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EVIDENCE OF HYBRIDIZATION BETWEEN *CYNOTILAPIA AFRA* AND *PSEUDOTROPHEUS ZEBRA* (TELEOSTEI: CICHLIDAE) FOLLOWING AN INTRALACUSTRINE TRANSLOCATION IN LAKE MALAWI.—The unusually diverse cichlid species flocks associated with the African Great Lakes represent one of the most exciting and challenging evolutionary phenomena known to biologists. Many mechanisms responsible for their evolutionary success have been proposed, including interspecific hybridization (Crapon de Caprona, 1986), although natural hybridization within the haplochromines has never been documented. Recent surveys conducted in 1991 and 1992, however, yielded nine specimens of a putative intergeneric hybrid between *Cynotilapia afra* (Günther), a species that was translocated from the northern part of the lake approximately 20 years ago (Ribbink et al., 1983), and *Pseudotropheus zebra* (Boulenger), a similarly colored species native to Thumbi West Island (14°05'S; 34°49'E) in southern Lake Malawi. These two species are naturally sympatric in other locations throughout the northern region of the lake; yet Thumbi West Island is the only site where we have found specimens representing possible hybridization. The purposes of this paper are to provide evidence for occurrence of haplochromine hybridization in Lake Malawi and to discuss the impact of intralacustrine translocations on the potential for locally endemic fauna to hybridize.

Adult fishes were collected by chase into a monofilament net (7 m × 1 m × 1.5 cm) while SCUBA diving. All specimens were collected in 1991 and 1992 from Mitande Rocks, a rocky reef adjacent to Thumbi West Island. As indicated below, *P. zebra* and *C. afra* are similarly colored at Mitande Rocks.

Cynotilapia afra.—Males are light blue along the posterior half of the lateral side, the anterior region is dark blue with seven black vertical bars, and the ventral region is black. Although the source of *C. afra* at Mitande Rocks is unknown, the color pattern of the introduced form most closely resembles that of *C. cf afra* from Mara Rocks, south of Usisya (Konings, 1990: 350). Color patterns follow: head light blue with one dark interorbital bar and infraorbital region and gular black; dorsal fin with proximal black band, white marginal band, faint orange lappets; caudal fin light blue with a brown-orange edge; anal fin blue-gray. The first two rays of the pectoral fins are black, the leading edges of the fins are blue, and the remainder of the fin is clear.

Females are dark blue laterally with six faint vertical bars. Other color patterns follow: head blue-green with one dark interorbital bar; gular region white; dorsal fin dusky gray with brown lappets; caudal fin light blue with a brown-orange edge; anal fin blue-gray. The first two rays of the pectoral fins are black, the leading edges of the fins are blue, and the remainder of the fin is clear.

Pseudotropheus zebra.—Males are blue laterally, with five to six dark vertical bars along the anterior two-thirds and very faint or no bars present on posterior one-third (Konings, 1990:461). Additional color patterns include head light blue with one dark interorbital bar; infraorbital region and gular blue-gray; dorsal fin light blue-gray with orange lappets on some rays; caudal and anal fins light blue; anal fin with three yellow-orange ocelli; pectoral fins gray and pelvic fins blue-black with white leading edges.

Females are gray-black laterally with five to six vertical bars; head gray-black; dorsal fin blue with a light blue marginal band and brown lappets. The anterior portion of the caudal fin is gray-black, and the posterior third is transparent gray, with blue markings and brown lappets. The proximal two-thirds of anal fin are black, and the distal one-third is transparent gray with a white leading edge.

Hybridization.—We first speculated that certain individuals were of hybrid origin because of the barring pattern on the dorsal fin. Unlike the putative parents at Mitande Rocks, the dorsal fin of the putative hybrids is characterized by disjunct barring (Fig. 1). In many specimens, it appeared as though the vertical bars of the body extended onto the dorsal fin. Although *P. zebra* and *C. afra* exhibit variation in dorsal-fin pigmentation among different geographic loca-

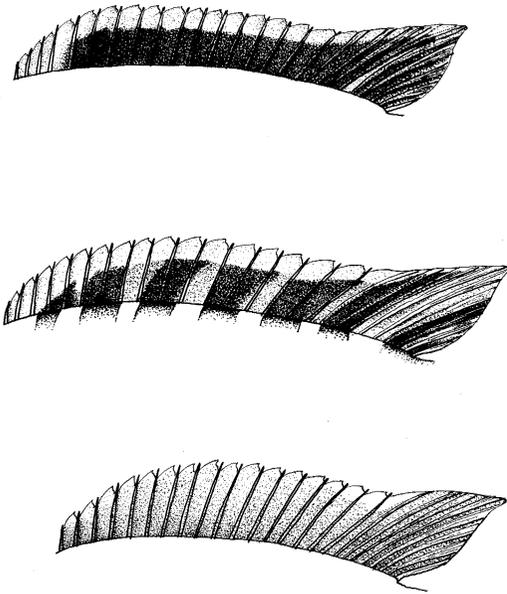


Fig. 1. Pigmentation of the dorsal fin of *Cynotilapia afra* (top), hybrid (center), and *Pseudotropheus zebra* (bottom) collected from Cape Maclear, Lake Malawi.

