A POSSIBLE INTERGENERIC CYPRINID HYBRID FROM LAKE TANGANYIKA

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SYNOPSIS

A series of fishes from Lunkungwe (Lake Tanganyika) were found to have characters intermediate between two endemic species, *Barbus tropidolepis* and *Varicorhinus tanganicae*. The likelihood of a hybrid origin for the Lunkungwe fishes is discussed and comments are made on the validity of the generic separation of the two putative parent species.

INTRODUCTION

During 1968 and 1969, Dr E. K. Balon of the Zoology Department, University of Guelph, Canada, collected eleven specimens of a cyprinid fish from Lunkungwe (5°45′S, 29°55′E), Lake Tanganyika. The largest specimen (133 mm SL) is now in the Museum of Zoology, University of Michigan (MZM 191573). The other ten specimens are in the Royal Ontario Museum (ROM 28132 and 28167).

These fishes are not referable to any known cyprinid species from Lake Tanganyika but are morphologically intermediate between *Varicorhinus tanganicae* and *Barbus tropidolepis*, species endemic to the Lake Tanganyika basin. From the data presented below it will be seen that the eleven Balon fishes are unlikely to represent extreme examples of either *Varicorhinus tanganicae* or *Barbus tropidolepis*.

In this paper I intend to put forward the hypothesis that these eleven fishes are hybrids between *Barbus tropidolepis* and *Varicorhinus tanganicae*.

Much of the evidence and discussion is, of necessity, similar to that given in Banister (1972). In that case the discovery of some fishes morphologically intermediate between *Barbus somereni* and *Varicorhinus ruwenzorii* was used as evidence for the hypothesized hybridization of these two species. Without breeding experiments, hybridization cannot be proved, but the circumstantial evidence is worth examining. Previously (Banister, 1972) I noted that the boundary between the African representatives of the genus *Barbus* and the genus *Varicorhinus* is

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vague. It has been shown (Groenewald, 1958 ; Gaigher, 1975) that under certain conditions some species of *Barbus* can change their mouth form and simulate the mouth type present in *Varicorhinus* species. Without an examination of more trenchant characters and without a knowledge of the previous history of the specimen, an individual fish could be placed with equal justification in either genus as the two genera are currently accepted (e.g. the definitions of Boulenger, 1909, and Jubb, 1968). These two definitions are, in the light of the known variation of some species, inadequate. The morphological intermediates described here, and *Barbus alluaudi* (Banister, 1972), raise further doubts about whether some species have been correctly assigned to the genus *Varicorhinus*. Work is in progress on the limits of the genera *Barbus* and *Varicorhinus*.

NOTES ON COUNTS AND MEASUREMENTS

The standard length (SL) was taken in the usual manner. The lateral line count (LL) was taken from the first pore-bearing scale behind the head to the scale lying lateral to the end of the hypurals. The body depth (D) is the maximum body depth, usually to be found just in front of the dorsal fin. The anterior limit for the head length (H) and snout length (Snt) was the premaxillary symphysis, with the premaxillae retracted. The posterior limit for the snout is the anterior margin of the orbit and for the head length is the most posterior part of the bony edge of the operculum. The term mouth width (MW) refers to the width across the lower jaw at the level of the angle of the mouth. The pectoral fin length (Pct) is the total length of the fin, measured in a straight line from the base of the first fin ray to the distal extremity of the fin. The measurements were taken in this way because of the ease of so doing with dial calipers, which were used on all fish except the smallest when dividers were used. The caudal peduncle length (CPl) is the horizontal distance from the posterior angle at the base of the last anal fin ray to the end of the hypurals and the caudal peduncle depth is the least depth of that part. The interorbital width (IO) was measured as the least distance between the bony edges of the interorbital space. The eye diameter (I) is the horizontal diameter of the visible part of the eye. Dsp symbolizes the height of the dorsal fin from the base of the first spine to the distal extremity of the longest fin ray. With any measurements which were repeatable on both sides of the fish (e.g. the anterior barbel, Ab or posterior barbel, Pb) the larger was taken except in cases where a deformity was obvious.

The majority of measurements were taken to the nearest millimetre, the exceptions were some measurements on small fishes ; these were taken to the nearest half millimetre. The mean is symbolized by $\bar{x}$, the standard deviation by s.d., the standard error by s.e. and the number of fish in the sample by n.

THE PUTATIVE HYBRIDS

Description. The description is based upon 11 fishes of 133, 105, 77, 69, 66, 59, 59, 58, 55, 55, 55 mm SL from Lunkungwe, Lake Tanganyika, ROM 28132, 28167 and MZM 191573. The largest specimen is shown in Fig. 1.

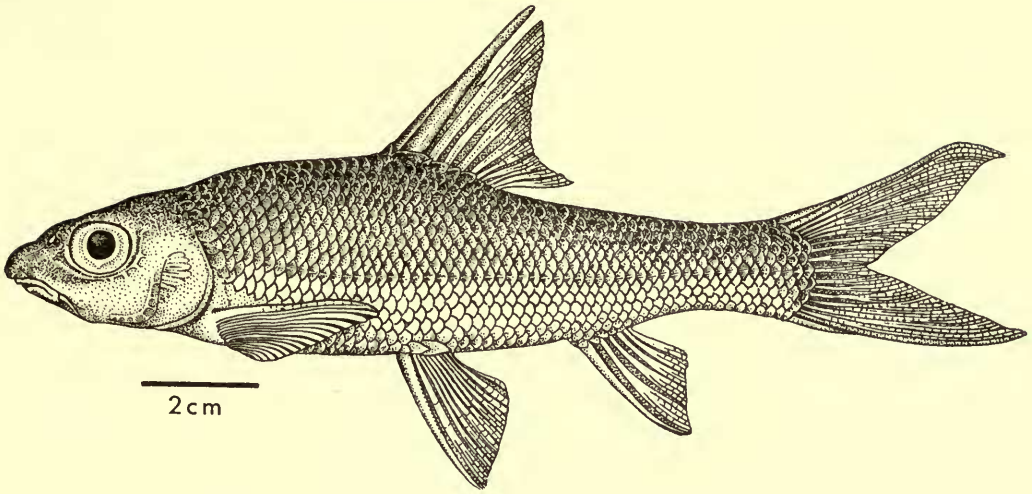

FIG. 1. The largest putative hybrid, a fish of 133 mm SL.

	x	s.d.	s.e.	range
SL	–	–	–	55 –133 mm
D	25·8	1·5	0·4	23·5–28·6
H	27·0	1·7	0·5	23·5–29·3
I	8·5	0·5	0·2	7·8– 9·3
IO	7·5	0·6	0·2	6·8– 8·8
MW	6·9	0·6	0·2	6·4– 8·5
Pct	21·3	1·1	0·3	19·6–28·6
CPl	18·9	1·5	0·5	15·3–21·0
CPd	10·9	0·7	0·2	9·8–11·7
Snt	7·8	1·1	0·6	6·8– 9·8
Ab	1·8	0·3	0·1	1·5– 2·3
Pb	3·2	0·5	0·2	2·5– 3·8

Unless stated otherwise, all measurements are expressed as a percentage of the standard length.

