Geophagus abalios, G. dicrozoster and G. winemilleri (Perciformes: Cichlidae), three new species from Venezuela

HERNÁN LÓPEZ-FERNÁNDEZ *¶ & DONALD C. TAPHORN **

* Section of Ecology and Evolutionary Biology, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX, 77843-2258, USA. E-mail: hlopez@tamu.edu
** Museo de Ciencias Naturales de Guanare, Universidad Nacional Experimental de Los Llanos Occidentales Ezequiel Zamora, Guanare, Portuguesa, 3323, Venezuela. E-mail: taphorn@cantv.net
¶ Author to whom correspondence should be sent

Abstract

We describe three new species of Geophagus from the Orinoco and Casiquiare drainages of Venezuela, bringing the total number of described species in the genus to fourteen, and of Venezuelan species to six. All three species are distinguished from G. grammepareius, G. taeniopareius, G. argyropectus and G. harreri by lacking an infraorbital stripe, which is either reduced to a preopercular mark or is absent. Geophagus abalios n. sp. reaches at least 163 mm SL; it is distinguished from G. dicrozoster n. sp., G. winemilleri n. sp., G. brachybranchus and G. proximus by lacking a preopercular mark. It can be further distinguished from the widely sympatric G. dicrozoster n. sp. by the squamation pattern, and upper jaw teeth arrangement. Preserved specimens of Geophagus abalios are distinguished from other Geophagus species without head markings except G. brokopondo by six vertical, parallel bars on the flank; it is distinguished from G. brokopondo by the anterior three bars, which are dorso-ventrally bisected by a clearer area, giving the impression of two thinner bars, whereas in the latter species all bars are solid; additionally, the sixth bar in G. abalios is elongate and restricted to the dorsal half of the caudal peduncle, above the lower lateral line, and in G. brokopondo the bar covers the entire caudal peduncle. Geophagus abalios is present in the llanos of the Orinoco drainage, reaching the Andean piedmont, the Río Caura in the Guyana Shield, and the higher Orinoco and Casiquiare drainages in Amazonas State. G. dicrozoster n. sp. and G. winemilleri n. sp. bear a preopercular mark, which distinguishes them from G. abalios n. sp., G. brokopondo, G. surinamensis, G. megasema, G. camopiensis, and G. altifrons, which lack head markings. G. dicrozoster n. sp. reaches at least 202 mm SL; preserved specimens are distinguished from other species with a preopercular mark by seven vertical, parallel lateral bars. The species is present in black water tributaries of the Orinoco in the Guyana Shield, and its middle and upper course, as well as in the Casiquiare and the headwaters of the Río Negro. G. winemilleri n. sp. reaches a maximum known size of 195 mm SL; preserved specimens are distinguished from other species with a preopercular mark by four broad, ventro-caudally inclined bars on the flank, plus a fainter bar on the dorsal portion of the caudal peduncle. G. winemilleri is described from the lower Casiquiare
drainage and the headwaters of the Río Negro in southern Venezuela, but may be distributed along the length of the Río Negro.

**Key words:** *Geophagus*, new species, Venezuela, Orinoco, Casiquiare, Río Negro

**Resumen**

Describimos tres especies nuevas de *Geophagus* de las cuencas de los ríos Orinoco y Casiquiare en Venezuela, elevando el número total de especies en el género a catorce, y las especies venezolanas a seis. Las tres especies se distinguen de *G. grammepareius, G. taeniopareius*, *G. argyroystictus* y *G. harreri* por no presentar una franja infraorbital, que está reducida a una marca preopercular o está completamente ausente. *G. abalios* alcanza 163 mm LE; se distingue de *G. dicrozoster* sp. nov., *G. winemilleri* sp. nov., *G. brachybranchus* y *G. proximus* por no presentar una marca preopercular. Además, se puede distinguir del ampliamente simpátrico *G. dicrozoster* por el patrón de escamación y por la distribución de los dientes de la mandíbula superior. Especímenes preservados de *G. abalios* se distinguen de otras especies de *Geophagus* sin marca preopercular, excepto *G. brokopondo*, por seis barras verticales y paralelas en el flanco; se distingue de *G. brokopondo* por las tres barras anteriores, que son bisecadas dorsoventralmente por un área más clara, dando la impresión de dos barras finas, mientras que en la otra especie todas las barras son sólidas; más aún, la sexta barra en *G. abalios* es alargada y restringida a la mitad dorsal del pedúnculo caudal, sobre la línea lateral, y en *G. brokopondo* la barra cubre completamente el pedúnculo. *G. abalios* está presente en los llanos de la cuenca del Orinoco, alcanzando el piedemonte andino, el Río Caura en el Escudo Guayanés y el alto Orinoco y la cuenca del Casiquiare en el Estado Amazonas. *G. dicrozoster* sp. nov. y *G. winemilleri* sp. nov. poseen una marca preopercular que los distingue de *G. abalios* sp. nov., *G. brokopondo*, *G. surinamensis, G. megasema, G. camopiensis* y *G. altifrons*, que carecen de marcas en la cabeza. *G. dicrozoster* sp. nov. alcanza 202 mm LE; especímenes preservados de *G. dicrozoster* se distinguen de otras especies con marca preopercular por poseer siete barras verticales paralelas sobre el flanco. La especie se distribuye en tributarios de aguas negras del Orinoco en el escudo Guayanés, y en sus cursos medio y alto, así como también en el Casiquiare y en las cabeceras del Río Negro. *G. winemilleri* sp. nov. alcanza 195 mm LE; especímenes preservados de *G. winemilleri* se distinguen de otras especies con marca opercular por cuatro barras anchas, inclinadas caudoventralmente en los flancos, y una barra menos visible sobre la porción dorsal del pedúnculo caudal. *G. winemilleri* se describe del curso bajo de la cuenca del Casiquiare y de las cabeceras del Río Negro en el sur de Venezuela, pero podría distribuirse a todo lo largo del Río Negro.

