Geographic variation of Barbus radiatus Peters, a widely distributed African cyprinid fish

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Synopsis

Barbus radiatus is a widely distributed, polytypic species with three recognized subspecies: *radiatus* Peters (1853), *aurantiacus* Boulenger (1910), and *profundus* Greenwood (1970). A phenetic analysis of relative similarity was conducted for specimens of *B. radiatus* from throughout its known range. The study focuses on several large population samples taken recently along the presumed central Zambian interface between the subspecies *aurantiacus* and *radiatus*. New data on meristic and morphometric variation in *B. radiatus* and recent rediscovery of typical *radiatus* in Lake Victoria demonstrate that *profundus* is a species distinct from *radiatus*. With respect to the remaining two subspecies, results indicate a populational mosaic of highly variable morphs rather than two discrete, allopatric morphs. Thus, *aurantiacus* is placed in synonymy of *radiatus*. It is hypothesized that the populational mosaic of morphology in *radiatus* reflects adaptive ecotypic responses to water temperature and current velocity. The characters which accounted for most of the geographic variation of *radiatus* were body depth, caudal peduncle length, longitudinal meristic counts, dorsal fin height, and orbit diameter.

Introduction

This study is a contribution to understanding morphological variation in populations of *Barbus*

radiatus, a widely distributed, polytypic species with three recognized subspecies: *radiatus* Peters (1853), *aurantiacus* Boulenger (1910), and *profundus* Greenwood (1970). The typical subspecies is distributed from the Aswa River in Uganda, southward to the Pongolo River in Natal, and westward to central Zambia where it interfaces with the western subspecies *aurantiacus* (Fig. 1). *B. r. profundus* is endemic to the deep waters of Lake Victoria.

It is proposed herein to accord full specific rank to *profundus* because this taxon has several characteristics which transcend variation in *radiatus*. Rationale for the change and a contrast of the two species are deferred to the systematic revision section. The following analysis of morphological variation will be confined to the two forms of *radiatus*.

B. r. radiatus generally has orbit diameter less than interorbital width, whereas, *aurantiacus* has orbit diameter greater than interorbital width. This is the only character that has proven to be diagnostic and, together with a presumed allopatric distribution, precludes synonymy of the two taxa. When the above criterion was used to classify *B. radiatus* from several recent collections made in Zambia, it became apparent that zoogeography of the two *radiatus* morphs was more complex than previously envisioned. A population referable to *aurantiacus* was found isolated in the Luongo River above Musonde Falls (Fig. 2 and 3); typical *radiatus* occurred just below the falls. This and other distributional anomalies as well as specimens difficult to refer to either morph suggested the need for further study.

Fig. 2. (a) *Barbus profundus* paratype, 52 mm, Lake Victoria (BMNH 1970.5.14:2–4); (b) *B. radiatus*, 67 mm, Lower Luongo River, Zambia (ROM 28075); (c) *B. radiatus*, 78 mm, Upper Luongo River, Zambia (ROM 28049), slender morph resembling *aurantiacus*.
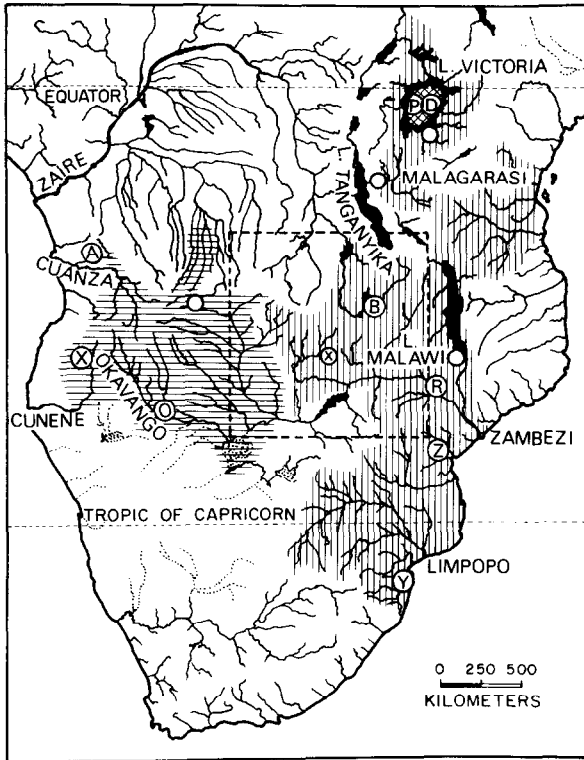
Fig. 1. Distribution in Africa of *B. r. radiatus* (vertical), *aurantiacus* (horizontal), and *profundus* (crossed) (after Greenwood 1970 and Bailey 1969). Circled letters indicate type localities: R = *radiatus*, synonyms are *doggetti* (D), *bangwelensis* (B), *palustris* (Z), and *rubellus* (Y). A = *aurantiacus*, synonyms are *rogersi* (X), and *okavangoensis* (O). P = *profundus*. The boxed area is enlarged in Fig. 3. Open circles indicate populations outside the boxed area that were studied herein.

There seems to be no agreement on which form of *B. radiatus* occurs in the Kafue, Bangweulu, or Upper Zambezi systems (Bell-Cross 1965, 1968, 1972; Greenwood 1963, 1970; Jubb 1967, 1968; Ladiges 1964). Taken together, the differing opinions of these authors support the observation that many populations of *B. radiatus* are difficult to categorize and may cast doubt on the validity of recognizing two subspecies. It was my objective to examine morphological variation of B. radiatus and thereby to reevaluate the need of recognizing two subspecies.