tions (Konings, 1990; pers. obs.), in the 68 collections made at Mitande Rocks prior to 1991, we never found individuals with disjunct barring in the dorsal fin, nor had it been reported in the literature. Body coloration in the putative hybrids is similar to the putative parents. Laterally, the ground color is blue with five to six vertical black bars. One of the putative hybrids, however, had five vertical bars on the left side and six on the right. Many individuals with disjunct barring in the dorsal fin, similar to those collected at Mitande Rocks in both 1991 and 1992, were videotaped in 1993 and 1994.

Hand-held specimens of the two putative parental taxa also can be discriminated by dentition patterns. *Cynotilapia afra* is characterized by the presence of widely spaced (1–5 in outer row of left lower jaw) conical teeth, whereas *P. zebra* has tightly packed (8–13 in outer row of left lower jaw) bicuspid teeth. *Pseudotropheus zebra* from Mitande Rocks never has conical teeth in the anterior three-fourths of the jaw although, on occasion, one or two of the small posterior teeth may be conical. Conversely, no bicuspid teeth have been observed in *C. afra* from Mitande Rocks. The presence of both conical and bicuspid teeth (Fig. 2) on the anterior portion of the jaws of those individuals with disjunct pigmentation of the dorsal fin further corroborates our hypothesis that these individuals were of hybrid origin.

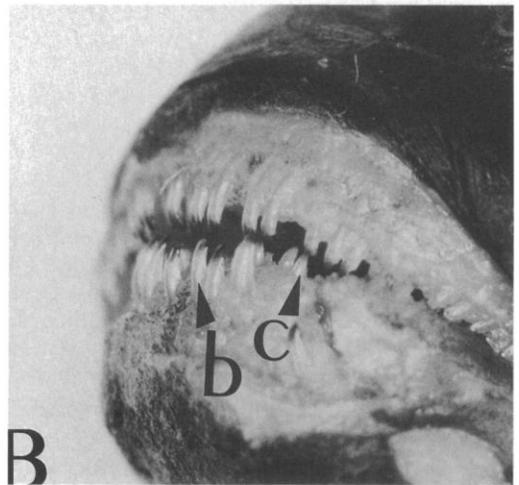


Fig. 2. Jaw teeth of *Cynotilapia afra* (A), hybrid (B; b = bicuspid, c = conical), and *Pseudotropheus zebra* (C).

Historically, identification of naturally occurring hybrids has depended on intermediacy of character states between the putative hybrid and the two putative parental forms. Neff and Smith (1979) criticized use of hybrid-description techniques that required a priori identification of the hybrid and suggested that principal components analysis should be used to delimit naturally occurring hybrids. In an attempt to support our initial hypothesis that observed color differences and dentition were indicative of hybridization, differences in body shape were analyzed using sheared principal components analysis (PCA) (Humphries et al., 1981; Bookstein et al., 1985) to compare the supposed hybrid to the two putative parental species.

Morphometric and meristic data were analyzed from 24 *C. afra*, 14 *P. zebra*, and nine putative hybrids that were collected in 1991 and 1992. Standard length was used throughout, and external counts and measurements follow Stauffer (1994). Except for gill-raker counts, which were recorded from the right side, all counts and measurements were made on the left side.

The first principal component of the morphometric data (Table 1), which may be interpreted as a size component (Humphries et al., 1981), accounted for 85% of the total variance. The second principal component accounted for 27.3% of the remaining 15% of the variance. Variables that had highest loadings on the sheared second principal component were posterior insertion of the dorsal fin to ventral edge of the caudal fin (0.44), posterior insertion of the anal fin to dorsal edge of caudal fin (0.43), pelvic-fin length (-0.43), and pectoral-fin length (-0.33).

The first principal component of the meristic data explained 49.3% of the total variance. Variables that loaded highly on the first principal component were number of teeth in outer row of the left lower jaw (0.26), number of cheek scales (0.21), number of teeth rows on the lower jaw (0.20), number of gill rakers on the first epibranchial (-0.18), number of teeth rows on the upper jaw (0.17), and number of dorsal-fin rays (-0.16).

