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Three New Sand-Dwelling Cichlids from Lake Malaŵi, Africa, with a Discussion of the Status of the Genus *Copadichromis* (Teleostei: Cichlidae)

JAY R. STAUFFER, JR., THOMAS J. LOVULLO, AND KENNETH R. MCKAYE

Three new species of the cichlid fish genus *Copadichromis* Eccles and Trewavas (Teleostei: Cichlidae) from Lake Malaŵi are described. The new species superficially resemble *Copadichromis eucinostomus* but are clearly distinguished by overall shape and meristic characters. The *C. eucinostomus* group is comprised of seven phenetically similar species, which lack lateral spots, have a silver lateral ground color with faint bars appearing in some individuals, and have 19 or fewer gill rakers on the outer ceratobranchial. Overall body shape, meristic characters, coloration, and behavior distinguish the three new species from each other. It is recommended that the name *C. eucinostomus* be restricted to the two original syntypes, now designated as a lectotype and paralectotype and cataloged into the Natural History Museum, London (BMNH.1921.9.6. 191-192).

THE acquisition of reproductive isolation without significant morphological changes probably poses the greatest problem to the taxonomist attempting to distinguish among African haplochromine cichlids (Lewis, 1982). Rapid speciation with marked changes only in coloration has occurred among allopatric cichlid populations apparently separated for only 3500 years (Greenwood, 1965). Numerous cichlid species lack distinctive morphometric differences and can only be distinguished by unique color patterns (Greenwood, 1974; Marsh et al., 1981). The absence of unequivocal morphological differences, however, does not preclude the assignment of specific status to these fishes. Genetic studies of sympatric color morphs of the rock-dwelling cichlids *Pseudotropheus zebra* (McKaye et al., 1984) and *Petrotilapia tridentiger* (McKaye et al., 1982) revealed significant differences in allele frequencies for several polymorphic loci. Furthermore, Stauffer and Boltz (1989) demonstrated that color differences in two sympatric species of the *P. zebra* complex were accompanied by differences in meristic characters, shape and detention of the pharyngeal bone, and body shape.

Male sand-dwelling cichlids build bowers which are aggressively defended and used as display sites during courtship (McKaye, 1983; McKaye et al., 1990). Different genera can be

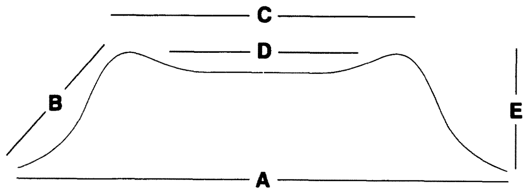

Fig. 1. Schematic illustrating measurements recorded for bowers constructed by breeding males of the *Copadichromis* group (A—width of base; B—slope length; C—outside top diameter; D—inside top diameter; and E—nest height).

distinguished from each other based on the form of the bowers the males build (McKaye and Stauffer, 1988; McKaye, 1991). Recently, McKaye et al. (in press) used morphological and genetic data in conjunction with bower shape to distinguish among *Tramitichromis* species. Eccles and Trewavas (1989) placed sand-dwelling species with small (lower jaw length 35–44% of HL) weak jaws and protrusible mouths in the genus *Copadichromis* Eccles and Trewavas, designating *Copadichromis quadrimaculatus* Regan as the type species. The group is locally known as utaka (Bertram et al., 1942) and, as recognized by Eccles and Trewavas (1989), may not be monophyletic. Within the genus, four species [*C. eucinostomus* (Regan), *C. flavimanus* (Iles), *C. inornatus* (Boulenger), and *C. prostoma* (Trewavas)] are phenetically similar in that they lack lateral spots anterior to the hypural plate, are silver laterally with faint bars appearing in some individuals, and possess 19 or fewer gill rakers on the outer ceratobranchial. We refer to these species as the *C. eucinostomus* group.

During the past decade, we have conducted extensive research on the ecology and behavior of sand-dwelling fishes in southern Lake Malaŵi (McKaye, 1984, 1991). In the course of these studies, we have observed males, fitting the description of *C. eucinostomus* (Trewavas, 1935; Iles, 1960) occupying bowers with three different, population-specific forms, which suggests that the different populations are distinct species. Unfortunately, we could not analyze the bower shape of *C. eucinostomus* topotypes because the type locality is simply "Lake Nyasa." Comparison of our material from southern Lake Malaŵi with the published accounts of this species was futile because they were based on specimens, which were not part of the type series and, thus, may not be *C. eucinostomus.* Iles' (1960) account of *C. eucinostomus* is based on the two cotypes and specimens "from both ends of Lake Nyasa." Eccles and Trewavas (1989) provided additional morphometric and meristic information based on the lectotype, paralectotype, and specimens from Karonga, Chilumba, Vua, and unknown localities in Lake Malaŵi. We postulate that not all of the these specimens were in fact *C. eucinostomus.* The purposes of this paper are to (1) describe three new species within the *C. eucinostomus* group using both morphological and behavioral data; (2) use behavioral data to distinguish selected members of this group from the genus *Tramitichromis*; and (3) provide an artificial key for the genus *Copadichromis* as it is now recognized.

