to the *B. alluaudi* value had the sample come from one of the other two species. Thus, for H, the probability of observing a mean of 23.10 is 0.1 for *V. ruwenzorii* and 0.1 for *B. somereni*. A low value of P

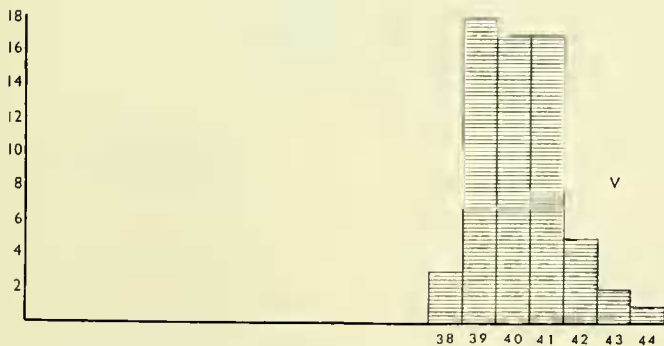
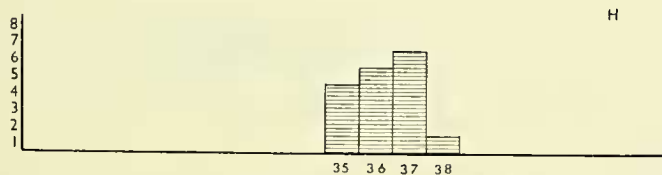
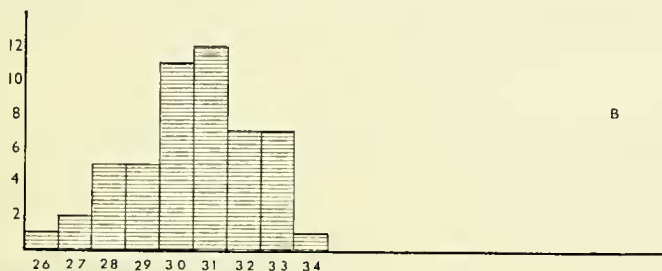


FIG. 22. Histograms to show the frequencies of the lateral line scale counts in *Varicorhinus ruwenzorii* (V); *Barbus somereni* (B); and *Barbus alluaudi* (H).

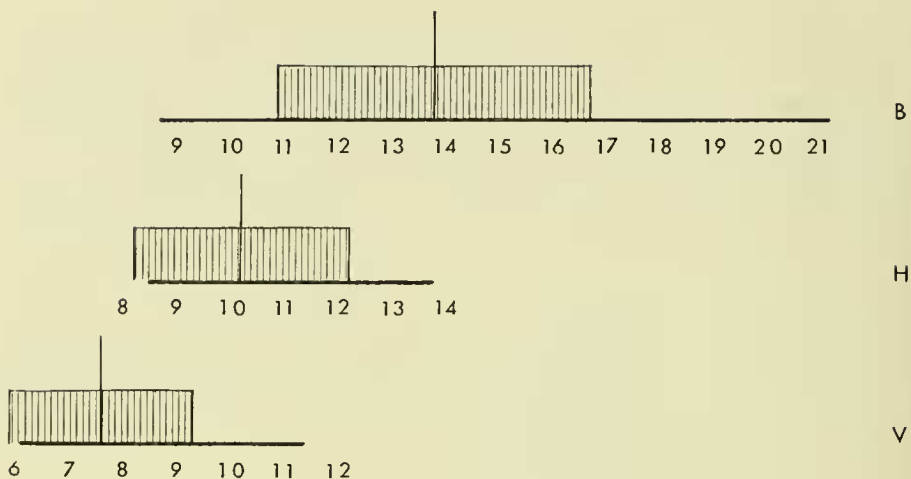


FIG. 23. A comparison of the ranges, mean and standard deviation of the dorsal spines in the three species. The base line represents the range; the vertical line represents the mean and the shaded area covers one standard deviation either side of the mean. The figures are the lengths of the dorsal spines expressed as a percentage of the standard length.