Methods and materials

This study encompasses material from 22 localities from throughout the known range of *B. radiatus* with an emphasis on the central Zambian interface
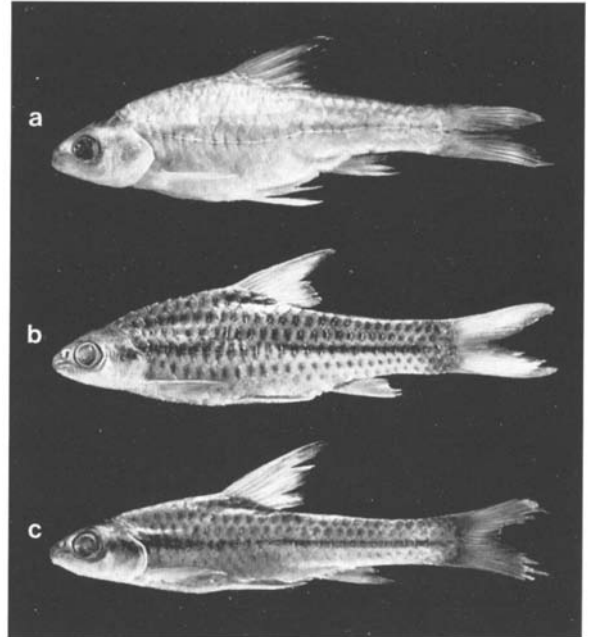
between the two subspecies (Fig. 1 and 3). For the following list of material examined, lots marked with an asterisk were not used in the principal components analysis. Size of specimens is given in standard length. Abbreviations for institutions are as follows: Albany Museum, Grahamstown (AMPF); British Museum (Natural History), London (BMNH); Natal Museum, Pietermaritzburg (NPB); Royal Ontario Museum, Toronto (ROM); Tervuren Museum, Tervuren (TM); and University of Michigan Museum of Zoology, Ann Arbor (UMMZ).

East of Zambia: Types. — BMNH 1904.5.19:24 *Barbus doggetti* holotype, 82 mm, Lake Victoria, W. Doggett; BMNH 1938.5.6:1–8 *Beirabarbus palustris* paratypes, (14)26–53 mm, swampy savannah 12 km from Beira, Moçambique, A. Herre, 30–IV–1936; BMNH 1960.11.5:1–2 and BMNH 1960.11.5:3–5 *Barbus rubellus* paratypes, *(5), Mzenyeni Pan, Ingwavuma District, Zululand, R. Crass, 17–IX–1956. Nontypes. — UMMZ 194962, 67 mm, Lake Victoria, depth 2 m in open water adjacent to dense *Vossia*, Mwanza, Tanzania, worm on hook and line, D. Stewart and R. Scully,
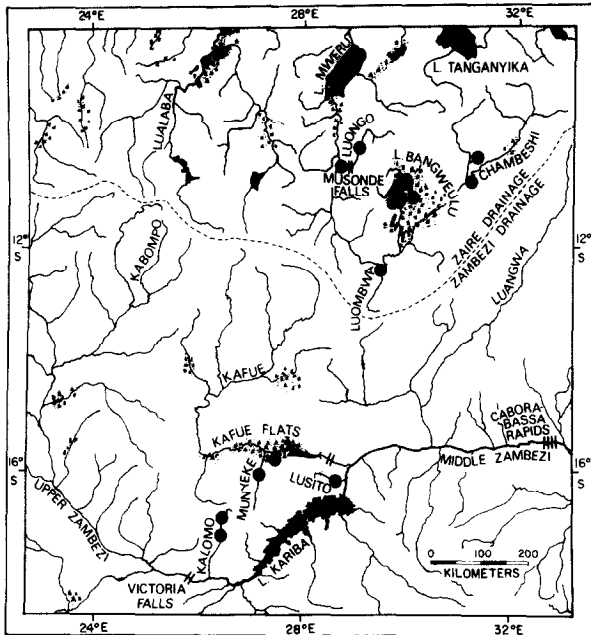
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Fig. 3. Zambian localities (●) for *B. radiatus* material used herein.

23–X–1973; UMMZ 198865, *74 mm, seasonal tributary of Lake Victoria, 32 km E of Mwanza, Tanzania, R. Scully, 12–IV–1974; BMNH 1971.6. 22:135–136, *(2)70–89 mm, Malagarasi River, Uvinga, Tanzania, P. Greenwood, R. Lowe-McConnell and G. Lockley, 18–IX–1952; BMNH 1932.11.15:343–360, *(meas. 10 of 20) 38–77 mm, Lake Malawi, Bar House and Deep Bay, Malawi, Christy; AMPF 1922, *(2)40–46 mm, Mzenyeni Pan, Ingwavuma District, Zululand, R. Crass, 17–IX–1956; AMPF 1266, *(2)38–41, Malambog-wenya River, Jozini, Pongolo River drainage, (R. Pott in mid-1960's?).

In Zambia: Types — BMNH 1905.11.10:6 *Barbus bangwelensis* holotype, 76 mm, Lake Bangweulu, F. Melland; BMNH 1910.1.26:5 *Barbus rogersi* paralectotype, *44 mm, Umsitu River, Kafue-Zambezi drainage, near Broken Hill (= Kabwe), Rogers. Nontypes. — ROM 28049, (meas. 25 of 174)30–117 mm, Upper Luongo River (above Musonde Falls), 16 km W of Mwenda, 0.5–4 m deep, 18–20 m wide, slow current, turbid water, macrophytes and some rocks, in deep grassy ravine, rotenone, E. Balon, 17–XI–1970; ROM 28075, (meas. 25 of 36)56–89 mm, Lower Luongo River (15 km below Musonde Falls), near ferry crossing, 0.2–1 m deep, 25–35 m wide, fast current,