Methods and Materials

Type material of the following species, cataloged into the Natural History Museum (London) were counted and measured: *C. eucinostomus* (BMNH.1921. 9.6.191-192), *C. flavimanus* (BMNH.1962.1962.10.18:12-16), *C. inornatus* (BMNH.1908.10.27.101-102), and *C. prostoma* (BMNH.1935.6.14.1817-1819). The three species described herein were collected in the vicinity of Nankumba Peninsula in southern Lake Malaŵi by chasing them into a monofilament net (7 m × 1 m; 1.5 cm mesh) while SCUBA diving. Standard length is used throughout and external counts, and measurements are those of Barel et al. (1977) and Stauffer (1991). Except for gill-raker counts, which were recorded from the right side, all counts and measurements were made on the left side of the fish. Abdominal and caudal vertebrae were enumerated from radiographs. Institutional abbreviations follow Leviton et al. (1985), except where noted.

The following parameters were recorded for each bower: width of base, slope length, outside top diameter, inside top diameter, and nest height (Fig. 1). Two measurements for each parameter (90° apart) were recorded for each bower. Differences in body shape and bower shape were analyzed using sheared principal components analysis (PCA; Humphries et al., 1981; Bookstein et al., 1985). This analysis restricts the size variation to the first component; thus, subsequent components are strictly shape related. Meristic differences were compared using PCA in which the correlation matrix was factored. Comparisons among the specimens examined were made by plotting the sheared second principal component against the first meristic component. Bowers of the three new species were compared by plotting the sheared second principal component against the sheared third principal component. Bower shape was considered a manifestation of a behavioral at-

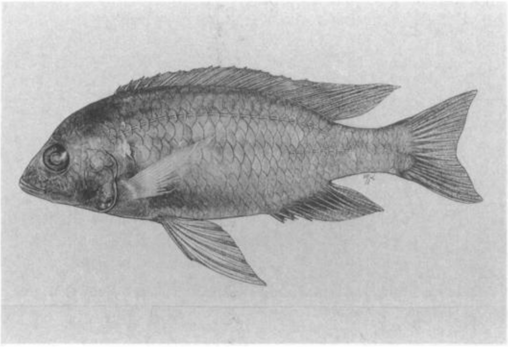

Fig. 2. Holotype of *Copadichromis conophoros* (PSU 2622.1).

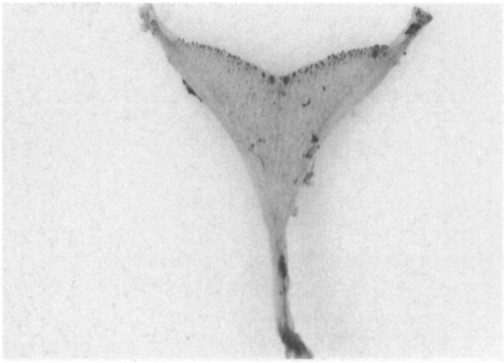

Fig. 3. Lower pharyngeal bone of *Copadichromis conophoros* (PSU 2622.2).

tribute. Male courtship patterns were recorded using a Sony V8 camera in an Amphibico underwater housing; the videotapes were cataloged into the Pennsylvania State University Fish Museum (PSU 2625).

Copadichromis conophoros n. sp.
Figs. 2–4

Holotype.—PSU 2622.1, adult male, 108.7 mm, Cape Maclear (14°05′S 34°54′E), Lake Malaŵi, Africa, 2–3 m, 12 Aug. 1988.

Paratypes.—PSU 2622.2, 8 (90.5–108.5 mm); USNM 324568, 8 (90.5–111.0 mm); Malaŵi Fisheries Unit (MFU) 7, 3 (95.8–102.1 mm); data as for holotype.

Diagnosis.—A protrusible jaw and fewer than 17 gill rakers on the outer ceratobranchial place *C. conophoros* in the *C. eucinostomus* group. *Copadichromis conophoros* is distinguished from other members of this group except *C. thines* by the presence of 13–15 gill rakers on the outer ceratobranchial. *Copadichromis conophorus'* heavily pigmented caudal fin differentiates it from *C. thinos.*

Description.—Jaws isognathous (Fig. 2) and protrusible; unicuspid teeth on jaws in three rows; 11 teeth in outer row of left lower jaw of holotype, 8–15 in paratypes. Lateral scales ctenoid; holotype with 34 pored lateral-line scales, paratypes with 33–34; pored scales posterior to hypural plate 1–2 (Table 1). Holotype with three scale rows on cheek, paratypes with 2–3. Lower pharyngeal bone triangular in outline with villiform teeth (Fig. 3). Gill rakers simple, outer arch with 13–15 on ceratobranchial, 4–6 on epibranchial, and one between ceratobranchial and epibranchial. Holotype with 12 abdominal and 17 caudal vertebrae, paratypes with 12–13 abdominal and 15–17 caudal vertebrae.

Lateral body coloration of males silver with blue and yellow highlights dorsally, fading to white ventrally; snout blue; head with black gular; dorsal fin clear proximally with midyellow stripe, distal one-quarter black with yellow lappets; dorsal and ventral rays of caudal fin black and center rays clear, membranes yellow with scattered melanophores; anal fin clear proximally, distal two-thirds black with yellow lappets; pelvic fins white on leading edge, with black stripe in middle, and black distally; pectoral fins clear. Lateral body coloration of females silver, dorsal one-third with purple hue fading to white ventrally; head gray dorsally fading to white ventrally with white gular; dorsal fin clear with yellow spots and lappets; caudal fin with black stripe in middle and faint yellow spots in membranes; anal fin clear with micromelanophores on distal two-thirds and with yellow tips; pelvic fins clear with white leading edge and first two membranes yellow.

Etymology.—The name conophorus, from the Greek meaning "cone-bearing," was chosen to reflect the cone-shaped bowers of breeding males (Fig. 4).