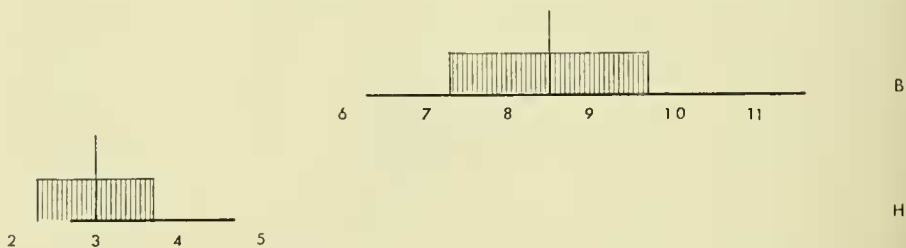


FIG. 24. A comparison of the posterior barbel lengths in *B. somereni* and *B. alluaudi*. Details as in fig. 23.

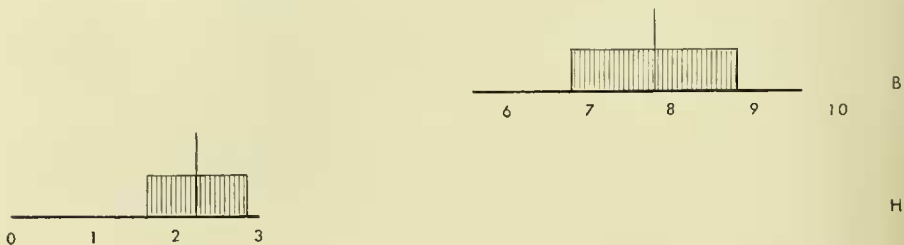


FIG. 25. A comparison of the anterior barbel lengths in *B. somereni* and *B. alluaudi*. Details as in fig. 23.

means that it is unlikely that the *B. alluaudi* differs from the putative parent species purely because of random variation. On this basis the values for the proportions of the dorsal spine (D.Sp.) provide strong evidence that the sample of *B. alluaudi* could not have come from either of the putative parent species.

It is most unlikely that the hybrids belong to either *V. ruwenzorii* or to *B. somereni* and the overall result hints most strongly at nearly perfect intermediacy.

Intermediacy has been advocated as a very significant distinguishing character of hybridisation by many authors (e.g. Hubbs, 1955; Berry and Low, 1970).

The lateral line scales for the three groups are compared in histogram form above (fig. 22). There is no overlap in the ranges of *B. somereni* and the hybrids, but the

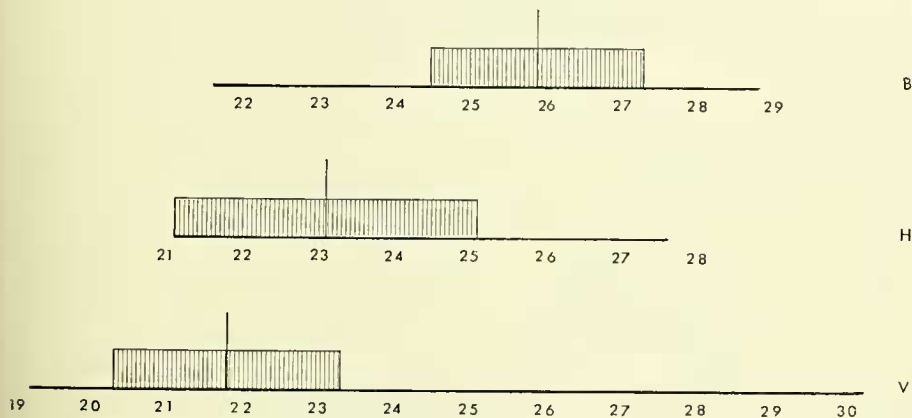


FIG. 26. A comparison of the head lengths of the three species. Details as in fig. 23.