A plot of the sheared second principal component of the morphometric data versus the first principal component of the meristic data illustrates no overlap between *C. afra* and *P. zebra* (Fig. 3). Two individual scores of the supposed hybrid are between the two minimum polygons formed by the two putative parental taxa, two lie within the polygon of *C. afra*, one within the polygon of *P. zebra*, and three lie outside the space encompassed by the minimum polygon clusters of the putative parents.

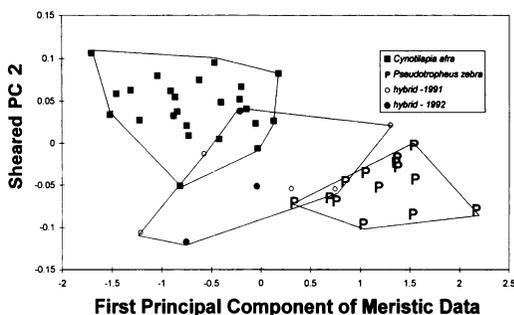


Fig. 3. Plot of second sheared principal component (morphometrics) and first principal component of meristic data from analysis of data from *Cynotilapia afra*, *Pseudotropheus zebra*, and putative hybrids.

An additional putative hybrid (not shown in Fig. 3) had 13 teeth in the outer row of the lower jaw and four rows of teeth on both upper and lower jaws, resulting in a high first principal component score (2.6), and suggesting phenotypic similarity to *P. zebra*. Pigmentation in its dorsal fin and the presence of conical teeth in the outer row of the lower jaw, however, led us to classify this individual as a hybrid or a back-cross. The position of putative hybrids relative to the minimum polygon clusters of parental forms did not change when this individual was eliminated from the sheared principal component analysis.

A total of 10 *C. afra*, 10 *P. zebra*, and five putative hybrids were screened for 15 enzymes using standard starch gel electrophoresis (Hillis and Moritz, 1990). Of 29 putative protein loci scored, two (aconitase and esterase-3) were polymorphic. All "populations" were in Hardy-Weinberg equilibrium, and allele frequencies did not differ significantly ($P < 0.05$), among the three taxa, even though the two putative parents are placed in different genera. Because of the lack of diagnostic alleles, allozyme data were inconclusive, and our hypothesis that the individuals are hybrids is supported primarily by morphological evidence.

Laboratory breeding experiments between the two putative parental taxa would enable us to directly compare laboratory-raised hybrids with specimens collected in situ. The location, however, from which the introduced population of *C. afra* originated is not known, and at this time, collection of rock-dwelling cichlids from Thumbi West Island is prohibited. Efforts are in progress to cross other populations of *C. cf. afra* and *P. zebra* in a series of mate choice experiments.

Hybridization among freshwater fishes is a common occurrence (Hubbs, 1955), and under artificial conditions, hybridization between hap-

TABLE 1. MORPHOMETRIC AND MERISTIC DATA FOR *Cynotilapia afra* (n = 24), *Pseudotropheus zebra* (n = 14), AND THE PUTATIVE HYBRID (n = 9). Values are mean (standard deviation).