The body is compressed, with smooth dorsal and ventral profiles. The deepest part of the body is just in front of the dorsal fin. The eye is large, protuberant and just visible in ventral view. The fleshy, rounded snout terminates in a rostral flap which is level with, but does not overhang, the mouth.

The anterior margin of the lower jaw is gently curved ; it has a sharp edge but lacks the conspicuous horny sheath present in specimens of *Varicorhinus tanganicae* (Pl. 2). Nevertheless, it has a shiny, padded appearance suggesting that a tough integument is present. The lower jaw is only slightly wider at its articulation than it is distally. The ventral face of the lower jaw is concave and the skin in this and the contiguous gular region bears numerous small papillae.

No lateral line pores are visible on the ventral surface of the lower jaw. There are two pairs of barbels. The short anterior barbels are usually hidden in a groove between the ventral edge of the lachrymal bone and lips. In the second largest

specimen (105 mm SL) a few isolated tubercles are present on the skin of the snout and the dorsal half of the lachrymal bone. The tubercles are about four times the diameter of the lateral line pores of the lachrymal bone.

In nine of the specimens the gill filaments could be seen clearly through a transparent zone in the centre of the opercular bone. In the other two fishes a dark patch of pigment was present through which the gill filaments could only just be discerned.

The peritoneum is dark grey/brown in the two specimens examined. The alimentary canal is narrow and much convoluted. There are 20+21 (f1), 20+22 (f3), 21+20 (f1), 21+21 (f2), 21+22 (f3) or 22+21 (f1) vertebrae including those comprising the Weberian mechanism.

From radiographs it can be seen that the angle of insertion of the pectoral fin is different in the three samples of fishes. The angle of insertion of the pectoral fin is here defined as the angle that a line through the mid-point of the first and last pectoral radials subtends with a line from the mid-point of the occipital condyle to the mid-point of the ural centrum. In the largest fish this angle is 30° ; in the other specimens it varied from 21° to 41°.

Dorsal fin. The dorsal fin has 4 simple rays and 9 (f11) branched rays. The last simple ray is thickened into a straight smooth spine ($\bar{x}=26{\cdot}3$, s.d.$=1{\cdot}5$, s.e.$=0{\cdot}5$, range$=23{\cdot}8$–$28{\cdot}5$). A low sheath of scales is present at the base of the dorsal fin.

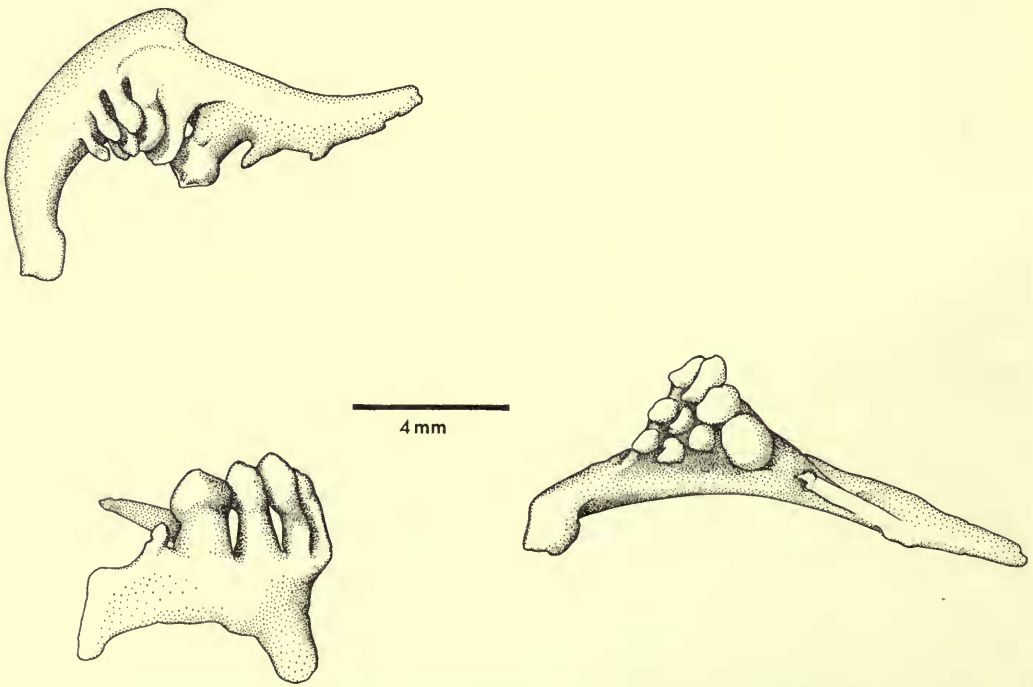

Fig. 2. The right pharyngeal bone of the largest hybrid.

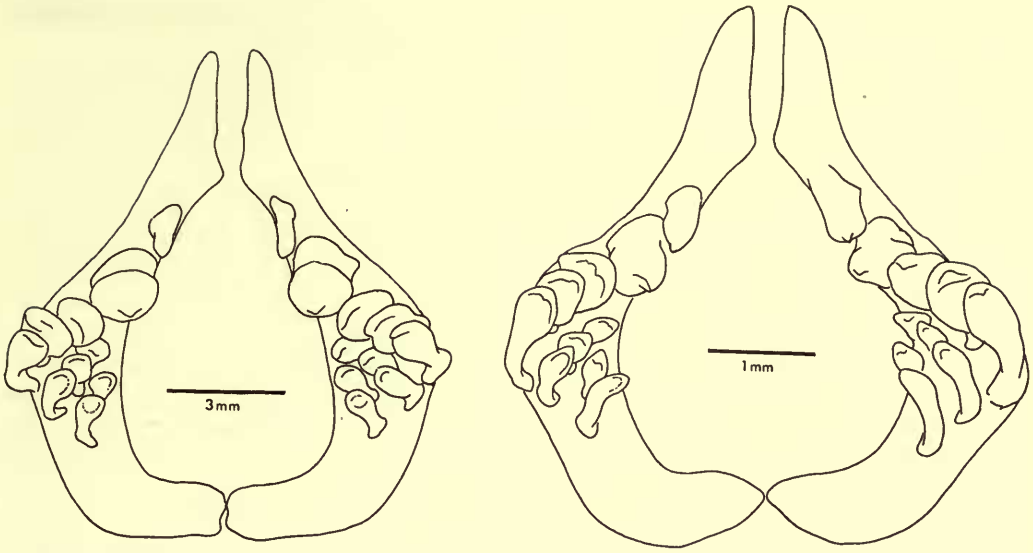

FIG. 3. Occlusal views of the pharyngeal bones of hybrids of 133 and 59 mm SL to show the arrangement of the tooth rows.

This sheath is highest anteriorly and is reduced to the level of the body contour by about the seventh or eighth branched ray. The origin of the dorsal fin is in advance of the pelvic fin.