rocky outcrops with gravel, sand and mud, in hillocks valley, rotenone, E. Balon, 18–XI–1970; BMNH 1943.7.27:221–230, (meas. 11 of 13)45–57 mm, Bangweulu Swamps, Chilui Island, Matipa, purchased, C. Ricardo and R. Owen, 4 to 20–XII–1936; BMNH 1932.12.16:124–143, (meas. 6 of 20)28–32 mm, Luombwa River, C. Pitman, 16–XII–1932; UMMZ 198863, (meas. 25 of 75) 28–53 mm, Chambeshi River at Kasama-Mpika highway, near shore, depth to 1 m, moderate current, clear water, sand and silt with macrophytes along shore, rotenone, R. M. Bailey and D. Stewart, 4–XI–1970; UMMZ 198862, (2)58–62 mm, tributary to Chambeshi River at road 53 km S of Kasama, swampy stream 0.5–4 m wide, 0.3 m deep, slow current, clear water, sand and gravel, *Typhus* and sedges, rotenone, R. M. Bailey and D. Stewart, 4–XI–1970; UMMZ 198864, (25)26–71 mm, Kafue Flats in Lochinvar National Park near Chunga, depth to 2 m, turbid water, muddy substrate, abundant macrophytes, rotenone and seine, J. Kapetsky and D. Stewart, 3 to 15–II–1970; UMMZ 198861, 46 mm, Munyeke Stream at Monze-Namwala road 41 km W of Lochinvar turn-off, seasonal tributary of Kafue Flats, dry to pools 1–8 m wide, 0.5 m deep, sand, gravel and rocks, rotenone and seine, R. M. Bailey and D. Stewart, 21–X–1970; ROM uncat., (meas. 25 of 51)36–53 mm, Kalomo River 12 km downstream from Kalomo township, braided stream averaging 3.5 m wide, 0.5 m deep, rapids and sand, also a pool with reeds, toxicant and seine, E. Balon, 29–IV–1969; ROM uncat., (meas. 11 of 13)80–90 mm, reservoir of Kalomo Dam on Kalomo River 163 km upstream from confluence with Zambezi River, 250–300 m wide in downstream third and less than 50 m wide in upstream half, gill net and seine, E. Balon, 5 to 7–II–1970; ROM uncat., 61 mm, Lusito River at Chipangula 26.5 km from confluence with Zambezi River, alternating rapids and pools at a large bend in the river, 10 m wide, gravel and large boulders, toxicant and seine, E. Balon, 22–IV–1969.

West of Zambia: Types. — BMNH 1911.6.1:78 *Barbus aurantiacus* lectotype, 76 mm, and BMNH 1911.6.1:79–80 paralectotypes, (2)46–65 mm, Rio Lucalla at Lucalla, Rio Cuanza drainage, Angola, W. Ansorge; BMNH 1949.12.30:1–10 *Beirabarbus okavangoensis* paratypes, (10)30–54 mm, Okavango River at Runtu, South West Africa, Eedes, 1939; BMNH 1907.6.29:149 *Barbus rogersi* lectotype, *48 mm, Rio Que, Rio Cunene drainage, Angola, W. Ansorge. Nontypes. — TM 160243–245, *(3)

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64–71 mm, and TM 160246–254, *(9)39–55 mm, Lac Colundo, Upper Zambezi River drainage, Angola, I-1955.

Subsequent reference to various populations is made using name of the river or lake from which the sample was taken. For type localities, name of the associated nominal species is used. The type of *doggetti* and two recently collected *radiatus* specimens from Lake Victoria are all referred to as 'doggetti'; also, two specimens from Mzenyeni Pan (type locality of *rubellus*) and two from the nearby Malambogwenya River are referred to as 'rubellus'.

Large population samples were subsampled to obtain a representative length range for both sexes and a total of up to 25 complete specimens. For samples of less than 25, all specimens from which a complete set of data could be taken were used. Data were taken for eleven morphometric characters with needle-point calipers to the nearest 0.1 mm and six meristic characters whenever possible (Table 1).

The fleshy orbital rim was difficult to measure accurately, especially in old material. Diameter of the orbit was measured as the horizontal distance from the posterior rim of the lachrymal (or the lateral ethmoid when it projected out) to the anterior rim of the suborbital behind the eye. The bony interorbital width was taken as least distance across the frontals (excluding the supraorbitals). This method gave values consistently lower than those reported by other authors but fulfilled the necessary criterion of being repeatable with a minimum of error for specimens of all sizes and all states of preservation.

A phenetic analysis of similarity among ten morphometric characters (Table 1) of 182 individual specimens from 16 populations was conducted using principal components analysis. Components were extracted from the correlation matrix of character vectors standardized to zero means and unit standard deviations. Methods are those used by Smith (1973) except that unscaled Eigenvectors were used herein. The components are defined by variates corresponding to the principal axes of the observations in multivariate space; the ith principal component is that linear compound of characters which explains the ith largest portion of the total character variance (Morrison 1967).

Principal components analysis is used here to summarize variation in morphology of *B. radiatus* and to identify characters with the greatest relative contribution to variation. A plot of projection scores for individuals against the first two principal components (Fig. 4) provides a convenient graphic display of relative similarity of specimens from various populations. Each specimen is considered a separate operational taxonomic unit and judgments about phenetic relationships are made according to which specimens cluster together in the multivariate hyperspace.

Table 1. Morphometric and meristic characters of *B. radiatus* that were examined; one through ten were used in the principal components analysis.

1. Standard length, tip of snout to caudal base.
2. Body depth, greatest dimension, usually at dorsal origin.
3. Caudal peduncle depth, least dimension.
4. Caudal peduncle length, posterior end of anal base to a vertical through caudal base.
5. Predorsal length, snout to dorsal fin origin.
6. Height of last unbranched dorsal ray, from structural base.
7. Head length, snout to tip of membranous opercular margin.
8. Snout length, tip to anterior bony orbital rim.
9. Interorbital width, least distance across frontals, measured medial to supraorbitals.
10. Diameter of orbit, bony margin from lachrymal or lateral ethmoid to rim of posterior suborbital.
11. Posterior barbel length.
12. Lateral line scales, pored scales to caudal base, excluding pored scales on caudal fin.
13. Predorsal scales, dorsal origin to occiput along midline.
14. Circumference scale count, rows around body just ahead of dorsal origin.
15. Circumpeduncular scale rows, around narrowest part of caudal peduncle.
16. Principal dorsal fin rays.
17. Postweberian vertebrae, excluding the urocentrum.