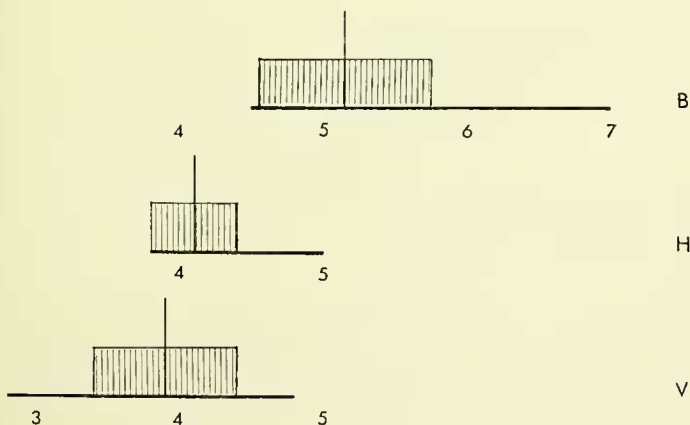


FIG. 27. A comparison of the eye diameters in the three species. Details as in fig. 23.

hybrids (1) and *V. ruwenzorii* (3) have 38 scales in common. The mean values for the hybrids and *V. ruwenzorii* are closer than those for *B. somereni* and the hybrids.

The range, mean and one standard deviation each side of the mean are shown graphically below. All are expressed as percentages of the standard length. Most of these graphs are self-explanatory and show the relation of the hybrid data to those of the parent species. The disappointing result for the mouth width has been mentioned above.

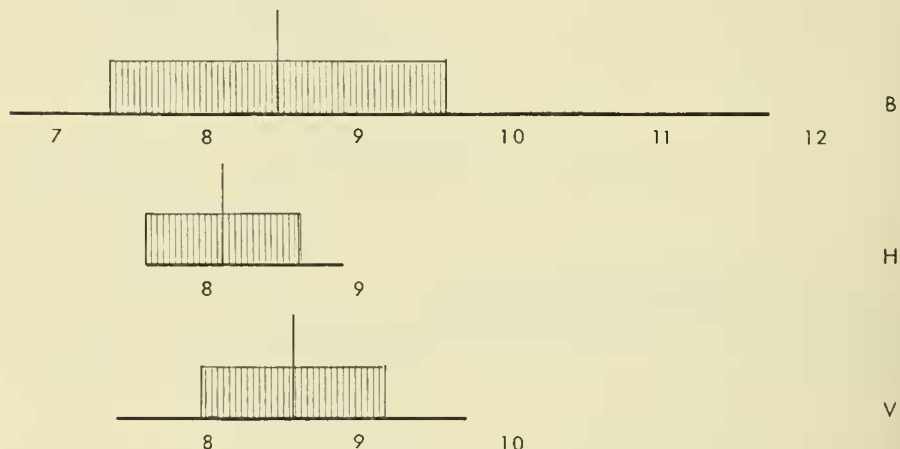


FIG. 28. A comparison of the interorbital widths in the three species. Details as in fig. 23.

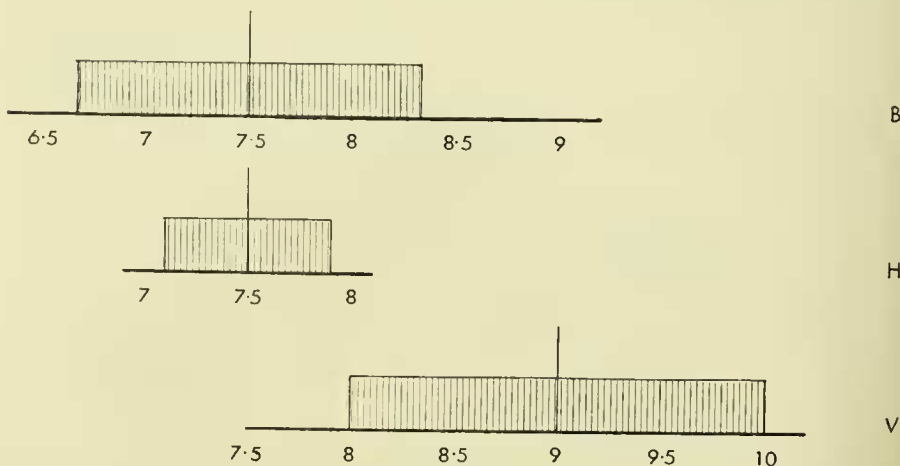


Fig. 29. A comparison of the mouth widths in the three species. Details as in fig. 23.

