Serranochromis altus, a New Species of Piscivorous Cichlid (Teleostei: Perciformes) from the Upper Zambezi River

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A new cichlid species, Serranochromis altus, from the Upper Zambezi River is described. It is sympatric with its deep-bodied sister species, S. angusticeps, within the Upper Zambezi and Kafue River drainages. Both immatures and adults of the new species can be distinguished from S. angusticeps on the basis of morphometric characters and color pattern, including the absence of distinct speckles on the face and chest and eye stripes that are diagnostic of the latter. Serranochromis altus has a shorter snout, larger eyes, wider head features, and longer pectoral fins than S. angusticeps of similar size. Both sexes of the new species mature at a larger size and appear to attain larger maximum sizes than S. angusticeps. During the low water period, S. altus inhabits deep regions of the main Zambezi River channel and feeds primarily on nocturnal mormyrid and schilbeid fishes. In contrast, S. angusticeps dwells in densely vegetated regions of quiet backwaters and lagoons of the Barotse floodplain where it ambushes small characids and cyprinids.

THE cichlid genus Serranochromis Regan contains nine nominal species from southern and central Africa that are distinguished from other cichlids by their large mouth size and piscivorous feeding habits. Trewavas (1964) revised the genus and provided a key and range maps. Following Bell-Cross's (1975) revision of south/central African Haplochromis species, Greenwood (1979) placed an additional eight species of smaller-mouthed, invertebrate-feeding cichlids within his Serranochromis subgenus Sargochromis. Serranochromis diversity is highest within the Upper Zambezi River drainage (including Okavango, Cuando/Chobe, and Kafue River drainages) with 10 species (Greenwood, 1979; Skelton et al., 1985), five of which are members of the piscivorous subgenus Serranochromis. The Chambeshi/Luapula River drainage (i.e., Zambian Congo system including lakes Mweru and Bangweulu) contains six nominal species, four from the subgenus Serranochromis that are shared with the Upper Zambezi, plus the endemics Serranochromis (S.) stappersi (Trewavas, 1964) and Serranochromis (Sar.) mellandi (Boulenger, 1905). In this paper, we describe a new species, Serranochromis (Serranochromis) altus, from the Upper Zambezi and Kafue Rivers. The new species is most similar to S. angusticeps (Boulenger, 1907), the species with which it seems to have been confused in earlier collections. Distinct ecological differences between these morphologically similar, sympatric species are documented.

Methods

Unless noted otherwise, determinations of morphological and meristic characters follow the criteria in Hubbs and Lagler (1958). Linear measurements less than 170 mm were made with vernier calipers to the nearest 0.1 mm, or with a transparent ruler to the nearest 1 mm if greater than 170 mm. All fish lengths are standard length (SL). Head length was measured from the tip of the snout to the most posterior extremity of the fleshy opercular flap; preorbital head depth was measured as a vertical line running through the anterior orbit margin from the dorsal midline to the ventral midline of the head; lower jaw length was the straight line distance between the anterior tip of the dentary bone to the posterior edge of the articular bone as estimated from external features; maxillary labial height was the maximum depth of the dermal covering of the posterolateral edge of the maxilla; width of the dentary tooth pad was the maximum distance between the lateral margins of the tooth-bearing surface with the jaws slightly open and without lateral distention of the lower jaw; internostril width was the straight line distance between the nostrils with jaws closed; body depth was the vertical distance from the dorsal midline at the dorsal-fin origin to the ventral midline. Principal component analysis was performed on 20 S. altus and 18 S. angusticeps from the Upper Zambezi with 21 log₁₀transformed morphometric characters from the



Fig. 1. Recently caught paratypes of Serranochromis altus (USNM 30843): 372 mm male in breeding condition above, 296 mm gravid female below.

covariance matrix and 10 meristic characters from the correlation matrix.