**Palabras clave:** *Geophagus*, especies nuevas, Venezuela, Orinoco, Casiquiare, Río Negro

**Introduction**

Gosse (1975) divided the South American genus *Geophagus* Heckel into several genera based on the number of supraneural bones. *Biotodoma* Eigenmann & Kennedy has 2 supraneurals, *Gymnogeophagus* de Miranda-Ribeiro has 0 and *Geophagus* has 1. Gosse’s definitions were later revised by Kullander (1986), who resurrected *Satanoperca* (Heckel) as distinct from *Geophagus*, and restricted the latter to include only species with paired
caudal extensions of the swimbladder lined by 6–12 ephemal “ribs”, and more caudal than precaudal vertebrae (see also Kullander & Nijsen 1989; Kullander et al. 1992). Kullander’s generic assignments have been corroborated by recent phylogenetic analyses of geophagine cichlids (Kullander 1998; Farias et al. 1999; 2000; 2001). As currently recognized, the genus Geophagus sensu stricto (Kullander 1986; Kullander & Nijsen 1989) includes eleven described species, and numerous others remain unnamed (e.g. Kullander 1986; Kullander et al. 1992; Kullander & Nijsen 1989; Weidner 2000).

Since Kullander (1986) and Kullander and Nijsen (1989), most populations of Geophagus referred to as G. surinamensis (Bloch) (Gosse 1975) have been recognized as different taxa. The Geophagus surinamensis “complex” includes 7 described species (G. surinamensis, G. brokopondo Kullander and Nijsen, G. brachybranchus Kullander and Nijsen, G. camopiensis Pellegrin, G. proximus (Castelnau), G. megasema Heckel and G. altifrons Heckel) and an undetermined number of undescribed species with deep bodies and heads, a mid-flank spot of variable size, and either with infraorbital stripe absent (e.g. G. surinamensis,) or limited to a preopercular black mark (e.g. G. brachybranchus). Geophagus species outside the G. surinamensis complex have a complete infraorbital stripe, including G. grammepareius Kullander and Taphorn, G. taeniopareius Kullander and Royero, G. argyrostictus Kullander, G. harreri Gosse and probably several undescribed species known to the aquarium trade (Weidner 2000).

Originally described from Surinam (Kullander & Nijsen 1989), Geophagus brachybranchus was identified from the Cuyuni drainage by S. O. Kullander and DCT (Taphorn et al. 1997), and is the only described species of the G. surinamensis complex known to occur in Venezuela. Other populations of Geophagus in the country have traditionally been identified as G. surinamensis (e.g. Mago-Leccia 1970; Axelrod 1971; Machado-Allison 1987), which is restricted to the Surinam and Marowijne rivers in eastern Surinam (Kullander & Nijsen 1989), or G. altifrons (Royero et al. 1992; Machado-Allison et al. 1993), which has an Amazonian distribution (Kullander 1986). These populations actually represented three undescribed species: two were identified by S. O. Kullander and DCT (1996 unpubl.) and the third by HLF and DCT (2002 unpubl.) during recent surveys of collections at the Museo de Ciencias Naturales de Guanare. Specimens of these three species appear to have been known for some time in the German aquarium trade, and two of them were referred to as Geophagus ‘stripetail’ or G. ‘Río Negro I’, and G. sp ‘Columbia’, respectively (Weidner 2000). In this paper, we describe these three new species from the Orinoco and Casiquiare drainages of Venezuela; provide maps of their known distribution, and a key for the identification of the Venezuelan species of Geophagus.