Life history.—*Copadichromis conophorus,* which is referred to as *C. eucinostomus* in early papers, forages in the water column, feeding primarily on zooplankton (McKaye, 1983, 1984; McKaye et al., 1990). Spawning occurs throughout the year but peaks from Jan. to March and Aug. to Sept. Males build cone-shaped bowers (Fig. 4; see McKaye et al., 1990) in large breeding arenas off sand beaches in water 3–10 m deep. The inside top diameter ranges from 9 cm to 18 cm

TABLE 1. MORPHOMETRIC AND MERISTIC CHARACTERS OF *Copadichromis conophorus*. Range and mean include holotype and 19 paratypes.

	Holotype	Mean	SD	Range
Standard length, mm	108.7	101.59	6.8	90.5–111.0
Head length, mm	32.0	28.7	2.3	24.9–32.0
Percent standard length				
Head length	29.4	28.3	0.7	27.3–29.9
Snout to dorsal-fin origin	32.7	31.4	0.9	29.9–32.8
Snout to pelvic-fin origin	36.8	35.8	1.3	33.8–38.8
Greatest body depth	36.8	33.7	1.5	31.2–36.8
Least caudal-peduncle depth	10.5	10.4	0.4	9.6–11.1
Caudal-peduncle length	15.9	17.0	1.1	14.3–19.4
Pectoral-fin length	30.8	30.6	1.5	28.6–34.0
Pelvic-fin length	32.5	33.1	1.8	30.1–36.3
Dorsal-fin base length	56.5	57.7	1.3	55.5–60.1
Percent head length				
Horizontal eye diameter	28.4	29.7	1.3	26.9–32.2
Vertical eye diameter	26.9	28.5	1.2	26.9–31.2
Snout length	30.9	32.0	1.4	29.1–34.2
Postorbital head length	40.0	40.0	1.0	38.1–41.5
Preorbital depth	20.9	20.1	1.3	18.1–22.1
Lower jaw length	35.9	36.6	2.0	32.8–39.3
Cheek depth	20.0	20.5	1.2	18.2–23.0
Head depth	86.6	90.7	4.6	83.8–99.3

	Holotype	Mode	Range
Counts			
Lateral-line scales	34	34	33–34
Pored scales posterior to lateral line	1	1	1–2
Scale rows on cheek	3	3	2–3
Dorsal-fin spines	17	17	16–17
Dorsal-fin rays	11	11	10–12
Anal-fin rays	9	9	9–10
Gill rakers on outer ceratobranchial	13	14	13–15
Gill rakers on outer epibranchial	6	5	4–6
Teeth in outer row of left lower jaw	11	12	8–15
Teeth rows on upper jaw	3	3	2–3
Teeth rows on lower jaw	3	3	—

and the outside top diameter from 16 cm to 30 cm (n = 10; Fig. 5).

Copadichromis cyclicos n. sp.
Figs. 6–7

Holotype.—PSU 2624.1, adult male, 115.6 mm, Kanchedza Island (13°58′S, 34°56′E), Lake Malaŵi, Africa, 2–3 m, 31 Jan. 1989.

Paratypes.—PSU 2624.2, 4 (66.6–116.6 mm); USNM 324569, 4 (79.5–121.2 mm); MFU 5, 3 (70.6–112.5 mm); data as for holotype.

Diagnosis.—The protrusible jaw and fewer than 17 gill rakers place *C. cyclicos* in the *C. eucinostomus* group. Its low number of gill rakers on the outer ceratobranchial (10–12) distinguishes it from all members of the *C. eucinostomus* group, except *C. thinos. Copadichromis cyclicos*' heavily pigmented caudal fin differentiates it from *C. thinos.*

Description.—Jaws isognathous (Fig. 6) and protrusible; unicuspid teeth on jaws in 2–3 rows; 14 teeth in outer row of left lower jaw of holotype, 8–17 in paratypes. Lateral scales ctenoid; holotype with 34 pored lateral-line scales, paratypes with 33–34; pored scales posterior to hypural plate 1–2 (Table 2.) Holotype with 3 scale rows on cheek, paratypes with 2–3. Lower pharyngeal bone triangular in outline with vil-

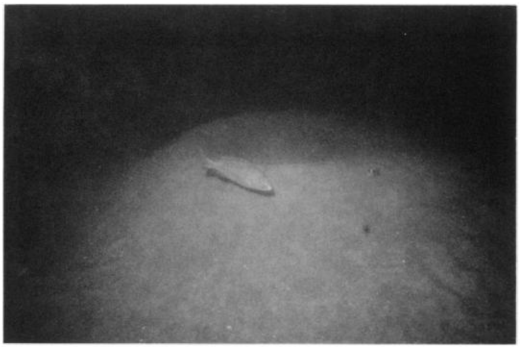

Fig. 4. Male *Copadichromis conophoros* defending bower, Cape Maclear, Lake Malaŵi.

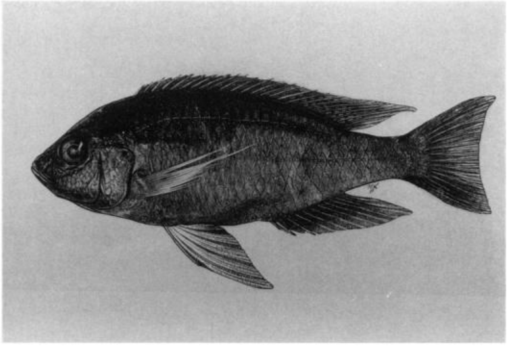

Fig. 6. Holotype of *Copadichromis cyclicos* (PSU 2624.1).

liform teeth (Fig. 7). Gill rakers simple, outer arch with 10–12 on ceratobranchial, 4–5 on epibranchial, and one between ceratobranchial and epibranchial. Holotype with 14 abdominal and 16 caudal vertebrae, paratypes with 12–14 abdominal and 16–17 caudal vertebrae.