Squamation. In the lateral line series there are 46 (f1), 47 (f1), 49 (f2), 50 (f1), 51 (f1), 52 (f2), 53 (f1), 54 (f1) or 56 (f1) scales. From the dorsal mid-line to the lateral line there are 10½ (f5) or 11½ (f6) scales. From the lateral line to the ventral mid-line there are 10½ (f2), 11½ (f3) or 12½ (f3) scales. This count was unobtainable on some specimens. Between the lateral line and the base of the pelvic fin there are 5½ (f5), 7 (f1) or 7½ (f4). Around the mid-point of the caudal peduncle there are 22 (f5) or 24 (f4) scales. The scales bear slightly diverging striations (Fig. 5).

Pharyngeal bones and teeth. The pharyngeal teeth number 2.3.5–5.3.2. The right pharyngeal bone of the largest specimen is shown in Fig. 2. The first (anterior) tooth of the inner row is short and slender and its alignment is more or less parallel with the adjacent edge of the second tooth. This tooth is large and stout with a mamilliform crown surmounted by a small recurved hook. The third, fourth and fifth teeth become progressively more slender and spatulate. The teeth of the second and third rows are smaller versions of the third, fourth and fifth teeth of the inner row. From the occlusal view of the pharyngeal bones the alignment of the middle and outer tooth rows can be seen. In about half of the specimens these two rows diverge from the first tooth of the middle row. In the rest of the specimens the rows are parallel. In two specimens one pattern is present on one bone and the others on its partner.

The mean tip-to-tip length of the pharyngeal bones of a specimen 105 mm SL is 10 mm and the mean length in a specimen of 59 mm SL is 6·3 mm. These figures

should be compared with the measurements of the pharyngeal bones of equal-sized *Barbus tropidolepis* and *Varicorhinus tanganicae* (pp. 179 and 183).

Gill-rakers. There are 15 (f5), 16 (f5) or 18 (f1) gill-rakers on the lower limb of the first gill-arch. The shape of the gill-rakers is intermediate between those of the putative parents; i.e. they are moderately thick with a clubbed or T-shaped extremity.

Coloration. These colour notes are based on alcohol-preserved specimens. The smaller fishes are lighter than the larger fishes. The body colour is yellow-brown, darker on the back than below the lateral line. The belly in some specimens has a pink tinge. There is a dark, broad mid-lateral stripe 3 or 4 scales deep caused by a concentration of pigment along the posterior edge of alternate scales in the rows at the edge of the band and on all the scales of the central rows. A distinct mid-dorsal stripe is present in several specimens. These stripes become less distinct in larger fishes as the body colour becomes progressively darker. All but two of the specimens have a clear spot on the operculum. The dorsal fin has a dark margin in small fishes but this becomes progressively fainter in larger fishes.

Distribution. All the specimens came from Lunkungwe, Lake Tanganyika. Dr Balon kindly provided the following details of the locality. The Lunkungwe River empties into a large bay on the eastern shore of central Lake Tanganyika about 100 km south of Kigoma in Tanzania. The river flows from the Kingwe mountains in a valley flanked by very steep foothills. The river gradient is steep. The width varies from 4 to 10 m, and there are rapids between rock outcrops and large boulders on the river bed. The fish were sampled about 2 km before the river empties into the lake. The river at this point flows swiftly but there are some pools with a plant resembling *Fontinalis* sp. The river is muddy when it empties into the lake and is bordered with reed thickets. The fish were poisoned with toxophene.

THE PUTATIVE PARENT SPECIES

Varicorhinus tanganicae (Boulenger, 1900)

Capoeta tanganicae Boulenger 1900 : 478.
Varicorhinus tanganicae : Boulenger, 1905 : 43 ; Poll, 1953 : 97.

Lectotype. A fish of 282 mm SL from the north end of Lake Tanganyika, one of the two syntypes, BMNH reg. no. 1906.9.6:9–10. The lectotype is the largest of the two specimens, the smaller specimen being designated a paralectotype.

Material examined. Apart from the syntypes the following specimens were used in this study: BMNH1936.6.15:731–751 ; 1955.12.20:900–903 ; 1955.12.20:881.

Description. Two separate samples of *Varicorhinus tanganicae* from Lake Tanganyika have been measured. One sample, of 24 fish from 48 to 282 mm SL, is intended to show the morphometric and meristic variation of the species. The other sample consists of five fishes of 59, 59, 80, 104 and 139 mm SL which are all the specimens available close to the size range of the hybrids. These are included to enable a detailed comparison to be made limiting, as far as possible, any distortion from allometry.

Sample 1 (n=24)

	$\bar{x}$	s.d.	s.e.	range
SL	–	–	–	48 -282 mm
D	25·9	2·1	0·4	23·0–30·0
H	22·7	2·4	0·5	14·6–26·0
I	6·3	0·9	0·2	4·6– 8·3
IO	9·1	0·9	9·2	7·4–10·6
MW	8·0	0·5	0·1	7·1– 9·5
Pct	19·7	1·2	0·2	16·6–21·4
CPl	17·2	0·9	0·2	15·1–18·9
CPd	12·8	0·9	0·3	10·4–14·7
Snt	7·3	0·6	0·1	6·4– 8·3
Ab	+	–	–	–
Pb	+	–	–	–
Dsp	19·8	3·0	0·6	12·6–24·8

It should be noted that although two pairs of barbels are invariably present in the specimens examined they are minute in the large fishes. Consequently barbel lengths are not included in this sample but are included in the 59–139 mm SL sample below.

Sample 2 (n=5)

	$\bar{x}$	s.d.	s.e.	range
SL	–	–	–	59 -139 mm
D	26·3	1·2	0·5	25·0–28·0
H	24·8	2·0	0·9	22·3–27·1
I	7·3	0·3	0·1	6·9– 7·6
IO	8·8	0·3	0·1	8·5– 9·3
MW	8·7	0·5	0·2	7·9– 9·3
Pct	20·5	1·2	0·5	18·9–22·0
CPl	15·4	1·4	0·6	13·5–17·3
CPd	10·5	0·5	0·2	10·0–11·0
Snt	6·8	0·5	0·2	6·3– 7·5
Ab (n = 4)	1·3	1·0	0·5	0·1– 2·6
Pb	3·1	1·3	0·6	1·4– 5·1
Dsp	23·9	2·3	1·0	21·2–27·3

Unless stated otherwise all measurements are expressed as a percentage of the standard length.

The body is compressed and streamlined, with smooth dorsal and ventral profiles. The snout is fleshy and bluntly rounded. The rostral flap almost overlaps the margin of the upper jaw on the ventral surface of the snout. The eye is large and protuberant usually visible from below, a feature that is more conspicuous in smaller specimens. In fishes of less than about 60 mm SL the anterior edge of the lower jaw is gently curved and lacks a horny covering. The lower jaw is straight-edged in larger fishes and has a sharp horny cutting edge.