Results

Meristics

Nearly every specimen had nine principal dorsal fin rays. The unbranched first ray was followed by eight (rarely nine) branched rays, the last of which was always split to the base. Circumference scale counts were also nearly invariate. Every specimen had 12 circumpeduncular scale rows and all but a few had 16 scale rows around the body just ahead of the dorsal fin origin. The typical pattern was three rows between the mid-dorsal row and lateral line plus three between the lateral line and mid-ventral row. Six of 14 *palustris* paratypes and the smaller *aurantiacus* paralectotype had the mid-

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Table 2 Frequency distributions of vertebrae and lateral line scale counts for *B. radiatus* from various localities. Lake Nabugabo data is from Greenwood (1963, lateral line; 1970, vertebrae).

Locality	Vertebrae					Lateral line scales						
	26	27	28	29	30	24	25	26	27	28	29	30
Upper Luongo River				25			1	2	15	6	1	
Ten Zambian localities	1	12	110	7	1	9	52	43	4			
B. palustris, paratypes	1	8	1			4	2	3				
Lake Nabugabo, Uganda				9	5			3	5	4	1	1

ventral row partially doubled to give possible counts of 17 rows.

Longitudinal meristic counts reveal some interesting variation (Table 2); the pattern for vertebrae closely parallels that for lateral line scales indicating a redundancy in these characters. It appears that specimens from the Upper Luongo have a mode of one myomere more than most other *radiatus*. *B. palustris* have a mode of one myomere less. Most of the variation in vertebrae counts seems to be due to addition or reduction of caudal vertebrae; there were typically 14 precaudal vertebrae. Specimens with less than 28 vertebrae often had two neural spines on the penultimate centrum. The single specimen from Munyeke Stream had 30 vertebrae. The Upper Luongo population had nine or ten predorsal scales compared to eight or nine for most other *radiatus*.

Phenetic similarities

Correlations between morphometric characters and the first two principal components indicate that the first component is simply related to size of the specimens (r = 0.97 to 1.00 for all characters). The second principal component is of greatest interest because effects due to size have been removed and the complex of characters with highest correlations are precisely those upon which the subspecies *radiatus* and *aurantiacus* were predicated. The second component is positively correlated with depth characteristics (r = 0.19, 0.22) and negatively correlated with each of the very different characters dorsal fin height (r = -0.17), caudal peduncle length (r = -0.13), and orbit diameter (r = -0.15). The first two components together account for 98.8 percent of the variation in the multivariate system. The Eigenvalue is 9.72 for the first component and 0.157 for the second.

The third and fourth components were extracted but were not significant.

The plot of projection scores for individuals on the first two principal components (Fig. 4) can be viewed as having size increasing from left to right on the horizontal axis. Diagonal trends in the plot reflect changes in morphology with growth. The vertical axis expresses the dichotomy between a *radiatus*-like morph at the top and an *aurantiacus*-like morph at the bottom. Correspondence between morphometric trends along the vertical axis and meristic trends (Table 2) is excellent. The *B. palustris* and Upper Luongo populations represent extremes in more or less equal and opposite directions. Specimens clustered to the top of the plot are deep-bodied with small eyes, low dorsal fin, and short caudal peduncle. The reverse is true of those to the bottom.

Differences between types considered synonyms of *radiatus* (i.e., *doggetti, bangwelensis*) and *aurantiacus* are bridged by variation in material from Zambia. Projection of the type specimens on the second component alone reveals the east-west cline which was part of the rationale for recognizing two subspecies. The holotype of *bangwelensis* is intermediate in form and historically it has been one of the more difficult to classify.

Morphometric proportions

The principal components analysis provided a general overview of the relative similarity of various populations and identified characters with the greatest relative contribution to variation. When these characters are expressed as percentage of standard length (SL) and analyzed individually (Fig. 5), the sources of variation along the second principal component are revealed in greater detail. The basis for positive and negative character cor-
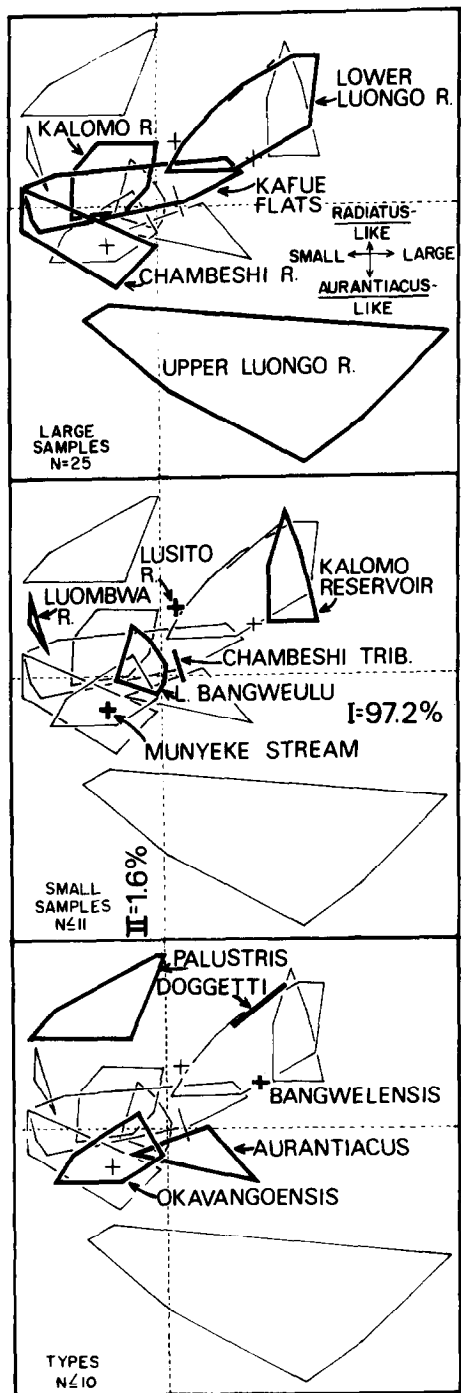
Fig. 4. Relative similarity of *B. radiatus* from selected populations as indicated by projection scores of individuals on the first two principal components. The cluster of points representing each population was circumscribed and individual points omitted. Different populations are successively highlighted in three views of the same plot.