Patterns of pigmentation of freshly captured specimens were noted and photographed in the field. Allozyme variation among gene products of 13 presumptive loci was evaluated for muscle and liver tissues from four *S. altus* (Fig. 1) and four *S. angusticeps* from the central Barotse floodplain region (15°26'S, 23°06'E). Electrophoretic procedures followed Murphy et al. (1990). Museum acronyms follow Leviton et al. (1985).

Serranochromis altus n. sp. Fig. 1

Holotype.—Male, USNM 308402, 301 mm, taken with hook and line by K. O. Winemiller along the west bank of the Zambezi River west of Mongu, Western Province, Zambia, 15°15'56"S, 22°55'36"E, 9 Sept. 1989. Winemiller; TNHC 17445,1 (96.4 mm), Zambezi River west Mongu, 25 Nov. 1989, K. O. Winemiller and L. C. Kelso-Winemiller; BMNH 1990.6.12:1-2, 2 (144.0, 151.0 mm), Mukakani, 1 Dec. 1989. K. O. Winemiller and L. C. Kelso-Winemiller. Kafue River: TNHC 17444, 1 (80.8 mm), junction Lufupa and Kafue Rivers, 30 Sept. 1989, K. O. Winemiller and L. C. Kelso-Winemiller.

Other material.—Twenty-one additional specimens collected from the central region of the Upper Zambezi between May and Dec. 1989 were not designated as paratypes. Ninety-five specimens taken from the commercial fishery at Mukakani between August and Oct. 1989 were examined for the ecological study.

Diagnosis .- A species of Serranochromis that greatly resembles S. angusticeps in having a deep body (depth at dorsal origin 2.3-3.1 in SL), steep, concave profile in the forehead region, and highly protrusible jaws; but can be distinguished from S. angusticeps by the following characters: no small red, rust, or brown spots or wormy patterns on head, jaws, chest or ventrum (distinct brown or gray spots present even in old preserved specimens of S. angusticeps); no brown or red spots on pelvic fins of adults (Fig. 2); no eye stripes on snout, cheek, opercle or forehead; lateral body stripe weakly developed in immatures less than 120 mm, completely absent in larger specimens; no spot on scales near base of pectoral fin (spot usually distinct in S. angusticeps); ripe and breeding males with dark olive/green rather than light olive/yellow head; male caudal fin with numerous small, dark red,

Paratypes.—Upper Zambezi, Barotse floodplain: TNHC 17457, 1 (237.5 mm), Namayula, 6 Sept. 1989, K. O. Winemiller; USNM 308404, 5 (94.7–117.6 mm), Luanginga River, Kalabo, 12 Oct. 1989, K. O. Winemiller, and L. C. Kelso-Winemiller, TNHC 17458, 1 (287 mm), Lisina, 9 Nov. 1989, K. O. Winemiller, TNHC 17447, 2 (121.0, 127.7 mm) Malakata, 19 Aug. 1989. C. Simusiko; USNM 30843, 2 (296, 372 mm), Mukakani 10 Nov. 1989, K. O. Winemiller and L. C. Kelso-Winemiller; AMNH 90201, 2 (179.5, 232.0 mm), Mukakani, 21 Nov. 1989, K. O. Winemiller; and L. C. Kelso-Winemiller; AMNH 99712, 2 (259, 299 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller and L. C. Kelso-Winemiller; MNH 99712, 2 (259, 299 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller and L. C. Kelso-Winemiller; MNH 99712, 2 (259, 299 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller and L. C. Kelso-Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller and L. C. Kelso-Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller and L. C. Kelso-Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), Mukakani, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), MUKANI, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), MUKANI, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), MUKANI, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), MUKANI, 24 Nov. 1989, K. O. Winemiller; MNH 99712, 2 (259, 290 mm), MUKANI, 24 Nov. 1989, K. O. WINE MUKANI, 24 Nov. 1989, K. O. WIN