Materials and methods

All measurements were taken using dial calipers to the nearest 0.1 mm when linear distance was less than 130 mm, and with a tape measure to the nearest mm when more than
Counts of fin rays and scales were made under a dissecting scope. Counts and measurement procedures follow those described in Kullander (1986) and Kullander and Nijssen (1989). Following Kullander et al. (1992) and Kullander (1996), scales in a horizontal row were counted on the row immediately above that one containing the lower lateral line (E1); rows above E1 (epaxial scales) are numbered E2 and higher, and rows below E1 are numbered H1 (hypaxial scales) and higher (Fig. 1). Vertebral counts were made from x-rayed and/or cleared and stained specimens following protocols in Dingerkus and Uhler (1977) or Taylor and Van Dyke (1985).


**FIGURE 1.** Diagrammatic representation of scale nomenclature, head markings and lateral bar patterns of *Geophagus* as used in this paper. Abbreviations are as follows: E1, first epaxial longitudinal series of scales, used to count number of longitudinal scales; E6, last epaxial longitudinal series of scales; H1–H5, hypaxial longitudinal series of scales; IOS, infraorbital stripe; MLS, mid-lateral spot; POM, preopercular mark; ULL, upper lateral line; LLL, lower lateral line; 1–7, lateral bars. Scale nomenclature after Kullander (1992, 1996). Infraorbital, preopercular and mid-lateral black markings are observable both in live and preserved specimens; lateral bar patterns are generally visible only on preserved specimens, and sometimes on stressed live specimens.
FIGURE 2. Diagrammatic representation of preopercular markings and lateral bars distinguishing Geophagus species within the G. surinamensis complex. a, G. dicrozoster, n. sp.; b, G. abalios n. sp.; c, G. winemilleri n. sp.; d, G. brokopondo; e, G. brachybranchus; f, G. surinamensis; g, G. proximus; h, G. megasema; i, G. camopiensis, and j, G. altifrons. Preopercular markings are visible in both live and preserved individuals; lateral bar patterns are generally visible only in preserved specimens.
Geophagus abalios n. sp.  
(Figs. 2b, 3–5, 9)


**Diagnosis.** The lack of head markings distinguishes *G. abalios* n. sp. from *Geophagus grammepareius*, *G. taeniopareius*, *G. harreri* and *G. argyroysticus*, which have a complete infraorbital stripe, and from *G. dicrozoster* n. sp., *G. winemilleri* n. sp., *G. brachybranchus* and *G. proximus*, which have a black preopercular marking. Preserved specimens of *Geophagus abalios* can be distinguished from all other *Geophagus* species without head markings except *G. brokopondo* by the possession of six vertical, parallel bars on the flank (Fig.1, 2); it can be distinguished from *G. brokopondo* by the anterior three bars, which are medially bisected by a clearer area, giving the impression of two thinner bars, whereas in the latter species all bars are solid; additionally, the sixth bar in *G. abalios* is elongate and restricted to the dorsal half of the caudal peduncle, above the lower lateral line, and in *G. brokopondo* the line covers the entire caudal peduncle (Fig. 2b and 2d).

**Description.** Based on holotype (163.0 mm SL) and 16 paratypes 45.5–192.0 mm SL with notes on variation among smaller specimens. Measurements and counts are summarized in Table 1. Sexes appear to be isomorphic.

Shape. Moderately elongate; dorsal outline more convex than ventral outline; head slightly broader ventrally than dorsally, chest flat; specimens 45.0 mm SL and smaller more elongate, with rounder nape; interorbital area moderately concave. Dorsal head profile straight, slightly concave in front of orbit, straight or slightly convex in specimens smaller than 112.0 mm SL, then sloping to dorsal-fin origin; dorsal-fin base descending, slightly convex to last ray, dorsal caudal peduncle forming a moderately concave curve to
caudal-fin base. Ventral head profile straight, slightly descending to pelvic-fin insertion; chest slightly convex in one specimen 192.0 mm SL; straight, horizontal from pelvic-fin insertion to origin of anal fin; anal-fin base straight, ascending; ventral caudal peduncle straight to slightly concave, slightly ascending or horizontal in specimens 45.0 mm SL and smaller; ventral caudal peduncle 1.5–1.6 times in dorsal. Lips moderately wide, lower without caudally expanded fold (see Kullander et al., 1992, Fig. 3). Maxilla reaching at most one third of the distance between nostril and orbit; ascending premaxillary process reaching slightly above midline of orbit. Opercle, preopercle, cleithrum, postcleithrum, and post-temporal lacking serration.

Scales. E1 33(4), 34(10), 35(3); scales between upper lateral line and dorsal fin 5.5–7.5 anteriorly, 2.5 posteriorly. Scales between lateral lines 2. Scales on upper lateral line 21(1), 22(4), 23(9), 24(1) and lower lateral line 13(1), 14(3), 15(6), 16(5). Anterior 1/3–1/2 of cheek naked, remainder with ctenoid scales; cheek scale rows 8–9. Opercle and sub-opercle covered with ctenoid scales. Interopercle with ctenoid scales caudally, otherwise naked. Single postorbital column of cycloid scales. Occipital and flank scales ctenoid. Circumpeduncular scale rows 7 above upper, 9 below lower lateral lines, ctenoid.