A series of six or seven lateral line pores is usually conspicuous on the skin of the ventral surface of each ramus of the lower jaw. Two pairs of small barbels are

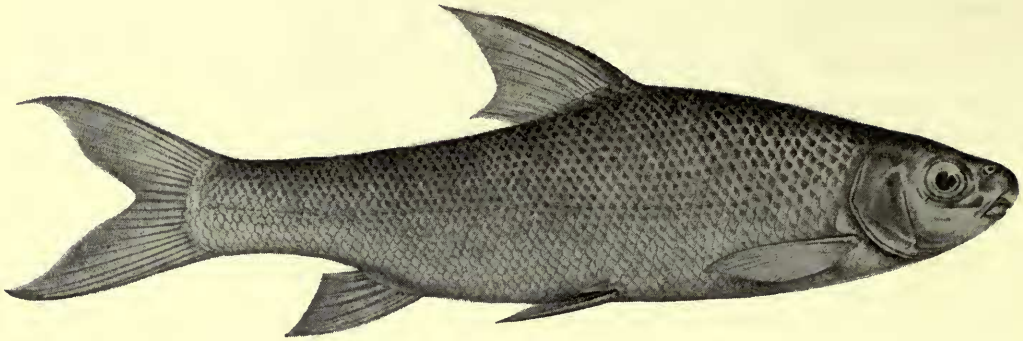

FIG. 4. *Varichorhinus tanganicae* (from Boulenger, 1901).

present. The anterior barbels can best be described as small prolongations of the postero-ventral corners of the rostral flap. The groove below the lachrymal bone is much narrower than in the Balon specimens. A few of the larger (more than about 200 mm SL) specimens have a scattering of small, poorly defined tubercles on the skin covering the lachrymal bone. The tubercles are non-contiguous and are about the same absolute size as those in the putative hybrids.

The peritoneum is dark grey-brown and the intestine is more convoluted than in the putative hybrids.

There are 20+21 (f1), 21+21 (f2), 21+22 (f4), 22+21 (f2) or 22+22 (f1) vertebrae in the ten specimens radiographed.

The angle of insertion of the pectoral fin varies between 37° and 51° in the ten specimens examined.

Dorsal fin. There are 4 unbranched rays and 8 (f4), 9 (f17) or 10 (f3) branched rays. The fourth simple ray is ossified into a straight smooth spine. The shape of

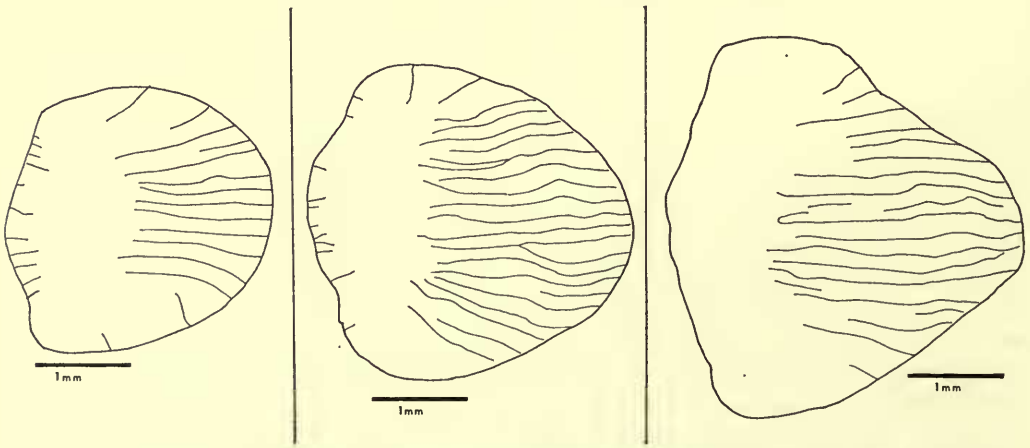

FIG. 5. A scale of a specimen of *Varichorhinus tanganicae* of 139 mm SL (left) a hybrid of 133 mm SL (centre) and a *Barbus tropidolepis* of 134 mm SL (right).

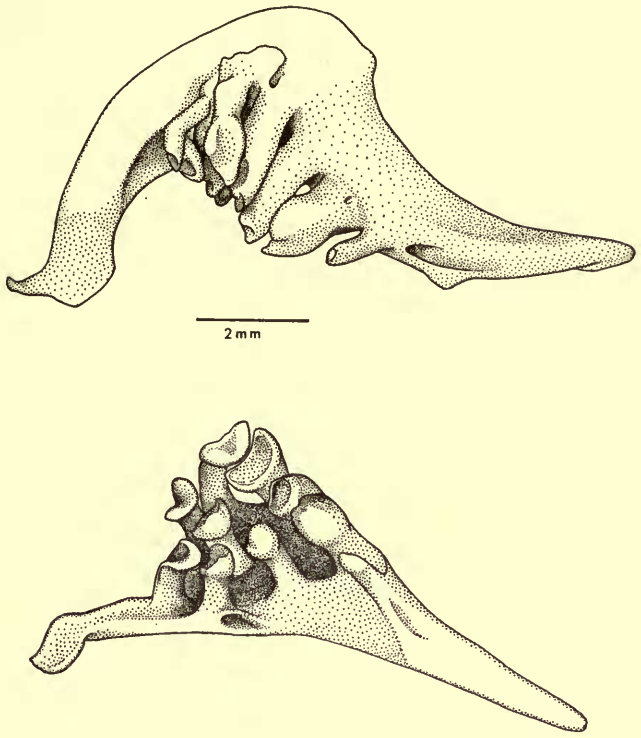

FIG. 6. The right pharyngeal bone of *Varicorhinus tanganicae* of 139 mm SL.

the dorsal fin is shown in Fig. 4. The anterior half of the base of the dorsal fin is surrounded by a low sheath of scales. The origin of the dorsal fin is in front of the origin of the pelvic fin.

Squamation. There are from 57 to 67 scales in the lateral line series: 57 (f2), 58 (f1), 60 (f2), 61 (f4), 62 (f2), 63 (f4), 64 (f4), 65 (f4), 67 (f1). There are $12\frac{1}{2}$ (f12), 13 (f9) or $14\frac{1}{2}$ (f3) scale rows from the dorsal mid-line to the lateral line. Between the lateral line and the ventral mid-line there are $12\frac{1}{2}$ (f1), $13\frac{1}{2}$ (f5), $14\frac{1}{2}$ (f6), $15\frac{1}{2}$ (f5), $16\frac{1}{2}$ (f2) or $17\frac{1}{2}$ (f1) scale rows. These scales could not be counted on some specimens. From the lateral line to the base of the pelvic fin there are 8 (f10), 9 (f12), 10 (f1) or 11 (f1) scales. Around the least circumference of the caudal peduncle there are 29 (f1), 30 (f5), 31 (f3), 32 (f6) or 33 (f2) scales.

The striations on the scales are radiate, but they tend to be more divergent in smaller fishes than in larger ones.

Pharyngeal bones and teeth. The pharyngeal teeth number 2.3.5–5.3.2 (Fig. 6). The teeth are slender and the posterior teeth in each row have spatulate crowns. The teeth are arranged in three parallel rows. The mean tip-to-tip measurement of the pharyngeal bones of a specimen of 104 mm SL is 8·9 mm and of a 60 mm SL specimen 6·0 mm.