Fig. 2. Recently caught female Serranochromis angusticeps (262 mm, top) and female S. altus (262 mm, bottom), both taken from Mukakani region on 10 Oct. 1989. Complete absence of small distinct spots on head, chest, and ventral regions is apparent in S. altus. Spotting on sides and dorsum of S. angusticeps is dark and distinct, whereas lateral spotting on S. altus is diffuse and faint.

purple, and indigo spots on a light pink and silver/indigo background (male S. angusticeps with black spots on dark grey or blue/grey); caudal fin and soft dorsal fin of immatures and adult females red or pink, dorsal fin with numerous dark spots (caudal and dorsal fins dark grey with profuse black spots in S. angusticeps); only few irregular spots near base of caudal fins of females and immatures; posterior edge of operculum with a broad, shallow notch (sometimes two shallow notches adjoined) resulting in concave vertical profile (straight or convex vertical profile in S. angusticeps); width of bony interorbital 5.3-5.9 in head length (HL) for individuals 80-130 mm, 4.3-5.3 for individuals 130-300 mm, 3.8-4.3 for individuals larger than 300 mm (Fig. 3); dentary tooth pad broad (Figs. 3, 4), maximum width 5.0-6.7 in HL for individuals 80-150 mm, 4.3-5.5 for individuals larger than 150 mm; 4-6 rows of short unicuspid teeth in anterior portion of premaxilla reducing to 2-4 rows posteriorly (in S. angusticeps, premaxillary tooth rows decline from 3 anteriorly to a single row posteriorly); 4-6 rows of short unicuspid teeth in anterior portion of dentary reducing to 3-4 posteriorly (in *S. angusticeps*, dentary tooth rows decline from 3 anteriorly to a single row posteriorly); ratio of median length to maximum width of tooth surface of lower pharyngeal bone 0.85 (0.75 in *S. angusticeps*).

Description.---Morphometric characters are given in Table 1; meristic characters given in Table 2. Figure 1 shows body form, pigmentation patterns, and fin shapes and positions for male and female; lower fish in Figure 5 illustrates the same for an immature. Body deep and laterally compressed, region of maximum depth usually near origin of dorsal fin or pelvic fins, region of maximum width at or just posterior to opercula. Head length 2.63-2.86 in SL for individuals 80-200 mm, 2.86-3.23 for individuals larger than 200 mm; dorsal profile of head concave, slopes at 30-35° from horizontal at snout tip. Mouth large and jaws highly protrusible; closed jaws angle upward, mandible angles 45-50° from horizontal from mouth corner; posterior edge of lower jaw not reaching anterior margin of eye; lower jaw more massive than



Fig. 3. Interspecific divergence in allometry of interorbit width, dentary tooth pad width, orbit length, and longest pectoral ray plotted based on 20 types of *Serranochromis altus* and 18 *S. angusticeps* (all characters except pectoral ray length are expressed as ratios of head length). Correlation of interorbit width data with linear regression is $r^2 = 0.73$, *S. altus*; $r^2 = 0.65$, *S. angusticeps*. Correlation of relative orbit length data with logistic regression is $r^2 = 0.88$, *S. altus*; $r^2 = 0.88$, *S. angusticeps*. Correlation of relative dentary pad width data with linear regression is $r^2 = 0.57$, *S. altus*; $r^2 = 0.62$, *S. angusticeps*.

upper. Premaxillary pedicles long, measuring 0.45-0.46 HL for individuals 80-150 mm, 0.42-0.44 HL for individuals >150 mm. Upper and lower jaw tooth pads broad (Fig. 4), teeth short, unicuspid and deeply embedded in dermal tissue; anterior teeth near midline longer than lateral teeth; 52-70 teeth in outer series of upper jaw; 50-58 teeth in outer series of lower jaw. Cheek deep, 2.7 in HL (2.2-3.4) with 6-8 scales in transverse series. Opercle rectangular, deeper than wide; small specimens with small notch in the middle of the posterior border; large specimens with a shallow, broad notch or sometimes two shallow notches adjoined, producing concave vertical profile of the posterior opercle. Gill rakers on posterior portion of anterior arch 11-14, usually 13.