Fin scales. Pectoral and pelvic fins naked. Dorsal fin with double or triple columns of ctenoid scales along interradial membranes to one third to one half of fin height. Scaly pad at base of dorsal fin formed by irregularly arranged small, ctenoid scales extending from first spine to fifth to seventh soft ray; specimens 55.5 mm SL or smaller, pad scales are cycloid or moderately ctenoid. Anal fin scaled on anterior section of soft portion, scales ctenoid, arranged in a single column along interradial membranes to one quarter to one third of fin height; anal fin naked in specimens 55.5 mm SL or less. Scaly pad on base of anal fin, scales small, ctenoid. Caudal fin entirely scaled except the tip of rays, and membranes between D3 and V3, scales ctenoid. Accessory caudal fin extension of lateral line between V4–V5, absent on dorsal lobe.

Fins. Dorsal XVII-11(1), XVII-12(1), XVIII-10(2), XVIII-11(6), XVIII-12(5), XIX-11(2); anal III-8(14), III-9(3). Dorsal spines increasing in length from first to sixth, equal length to ninth, then slightly shorter; lose membranes behind spine tips (lappets) acutely pointed, up to 1/3 the length of spines. Soft portion moderately expanded and pointed, reaching about 1/3 of caudal-fin length, rays 3–6 longest but not produced into filaments; specimens 56.0 mm SL and smaller with rounded soft portion, not quite reaching caudal-fin base. Anal fin pointed, with 2nd and 3rd soft rays slightly produced, not reaching caudal fin or barely beyond its base in specimens 90.6 and 192.0 mm SL. Caudal fin emarginate with lobes of approximately the same length and without filaments; one specimen 112.1 mm SL with slightly produced rays D8 and V8. Pectoral fin elongate, more or less triangular, longest at 4th ray, reaching 1st or 2nd anal-fin soft rays, then progressively shorter ventrally. Pelvic fin triangular, first ray produced into a filament reaching 5th anal-fin soft ray; in one specimen 112.1 mm SL reaching over 1/2 of caudal-fin length; specimens 45.5 mm SL or less with rays only slightly produced, reaching at most 1st spine of anal fin.
Teeth. Outer row of upper jaw with 10–28, blunt, slightly recurved unicuspid teeth; much larger than in inner rows, extending along most of premaxillary length. 2–3 inner rows, separated by a clear gap from outer row; teeth very thin, pointed, straight or slightly recurved unicuspids. Inner rows parallel to outer over its length, not forming a tight pad. Outer row of lower jaw with 6–25 unicuspid, blunt, slightly recurved unicuspids; medial 4–5 teeth larger than rest on outer row, cylindrical, slightly recurved, blunt and more labially positioned than rest of row. Inner rows 3–4, only on medial third of dentary, separated
from outer row by distinct gap; teeth long, thin, straight or slightly recurved, much smaller than outer row.

Gills. External rakers on first gill arch: 9(5), 10(3) on epibranchial lobe, 1 in angle and 12(7), 13(2) on ceratobranchial, none on hypobranchial. Microbranchiospines on the outer face of second to fourth arches. Gill filaments with narrow basal skin cover.

Tooth plates. Lower pharyngeal tooth plate elongate; width of bone 80% of length; dentigerous area 80% of width; 30 teeth in posterior row, 10 in median row. Anteriormost teeth subconical or subcylindrical, erect; most teeth laterally compressed and with small, low ridge rostrally, cusps on caudal half of teeth; lateral marginal teeth on anterior half like anteriormost, on caudal half smaller and thinner; posteromedial teeth much larger, nearly round in circumference, posterior cusps, almost blunt (Fig. 5). Ceratobranchial 4 with 4 toothplates with 11, 28, 6 and 4 teeth.