The graph for the interorbital width (fig. 28) shows two interesting factors. Firstly that the mean interorbital widths differ hardly at all in the parent species but both are slightly greater than in the hybrid. The increased mouth width in the *Varicorhinus* is not therefore reflected by an overall increase in head width. The visibility of the eyes in ventral view in the three groups of fishes has been noted above. The large standard deviation for this character in *B. somereni* (Table on page 282) is due to the relatively wider interorbital space in the very large *Barbus somereni*. The second point is that this is the only character in which the hybrid is not intermediate. There are instances of similarly anomalous results in hybrids. Steinitz and Ben Tuvia (1957) noticed the same phenomenon for the head length/eye diameter ratios in *Barbus longiceps* and *Capoeta damascinus* hybrids.

Hybrids may also have meristic characters which show great variability. Hubbs (1956) observed the great variability of the F_1 hybrids of *Notropis lepidus* and *N. prosperinus* which in some characters exceeds the range of the parent species, e.g. in the number of dorsal and anal fin rays. Hubbs (1951) describes the increase beyond the parental ranges of the anal fin rays of the hybrids between *Notropis heterolepis* and *Hybognathus hankinsoni*. The Steinitz and Ben Tuvia results most closely resemble the interorbital width results shown above.

The pharyngeal bones in the hybrids have either four (as in the types) or five teeth in the inner row. The size of the fifth tooth, when present, is of some importance; it is always smaller than the same tooth in an equally large pharyngeal bone from *B. somereni*; in other words it is satisfactorily intermediate. The presence of only 4 teeth in the Wimi river specimens is more difficult to understand, for it reflects the *Varicorhinus* condition perfectly.

With such a small sample of hybrids and without a complete size range it is unwise to speculate on reasons for the possession of four or five teeth. Various other characters which are not readily quantifiable e.g. the shape of the bones of the jaws and suspensoria still serve to show the mixture of parental characters present in the hybrids.

The nine specimens collected by the Imperial College expedition were all males. Assuming that the fishes do not segregate by sexes the chances of a random sample all being male is sufficiently low to suggest that the sex ratio is unbalanced. Holčík and deWit (1962b) noticed that all of the F_1 of a *Rhodeus sericeus*, *Rhodeus ocellatus* cross were male. Hubbs and Hubbs (1932) observed the predominance of male offspring in sunfish (Centrarchidae) hybrids. Hubbs (1961), reviewing earlier work, points out that the F_1 male hybrids are usually sterile, although occasional exceptions are found both in the sense of an individual within a brood and in cases like *Molliensia sphenops* and *Molliensia latipinna* where the males are almost fully fertile but the females only rarely so. If the males are sterile (as the lack of evidence of F_2 generations and backcrosses would suggest) then this might be displayed in the detailed structure of the testes. Accordingly, a hybrid specimen and a male of *B. somereni* of approximately the same size, caught on the same day, were compared. None of the specimens was preserved especially for histological examination, so this comparison of two specimens, treated in the same way, was the best that could be done. The specimens were preserved in formalin on the same day they were

captured but the preservative must have taken some time to become fully effective as decay was evident in the alimentary canal (p. 271). It could only be assumed that both specimens had undergone the same post-mortem changes and that a comparison between the two would have some validity.

The testes of the hybrid were longer than those of the *B. somereni* by about a quarter and thicker by the same amount. Histological sections were prepared as described above (p. 265).

The sections of the hybrid testes showed large vacuoles, hardly any interstitial tissue and the sperm mother nuclei gave an appearance of abnormality especially in the variation of size and shape when compared with the *B. somereni* sperm mother nuclei. In *Barbus somereni* there were no vacuoles, plenty of interstitial tissue and clumps of sperm. With the naked eye the D.N.A. stain showed up in dense patches in the *Barbus somereni* but only diffusely in the hybrid testes sections.