Dorsal-fin origin approximately even with pectoral-fin origin, but anterior to origin of pelvic fins; dorsal-fin rays XV-XVI,15-18, usually XV,16 (usually XV,17 in *S. angusticeps*); pectoral-fin rays 13-15, usually 14 (usually 13 in *S. angusticeps*). Caudal peduncle longer than deep in individuals less than 120 mm; peduncle length approximately equal to or shorter than depth in individuals greater than 120 mm. Scales weakly ctenoid, with some slightly denticulate. Tips of folded pelvic fins not reaching anal origin, pelvic fins longer in mature males than females and immatures. Pectoral fin rounded, height approximately equal to length; length of longest pectoral ray 4.8 in SL (4.5-5.8). Caudal fin rounded; length 4.0 in SL (3.7-4.3); series of 3-5 scales covering base. Dorsal and anal fins of adults terminate posteriorly in an acute angle, rounded in immatures. Relative lengths of dorsal and anal rays approximately equal in the two sexes among immature size classes; relative lengths of dorsal and anal rays longer in mature males (dorsal 0.23-0.28 SL, anal 0.19-0.24 SL, n = 4) than mature females (dorsal 0.21-0.23) SL, anal 0.18-0.21 SL, n = 4).

Color in life.—Body very light silver/grey or olive/grey, dorsum darker olive/grey, ventrum and chest white; 5–9 faint, diffuse grey/brown vertical bars on flanks of immatures, sometimes appear as broad faint bars on flanks of freshly captured adults; faint grey/brown or grey/olive pigmentation along the anterior edges of



Fig. 4. Premaxillary and dentary tooth pads of *Serranochromis altus* (paratype USNM 30843, 372 mm, left) and *S. angusticeps* (280 mm, right) from Mukakani region. Maximum widths of each tooth pad are given in mm.

flank scales, flank scale pigments much darker in ripe and breeding adults resulting in crosshatched or checkered appearance; head plain but darker on dorsum; no distinct eye streaks or spots on head; sometimes faint grey/brown or grey/olive blotches on cheek and operculum; head and chest of ripe and breeding adults green/olive, much darker in males; indistinct black spot on opercular flap; iris gold/brown, orange in small immatures; pectoral fin transparent without spots; no spot on scales at base of pectoral fin; caudal fin pink or red in immatures and females, only a few irregular spots near caudal peduncle; caudal fin of males with small dark red, purple, or indigo spots on a pink and light silver/indigo background; distal half of soft dorsal and anal fins of adults with small red, purple or indigo spots on silver/indigo and pink background; dorsal and caudal fins of adults with thin orange or yellow/orange band along distal margin; anal fin of adults with yellow band along distal margin, yellow coloration sometimes fading proximally midway into fin; anal

fin of adults light blue near base fading to silver/indigo distally; anal fin of both sexes with 30-40 large pink or pink/orange ovate spots, each ringed with a transparent, white ocellus ("egg dummies"); ocelli of ripe and breeding fishes entirely or partly surrounded by a dark indigo ring that fades into lighter background coloration; pelvic fins yellow/orange and unspotted in females and unripe males, black in ripe and breeding males.

Color in alcohol.—Background color fading to light grey, tan, or white; pigmentation at base of flank scales grey or brown; fin spots dark grey or brown; opercular spot black; background color of fins diffuse, light grey; distal border of dorsal, caudal, and anal fins of adults with pale band; ocelli around anal-fin spots very pale in mature fishes, difficult to see in some preserved specimens, absent in immatures; mouth and cheeks with diffuse, light-grey patchy pigmentation but no spots or eye-stripe complex (head, chest, and ventrum spots of *S. angusticeps* appear