Lateral body coloration of males silver/gray with blue and yellow highlights on dorsal third, fading to white ventrally; snout blue, cheek gray with yellow highlights, dark gray opercular spot; gular black; dorsal fin gray with yellow spots, white marginal band and yellow lappets; caudal fin dark gray with yellow spots; anal fin dark gray with 4–6 yellow ocelli with white borders; pelvic fin with spine and first ray black, remainder clear; pectoral fin clear. Females silvery overall, with orange spots on dorsal fin, but no ocelli on anal fin.

Etymology.—The name cyclicos, from the Greek meaning "circular" was chosen to reflect the courtship dance of breeding males.

Life history.—*Copadichromis cyclicos* forages in the water column, feeding primarily on zooplankton. Spawning occurs throughout the year but with two peaks, Jan. to March and Aug. to Sept. Males build cone-shaped bowers in breeding arenas over sand, at water depths of 3–7 m. The inside top diameter ranges from 14 cm to 20 cm and the outside top diameter from 25 cm to 38 cm (Fig. 5).

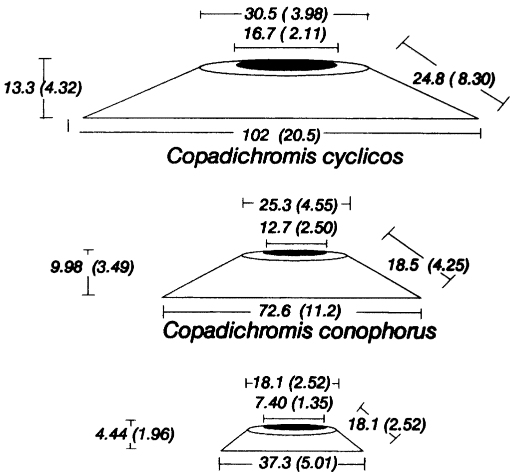

Fig. 5. Comparisons of bower sizes of *Copadichromis conophorus* (n = 10) *Copadichromis cyclicos* (n = 10), and *Copadichromis thinos* (n = 24) showing mean dimensions (cm) with standard deviations in parentheses.

Copadichromis thinos
Figs. 8–9

Holotype.—PSU 2623.1, adult male, 78.4 mm, Mazinzi Reef (13°53′S, 34°59′E), Lake Malaŵi, Africa 10–15 m, 31 Jan. 1988.

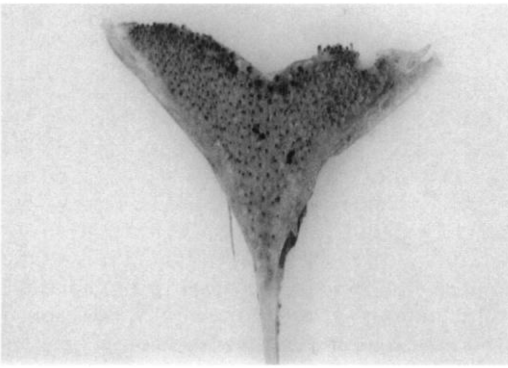

Fig. 7. Lower pharyngeal bone of *Copadichromis cyclicos* (PSU 2624.2).

TABLE 2. MORPHOMETRIC AND MERISTIC CHARACTERS OF *Copadichromis cyclicos*. Range and mean include holotype and 11 paratypes.

	Holotype	Mean	SD	Range
Standard length, mm	115.6	102.9	20.5	66.6–121.2
Head length, mm	32.7	29.7	5.7	19.1–36.5
Percent standard length				
Head length	28.3	28.9	0.9	27.8–31.3
Snout to dorsal-fin origin	31.2	32.3	1.4	30.2–35.3
Snout to pelvic-fin origin	35.9	35.9	1.4	33.8–39.0
Greatest body depth	36.1	33.1	1.6	30.6–36.1
Least caudal-peduncle depth	10.7	10.6	0.4	9.8–11.4
Caudal-peduncle length	15.7	16.6	0.9	14.8–18.1
Pectoral-fin length	30.0	29.5	1.7	26.9–33.2
Pelvic-fin length	31.4	31.2	4.6	22.8–36.0
Dorsal-fin base length	59.3	57.8	1.5	54.2–59.7
Percent head length				
Horizontal eye diameter	30.0	32.1	2.7	28.8–37.1
Vertical eye diameter	30.6	31.7	2.7	28.2–36.1
Snout length	36.1	32.7	1.9	29.8–36.1
Postorbital head length	39.1	39.0	1.8	34.4–40.7
Preorbital depth	21.1	20.4	1.8	16.7–22.4
Lower jaw length	36.1	36.5	2.3	33.0–40.9
Cheek depth	25.4	21.6	2.4	17.3–25.4
Head depth	92.7	86.8	6.0	75.1–95.3

	Holotype	Mode	Range
Counts			
Lateral-line scales	34	34	33–34
Pored scales posterior to lateral line	1	1	1–2
Scale rows on cheek	4	3	3–4
Dorsal-fin spines	17	17	16–17
Dorsal-fin rays	11	11	10–12
Anal-fin rays	9	9	8–9
Gill rakers on outer ceratobranchial	12	11	10–12
Gill rakers on outer epibranchial	4	4	4–5
Teeth in outer row of left lower jaw	14	14	8–17
Teeth rows on upper jaw	3	3	2–3
Teeth rows on lower jaw	2	2	2–3

Paratypes.—PSU 2623.2, 4 (71.7–73.9 mm); USNM 324570, 3 (67.5–74.8 mm); MFU 5, 2 (73.7–76.1 mm); data as for holotype.