Color pattern in alcohol (Fig. 3). Base color grayish yellow; nape, snout and upper lip darker gray, fading caudally to base color towards cheek; lower lip yellowish white. No markings on the head, preopercule immaculate. Opercle darker on dorsal third; lower half of opercle and subopercle dusky yellow; silvery white in some specimens, probably depending on preservation. Ventrally, gill cover yellowish white; white in some specimens; branchiostegal membrane grayish. Chest white laterally and ventrally; in best preserved specimens white extends ventrally to base of caudal fin and to scale row H3 on caudal peduncle (Fig. 1). Flanks with 6, dorso-ventrally directed, yellowish-gray bars fading or disappearing ventrally (Fig. 2b). Bar 1 expands from the 4th or 5th predorsal scale to the base of the 4th dorsal-fin spine; its anterior edge delimited by the extrascapular and its posterior edge descending vertically and disappearing ventrally at the pectoral-fin insertion. Bar 2 extends between the 6th and 8th dorsal-fin spines, and runs vertically to H7.
Bar 3 extends between the 10th and 13th dorsal-fin spines, and runs parallel to bar 2, fading ventrally at H6–H7. Bars 1–3 are generally bisected dorso-ventrally by a lighter column about 1 scale wide, giving the appearance of being two narrow bars in some specimens; this feature may be lost on poorly preserved specimens. A diffuse, blackish medial spot coincides with bar 3, extending rostro-caudally between scales 11–12 and 14–15 of E3 and dorso-ventrally between E3 and E1, such that the upper lateral line traverses the uppermost row of scales of the spot. Bar 4 extends between the bases of dorsal-fin spines 13–14 to 16–18, descends vertically and fades at H4–H5. Bar 5 extends between the first soft ray and ray 4–5 of dorsal fin, it descends vertically and disappears at H3–H4; in other specimens the bar is located between the last dorsal-fin spine and ray 3. Bar 6 extends from the base of the 6–7 (4–5 in some specimens) dorsal-fin rays and extends to the base of the caudal fin; bar is restricted to dorsal portion of caudal peduncle, above lower lateral line, and is longer horizontally than vertically (Fig. 2b).

Dorsal fin dusky, lappets dark gray or blackish, forming a dark edge along fin; soft and posterior third of spinous portion white-spotted on interradial membranes; four distinguishable longitudinal, parallel, grayish stripes alternate with light stripes along most of fin, turning almost hyaline rostrally; number of stripes increases with size to 6 in a 192.0 mm SL specimen. Anal fin hyaline to slightly dusky; 4 longitudinal, parallel gray stripes along soft portion of fin (5 in largest specimen). Caudal fin dusky, with round, whitish spots increasing in size towards dorsal edge; spots develop into horizontal stripes in larger specimens and a 192.0 mm SL specimen shows virtually no spots; specimens 55.5 mm SL and smaller with 4 dark, vertical bars. Pectoral fin immaculate. Pelvic fin whitish gray, dusky distally; dusky in largest specimen (192.0 mm SL), spine and first ray whitish gray to dusky.

**Live colors** (Fig. 4). Background color greenish gray, breeding specimens more metallic gray. Head without markings except for iridescent blue on the upper lip, continued as a stripe extending to the corner of the preopercule, and a slight marking of the same color on the ventral edge of orbit. A variable number of iridescent blue spots on the preopercule apparently limited to breeding specimens. Six yellow stripes extend between the base of dorsal and H4–5; in adult, breeding specimens, dorsalmost stripes appear as brownish-orange vermiculations and spots. Ventrum distinctly white; breeding adults with bright orange or red chest. Dorsal and anal fins reddish with faint iridescent blue horizontal banding that turns brighter during breeding; caudal brownish red with iridescent blue spots and bands in no clear pattern; pelvic reddish orange with iridescent blue banding, first ray white or very light blue. An aquarium photograph in Weidner (2000: 148, Fig. 1) of an unidentified *Geophagus* from Venezuela is undoubtedly of a mature adult of *G. abalios*.

**Distribution and habitat.** (Fig. 9) *Geophagus abalios* is commonly found in black or clear water rivers in the llanos, and is known from the Apure, Cinaruco-Capanaparo, and Aguaro-Guariquito drainages. Its current northern-most collection locality is “Las
Majaguas” dam in the Río Cojedes, where it was probably introduced by recommendation of the Venezuelan ichthyologist A. Fernández-Yépez. According to his account (Fernández-Yépez and Anton, 1966), Geophagus species were not naturally present in the reservoir, and he recommended the introduction of “Geophagus surinamensis” along with some other species, presumably for sport fishing purposes. G. abalios reaches the Andean piedmont to the west, and is the only Geophagus found in clear to white water seasonal lagoons along the main-stem of the Orinoco to the east (Rodríguez and Lewis Jr. 1990; 1994). The species appears restricted to the Caura drainage on the Guyana Shield, but it extends into the tributaries of the middle and upper Orinoco, including the Ventuari, Mavaca, and along the Río Casiquiare, nearly to the headwaters of the Río Negro.

**Etymology.** From the Greek α, not or without and βαλίος, spotted. In reference to the lack of preopercular markings. To be regarded as an adjective in masculine form.

*Geophagus dicrozoster* n. sp.

(Figs. 2a, 6–9)

**Holotype.** MCNG 40996, 193.0 mm SL; Venezuela: Apure: Río Cinaruco: Laguna Larga (6.5339°N 67.4150°W); D.A. Arrington and J. Arrington, 13 April 1999.


**Diagnosis.** A preopercular mark distinguishes *Geophagus dicrozoster* n. sp. from *G. grammepareius*, *G. taeniopareius*, *G. argyrostictus* and *G. harreri*, which have a complete infraorbital stripe (Fig. 1), and from *G. abalios* n. sp., *G. brokopondo*, *G. surinamensis*, *G. megasema*, *G. camopiensis*, and *G. altifrons*, which lack head markings. Preserved specimens of *G. dicrozoster* can be distinguished from other species with preopercular mark by the possession of seven vertical, parallel lateral bars, as opposite to *G. winemilleri* n. sp. (4 bars) and *G. brachybranchus* and *G. proximus* (no bars) (Fig. 2).