Lateral line scales	37 (2)	38* (10)	39	(8)	
Upper lateral line series	22 (6)	23* (9)	24	(5)	
Lower lateral line series	16 (7)	17* (11)	18	(2)	
Scale rows above lateral line	7 (3)	8* (9)	9	(8)	
Scale rows below lateral line	9 (6)	10* (8)	11	(6)	
Dorsal spines	XV* (16)	XVI (4)		• •	
Dorsal rays	15 (3)	16* (10)	17	(6)	18(1)
Anal spines	III* (20)			• •	.,
Anal rays	11 (4)	12* (14)	13	(2)	
Pectoral rays	13 (3)	14* (16)	15	(1)	
Gill rakers of lower arch	11 (2)	12 (5)	13*	• (11)	14 (2)
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TABLE 2. FREQUENCY DISTRIBUTIONS FOR MERISTIC CHARACTERS IN Serranochromis altus.

* Counts for the holotype (USNM 308402).

vango drainage in Botswana and Namibia that lack distinct spots on the head and possibly correspond to the new species.

Comparisons.-Figure 6 illustrates clearly the greater relative widths of head features in S. altus compared with S. angusticeps. Multivariate PCA performed on morphometric characteristics showed complete separation of S. altus and S. angusticeps on a plot of PC axes 2 and 3 (Fig. 7). Because similar SL ranges were examined (S. altus, 80.8-372 mm; S. angusticeps, 74.9-280 mm) the first PC axis, a body length discriminator, revealed few interspecific differences. Morphometric characters with highest eigenvalues for PC 2 were snout length (0.50), interorbital width (-0.37), lower-jaw tooth-pad width (-0.36), orbit diameter (-0.34), internostril width (-0.27), and pectoral-fin length (-0.25). PCA using meristic characters revealed large interspecific overlap, although dorsal fin, lateral line, and gillraker counts contributed to a small degree of separation on PC 1 and 2. Ranges of meristic characters of S. altus listed in Table 2 were the same for S. angusticeps.

Allozyme data reveal two fixed differences between S. altus and S. angusticeps among 26 comparisons (2 tissues, 18 presumptive loci). Complete allelic differentiation was observed for phosphoglucomutase (Pgm) in skeletal muscle and mannosephosphate isomerase (Mpi) in liver.

Ecology.—We captured 15 adult *S. altus* from deep shoreline regions of the main river channel during the low water period of the Barotse floodplain of the Upper Zambezi River. All 51 were located near dense aquatic vegetation close to swift current. Four adult *S. altus* were cap-

tured near dense vegetation in lagoons adjoining the main river channel. In contrast, 23 of 28 S. angusticeps were captured from lagoons and quiet backwaters, either within or near aquatic vegetation. Serranochromis robustus (Günther) was the only other member of the subgenus commonly found inhabiting swift regions of the main channel of the Zambezi River, usually near the substrate and not in close proximity to dense vegetation (Winemiller, 1991).

Examination of gonads from specimens obtained from the commercial floodplain fishery indicated that most S. altus had attained spawning condition by October 1989, and breeding was initiated just prior to the annual rains in December and January. Data are not available to determine whether multiple spawnings occur during the four- to five-month flood period on the Barotse plain. Based on the condition of gonads from 56 individuals taken during Oct.-Dec. 1989, female S. altus mature at approximately 250 mm and males at approximately 300 mm. Based on fishes collected during the same period from the same region, we estimated female S. angusticeps maturation at 175-200 mm (n = 64) and male maturation at 250 mm (n =63). The maximum size recorded for S. altus females was 374 mm, and 410 mm for males. The largest female S. angusticeps was 318 mm and the largest male was 380 mm. Serranochromis altus is assumed to mouth brood, as do all other members of the genus that have been investigated. Ocellated spots ("egg dummies") on the anal fin and relatively low clutch sizes for a fish of this size support this contention. Seven S. altus females examined during November (225-304 mm) averaged 920 mature oocytes (range 394-1454), whereas 20 S. angusti-



Fig. 5. Recently preserved, immature specimens of Serranochromis angusticeps (95.3 mm, TNHC 17449, above) and S. altus (94.7 mm, paratype USNM 308404, below), both taken from the Luanginga River at Kalabo on 12 Oct. 1989. Serranochromis angusticeps shows a more developed lateral stripe, eye-stripe complex, head and chest spotting, smaller eye, and longer snout in contrast with S. altus.