relations with component two can be easily seen in comparison of trends for body depth and dorsal fin height. The pattern for orbit diameter and interorbital width is remarkably similar to that for dorsal height. Interorbital width did not emerge as important in the principal components analysis but is included here because of its prior use as a diagnostic character. The pattern for caudal peduncle length also follows that for dorsal fin height in the eastern and Zaire drainage populations but is less consistent for the other localities. An important result with respect to the systematics of *radiatus* is the observation that a spectrum of population morphs occurs in each of the regions studied. Data on the lectotype of *B. radiatus* (Fig. 5) indicate that it would cluster near *okavangoensis* if included in the principal components analysis (Fig. 4). It might also be noted that for any given population, one or more characters may have 95% confidence limits of the mean non-overlapping with the limits for several other population means.

Body-depth variation was similar to that for caudal peduncle depth indicating a redundancy in these two characters. Variation in depth may be in part a function of the nutritional state or reproductive condition of individuals comprising a population. The Chambeshi River sample included some specimens which appeared emaciated but all other populations appeared to be in good condition. The Kalomo Reservoir sample was all large, gravid females but the sample mean was not significantly different from that of the Kalomo River sample which included much smaller specimens (Fig. 5). Where adequate samples were available, it was consistently observed that males and females had similar mean depth but the females were more variable.

Caudal peduncle length may vary with changes in vertebral number but the correspondence is not as good as might be expected. Mean length of the last caudal centrum was determined from x-rays of ten Upper Luongo specimens to be 1.8% of SL. The range in caudal peduncle length for that sample spans almost four percent of SL but every specimen has 29 vertebrae. Having an extra caudal vertebra might account for only half the difference in mean peduncle length between Upper and Lower Luongo populations. Also, the Munyeke specimen with 30 vertebrae has a relatively short caudal peduncle.

Posterior barbel length was difficult to measure accurately as measurements were typically between

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	POPULATION	n : S.L. (mm)	Body Depth 22 24 26 28 30 32 34	Dorsal Fin Height 22 24 26 28 30 32	Orbit Diameter 8 10 12	Inter-orbital 4 6 8	Caudal Peduncle Length 16 18 20 22 24 26
EAST	B.'doggetti'	3:67-82					
	Malagarasi R.	2:70-89					
	L. Malawi	10:38-77				N.D.	
	B. radiatus	1:35					
	B. palustris	14:26-53		n:9			n:10
	B.'rubellus'	4:38-46					
ZAMBIAN DRAINAGES — Zaire	B. bangwelensis	1:76					
	L. Bangweulu	11:45-57					
	Luombwa R.	6:28-32					
	Chambeshi R.	25:28-53					
	Chambeshi Trib.	2:58-62					
	Lower Luongo R.	25:56-89					
	Upper Luongo R.	25:30-117					
ZAMBIAN DRAINAGES — Zambezi	Kafue Flats	25:26-71					
	Munyeke Stream	1:46					
	Kalomo R.	25:36-53					
	Kalomo Res.	11:80-90					
	Lusito R.	1:61					
WEST	B. aurantiacus	3:46-76					
	B. okavangoensis	10:30-54					
	B. rogersi	2:44-48		n:1			
	L. Colundo	12:39-71	N.D.	N.D.			N.D.

Fig. 5. Variation of selected morphometric characters of *B. radiatus.* Parameters illustrated are the mean (vertical bar), range (horizontal bar), and 95% confidence limits for the mean (Blocks). Confidence limits were approximated using a method based on Fieller's Theorem (Goldstein 1964: 184–187); these are often asymmetrical relative to the mean because the method takes into account the compound variance of ratios. Confidence limits for samples less than five are wider than the range of observations and not plotted. Data for the lecotype of *B. radiatus* are from Greenwood (1963). N. D. = no data.

0.5 and 1 mm. Range of observations (as percentage of SL) overlapped broadly for all populations and no useful patterns of variation in barbel length were detected.

Allometry

Upper and Lower Luongo River populations have divergent trends toward lower and upper corners of the principal components plot (Fig. 4) which may reflect allometric growth of various characters. Slope of the relationship between dorsal fin height (as a percentage of SL) and standard length appeared to differ slightly for the two Luongo River populations; this may contribute to the divergent trends observed. Dorsal fin height as a percentage of SL was found to decrease with increasing size. For each of the two Luongo River samples, small specimens had dorsal fins roughly three percent of SL longer than large fish, but the data were highly variable. This basically agrees with Banister's (1973: Fig. 55) findings for *B. intermedius* and other species of large *Barbus*; as size increases, they have a negative exponential trend in dorsal spine length as a percentage of SL. Such negative allometry probably contributes to the wide range of dorsal fin height observations for various *radiatus* populations (Fig. 5) and may partially explain the short fins of the Kalomo Reservoir specimens.

A ratio of orbit diameter and interorbital width has been used to distinguish *aurantiacus* from *radiatus*. These same characters are noted for their allometric growth changes in a wide variety of

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fishes. Greenwood (1963:23) noted that the ratio of these characters seems to change with increasing size of *aurantiacus* but remains nearly constant in *radiatus*. The same pattern emerges if values for these two characters are plotted versus standard length for the two Luongo populations (Fig. 6). Slopes of the first principal axes fit through each bivariate scatter of points indicate that for the Lower Luongo population, growth rate of both characters relative to standard length is similar (i.e., the axes are nearly parallel). This contrasts with the Upper Luongo population where the two axes diverge with increasing size. Convergence of orbit-size axes for small specimens of the two populations combined with intersection of the interorbital axes points out a possible source of error in using these measurements to diagnose taxa.