Gill-rakers. In the 14 specimens examined the number of gill rakers on the lower limb of the first gill arch is 17 (f1), 18 (f4), 19 (f7) or 20 (f2). The gill rakers are slender, conical and bear small lateral projections.

Coloration. Live fishes were described by Poll (1953) as brown to grey on the back, paler ventrally. A silver sheen is usually present and the fins are pale grey. Preserved specimens are usually a pale yellow/brown in colour although the larger specimens tend to be greyer.

Distribution. This species is confined to the Lake Tanganyika basin. According to Poll (1953) it is found in both the lake and the affluent rivers, even in the rapids of the inflowing streams. In the lake it is commonest in rocky areas near to the mouths of streams. It ascends rivers to breed. Small fishes (less than 80 mm SL) are rare in the lake and seem to spend the early part of their lives in the streams. In both the lake and the feeder streams *Varicorhinus tanganicae* is found feeding in sandy, gravelly or rocky regions, rummaging for insect larvae. Ostracods, worms and diatoms mixed with grains of sand are also found in the alimentary canal (Balon, pers. comm.).

Barbus tropidolepis Boulenger, 1900

For synonymy see Banister (1973).

Material examined. In addition to the syntypes, the following specimens were examined: BMNH1955.12.20:737–740; 1955.12.20:775–792; 1955.12.20:795–799; 1955.12.20:806–815; 1955.12.20:1169–1171.

Description. Two separate samples of *Barbus tropidolepis* were measured. The first, a sample of 47 fishes from Lake Tanganyika, are between 99 and 365 mm SL and serve to show the variation of morphometric characters in the species (taken from Banister, 1973). The second sample is of ten fishes and represents all the available specimens within the size range of the putative hybrids. These ten fishes are of 56 (2), 59 (2), 60, 66, 69, 75, 105 and 134 mm SL.

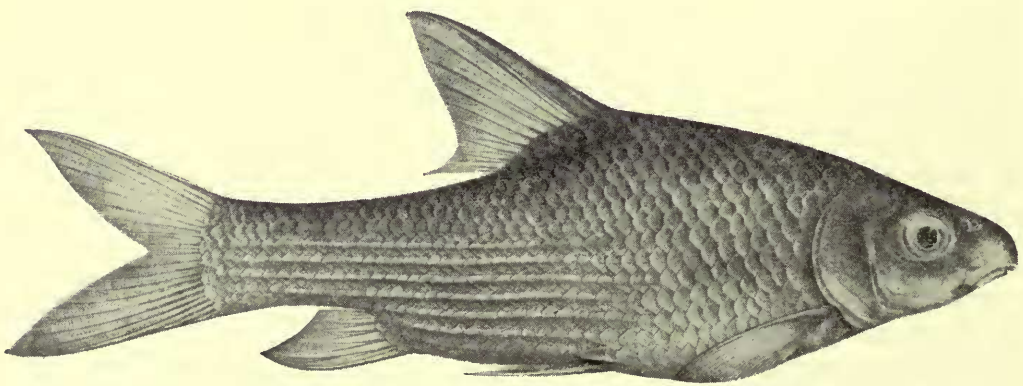

Fig. 7. *Barbus tropidolepis* (from Boulenger, 1901).

Sample 1 (n=47)

	$\bar{x}$	s.d.	s.e.	range
SL	–	–	–	99 –365 mm
D	28·8	2·7	0·6	25·0–33·7
H	27·0	1·4	0·3	24·8–30·1
I	9·4	1·3	0·3	7·0–11·0
IO	9·0	1·5	9·3	7·4–11·4
MW	6·4	0·8	0·2	5·2– 8·8
Pct	20·8	1·0	0·2	19·1–23·9
CPl	14·9	1·2	0·3	12·9–17·7
CPd	11·7	0·9	0·2	10·1–13·7
Snt	8·4	1·0	0·2	5·2– 9·3
Dsp	25·8	2·7	0·6	20·8–30·0

Sample 2 (n=10)

	$\bar{x}$	s.d.	s.e.	range
SL	–	–	–	56 –134 mm
D	26·3	2·2	0·7	23·4–30·6
H	27·2	0·7	0·2	25·9–28·8
I	8·8	0·6	0·2	8·2–10·2
IO	8·7	0·6	0·2	7·6– 9·7
MW	5·9	0·5	0·1	5·1– 6·7
Pct	20·4	1·7	0·5	16·6–22·6
CPl	14·3	1·0	0·3	12·0–15·3
CPd	11·2	0·6	0·2	10·5–12·1
Snt	7·3	0·6	0·2	6·5– 8·2
Dsp	28·2	1·5	0·5	25·0–30·6

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

The body has a compressed, fusiform shape. The blunt snout lacks a rostral flap. Only a very shallow groove is present between the edge of the lachrymal bone and the snout. The eye is protuberant and conspicuous in ventral view.

The mouth is subterminal. The lower jaw is narrow with a soft, curved, anterior margin. The lower lip is often discontinuous medially. A few specimens have the lips slightly thickened. The gular surface is deeply folded. There is no anterior barbel and the posterior barbel is represented by a very small papilla. Although invariably present, this barbel is too short to measure accurately.

Small, scattered tubercles are present on the skin covering the dorsal part of the lachrymal bone as well as between the orbit and the nostrils. The tubercles are smaller than those of *Varicorhinus tanganicae* or the Balon specimens. In common with *Varicorhinus tanganicae* a series of 6 or 7 lateral line pores is conspicuous on the ventral surface of each ramus of the lower jaw. The peritoneum is mid-brown in colour.

In the 14 specimens radiographed there are 18+22 (f1), 19+21 (f4), 19+22 (f8) or 19+23 (f1) vertebrae. The angle of insertion of the pectoral fin varies from 12° to 23° in the specimens radiographed.

Dorsal fin. There are 4 unbranched rays (not 3 as reported by Boulenger, 1911, and Worthington & Ricardo, 1937). The last unbranched ray forms a smooth

straight spine. There are 9 (rarely 10) branched rays. The dorsal margin of the dorsal fin has a characteristic shape which can be seen in Fig. 7. The origin of the dorsal fin is directly above or slightly in advance of the pelvic fins.

Squamation. There are from 39 to 44 scales in the lateral line series: 39 (f2), 40 (f9), 41 (f11), 42 (f13), 43 (f9), 44 (f3). There are $8\frac{1}{2}$ (rarely $7\frac{1}{2}$) scale rows between the dorsal mid-line and the lateral line and $8\frac{1}{2}$ (rarely $7\frac{1}{2}$, very rarely $9\frac{1}{2}$) scale rows between the lateral line and the ventral mid-line. Around the least circumference of the caudal peduncle there are 16 (f34), 17 (f6) or 18 (f7) scales. The ridges of fat that may occur on the scales of this species (see Banister, 1973) do not occur in the putative hybrids nor in *Varicorhinus tanganicae.* The scale striations are more or less parallel. The posterior margin of each scale is markedly lobate.