I have no information about the testicular cycle in *Barbus somereni* so I cannot justifiably draw any conclusions from these meagre observations. Much more histological work is necessary before any valid conclusions can be reached about the possible sterility of the testes of *B. alluaudi*.

With these assumptions, which is all the evidence currently available, it would seem that the sex ratio in *Barbus alluaudi* is unbalanced. This suggests that the fishes referred to *Barbus alluaudi* are hybrids.

The question why the hybrids should be relatively common in the Mubuku river is difficult to answer. The spawning habits of cyprinids are such that chance fertilisation of an egg by a foreign sperm is quite possible and has apparently not infrequently happened in North America and Europe, so an occasional hybrid would not be too surprising. However, the breeding habits of *Barbus somereni* and *Varicorhinus ruwenzorii* are not known. It can only be assumed that the eggs are freely scattered and the sperm shed into the water in their proximity as generally happens in cyprinids. But whether these two species breed at the same time or not is unknown.

Barbus somereni is either rare in the Mubuku or inhabits parts as yet uncollected. The Imperial College Expedition caught none in the Mubuku but found they were plentiful in the Sibwe (fig. 1). Ian Dunn collected only one specimen in the Mubuku. *Varicorhinus ruwenzorii*, on the other hand, is as abundant in the Sibwe as in the Mubuku.

It is possibly significant that *B. alluaudi* is commonest in the Mubuku river where *B. somereni* is scarce. Hubbs (1951) identified the unique specimen of *Notropis germanus* as a hybrid between *Hybognathus hankinsoni* and *Notropis heterolepis*. The interest here lies in the fact that *N. heterolepis* no longer lives in the Smoky Hill river where the hybrid was collected. It appears to have been rare in 1885 when '*N. germanus*' was collected. Only one specimen of this cross is known and Hubbs suggested that the *N. heterolepis* hybridised when their numbers became very low. Similar evidence is put forward for catostomids by Hubbs and Miller (1952). Perhaps the relative abundance of the hybrid in the Mubuku river is due to the disparity in numbers between *Barbus somereni* and *Varicorhinus ruwenzorii*.

The evidence for the hybrid origin is circumstantial, but the two arguments in

favour of this hypothesis are, (i) the presence of only three large cyprinids in the streams in question with the rarest of the three displaying conspicuous morphological intermediacy between the other two, (ii) the fact that *Barbus alluaudi* is most frequently encountered in a stream where one of the putative parent species is very scarce.

Although this does not prove the hybrid origin of *Barbus alluaudi*, the morphological intermediacy of this nominal species does conform to previously studied interspecific fish hybrids. On the balance of evidence I suggest that *Barbus alluaudi* is an intergeneric hybrid between the cyprinid species *Barbus somereni* and *Varicorhinus ruwenzorii*.

SUMMARY

The three species of large cyprinids living in the streams on the Ruwenzori mountain range, Uganda viz. *Barbus somereni*, *Varicorhinus ruwenzorii* and *Barbus alluaudi* are described. The comparative scarcity of *B. alluaudi* (about 6 per cent of the population at one site) and the fact that many of its characters are intermediate between those of the other two species suggest that it is a hybrid. Further arguments in favour of this hypothesis are the apparently unbalanced sex ratio in *B. alluaudi* and the fact that it is most abundant where one of the putative parent species is rare.

The intermediate characters of *B. alluaudi* are discussed and compared with those of *Barbus somereni* and *Varicorhinus ruwenzorii*.

The hybrid origin of *B. alluaudi* cannot be proved but a strong circumstantial case can be constructed for it.

ACKNOWLEDGEMENTS

I am delighted to be able to express my gratitude to Dr. P. H. Greenwood for criticising the manuscript and for spending many hours discussing the problem with me. I am greatly indebted to Mrs Sharon Chambers and Mr Gordon Howes for the illustrations and to Miss Margaret McLellan for preparing the graphs and helping with the measurements and calculations. The statistical analyses could not have been done without the advice of Dr M. Hills and lastly I could not have studied the specimens had it not been for Dr Ian Dunn, Mr Paul Ready and Mr Tim Slade who collected the fishes.