If the same analysis is made using the conventional exponential model for allometric growth, fit of the axes through the scatter of points is only slightly improved. The exponential model indicates, however, that orbit and interorbital axes are nearly parallel for the Upper Luongo population
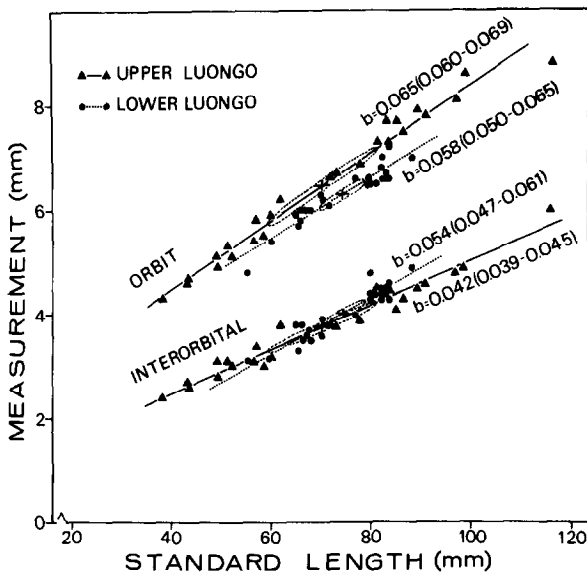
and converge with increasing size for the Lower Luongo population. Unfortunately, the lack of very small specimens for each population makes it difficult to resolve the actual growth pattern that gives rise to each morph of *radiatus*. Apparently, relative growth rates of various body parts during very early life are especially important in moderating the ultimate form of the fish (Barlow 1961).

Systematic revisions

The results indicate that there are not two discrete allopatric morphs of *radiatus*. Instead there is a populational mosaic of highly variable morphs. It is thus reasonable to place *aurantiacus* in the synonymy of *radiatus*. With the expanded data base now available (see below) it is also apparent that morphology of *profundus* is well outside the bounds of the most extreme morphs of *radiatus* discussed above; *profundus* should be elevated from subspecific rank.

Barbus radiatus Peters
Fig. 2b,c

Barbus radiatus Peters 1853:783 (the larger of two syntypes was designated lectotype by Greenwood 1963, the paralectotype was not identified).
Barbus doggetti Boulenger 1904:450.
Barbus bangwelensis Boulenger 1905:643–644.
Barbus aurantiacus Boulenger 1910:554 (lectotype designated by Greenwood 1962).
Barbus rogersi Boulenger 1911:180, Fig. 158 (lectotype designated by Greenwood 1962).
Beirabarbus palustris Herre 1936:100.
Beirabarbus okavangoensis Barnard 1941:470–471.
Barbus rubellus Crass 1960:431–433, Fig. 1 (paratypes polyspecific, see below).

Diagnosis

A species of *Barbus* with well developed sensory pitlines covering the head; it is thus classified in the subgenus *Enteromius* Cope 1869 (Greenwood 1970). This character alone separates *radiatus* from all other species of *Barbus* known from within its distribution range except *profundus* (Fig. 1). Diagnostic characters for separating *radiatus* from *profundus* are presented in Table 3. Among the eleven species now classified in *Enteromius* (nine in West Africa), *radiatus* is distinguished for the most part by its short but ever-present posterior barbels which were minute to at most 2.6% of SL for the specimens which I measured (n = 160). Greenwood

Fig. 6. Change in orbit diameter and interorbital width versus size of *radiatus* from allopatric populations in the Luongo River as indicated by slope (b and 95% confidence limits of b) of the first principal axis through each bivariate scatter of observations. The 95% confidence elipse for each bivariate mean (+) is also given. Statistical procedures are from Sokal & Rholf (1969: 526–532) with one change recommended by Ricker (1973: 415, footnote).

Table 3. Contrasting characteristics of *Barbus radiatus* and *B. profundus* (based on Greenwood 1970, and most of the material examined herein).

Character	radiatus	profundus
Barbels	usually 4 present	absent
Second pharyngeal tooth of primary row	always stouter and taller than other teeth	not enlarged
Circumpeduncular scale rows	always 12	mode 9, 8 to 11
Circumference scale rows	16 (17)	16 to 18
Ratio height:length of exposed surface on lateral line scale below dorsal fin origin	$\overline{X} = 2.68$, 2.50 to 2.78, 11 paratypes of *palustris*	$\overline{X} = 3.48$, 2.67 to 4.46, n = 23
Postweberian vertebrae	mode 28, 27 to 29 (30)	mode 30, 29 to 31
Interparietal fontanelle	usually closed at a size of 30 mm	often open to a size of 40 mm
Habitat in Lake Victoria	littoral zone and both ephemeral and permanent tributaries	deep water only, 18 to 65 m

(1962:197) reports an average of 2.3% of SL and a maximum of 5.6%. Six of the West African species of *Enteromius* have barbels. Of these, *ablabes* (Bleeker) 1863 is perhaps the most similar to *radiatus* but differs in having longer posterior barbels (5.7 to 8.9% SL, Hopson and Hopson 1965).