Pharyngeal bones and teeth. The pharyngeal teeth usually number 2.3.5–5.3.2. The first tooth of the inner row is very small and may be absent. When absent, its locus is marked by a small pinnacle of bone. The second tooth of the inner row is stout with a molariform crown. The remaining three teeth in this row become progressively thinner. The crowns of especially the third and fourth teeth are almost as wide as that of the second tooth but are not so long, i.e. they are kidney-shaped when viewed from an occlusal position (see Fig. 9).

The alignment of the second and third rows is characteristic in that the first tooth of the second row is displaced slightly so that the second and third tooth rows

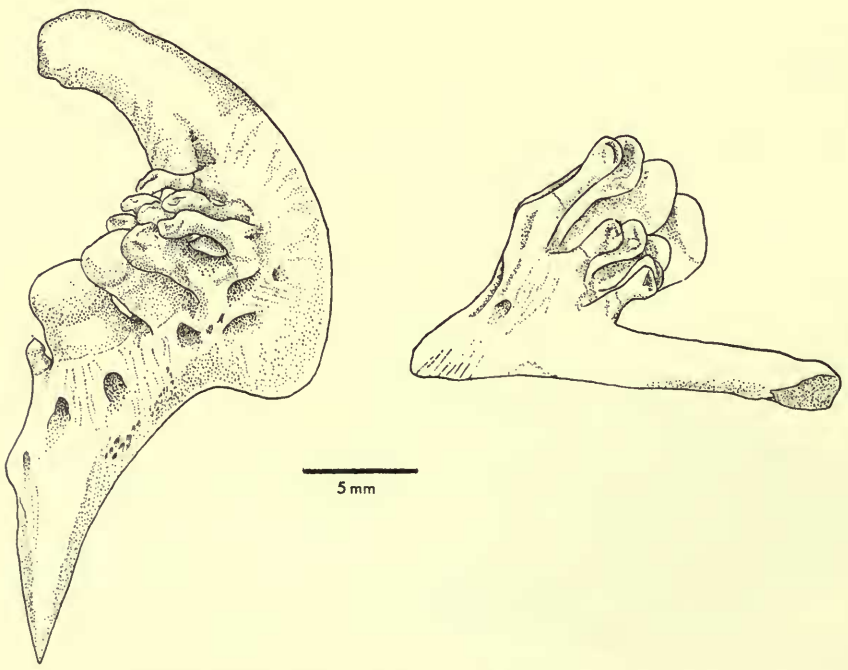

FIG. 8. The right pharyngeal bone of *Barbus tropidolepis* (from Banister, 1973).

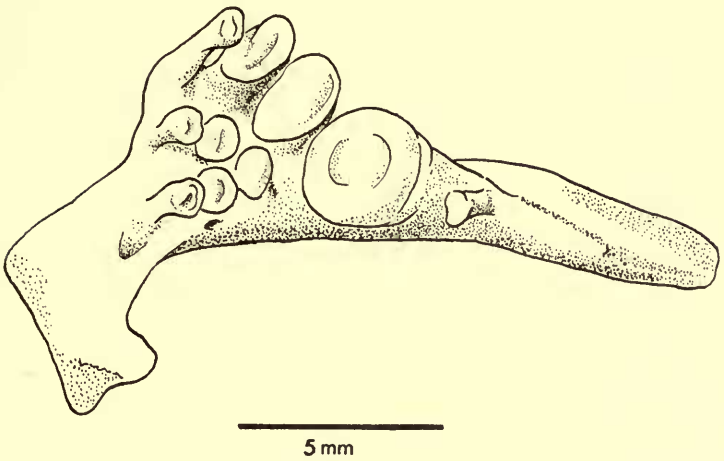

FIG. 9. Occlusal view of the right pharyngeal bone of *Barbus tropidolepis* (from Banister, 1973).

appear to radiate from it, rather than lying parallel to each other. The mean tip-to-tip length of the pharyngeal bones from a specimen of 105 mm SL is 13·5 mm and the mean for the pharyngeal bones from a fish of 60 mm SL is 7·5 mm.

Gill-rakers. There are 13 (f10), 14 (f4) or 15 (f2) gill-rakers on the lower limb of the first gill-arch in the 16 specimens examined. The gill-rakers are broad based with the outside edge produced forwards as a hook.

Coloration. The colour of live fishes, as described by Poll (1953), is grey or olive on the back, lighter ventrally. There is no noticeable colour pattern. Preserved fishes are brown on the body. Small specimens (less than about 90 mm) have a dark margin to the dorsal fin ; otherwise the fins are pale brown.

Habitat. This species is found in Lake Tanganyika to a depth of 25 m. It also occurs in feeder streams, especially in the breeding season (Poll, 1953).

DISCUSSION

There are three possible ways of regarding Balon's anomalous fishes. They could represent a new species, they could be hybrids or they could represent extreme representatives of a known species. The Balon specimens are very much rarer in the wild than either *Barbus tropidolepis* or *Varicorhinus tanganicae* and they have only been found at one locality. Hubbs, Hubbs & Johnson (1943) quote, for two species of North American Catostomidae captured in the same river system, a proportion of hybrids to parents of 4·2 and 6·4%. They also state that some hybrids are much rarer and the proportion may be about 1%.

There is no quantitative information available about the Balon specimens. However, Balon (pers. comm.) has stated that they occur with *Barbus tropidolepis* and *Varicorhinus tanganicae* and are very much rarer than either. This information, coupled with the conspicuous morphological intermediacy between *Barbus tropidolepis*

and *Varicorhinus tanganicae* possessed by the Balon fish, suggests it is unlikely that they represent a true species.

The consistent differences between *Barbus tropidolepis* and *Varicorhinus tanganicae* in morphometric and meristic characters leave no doubt as to their specific distinctness. The differences in mouth form and associated feeding structures could arguably be the result of particular responses to the environment (Groenewald, 1958), but this is unlikely because of the discrete differences in other, and apparently unrelated, characters.

The morphometric intermediacy of aquarium-bred, and thus indisputable, hybrids has often been noted (e.g. Holčik & de Witt, 1962a, b ; Hubbs & Miller, 1952). Hubbs (1955) described the morphological intermediacy of hybrids in the wild. Berry & Low (1970) and Hubbs (1955) advocate intermediacy as a very significant character of hybridization.

Unfortunately, the supporting evidence for hybridization that was used in the case of *Barbus alluaudi* (Banister, 1972) has not been available in this instance. For example, I have not been able to examine the gonads because of their inadequate preservation and I have but little information of the frequency of the occurrence of the Balon fishes in the wild. Therefore, the case rests solely on morphological evidence.