Diagnosis.—The protrusible mouth and fewer than 17 gill rakers place *C. thinos* in the *C. eucinostomus* group. Its low number of gill rakers on the outer ceratobranchial (11–13) distinguishes it from the *C. eucinostomus* syntypes. The small size (67.5–78.4 mm) and pigmentation differentiate it from *C. conophorus* and *C. cyclicos*. *Copadichromis thinos* males' distal portion of their caudal fins is transparent with yellow spots, whereas males of other members of this species group have heavily pigmented caudal fins.

Description.—Jaws isognathous (Fig. 8) and protrusible; unicuspid teeth on jaws in 2–3 rows; 13 teeth in outer row of left lower jaw of holotype, 11–14 in paratypes. Lateral scales ctenoid; holotype with 34 pored lateral-line scales, paratypes with 32–34; pored scales posterior to hypural plate 1–2 (Table 3). Holotype with 3 scale rows on cheek, paratypes with 2–3. Lower pharyngeal bone triangular in outline with villiform teeth (Fig. 9). Gill rakers simple, outer arch with 11–13 on ceratobranchial, 4–5 on epibranchial, and one between ceratobranchial and epibranchial. Holotype with 12 abdominal and 17 caudal vertebrae, paratypes with 11–12 abdominal and 15–17 caudal vertebrae.

Lateral body coloration of males silver with blue highlights; dorsal third blue/gray, fading to white ventrally; head gray, gular white with scattered micromelanophores; dorsal fin gray with yellow spots and orange/yellow lappets;

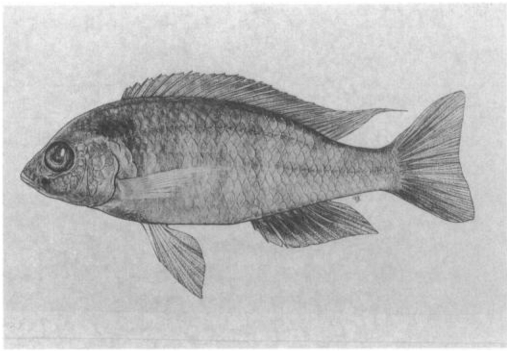

Fig. 8. Holotype of *Copadichromis thinos* (PSU 2623.1).

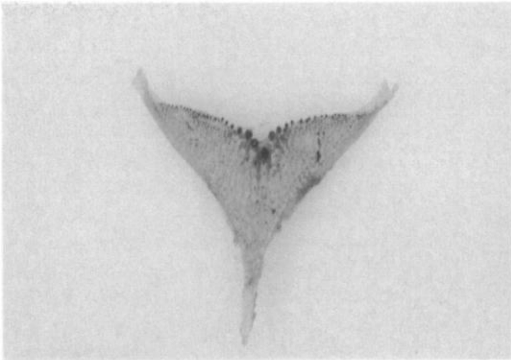

Fig. 9. Lower pharyngeal bone of *Copadichromis thinos* (PSU 2623.2).

distal portion of caudal fin clear with yellow spots; anal fin clear with 4–6 yellow ocelli; pelvic fin clear with anterior 2 rays yellow; pectoral fin clear. Coloration of females similar but not as intense; ocelli present on anal fin.

Etymology.—The name thinos, from the Greek meaning "sand-hill," was chosen to reflect the sand platform on which this species spawns.

Life history.—*Copadichromis thinos* forages in the water column, feeding primarily on zooplankton. Spawning occurs sporadically throughout the year but peaks between Jan. and March. Males build cone-shaped bowers in breeding arenas on the rock/sand interface, at water depths of 15–25 m. Bowers were typically smaller than those built by the other two species (Fig. 5). The inside top diameter ranges from 5 cm to 10 cm and the outside top diameter from 13 cm to 25 cm (Fig. 5).

Discussion

Size accounts for 92% of the total variance of the PCA of the morphometric data. The second principal component accounts for 2.8% of the remaining variance. Variables with the highest loadings on the sheared second principal component are eye diameter, preorbital depth, distance between the posterior dorsal fin and the posterior anal fin, and caudal-peduncle length (Table 4). The first principal component of the meristic data explains 53.1% of the variance. Variables with the highest loadings on the first principal component (meristic data) are the number of gill rakers on the ceratobranchial (0.30), number of dorsal-fin rays (0.27), and number of cheek scales (−0.28).