Fig. 6. Dorsal view of head of male Serranochromis altus (409 mm, right) and male S. angusticeps (363 mm, left), both taken from Mukakani region of central Barotse floodplain on 3 Oct. 1989.



Fig. 7. Separation of Serranochromis altus and S. angusticeps in a plot of principal components 2 and 3 based on the covariance matrix of 21 log-transformed morphometric characters. The two species showed nearly identical ranges of values on the first PC axis, a body length discriminator.

ceps (213–318 mm) averaged 627 oocytes (range 130–1058).

Examination of contents from 114 stomachs of S. altus from central floodplain showed it feeding primarily on nocturnal mormyrids and a schilbeid catfish (Table 3). Sympatric S. angusticeps fed mostly on small diurnal characids and cyprinids (Barbus spp.) during the same period (Table 3). Our gillnet capture data suggest that S. altus may be primarily a crepuscular or nocturnal forager. The only two S. altus captured with hook and line were taken just before dusk, whereas daytime angling along the shore of the primary Zambezi River channel yielded only S. robustus.

DISCUSSION

Trewavas (1964) recognized eight nominal species of predatory Serranochromis from southcentral Africa but only one Upper Zambezi species, S. angusticeps, with a deep, laterally compressed body, highly protrusible jaw apparatus, and steeply sloping, concave forehead profile. Trewavas considered S. angusticeps, S. stappersi, and S. spei a trio of allopatric sister species all having numerous close-set teeth, oblique mouth, and long premaxillary pedicles. Both S. stappersi

of Lake Mweru/lower Luapula River and S. spei of the upper Kasai River (eastern Zaire) have much shorter premaxillary pedicles and snouts than both S. angusticeps and S. altus. Trewavas also discussed the close affinities of S. stappersi with S. macrocephalus and S. longimanus, the latter two from Upper Zambezi drainages. In our view, S. altus and S. angusticeps represent sympatric sister species having very similar morphologies but major ecological differences. Numerous opportunities for allopatric speciation and subsequent dispersal and reunion of the two divergent forms would have existed during the dynamic geological and physiographic history of the Upper Zambezi region (summarized by Jubb, 1967; Balon, 1974; Bell-Cross and Minshull, 1988).

Earlier taxonomic and field studies appear to have confused S. altus as the male phenotype of S. angusticeps. Jubb (1961, 1967) described the speckle-faced phenotype as corresponding to females and immatures of S. angusticeps. Our examinations of hundreds of S angusticeps from the Upper Zambezi River of Zambia revealed that all males and females have distinct brown or red spots on the mouth, cheek, opercula, chest, and pelvic fins. Additionally, most, S. angusticeps specimens show at least some devel-

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	Serranoo	Serranchromis angusticeps	
Prey category	% Frequency	% Volume (ml)	% Frequency
Detritus/substrate			 Berning and Berning a Berning and Berning and Berning
Amphipoda (Crustacea)			
Ostracoda (Crustacea)			
Decapoda (Crustacea)			
Ephemeroptera (Insecta)			
Hippopotamyrus discorhynchus (Mormyridae)			
Marcusenius macrolepidotus (Mormyridae)			
Mormyrus lacerda (Mormyridae)			
Alestes lateralis (Characidae)			
Micralestes acutidens (Characidae)			
Barbus haasianus (Cyprinidae)			
Barbus paludinosus			
Barbus poechii			
Barbus puellus			
Schilbe mystus (Schilbeidae)			
Aplocheilichthys katangae (Cyprinodontidae)			
Pseudocrenilabrus philander (Cichlidae)			
Sargochromis codringtonii (Cichlidae)			
Tilapia sparrmanii (Cichlidae)			
Ctenopoma sp. (Anabantidae)			
Unidentified fish			
Percent empty stomachs	77	.2	