Comments

Five paratypes of *rubellus* were examined at the BMNH but were not included in the foregoing analysis because all had been dessicated and the series was polyspecific. One large specimen was referable to *radiatus* but a second specimen in the same lot (BMNH 1960.11.5:1–2; original NPB numbers missing) and three in another lot (BMNH 1960.11.5:3–5; formerly NPB 150/2,4,7) were tentatively identified as *B. annectens*. The large specimen contrasted noticeably with the others in having sensory pitlines readily visible on the head (absent in the others), much shorter barbels, longer snout, and a different gill raker morphology. The shortest snout which I observed for *radiatus* was 6.8% of SL (range 6.8 to 8.8, n = 209) and the long-

est barbel observed was 2.6% of SL. On the basis of these two characters, the holotype and half of the paratypes of *rubellus* are referable to *radiatus* (Crass 1960; Table II, NPB 146/1–8) and the remaining paratypes (NPB 150/1–7) are some other species, perhaps *annectens*. *B. radiatus* typically have three relatively slender, pointed and spaced gill rakers on the lower limb of the anterior arch with two or three pad-like rakers below them. In contrast, *annectens* (AMPF 1265) and NPB 150/2,4,7 have about eight pad-like, contiguous gill rakers on the lower anterior arch. Dr. R. Jubb was kind enough to reexamine the holotype of *rubellus* and confirmed that it is *radiatus*.

Zoogeography

B. radiatus is reported here for the first time from the Lake Tanganyika drainage where it was collected in the Malagarasi River, Tanzania. The species has also been collected near Maun, Botswana, where it is common (K. Banister, letter of 4 June 1976). It seems likely that future explorations will bring new range extensions.

When *profundus* was discovered, *radiatus* was known from Lake Victoria only by the type of *doggetti* (1904, precise locality unknown). Several years of intensive collecting by personnel of the East African Freshwater Fisheries Research Organization established that *radiatus* occur in larger, permanent tributaries to the lake but no new specimens were found in the lake proper or its ephemeral tributaries. It was thus suspected that the *doggetti* type came from a tributary and *profundus* was thought to be a lacustrine subspecies (Greenwood 1970).

In 1973, I spent a week with Mr. R. Scully who was then with USAID/EAFFRO in Mwanza, Tanzania. Intent on seeing some of the fascinating Lake Victoria cichlids, I baited a small hook with earthworm and began fishing. Much to my surprise, I caught a *Barbus radiatus*. Subsequently, Mr. Scully has sent me a single gravid female *radiatus* which he collected in a tributary to Speke Gulf that flows only during the heavy rains of March and April. These new records dispel prior concerns about the apparent absence of typical *radiatus* in the lake proper and support the arguments given herein for elevating *profundus*; but obviously, they do not demonstrate sympatry as there remains a 16 m depth segregation.

Barbus profundus Greenwood
Fig. 2a

Barbus radiatus profundus Greenwood 1970:1–13; illustrated pharyngeal teeth only, Fig. 1A.

Holotype: BMNH 1970.5.14:1,59 mm, 2°09′5″S, 32° 35′ 5″E, Sta.T267, depth 57 m, mud, Lake Victoria, trawl, P. Greenwood, 27–II–1970. Paratypes. — (All lot numbers are prefixed by BMNH 1970.5.14:) 2–4, (3)52–57 mm, same data as holotype; 6–8, (3)38–55 mm, 0° 50′ 0″S, 32° 35′ 0″E, Sta.U389, 60–61 m, mud; 10–12, (3)54–57 mm, 0° 38′ 5″S, 32° 30′ 0″E, Sta.U382, 52 m, mud; 18, 57 mm, 2° 12′ 5″S, 32° 45′ 5″E, Sta. 237, 50 m, hard mud; 40–42, (3) 54–58 mm, 1° 30′ 0″S, 32°23′5″E, Sta.T233, 62–64 m, mud; 43, 58 mm, 0° 02′ 0″S, 32° 27′ 0″E, Sta.220, 59–62 m, mud; 44–46, (3)54–60 mm, 1° 12′ 0″S, 32° 22′ 0″E, Sta.222, 54–57 m, clay; 80–83, (4)52–63 mm, 0° 45′ 0″S, 32° 38′0″E, Sta.U388, 56–57 m, mud; 97–98, (2)52–57 mm, 1° 32′ 0″S, 32° 17′ 5″E, Sta.T271, 56–58 m, clay; (one paratype not seen). All from Lake Victoria, trawl, P. Greenwood, 15 to 28–II–1970.

Diagnosis

A species of the subgenus *Enteromius*. No maxillary barbels, a mode of nine (8 to 11) circumpeduncular scale rows, and other characters (Table 3) readily distinguish *profundus* from *radiatus* (the only other *Enteromius* known from the Lake Victoria basin). In West Africa there are three known species of *Enteromius* which lack barbels. Of these, *aspilus* Boulenger 1907 has 12 circumpeduncular scale rows. Both *jae* Boulenger 1903 and *sylvaticus* Loiselle and Welcomme 1971 have the lateral line greatly reduced or absent in contrast to the complete lateral line pore series in *profundus*.

Comments

Circumpenduncular scale row count provided complete separation of *profundus* and *radiatus* when counted at the point of least peduncle depth. Greenwood reported a modal count of 10 rows and two *profundus* with 12 rows, but apparently his counts were made slightly anterior to mine (P. Greenwood, personal communication); the caudal peduncle tapers somewhat in *profundus*. Frequencies for 22 of the *profundus* types were as follows:

8 rows (3 fish including the holotype), 9(14), 10(3), 11(2). Circumference scale row counts are less diagnostic but almost half of the type specimens of *profundus* have more than 16 rows; this may be a useful supplementary character.

An important squamation character not mentioned in the original description of *profundus* is the extremely tall, narrow (columnar) lateral line scales. The ratio of height to length of exposed surface on a lateral line scale below the dorsal fin origin is a useful diagnostic character (Table 3). The *palustris* population was chosen to contrast with *profundus* because it is the most extreme in this character. Only one of 23 *profundus* fell within the range for *palustris*. The holotype of *doggetti* and a second specimen from Lake Victoria had an average ratio of 2.18, the type of *bangwelensis* had 2.25, and three *aurantiacus* types averaged 2.44.