When the sheared second principal component of the morphometric data is plotted against the first principal component of the meristic data, the clusters formed by the three new species do not overlap with the previously described fishes in the *C. eucinostomus* group (Fig. 10). *Copadichromis prostoma* differs from all other members of this group in both sheared second principal components (morphometric data) and first principal components of the meristic data. It is further distinguished because of the presence of a dark lateral stripe. Similarly, *C. flavimanus* and *C. inornatus* are quite distinct from the three species described herein and are separated primarily along the first principal component of the meristic data. Although shape differences between old and freshly preserved specimens could be partly artifactual, meristic characters of preserved specimens would not change with time. Additionally, those minimum polygon clusters formed by *C. conophorus* and *C. cyclicos* do not overlap. *Copadichromis conophorus* has 13–15 gill rakers on the outer ceratobranchial, whereas *C. cyclicos* has 10–12. *Copadichromis thinos* is clearly intermediate between these two species (Fig. 10); however, a MANOVA in conjunction with a Hotelling-Lawley trace demonstrated that these three minimum polygon clusters were significantly different ($P < 0.05$) from each other. Furthermore, because the clusters were significantly different ($P < 0.05$) along the first principal component (meristic data) axis independent of the sheared second principal component axis, a Duncan's Multiple Range test was used to demonstrate that all three clusters were significantly ($P < 0.05$) different from each other.

Observations have demonstrated that members within a genus of Lake Malaŵi hapolchromines build similarly shaped bowers (McKaye, 1991), and preliminary evidence indicates that members of different genera exhibit different courtship dances. For example, the three species described herein have a circular courtship movement, whereas the sympatric *Tramitichromis* spp. use a figure-eight

TABLE 3. MORPHOMETRIC AND MERISTIC CHARACTERS OF *Copadichromis thinos*. Range and mean include holotype and nine paratypes.

	Holotype	Mean	SD	Range
Standard length, mm	78.4	73.3	3.1	67.5–78.4
Head length, mm	22.9	21.5	0.9	19.8–22.9
Percent standard length				
Head length	29.2	29.3	0.7	28.3–30.7
Snout to dorsal-fin origin	33.8	33.1	1.2	31.4–34.7
Snout to pelvic-fin origin	33.9	33.8	0.7	33.1–35.3
Greatest body depth	32.1	31.4	1.4	29.6–34.2
Least caudal-peduncle depth	11.2	10.3	0.5	9.5–11.2
Caudal-peduncle length	15.1	16.2	0.8	14.8–17.6
Pectoral-fin length	30.6	30.3	1.4	27.8–32.3
Pelvic-fin length	30.9	31.2	1.0	29.5–33.1
Dorsal-fin base length	58.0	56.5	1.4	54.0–59.0
Percent head length				
Horizontal eye diameter	32.3	34.0	0.9	32.3–35.4
Vertical eye diameter	32.3	32.7	1.3	30.4–35.0
Snout length	33.6	31.3	1.2	29.4–33.6
Postorbital head length	40.2	40.0	2.2	35.5–43.4
Preorbital depth	24.0	18.7	2.5	15.9–24.0
Lower jaw length	34.9	35.5	2.5	30.2–38.6
Cheek depth	20.5	18.9	1.2	17.0–20.7
Head depth	82.5	83.4	3.4	79.9–90.0

	Holotype	Mode	Range
Counts			
Lateral-line scales	34	34	32–34
Pored scales posterior to lateral line	1	1	1–2
Scale rows on cheek	3	3	2–3
Dorsal-fin spines	16	16	16–17
Dorsal-fin rays	11	11	10–12
Anal-fin rays	9	9	9–9
Gill rakers on outer ceratobranchial	12	12	11–13
Gill rakers on outer epibranchial	4	4	4–5
Teeth in outer row of left lower jaw	13	12	11–14
Teeth rows on upper jaw	3	3	2–3
Teeth rows on lower jaw	3	3	3–3

courtship movement (PSU 2625). For the three new species described herein, no differences among courtship patterns of breeding males could be discerned; however, because the spawning platforms of each species are constructed by breeding males, we considered bower shape a manifestation of a behavioral pattern and used this character to further delimit the species. A plot of the sheared second principal component against the sheared third principal component demonstrated that the bower shapes of the three species were different (Fig. 11). There was no overlap between the clusters formed by *C. cyclicos* and *C. thinos*. The bowers of *C. conophorus* were intermediate in shape between those of *C. cyclicos* and *C. thinos*; however, all three species' bowers were significantly different ($P < 0.05$) from each other, along the sheared second principal component axis (ANOVA, Duncan's Multiple Range test).

The inside top diameter was chosen as the most appropriate dimension with which to compare size of the bowers among the three species described herein. In a series of experiments, McKaye et al. (1990) observed that when *C. conophorus*' bowers were leveled, reconstruction began within 24 h. Bower height and width of the base continued to increase over a 10-day period; however, the inside top diameter reached its preleveled dimensions within 24 h and remained constant. The inside top diameters of the bowers of the *C. conophorus*, *C. cyclicos*,

TABLE 4. VARIABLE LOADINGS ON SIZE AND THE FIRST TWO SHEARED PRINCIPAL COMPONENTS (SHAPE FACTORS) FOR *Copadichromis eucinostomus* (n = 2), *Copadichromis conophorus* (n = 20), *Copadichromis cyclicos* (n = 12), *Copadichromis thinos* (n = 11), *Copadichromis inornatus* (n = 2), *Copadichromis prostoma* (n = 3), AND *Copadichromis flavimanus* (n = 5).