The 11 Balon fishes have 45–56 scales in the lateral line series. This is a wide range for a small sample. There are only five species of large *Barbus* and *Varicorhinus* in Lake Tanganyika. *Barbus tropidolepis* has 39–44 (n=47) scales ; *Varicorhinus tanganicae* has 57–67 (n=24) ; *Varicorhinus leleupanus* has 42 or 43 (n=2) ; *Barbus platyrhinus* has 38–41 (n=7) ; and *Barbus caudovittatus* has 24–30 (n=47). Considering just the lateral line scale counts, no overlap exists between any of the recognized species and the Balon specimens ; which alone tends to render unlikely the hypothesis that these specimens represent extreme forms of any known species.

Only one of the five species of *Varicorhinus* and large *Barbus* in Lake Tanganyika has smaller scales than the fishes under consideration, i.e. *Varicorhinus tanganicae* with 57–67 scales in the lateral line series. This species, therefore, is a certain candidate as one of the parents of the putative hybrids.

On the basis of the scales alone, *Barbus caudovittatus* can surely be eliminated as the other parent, but this still leaves *Barbus platyrhinus*, *Barbus tropidolepis* and *Varicorhinus leleupanus*. The bulky body of *Barbus platyrhinus* is not reflected in the streamline shape of the Balon fishes. A hybrid between *Varicorhinus leleupanus* and *Varicorhinus tanganicae* would be very likely to have a wide, horny-edged 'sector' mouth. The Balon fishes do not have a wide, horny-edged 'sector' mouth. Furthermore, *Varicorhinus leleupanus* has not been recorded from the Lunkungwe area of Lake Tanganyika. In the wild, the Balon fishes occur together with both *Barbus tropidolepis* and *Varicorhinus tanganicae*.

The range, mean and one standard deviation each side of the mean for seven morphometric characters of the putative hybrids and probable parent species are given in Table 2. The characters chosen (H, I, IO, MW, Dsp, Ab, Pb) are the same as were considered when discussing the hybrid origin of *Barbus alluaudi*

(Banister, 1972). The choice was made partly for comparison with the *Barbus alluaudi* situation and partly because these are the only morphometric characters in which the putative parent species differ significantly from each other and/or from the hybrid. The samples of *Barbus tropidolepis* and *Varicorhinus tanganicae* are from the same size range as the putative hybrids.

The number of vertebrae and the number of gill-rakers on the lower limb of the first gill-arch in the Balon fishes are intermediate between those of the putative parents (Table 1). The pharyngeal bone length and the angle of insertion of the

TABLE 1

	Total no. of vertebrae	Gill-rakers	Pectoral insertion angle
B.t.	40–42 (n = 14)	13–15 (n = 16)	12–23° (n = 9)
Hyb.	40–43 (n = 11)	15–18 (n = 11)	21–40° (n = 11)
V.t.	41–44 (n = 10)	17–20 (n = 14)	37–51° (n = 12)

Mean length of pharyngeal bones

	SL (mm)	Ph. length (mm)
V.t.	60	6·0
V.t.	104	8·9
Hyb.	59	6·3
Hyb.	105	10·0
B.t.	60	7·5
B.t.	105	13·5

pectoral fin show the same intermediacy, as does the alignment of the pharyngeal teeth.

The possibility that the Balon fishes represent an extreme example of either putative parent species must now be considered. The techniques of Schultz & Schaeffer (1936) and of Hubbs, Hubbs & Johnson (1943) have been used to evaluate the probability of a character of the sample under examination falling within the

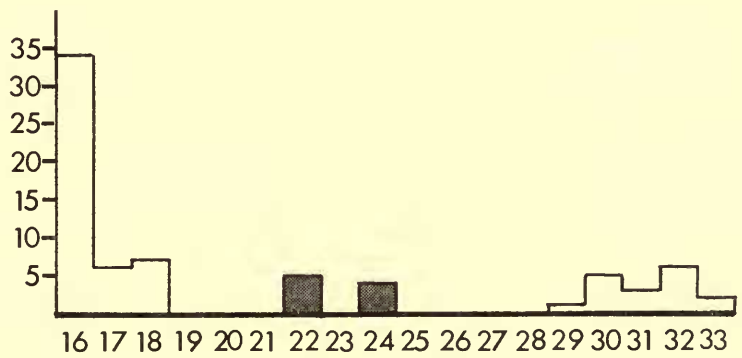

FIG. 10. A histogram of the frequencies of the lateral line scale counts in *Barbus tropidolepis* (left), the hybrids (black, centre) and *Varicorhinus tanganicae* (right).

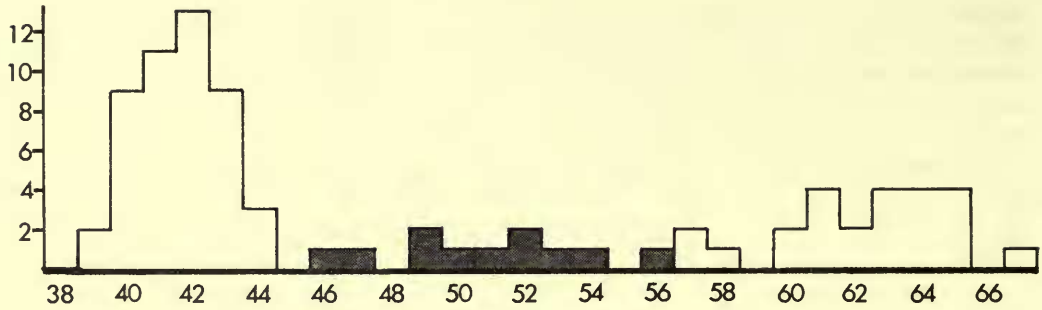

FIG. 11. A histogram of the frequencies of the scale counts around the least circumference of the caudal peduncle in *Barbus tropidolepis* (left), the hybrids (black, centre) and *Varicorhinus tanganicae* (right).

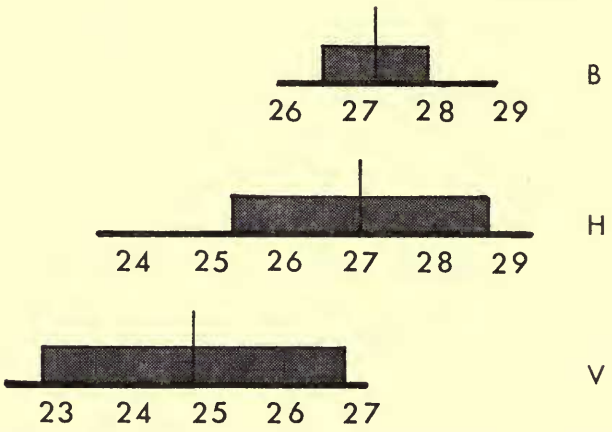

FIG. 12. A comparison of the range, mean and standard deviations of the head length in the three forms. The base line represents the range, the vertical line the mean and the black area covers one standard deviation either side of the mean. The figures are the lengths of the heads expressed as a percentage of the standard length. B = *Barbus tropidolepis*, V = *Varicorhinus tanganicae*, H = hybrids.