**Description.** Based on holotype (193.0 mm SL) and the 19 paratypes 63.4–202.0 mm SL with notes on variation among smaller specimens. Measurements and counts are summarized in Table 1. Sexes appear to be isomorphic.

**TABLE 1.** Morphometrics of *Geophagus winemilleri*, *G. abalios*, and *G. dicrozoster*. Numbers in bold highlight morphometric differences among the species.

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**Shape.** Moderately elongate; dorsal outline more convex than ventral outline; head broader ventrally than dorsally; specimens 63.4 mm SL and smaller more elongate; interorbital area moderately concave. Dorsal head profile moderately convex, ascending to dorsal-fin origin, except in front of orbit where slightly concave, in specimens smaller than 65.0 mm SL, straight from orbit to dorsal-fin origin; dorsal-fin base descending, arched to
last ray, then forming a horizontal, moderately concave line to caudal-fin insertion. Ventral head profile straight, slightly descending to chest; slightly convex to pelvic-fin insertion; straight, horizontal from pelvic-fin insertion to origin of anal fin; anal-fin base slightly convex, ascending; ventral caudal peduncle moderately concave, slightly ascending or horizontal in specimens 64.0 mm SL and smaller. Lips moderately wide, lower with slightly caudally expanded fold (see Kullander et al., 1992, Fig. 3). Maxilla reaching 1/3–2/3 of the distance between nostril and orbit; ascending premaxillary process reaching slightly above midline of orbit. Opercle, preopercle, cleithrum, postcleithrum, and posttemporal lacking serration.

Scales. E1 34(3), 35(7), 36(8), 38(2); scales between upper lateral line and dorsal fin 6.5–8.5 anteriorly, 2.5–3.5 posteriorly. Scales between lateral lines 2. Scales on upper lateral line 19(1), 20(7), 21(8), 22(4) and lower lateral line 14(1), 15(4), 16(3), 17(9), 18(3). Anterior half of cheek naked, remainder with ctenoid scales; cheek scale rows 9–10. Opercle covered with ctenoid scales. Caudo-ventral area of subopercle naked, remainder with ctenoid scales. Interopercle with cycloid scales caudally. Single postorbital column of ctenoid scales, particularly in largest specimens. Occipital and flank scales ctenoid. Circumpeduncular scale rows 7–9 above upper, 9–11 below lower lateral line, ctenoid.

Fin scales. Anal, pectoral and pelvic fins naked. Dorsal fin scaled on spinous and soft portions, scales ctenoid, and arranged in double or triple columns along interradial membranes up to one third to one half of fin height. Scaly pad at base of dorsal formed by irregularly arranged small, ctenoid scales extending from first spine to third to seventh soft ray. Anal scaleless, scaly pad on base of anal absent, at most a few small scales on base of anterior portion of fin, moderately ctenoid. Caudal fin scaled along its entire surface, except the tip of rays, and part of membranes between D3 and V3, scales ctenoid. Accessory caudal fin extension of lateral line between V4–V5, absent on dorsal lobe.

Fins. Dorsal XVI-12(2), XVI-13(1), XVII-11(2), XVII-12(9), XVII-13(1), XVIII-11(2), XVIII-12(2); anal III-7(1), III-8(18), III-9(1). Dorsal-fin spines increasing in length from first to sixth, equal length to ninth, then slightly shorter; lappets pointed, short; soft portion round, reaching just beyond caudal-fin insertion; moderately pointed in a 202.0 mm SL, and reaching about a third of caudal-fin length; rays 4–6 longest but not produced into filaments; in specimens 63.0 mm SL and smaller dorsal fin not reaching caudal-fin insertion. Anal fin round, moderately pointed in largest specimens, with rays 2–5 longest, not reaching caudal fin or barely beyond its base in largest specimens. Caudal fin emarginate with lobes of approximately the same length and without filaments; one specimen 120.2 mm SL with slightly produced ray D8. Pectoral fin elongate, more or less triangular, longest at 4th ray, reaching 1st or 2nd anal-fin spines, then progressively shorter ventrally. Pelvic fin triangular, first ray produced into a filament reaching 3rd anal-fin soft ray; in a specimen 202.0 mm SL almost reaching caudal-fin insertion; specimens 45.5 mm SL or less with slightly or not produced rays, reaching at most 1st anal-fin spine.
Teeth. Outer row of upper jaw with 17–26 approximately cylindrical, frequently blunt, slightly recurved, unicuspids teeth; larger than in inner rows, extending along most of premaxillary length; 6–7 inner rows, separated by a clear gap from outer row; teeth on inner row thin, slightly recurved unicuspids, forming a pad. Outer row of lower jaw with 16–22 blunt, slightly recurved unicuspids teeth; median 3 teeth more labially positioned than rest of row; inner rows 6 (4 in small specimens), forming a pad, separated from outer row by distinct gap; teeth thin, slightly recurved unicuspids.