	PC1	Sheared PC2	Sheared PC3
Standard length	−0.21	−0.02	0.03
Head length	−0.20	−0.05	−0.15
Snout length	−0.23	0.17	−0.30
Postorbital head length	−0.22	0.13	0.01
Horizontal eye diameter	−0.12	−0.43	−0.41
Vertical eye diameter	−0.13	−0.42	−0.45
Preorbital depth	−0.30	0.70	−0.37
Head depth	−0.25	−0.09	0.09
Snout to dorsal-fin origin	−0.19	−0.00	−0.12
Snout to pelvic-fin origin	−0.23	−0.14	−0.05
Dorsal-fin base length	−0.23	−0.01	0.04
Least caudal-peduncle depth	−0.22	−0.08	0.02
Caudal-peduncle length	−0.21	−0.17	0.21
Anterior dorsal to anterior anal	−0.24	−0.10	0.00
Posterior dorsal to poseterior anal	−0.20	−0.03	0.43
Anterior dorsal to posterior anal	−0.23	0.03	0.07
Posterior dorsal to anterior anal	−0.22	−0.07	0.22
Posterior dorsal to ventral caudal	−0.20	0.14	0.10
Posterior anal to dorsal caudal	−0.22	−0.02	0.22
Anterior dorsal to pelvic-fin origin	−0.26	−0.09	0.07
Posterior dorsal to pelvic-fin origin	−0.23	−0.03	0.15

and *C. thinos* were significantly different from each other (ANOVA/Duncan's Multiple Range test, $P < 0.05$).

In her classic work on Lake Malaŵi fishes, Trewavas (1935) recognized the close affinities between the following six species based on morphological and feeding similarities: *Copadichromis eucinostomus, C. inornatus* (Boulenger), *C. cyaneus* (Trewavas), *C. prostoma, C. chrysonotus* (Boulenger), and *C. quadrimaculatus*. Subsequently, Iles (1960) described *C. flavimanus, C. mloto* (Iles), *C. virginalis* (Iles), *C. boadzulu* (Iles), *C. trimaculatus* (Iles). *C. nkatae* (Iles) *C. jacksoni* (Iles), *C. borleyi* (Iles), *C. pleurostigmoides* (Iles), and *C. likomae* (Iles) and placed them in the zooplankton feeding group. Eccles and Trewavas (1989) included *C. pleurostigma* (Trewavas) in this group. Most recently, Konings (1990) described *C. azureus* Konings, *C. mbenjii* Konings, and *C. verduyni* Konings and suggested that *C. prostoma, C. eucinostomus,* and *C. boadzulu* be placed in the genus *Nyassachromis* Eccles and

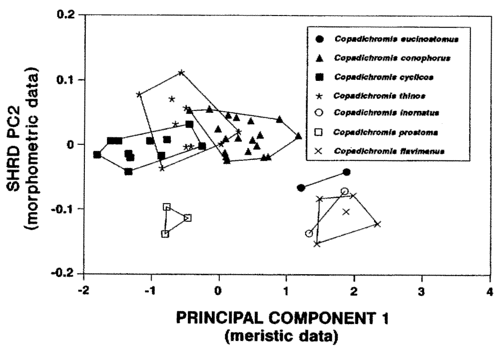

Fig. 10. Plot of individual sheared second principal component scores (morphometric data) and first principal component scores (meristic data) of members of the *Copadichromis eucinostomus* group.

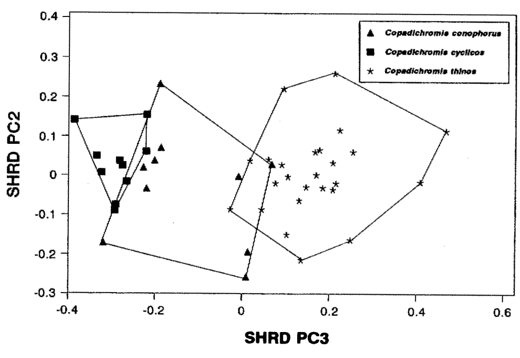

Fig. 11. Plot of individual sheared principal component scores of bower-shape of *Copadichromis conophorus, Copadichromis cyclicos,* and *Copadichromis thinos.*

Trewavas, based on the longitudinal pigmentation pattern and habitat preference of spawning males. The longitudinal pigmentation pattern is considered plesiomorphic, however (Eccles and Trewavas, 1989); and we contend that too little is known about the breeding biology of this group to diagnose habitat preference of breeding males. In the diagnosis of *Nyassachromis*, Eccles and Trewavas (1989) state that, in species for which "the form of the gut is known, it is long and coiled." The guts of *C. eucinostomus, C. conophorus, C. copadichromis*, and *C. thinos* are not long and coiled; we, therefore, reject Konings' (1990) inclusion of these four species in *Nyassachromis*. We do concur with Eccles and Trewavas' (1989) conjecture that *Copadichromis* may not be monophyletic (Hennig, 1979).

In summary, we have described three new species of *Copadichromis* that have historically been confused with *C. eucinostomus* (Ribbink et al., 1983; McKaye, 1983; Lewis et al., 1986). Although *Copadichromis*, as recognized by Eccles and Trewavas (1989), may not be monophyletic, too little information on the genetics, morphology, and behavior is available to warrant splitting the genus at this time. Morphological similarities (pigmentation patterns and 19 or fewer gill rakers on the outer ceratobranchial) enabled us to provisionally define the *C. eucinostomus* group, within the genus. We have distinguished three new species from each other and from other species in this group based on morphological characteristics. Additionally, we have used a facet of behavior, bower-shape and size, to discern further differences among the three new species. Because the type locality of *C. eucinostomus* is merely Lake Nyasa, we were prohibited from collecting or observing topotypes to define this species more rigorously. Eccles and Trewavas (1989) also had difficulty characterizing this species, as evidenced by it appearing in two different couplets in their key. We recommend, therefore, that *C. eucinostomus* be restricted to the lectotype and paralectotype currently cataloged into the Natural History Museum (London) (BMNH.1921.9.6.191-192).