Character	<i>C. afra</i>	<i>P. zebra</i>	Hybrid
Standard length (mm)	74.1 (6.10)	78.1 (9.13)	70.9 (3.36)
Head length (mm)	22.2 (1.63)	24.2 (3.00)	21.9 (1.04)
Percent head length			
Snout length	33.2 (3.22)	33.6 (6.00)	34.7 (2.26)
Postorbital head length	39.5 (3.48)	39.4 (4.64)	38.8 (2.68)
Horizontal eye diameter	31.9 (2.84)	32.7 (3.81)	33.2 (2.32)
Vertical eye diameter	32.1 (2.87)	32.6 (4.04)	33.5 (2.30)
Head depth	105.8 (11.7)	102.8 (14.3)	94.5 (6.56)
Preorbital depth	20.1 (2.21)	21.1 (3.63)	19.5 (2.25)
Cheek depth	28.0 (3.53)	27.2 (4.57)	27.4 (2.57)
Percent standard length			
Head length	30.0 (2.20)	31.0 (3.84)	30.9 (1.47)
Snout to dorsal fin	33.0 (3.20)	34.4 (4.32)	34.5 (2.17)
Snout to pelvic fin	38.0 (3.13)	38.5 (4.93)	37.1 (3.45)
Dorsal-fin base length	60.9 (5.55)	61.8 (7.54)	62.2 (4.53)
Anterior dorsal to anterior anal	50.8 (4.75)	52.1 (6.70)	50.6 (4.18)
Anterior dorsal to posterior anal	63.6 (6.23)	65.0 (8.42)	64.7 (4.68)
Posterior dorsal to anterior anal	31.3 (3.04)	31.7 (4.43)	30.7 (1.76)
Posterior dorsal to posterior anal	16.4 (1.78)	16.5 (2.41)	15.7 (1.03)
Posterior of dorsal to ventral of caudal	19.6 (2.28)	18.4 (2.13)	17.3 (0.74)
Posterior of anal to dorsal of caudal	22.9 (2.65)	21.9 (2.59)	20.3 (1.05)
Posterior of dorsal to pelvic fin	57.0 (5.07)	56.9 (6.95)	56.6 (4.40)
Anterior of dorsal to pelvic fin	35.1 (3.84)	36.3 (5.35)	34.0 (3.13)
Caudal peduncle length	15.2 (1.51)	14.2 (1.79)	11.0 (0.93)
Least caudal peduncle depth	12.6 (1.23)	12.9 (1.80)	8.5 (0.55)
Dorsal-fin spines	17.1 (0.50)	17.4 (0.51)	17.3 (0.92)
Dorsal-fin rays	8.8 (0.46)	8.5 (0.61)	8.8 (0.35)
Anal-fin rays	7.1 (0.32)	6.8 (0.37)	7.0 (0.00)
Pelvic-fin rays	13.0 (0.00)	13.0 (0.22)	13.3 (0.52)
Lateral-line scales	31.3 (0.89)	31.1 (0.85)	32.5 (0.53)
Cheek scales	3.3 (0.50)	4.1 (0.59)	3.6 (0.74)
Gill rakers on 1st epibranchial	2.6 (0.48)	2.7 (0.44)	2.7 (0.46)
Gill rakers on 1st ceratobranchial	13.1 (1.07)	12.2 (1.15)	12.3 (1.30)
Teeth in outer row of left lower jaw	3.4 (0.96)	8.8 (3.02)	7.0 (3.02)
Teeth rows on upper jaw	2.0 (0.40)	2.8 (0.59)	3.0 (0.76)
Teeth rows on lower jaw	2.5 (0.51)	3.0 (0.60)	2.6 (0.92)

lochromine cichlids has been successful (Loiselle, 1971; McElroy and Kornfield, 1993). Frequency of hybridization under natural conditions often is associated with crowding of spawning fishes, cohabitation of rare and abundant fish, occurrence of abiotic stress, and presence of nonnative species (Stauffer et al., 1979; Crapon de Caprona and Fritzsche, 1984). Hubbs (1961) postulated that behavioral blocks to interspecific hybridization may often break down as a result of species introductions.

We contend that the nine specimens described herein are of hybrid origin. We dismiss an alternative hypothesis that the individuals represent an alternative morphotype of one of

the parental species or represent a previously undescribed taxa. First, Ribbink et al. (1983) during the mid-1970s conducted an extensive survey of Lake Malawi rock-dwelling cichlids and did not report observing specimens such as those described here. Second, 68 collections from Thumbi West Island between 1983 and 1990 produced no specimens with similar coloration or tooth pattern (J. R. Stauffer and K. R. McKaye, unpubl.). Finally, possession of both bicuspid and conical teeth and disrupted barring pattern in the dorsal fin is clearly intermediate between the two putative parental species.

Hybridization between these two species pos-

sibly has occurred as a direct result of translocation of *C. afra* to Thumbi West Island approximately 20 years ago. Naturally occurring, sympatric populations of *C. afra* and *P. zebra* inhabit a rocky shoreline at Nkhata Bay, in the northern region of the lake. Examination of dorsal-fin pigmentation of approximately 200 individuals of these two species from Nkhata Bay provided no indication of disjunct barring or possession of both bicuspid and conical teeth in the same individual. Several factors may contribute to hybridization of these two species at Mitande Rocks but not at Nkhata Bay. One factor may be that premating isolating mechanisms that evolved in native sympatric populations may be more exacting than those present in allopatric populations.