The caudal fin of *profundus* seems to be more deeply forked than in *radiatus* but no attempt was made to quantify this character. Finally, color pattern may prove to be a useful character for separating specimens preserved in formalin. The only specimen of *radiatus* definitely known to come from Lake Victoria proper (UMMZ 194962) was preserved in formalin and closely resembles specimens from the Lower Luongo River (Fig. 2b). There are discrete longitudinal rows of dark brown spots which contrast noticeably with the diffuse color pattern of *profundus* (Fig. 2a).

Speculation

Rejection of the premise that there are two subspecies of *radiatus* invites a new explanation for the morphological variation that has caused so much confusion. Given the present lacunae of knowledge on the biology of African *Barbus* and on the physical environment where they live, an explanation is not yet possible. Yet, if an understanding of such variation can be useful for resolution of systematic problems with other species of *Barbus*, then an explanation should ultimately be sought and a working hypothesis might now be useful. It is hypothesized that the populational mosaic of morphology in *radiatus* reflects adaptive ecotypic responses to water temperature and current velocity. The hypothesis is not new as it has been evoked and tested numerous times for a variety of fishes, including cyprinids, but so far has not been

suggested as applicable to *Barbus*. Supporting evidence for such responses in *Barbus* is indirect but certainly warrants consideration.

Longitudinal meristic counts and head proportions such as orbit diameter contribute to variation in *radiatus*. These characters have been shown in other fishes to respond to water temperature during some critical embryological stage. Some of the first observations of temperature effects on morphology and meristics of fish were made over fifty years ago (Jordan 1891; Hubbs 1922, 1926). The numerous studies made since then have been reviewed by Barlow (1961) and Fowler (1970). A generalization that has developed from prior studies is that populations in relatively colder water attain a larger size, have higher longitudinal meristic counts, and may also have relatively larger or smaller orbit than their warm-water conspecifics. A genetic component has sometimes been shown to be associated with what otherwise seems to be an environmental morphocline (Fowler 1970). However, laboratory studies have shown that the relationship of temperature to vertebral number is often a U-shaped function for a group of siblings with lowest vertebral number occurring at some intermediate temperature. Thus, minor genetic changes may lead to adaptation of a population to local conditions and year to year environmental fluctuations at a given locality may also contribute to meristic and morphometric variation.

Body depth, caudal peduncle length, and dorsal fin height also accounted for much of the variation between *radiatus* populations. It has been documented that fast-water populations of a given species tend to have a more attenuate body with slender caudal peduncle and relatively longer fins than their quiet-water conspecifics (Hubbs 1941, Smith 1966). Such morphological adaptations to fast-moving water are likely to be genetically determined but could also be influenced by factors such as temperature (i.e., through an increase in number of vertebrae).

By comparing published accounts for other fishes to observations on *radiatus* it can be inferred that *aurantiacus*-like morphs inhabit relatively cooler and perhaps also faster-flowing waters. Conversely, *radiatus*-like morphs may develop in warmer water and live in quieter water. Relative temperature stability (or climatic equability) of various habitats may also affect morphology (Smith & Koehn 1971). Both laboratory and field studies are needed to test the above hypothesis

and thereby, to determine the importance of ecotypic and genetic factors as contributors to geographic variation in *radiatus*.

The Upper Luongo and *palustris* populations represent the most extreme morphs of *radiatus* known (Fig. 4; Table 2). *B. palustris* was collected on a floodplain near sea level where the coast is warmed by the Moçambique Current, a southward deflection of the warm South Equatorial Current of the Indian Ocean (Jubb 1967). Both mean annual temperature and rainfall are relatively high near Beira.

In contrast, the Upper Luongo River is located on the central African plateau +1000 m above sea level and its *radiatus* population is isolated above Musonde Falls, an apparent barrier to upstream migration of several fish species. Thus confined, they may be obliged to reside in cooler, faster-flowing water than is usual for the species. There is a small reservoir on the Luongo just above Musonde Falls and this may warm the stream flow before it reaches *radiatus* in the Lower Luongo. Unfortunately there are no water temperature data for the Luongo River; I can only speculate.

Individuals of the Upper Luongo population (Fig. 2c) attain a larger size than those of any other population, have high longitudinal meristic counts, have attenuate body with caudal peduncle longer than can be accounted for by the presence of an extra vertebra, and have the first principal dorsal fin ray more strongly ossified than in any other population (i.e., movable segments only near the tip). A good case might be made for considering the Upper Luongo population to be a subspecies or perhaps even a distinct species as it seems to be isolated and a large majority of individuals can be discriminated from their nearest neighbors in the Lower Luongo.

It would be harder to make a case for specific recognition of the *palustris* population as it may routinely mix with adjacent coastal river populations via floodplains during exceptionally wet years (Farquharson 1962). These include the Lower Zambezi to the north with the type locality of *B. radiatus* and the Pongolo system with *rubellus* to the south (Fig. 3). Yet, as noted above, *palustris* deviates from the norm in an almost equal and opposite way from the Upper Luongo population. The morphology of *palustris* and high meristic counts of the Lake Nabugabu population (Table 2) argue against naming the Upper Luongo population at this time, especially since it is dis-

tinguished entirely by characters known to be strongly influenced by environmental factors (Alizarin preparations of Upper and Lower Luongo specimens were compared; except for vertebral number, they agreed in every detail).

Tilapia baloni is also isolated in the Upper Luongo River and it differs morphologically from its allopatric sister species, *T. sparrmanii*, in many of the same ways that Upper Luongo *radiatus* are distinguished (Trewavas & Stewart 1975). However, *baloni* has a distinctive color pattern and other characters which indicate that important genetic changes are involved. The possibility remains that Upper Luongo *radiatus* are equally different genetically. There is good evidence to indicate that Upper Luongo fishes have had a long history of isolation but the details are beyond the scope of this paper. The evidence includes unique morphology of various species populations living there as well as complete exclusion of several genera by Musonde Falls. Suffice it to say that further studies on Upper Luongo fishes will be worthwhile.

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