Gills. External rakers on first gill arch; 10(11), 11(1) on epibranchial lobe, 1 in angle and 12(3), 13(7), 14(2) on ceratobranchial, none on hypobranchial. Microbranchiospines on the outer face of second to fourth arches. Gill filaments with narrow basal skin cover.

Tooth plates. Lower pharyngeal tooth plate elongate (Fig. 8); width of bone 80–82% of length; dentigerous area 80% of width; 28 teeth in posterior row, 11 in median row. Anteriormost teeth subconical, laterally compressed and erect; cusps posterior, slightly curved rostrad, small rostral edge ridge; lateral marginal teeth with same cusp pattern, teeth thinner and more laterally compressed towards caudal edge of plate; posteromedial teeth much larger, almost cylindrical, cusps posterior, almost blunt. Ceratobranchial 4 with 5 toothplates with 4–6, 5–7, 5–13, 6–11 and 3–7 teeth; one of two specimens with 7 toothplates with 6, 4, 5, 5, 4, 3 and 3 teeth on left side.

Vertebrae. 14+18=32(1), 14+19=33(10), 15+18=33(3), 15+19=34(1); 11–12 epihemal ribs.

**FIGURE 7.** *Geophagus dicrozoster.* Uncatalogued specimen, young adult immediately after capture at the type locality: Laguna Larga, Rio Cinaruco, Apure State, Venezuela. 6.3335°N, 67.2471°W.

**Color pattern in alcohol** (Fig. 6). Background color grayish yellow; nape, snout, upper lip and naked portion of cheek darker gray, scaled portion of cheek lighter; lower lip yellowish white. Vertical, blackish mark in the corner of the preopercule, continued into the interopercule as a faint spot; indistinguishable or faded in specimens smaller than 65.0
Operculum with a dark, brown spot on dorsal edge, reaching first scale of upper lateral line, otherwise uniformly dusky yellow or silvery white in some specimens probably depending on preservation. Ventrally, gill cover dusky yellow or yellowish white in some specimens; branchiostegal membrane also yellowish, grayish brown in one specimen 202.0 mm SL. Chest yellow laterally and ventrally, white in many specimens, juveniles with distinctive silvery-white chest region; in best preserved specimens dusky yellow or white extends ventrally to base of caudal fin and to H3 on caudal peduncle flanks. Flanks with 7, dorso-ventrally directed, dark-gray bars fading or disappearing ventrally (Fig. 2a). Bar 1 expands from the 7th–8th predorsal scale to the base of the dorsal fin between spines 4–5 forming an inverted triangle; its anterior edge roughly delimited by the extrascapular and its posterior edge descending ventrally to the pectoral-fin insertion. Bar 2 extends between the base of dorsal-fin spines 6–7 and 9, and runs vertically to H6–7. Bar 3 extends between the base of dorsal-fin spines 10–11 and 12–13, descends ventrally and slightly caudally oriented, fading progressively to H6–7. A well-demarcated, black medial spot is located on bar 3, extending rostro-caudally between scales 11 and 14–15 of E3 and dorso-ventrally between the lower half of E4 and E1, such that the upper lateral line traverses the dorsal 1/4–1/3 of the spot. Bar 4 extends between the bases of dorsal-fin spines 14–15 to 17, and descends ventro-caudally to the upper lateral line, where it merges with bar 5 such that the two bars form a “Y” shaped figure (Fig. 2a); in specimens 50.0 mm SL or less, bar 4 may appear as a spot on the base of the dorsal, not quite reaching bar 5. Bar 5 extends between the base of dorsal-fin spine 18 and ray 1 or rays 1–2 and rays 4–5, it descends vertically fading at H1–2. Bar 6 extends from the base of the 7–8 dorsal fin rays to the second postdorsal scale in the caudal peduncle, descends vertically and fades at H1–2. Bar 7 covers the area between the last 4–5 lower lateral line scales and the base of the caudal fin, disappearing ventrally at H2.

**FIGURE 8.** *Geophagus dicrozoster.* Occlusal aspect of lower pharyngeal tooth plate; from MCNG 40623, 88.4 mm SL; scale bar 1 mm.
Dorsal fin dusky, lappets dark gray or blackish, forming a faint dark edge along fin; dorsal fin immaculate except a few indistinct whitish spots in the membranes of caudal half of soft portion; in specimens 63.0 mm SL or smaller, three dusky longitudinal, parallel stripes alternate with light stripes along soft portion of dorsal fin. Anal fin hyaline to slightly dusky; 4 longitudinal, parallel gray bands along soft portion; largest specimen with dark gray lappets. Caudal fin gray-brown, with whitish longitudinal bands of variable length and elongate spots, forming no evident pattern; specimens up to 85.0 mm SL with 4 dark, vertical bands that gradually turn into the above described pattern with increasing size. Pectoral fin immaculate. Pelvic fin dusky, darker distally; spine and first ray whitish gray to dusky.