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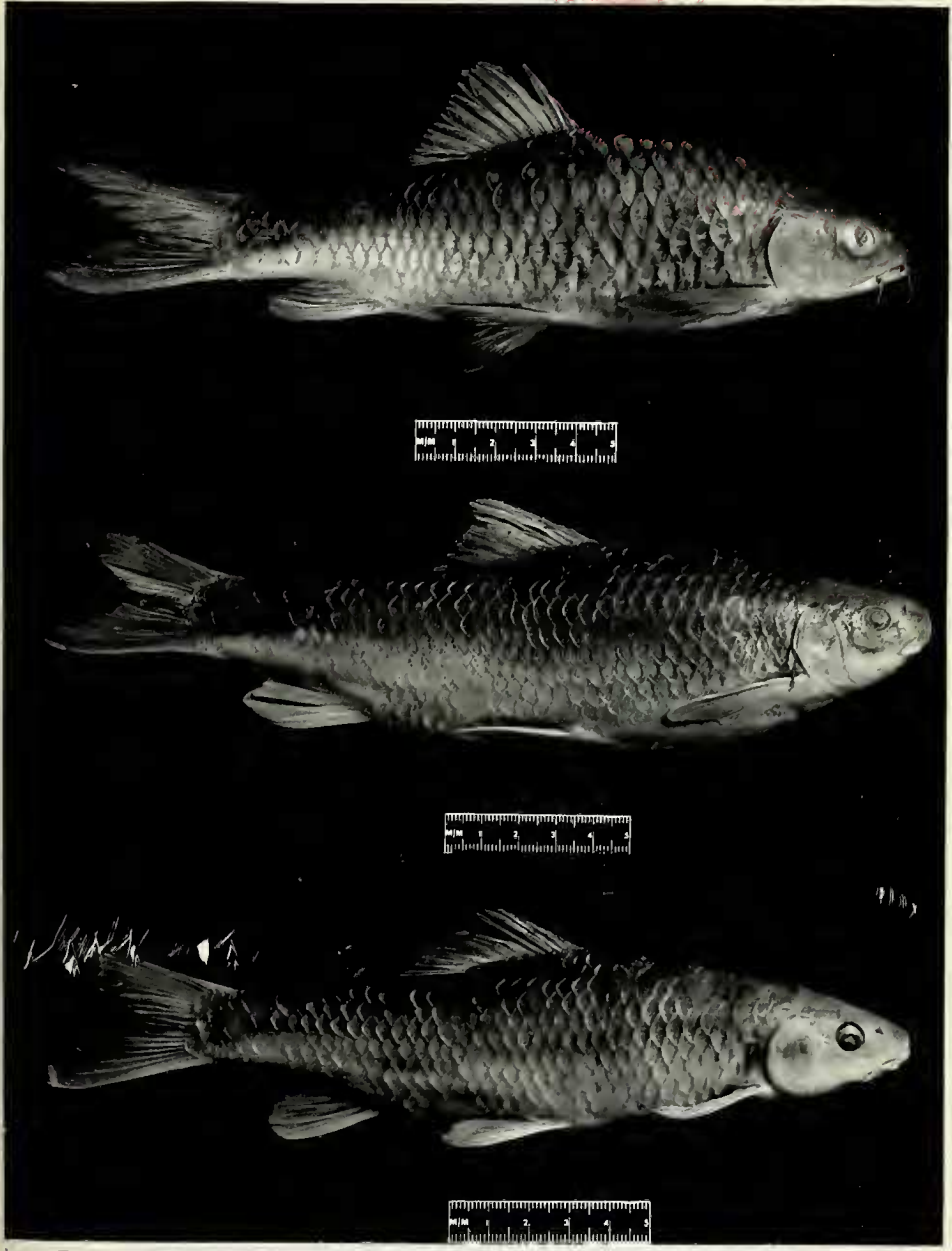
PLATE I

(a) *Barbus somereni*

(b) *Varicorhinus ruwenzorii*

(c) *Barbus alluaudi*. A specimen from the Mubuku river collected by the Imperial College Expedition.

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(a)

(b)

(c)