 TABLE 3. GUT CONTENTS OF UPPER ZAMBEZI Serranochromis altus (n EXAMINED = 114) AND Serranochromis angusticeps (n EXAMINED = 238).

opment of the eye-stripe complex. In contrast, neither males nor females of S. altus showed either facial spotting or eye stripes. Jubb's (1967) figure 201 could correspond to the phenotype of S. altus, whereas his plates 43 and 44 (reproduced by Bell-Cross and Minshull, 1988) illustrate fairly accurately the typical coloration pattern of both male and female S. angusticeps. Boulenger's (1911) plate XLII (reproduced by Trewavas, 1969) accurately represents pigmentation patterns of immatures (listed as female) and adults of both sexes (listed as male) in S. angusticeps. Juvenile S. altus and S. angusticeps can be quickly separated by pigmentation pattern alone (Fig. 5).

Boulenger's (1907) original description of Paratilapia angusticeps includes the distinctive character of a very strongly compressed head (head depth 2.6-3 times in total length). Trewavas (1964) discovered six specimens of S. macrocephalus in the jar with the six specimens she designated as the lectotype and five paralectotypes of S. angusticeps. The types of S. angusticeps were collected by Ansorge at Mossamedes, Angola (exact drainage undetermined, but according to Bell-Cross and Minshull [1988], it probably corresponds to the Cunene drainage where the species is known to occur). Trewavas (1964) considered Castelnau's (1861) Chromys levaillantii a probable senior synonym of S. angusticeps. Because the type of C. levaillantii is lost and the name had not been used until 1963 in a brief amendment sheet for Jubb (1961), she designated it a nomen oblitum. The name could not have applied to S. altus, because Castelnau (1861) clearly identified red spotting on the head and body in the original description.

Descriptions associated with junior synonyms of S. angusticeps listed by Trewavas (1964) clearly identify either eye stripes or red spotting on the mouth, cheek, and opercle in this species. Boulenger's (1908) Paratilapia kafuensis (later placed in synonymy of P. angusticeps by Boulenger) was based on a single Kafue River specimen having "a dark oblique band from the eye to the maxillary," a character present in S. angusticeps but never present in S. altus. Ricardo-Bertram (1943) attempted to resurrect S. kafuensis, but her description includes "large numbers of small red spots on the under part of the head," a feature diagnostic for S. angusticeps but not present in S. altus.

According to Greenwood (1979), the anal-fin spots of Serranochromis species are nonocellate and, for some species, differ little from the spots on other medial fins. The putative Serranochromis condition contrasts with the distinct eggdummies on anal fins of Haplochromis species. While expressing concern for a paucity of fresh material for examination of pigment patterns, Greenwood suggested that distinct ocellation and reductions in the number of anal-fin spots might constitute a synapomorphy in haplochromine cichlids. Our examinations of hundreds of freshly caught Serranochromis, representing seven common Upper Zambezi species (S. thumbergi and S. longimanus excluded), identified distinct ocelli around the anal-fin spots of all large adults in the piscivorous subgenus Serranochromis. Transparent white ocelli were generally absent in smaller size classes of most species. Ocellated anal-fin spots showed greatest contrast with the dark background coloration of the fin among prespawning male S. altus. Anal-fin ocelli are discernable to varying degrees in large, preserved specimens of S. altus and S. angusticeps (SL > 230 mm). We suspect that few large, sexually mature Serranochromis specimens have been deposited in museums. In addition, Greenwood (1979) cited a range of two to three tooth rows in the anterior region of both upper and lower jaws in the genus Serranochromis. In all species of Serranochromis that we have examined, the number of jaw tooth rows tends to increase with size. In agreement with Greenwood's generic diagnosis, the largest S. angusticeps we examined (280 mm) had three anterior tooth rows (reducing to a single outer row posteriorly). In contrast, large S. altus (SL > 230) had from three to six rows anteriorly with a gradual reduction to two to three rows posteriorly.