Rosen (1979:277) stated that “. . . reproductive compatibility is an attribute of the members of the ancestral species, which is gradually diminished and ultimately lost. . . .” Given the relatively recent evolution of Lake Malaŵi species flock, it is possible that the primitive character state of “reproductive compatibility” has not been lost between the majority of endemic species and that syntopic species maintain reproductive cohesion via premating isolating mechanisms. The similarity of color patterns between introduced and native cichlids may have been the catalyst that induced the hybridization reported here. Finally, differences in population densities of the two parental species at Nkhata Bay and Thumbi West Island may have influenced occurrence of hybridization. At Nkhata Bay, where both putative parental forms are native, estimates of the number of territorial males of *C. afra* and *P. zebra* per 50 m² were 25 and 20, respectively (Ribbink et al., 1983). At Thumbi West Island, however, Ribbink et al. (1983) estimated the density of native, territorial male *P. zebra* (60 individuals per 50 m²) to be far greater than that of translocated *C. afra* (three individuals per 50 m²). This suggests that *C. afra* females would have fewer conspecific males with which to mate, increasing the chance of heterospecific mate selection. Crapon de Caprona and Fritzsche (1984) suggested that similar accidental hybridizations may have occurred under “forced conditions” in Lake Victoria.

Because of the evidence presented here, we strongly condemn intralacustrine translocations of fishes within Lake Malaŵi. Hybridization of introduced and native taxa could cause extinction of indigenous fishes, or through introgression, alter gene pools (Stauffer, 1984).

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LONG-TERM EFFECT OF TAIL LOSS ON HOME-RANGE SIZE AND ACCESS TO FEMALES IN MALE LIZARDS (*PSAMMODROMUS ALGIRUS*).—The home-range size of lizards can vary according to different factors as, for example, body size and energetic requirements (Turner et al., 1969), sex (Rose, 1982), foraging mode (Rose, 1982), visibility (Eason and Stamps, 1992), reproductive season (Rose, 1982), population density (Rose, 1982), food availability (Guyer, 1988; Simon, 1975; but see Waldschmidt, 1983), activity constraints (Ruby and Dunham, 1987), female availability (Schoener and Schoener, 1982), and/or stress (DeNardo and Sinervo, 1994).

Numerous lizards autotomize their tails to escape from predators, and this has the immediate benefit of survival (Bellairs and Bryant, 1985). However, tailless lizards incur various costs during the tail regeneration period (Wilson, 1992; Martín and Salvador, 1992, 1993). Home-range size may also be affected by tail loss. Salvador et al. (In Press) showed in a field experiment that males of the lacertid lizard *Psammodromus algirus* decreased the size of their home range an average of 64% after tail loss and had access to fewer females. In that experiment, only the short-term effects of tail loss were examined

because tail manipulation and home-range reduction occurred during the same reproductive season (April–May). Here, we present data that show long-term effects of tail loss on home-range size and potential access to females in *P. algirus* males.

Methods.—We conducted fieldwork during spring 1994 in a deciduous oak-forest (*Quercus pyrenaica*) near Navacerrada (40°44'N, 4°00'W), central Spain, where we established a 1.5-ha plot with markers every 10 m. During 21–29 March, immediately after lizards emerged from hibernation, we captured by noosing 23 large males [snout–vent length (SVL) = 80–85 mm]. For each individual, we recorded whether the tail was complete or regenerated. Growth rates of regenerating tails are unknown in *P. algirus*, so our sample of males with regenerated tails included males with tails lost one or more years before. Lizards were measured (SVL and tail), marked with paint, and released at their capture site on the same day. Females noosed in the home ranges of males during April were handled in the same way.

We noted the location of each large male once every two days during April. Thus, we mapped 15 locations for each male. This is more locations than usually used in other home-range studies (Rose, 1982); and although home range can increase with number of mapped points, since our sample size was the same for all individuals, any possible bias should affect all males similarly. Home-range area was measured by the convex polygon method (Rose, 1982).

Results.—Snout–vent lengths of males with complete tails (\bar{x} = 82.3 mm, SE = 0.7, n = 11) or regenerated tails (\bar{x} = 82.1 mm, SE = 0.6 mm, n = 12) did not significantly differ (2-tailed Mann-Whitney U-test: U = 92.0, P = 0.80). However, tail lengths of males with regenerated tails (\bar{x} = 129.9 mm, SE = 8.9, n = 11) were significantly shorter than those of males with complete tails (\bar{x} = 174.1 mm, SE = 5.4, n = 12) (Mann-Whitney 1-tailed test: U = 17.5, P = 0.005). Home-range sizes of males with regenerated tails (\bar{x} = 213.4 m², SE = 41.5) were significantly smaller than those of males with complete tails (\bar{x} = 397.4 m², SE = 36.6) (Mann-Whitney 2-tailed test, U = 10, P = 0.001). Moreover, home-range size was significantly correlated with tail length for pooled data (Spearman rank correlation: r_s = 0.739, P < 0.0001, n = 23; Fig. 1). Home-range size was also significantly correlated with the number of females with overlapping areas (r_s = 0.49, P = 0.016, n = 23). The number of females resident in the