Artificial Key to the Species of *Copadichromis*

Copadichromis, as diagnosed, consists of small- to medium-sized planktivores with weak jaws and elongated premaxillary pedicels whose bones can be thrust forward to form a protrusible mouth (Eccles and Trewavas, 1989). Although members of the genus share morphological characters, it is most probably not monophyletic (Hennig, 1979); additional information on the morphology, genetics, and behavior of this group is needed, however, before its phylogeny can be resolved. The following key is presented to provisionally define and characterize members of this group. The key was constructed using characters reported in Eccles and Trewavas (1989),[1] Iles (1960),[2] Konings (1990),[3] and via direct examination of type material.[4] Numerous currently undescribed species will likely be placed in this genus.

1 (a) One or more distinct dark spots or horizontal stripes laterally 2
1 (b) Distinct spots or horizontal stripes absent laterally 17
2 (a) One or more horizontal stripes laterally; a single caudal spot may be present 3
2 (b) At least one lateral spot anterior to hypural plate 5
3 (a) Fewer than 17 gill rakers on outer ceratobranchial ..... *C. prostoma*[1,4]
3 (b) More than 17 gill rakers on outer ceratobranchial 4
4 (a) Caudal spot absent; horizontal band distinct ..... *C. boadzulu*[1,2]
4 (b) Caudal spot present; horizontal band indistinct ..... *C. cyaneus*[2,4]
5 (a) Fewer than 18 gill rakers on outer ceratobranchial and three distinct lateral spots 6
5 (b) 18 or more gill rakers on outer ceratobranchial or if fewer than 18 gill rakers, only one lateral spot 9
6 (a) Instestine approximately five times standard length ..... *C. trimaculatus*[1,4]
6 (b) Intestine less than four times standard length 7
7 (a) Supra-pectoral spot entirely below the upper lateral line ..... *C. verduyni*[3]
7 (b) Supra-pectoral spot overlapping the upper lateral line 8
8 (a) Dorsal portion of head flat; 14–18 slender gill rakers (gill-raker length more than twice gill-raker width at base) on outer ceratobranchial ..... *C. azureus*[3]
8 (b) Dorsal portion of head flat; 14–15 sort thick gill rakers (gill-raker length less than twice gill-raker width at base) on outer ceratobranchial ..... *C. mbenjii*[3]
9 (a) Supra-pectoral spot large, covering three or four longitudinal scales 10
9 (b) Supra-pectoral spot small, not covering more than two longitudinal scales 12
10 (a) Supra-anal spot present ..... *C. quadrimaculatus*[1,4]
10 (b) Supra-anal spot absent 11
11 (a) 17–18 gill rakers on outer ceratobranchial ..... *C. pleurostigma*[1,4]
11 (b) 22–25 gill rakers on outer ceratobranchial ..... *C. pleurostigmoides*[1,4]
12 (a) 24–28 gill rakers on outer ceratobranchial ..... *C. likomae*[1,4]
12 (b) 19–23 gill rakers on outer ceratobranchial 13
13 (a) Total number of dorsal-fin elements 29–30 ..... *C. jacksoni*[1,2,4]
13 (b) Total number of dorsal-fin elements 28 or fewer 14
14 (a) Distinct green hue in freshly collected specimens; three scale rows above upper lateral line 15
14 (b) Yellow diamond-shaped spots under scales; four scale rows above upper lateral line ..... *C. borleyi*[1,4]
15 (a) Premaxillary pedicels 27–30% of head length ..... *C. chrysonotus*[4]
15 (b) Premaxillary pedicels 34–40% of head length ..... *C. nkatae*[4]
16 (a) 10–19 gill rakers on outer ceratobranchial 18
16 (b) 21–25 gill rakers on outer ceratobranchial 17
17 (a) Body depth equal to or less than 30% standard length ..... *C. mloto*[1,4]
17 (b) Body depth greater than 30% standard length ..... *C. virginalis*[1,4]
18 (a) 17 or more gill rakers on outer ceratobranchial 19
18 (b) Fewer than 17 gill rakers on outer ceratobranchial 20
19 (a) 15 dorsal spines; 17 gill rakers on outer ceratobranchial ..... *C. eucinostomus*[1,4]
19 (b) 16-17 dorsal spines; more than 17 gill rakers on outer ceratobranchial ..... *C. flavimanus*[4]
20 (a) A total of 22 or more gill rakers on outer arch, including those on the epibranchial, ceratobranchial, and the one between ..... *C. inornatus*[4]
20 (b) Fewer than 22 gill rakers on outer arch 21
21 (a) Distal portion of caudal transparent with yellow spots ..... *C. thinos*[4]
21 (b) Micromelanophores scattered throughout the caudal fin 22
22 (a) 13–15 gill rakers on outer ceratobranchial ..... *C. conophorus*[4]
22 (b) 10–12 gill rakers on outer ceratobranchial ..... *C. cyclicos*[4]

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(JRS, TJL) SCHOOL OF FOREST RESOURCES, PENNSYLVANIA STATE UNIVERSITY, UNIVERSITY PARK, PENNSYLVANIA 16802; AND (KRM) APPALACHIAN ENVIRONMENTAL LABORATORY, UNIVERSITY OF MARYLAND SYSTEM, FROSTBURG, MARYLAND 21532. Submitted 15 Oct. 1992. Accepted 24 Dec. 1992. Section editor: R. Winterbottom.