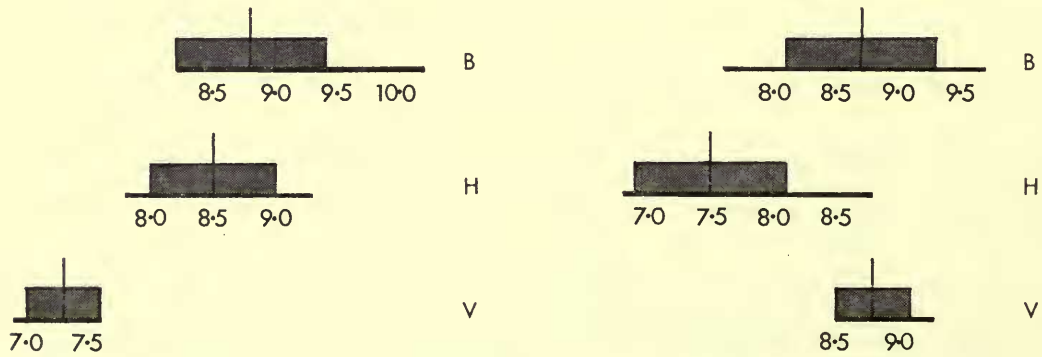

FIG. 13. Comparisons of the eye diameter (left) and interorbital width (right) in the three forms. Details as in Fig. 12.

range of that character in either of the putative parent species. The results are shown in Table 2.

TABLE 2

Character	n	$\bar{x}$	s.d.	% B	% V	P
H						
V. t.	5	24·82	2·05			0·4
Hyb.	11	26·97	1·72	91	9	
B. t.	10	27·18	0·77			0·7
I						
V. t.	5	7·30	0·30			0·1
Hyb.	11	8·54	0·55	81	19	
B. t.	10	8·83	0·61			0·25
IO						
V. t.	5	8·78	0·31			0·1
Hyb.	11	7·46	0·63	–	–	
B. t.	10	8·66	0·66			0·1
MW						
V. t.	5	8·72	0·55			0·1
Hyb.	11	6·86	0·63	52	48	
B. t.	10	5·90	0·51			0·1
Dsp						
V. t.	5	23·94	2·35			0·4
Hyb.	11	26.34	1.52	44	56	
B. t.	10	28·2	1·59			0·1
Ab						
V. t.	5	1·35	1·06			0·1
Hyb.	11	1·80	0·28	–	–	
B. t.	10					–
Pb						
V. t.	5	3·06	1·36	–	–	0·78
Hyb.	11	3·24	0·54			–
B. t.	10					

For the characters H, I, MW and Dsp the mean for the hybrid lies between the means for the other two species. The % B refers to the percentage proximity of this mean to the mean for *Barbus tropidolepis* and the % V refers to the percentage proximity to the *Varicorhinus tanganicae* mean. The probability, P, refers to the probability of observing a mean equal to the Balon specimen value if the sample had come from one of the other two species.

The morphometric measurements of the putative hybrids are satisfactorily intermediate for the characters MW and Dsp. However, the head length results are not as significant as they were for *Barbus alluaudi* (Banister, 1972). In that case the percentage likeness of the head length to each of the putative parents is

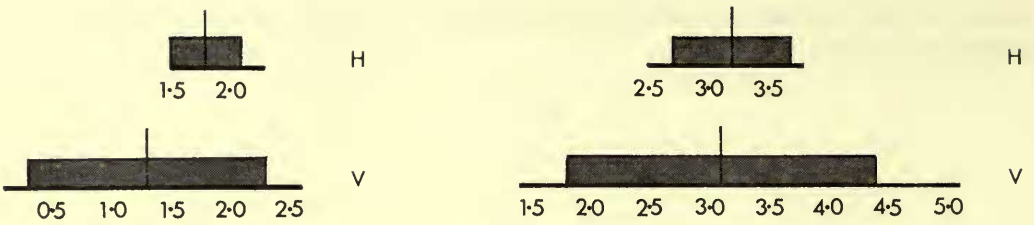

FIG. 14. Comparisons of the anterior (left) and posterior (right) barbel lengths in the three forms. Details as in Fig. 12.

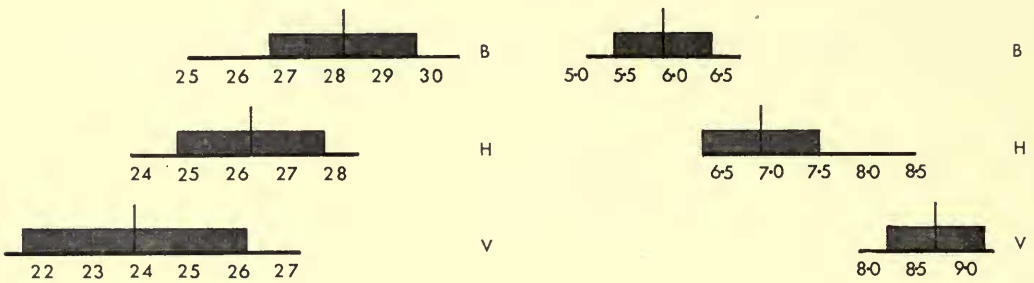

FIG. 15. Comparisons of the dorsal spine length (left) and the mouth width (right) in the three forms. Details as in Fig. 12.

69 and 31% respectively. It can be seen from Table 2 that the head-length of the Balon fish is much closer to that of *Barbus tropidolepis* than to that of *Varicorhinus tanganicae* (% B = 91 ; % V = 9). One striking similarity between *Barbus alluaudi* and the Balon fishes can be seen in the interorbital width. In both cases, the hybrid interorbital width is less than that of the putative parents, the latter differing but little from each other in this character.

Although generally it is true to say that African *Barbus* species have longer barbels than African *Varicorhinus* species, it is not true in this case. What little difference exists between the putative hybrids and *Varicorhinus tanganicae* shows that the hybrid has slightly longer barbels.

The results of the morphometric characters analysed in Table 1 and the characters described in the earlier part of the text indicate that it is unlikely that the Balon specimens are extreme forms of either *Barbus tropidolepis* or *Varicorhinus tanganicae*. The degree of intermediacy hints most strongly at a hybrid origin.

The evidence for the hybrid origin of the Balon fish is circumstantial and rests solely on the fact that in many characters these specimens are intermediate between *Barbus tropidolepis* and *Varicorhinus tanganicae*. This is the second example of hybridization between species of the genera *Barbus* and *Varicorhinus* in Africa. Such intergeneric hybridization raises doubts about the validity of the two genera. The mouth shape is the main character used to distinguish the two genera and yet this has been shown (Groenewald, 1958 ; Banister, 1973) to be a variable feature of little value at the generic level. Some *Barbus* species show extra-limital variation and achieve the *Varicorhinus* facies, or at least a close approximation to it. In

all probability the true situation is that the genus *Varicorhinus* is polyphyletic and contains some species whose phyletic status may be best expressed by placing them in the genus *Barbus*. A full revision of the genus *Varicorhinus* is needed to clarify these anomalies. This work is in progress.

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PLATE 1

A hybrid (top) of 133 mm SL, *Varicorhinus tanganicae* (centre) and *Barbus tropidolepis* (bottom).