Our ecological data indicate that S. altus is primarily a channel dweller, whereas S. angusticeps inhabits vegetated lagoons and shallow backwaters of the Barotse floodplain. Our data also suggest that S. altus mature at larger sizes and attain larger maximum sizes than S. angusticeps. The maximum size of 2.5 kg reported for S. angusticeps from the Upper Zambezi sport fishery (Jackson, 1961; Bell-Cross and Minshull, 1988) probably corresponds to S. altus. Bell-Cross and Minshull (1988) suggested that S. angusticeps attains a larger size in the Upper Zambezi than in neighboring drainages, which suggests that S. altus might be very rare in the Okavango system. P. H. Skelton (pers. comm.) reported that speckle-faced S. angusticeps far outnumber nonspotted forms (S. cf. altus) in the AMG. We await specimens to confirm identification of the latter as the new species.

COMPARATIVE MATERIAL EXAMINED

Serranochromis angusticeps, Fisheries Department collection, Chilanga, Zambia: Kafue flats 185, 240, 201, 205 mm; Kafue/Mulungushi Dam 270 mm; Kafue/Lake Kashiba 231 mm; Kafue/Chunga Lagoon 195.5, 198 mm; Kafue/Kakoma Dam 197 mm; Kafue/Namwala 97.5, 68.5; Kafue/Chianu Lagoon 55.0 mm; Chambeshi/Mbesuma 200 mm; Lake Bangweulu/Kaoma Point 189; Lake Tanganyika/Chira 307 mm. Upper Zambezi, Barotse floodplain: TNHC 17451, 1 (130.5), Kama, 28 June 1989; TNHC 17481, 1 (253), Leyolelo, 10 July 1989; TNHC 17448, 2 (126.6, 132.7), Malakata, 19 Aug. 1989; TNHC 17474, 3 (137.2-236), Namayula, 4 Sept. 1989; TNHC 17447, 5 (74.9-124.7), Luanginga River, Kalabo, 12 Oct. 1989; TNHC 17478, 1 (230.5), Lisina, 9 Nov. 1989; TNHC 17454, 2 (198.1-233), Mukakani, 21 Nov. 1989; TNHC 17446, 1 (103.2), Zambezi River west Mongu, 25 Nov.

Acknowledgments

We thank E. Muyanga, P. H. Skelton, V. G. Springer, and D. J. Stewart for contributing literature and information concerning Serranochromis. We are also grateful to D. M. Hillis for the use of his laboratory facilities for the allozyme analysis and R. De Sa and P. Chippindale for their technical assistance. We thank the government of Zambia, especially the Member of Central Committee for Western Province, for permission to work in Western Province, and members of the Fisheries Department of Zambia for their participation in field work, especially staff in Western Province: G. Milindi, J. Masinja, Sinda, M. Nuambe, P. Mayonde, Nsangu, Mwiba, H. Moanga, and Zimba. Missionary Oblates International of Zambia and the Mongu Nutrition Center provided many crucial forms of logistical support in Western Province. We are forever indebted to W. Ritter, J. Ritter, and M. Zbylski for their numerous contributions to our work and welfare. W. Ritter, T. Ulvolden, and G. Widmaier assisted in several of the Barotse field collections. T. Dowling, C. Bell, L. Bell, M. McCallie, L. Dean, J. Dean, and S. Mee of the U.S. Embassy in Lusaka provided housing, food, and varied forms of support during our stay in Zambia. We are grateful to all of them. Helpful comments on an earlier draft of the report were provided by F. Pezold, D. Stewart, and P. Skelton.

Funding for field research was furnished by the United States Center for International Exchange of Scholars and the United States Information Service in the form of a Fulbright Research Grant to the first author. The Texas Memorial Museum provided funds for shipping and curation of Zambezi specimens.

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