**Live colors** (Fig. 7). Dark markings as in alcohol specimens. Background color yellowish olive green; head silvery with yellow on gill cover, snout gray, upper lip iridescent blue extending behind lips to preopercular mark. Dorsal fin reddish with faint iridescent blue spots, especially on the soft portion; some specimens with proximal third of spiny portion yellow, probably due to breeding condition; anal fin red or reddish with distinctive iridescent blue horizontal banding; caudal fin reddish with a variable pattern of iridescent blue stripes and spots. Five to seven faint, yellow horizontal stripes alternating with olive green along body, but not always distinct.
**Distribution and habitat** (Fig. 9). *Geophagus dicrozoster* is common in the black waters of the Caura and Caroni drainages of the Guyana Shield; it is also present in all major tributaries of the middle and upper Orinoco, including the drainages of the Cata-niapo, Ventuari, Atabapo, Ocarno, and Mavaca, as well as the Casiquiare and the headwaters of the Río Negro. In the llanos, *G. dicrozoster* is restricted to the moderately black-watered Río Cinaruco, although further collections will likely show its presence in the nearby Río Capanaparo and its tributaries. No specimens have been captured from white water, or from llanos clear water drainages as the Aguaro-Guariquito.

**Etymology.** From the Greek *dikros*, forked, and *zoster*, belt. Given in reference to the “Y” formed by lateral bars 4 and 5. To be regarded as an adjective in masculine form.

*Geophagus winemilleri* n. sp.

(Figs. 2c, 10–13)


![Figure 10](Image)

**FIGURE 10.** *Geophagus winemilleri*. Holotype, MCNG 35486, 195.0 mm SL. Venezuela: Amazonas: Río Siapa: Laguna Yocuta, (2.1347° N 66.3742° W).

**Paratypes.** MCNG 12227, 9, 24.5–47.3 mm SL (4 measured); Venezuela: Amazonas: Río Casiquiare: El Porvenir, approx. 60 Km. from confluence with Río Negro (2.0833° N 66.5° W); L. Nico, E. Conde, P. Cardozo, G. Aymard and B. Stergios, 15 April 1985. — AMNH 233637 (ex-MCNG 12301), 1, 188.0 mm SL; Venezuela: Amazonas: Caño Emoni, 2 Km. upstream from confluence with Río Siapa (2.1167° N 66.3333° W); L. Nico, E. Conde, P. Cardozo, G. Aymard and B. Stergios, 17 April 1985. — MCNG 37858, 29, 19.2–149.0 mm SL (5 measured); Venezuela: Amazonas: Río Casiquiare: Isla Cuamate,

**Diagnosis.** A preopercular mark distinguishes *Geophagus winemilleri* from *G. grammipareius*, *G. argyrodictus* and *G. harreri*, which have a complete infraorbital stripe, and from *G. abalios* n. sp., *G. brokopondo*, *G. surinamensis*, *G. megasema*, *G. camopiensis*, and *G. altifrons*, which lack head markings. Preserved specimens of *G. winemilleri* can be distinguished from other species with preopercular mark by the possession of 4 ventrally-inclined, parallel lateral bars, as opposite to *G. dicrozoster* n. sp. (7 bars) and *G. brachybranchus* and *G. proximus* (no bars) (Fig. 2).

**Description.** Based on holotype (195.0 mm SL) with notes on variation in 14 paratypes 41.8 to 188.0 mm SL. Measurements and counts are summarized in Table 1. Sexes appear to be isomorphic.

**Shape.** Moderately elongate; dorsal outline more convex than ventral outline; head broader ventrally than dorsally; specimens 45.0 mm SL and smaller with rounder nape; interorbital area moderately concave. Dorsal head profile slightly curved above upper lip, then straight, steeply ascending to orbit, slightly convex or straight (specimens smaller than 118.0 mm SL) in front of orbit, then sloping to dorsal-fin origin; descending, slightly convex to last ray of dorsal fin, then straight, almost horizontal to caudal-fin base. Ventral head profile straight, slightly descending; chest moderately convex; straight, horizontal from pelvic-fin insertion to origin of anal fin; anal-fin base straight, slightly ascending; ventral caudal peduncle straight, slightly ascending; caudal peduncle about 1.5 times longer ventrally than dorsally. Lips moderately wide, lower with slightly caudally expanded fold (see Kullander et al., 1992, Fig.3). Maxilla not quite reaching middle vertical line between nostril and orbit; ascending premaxillary process reaching lower half of orbit. Opercle, preopercle, cleithrum, postmaxillary process reaching lower half of orbit. Opercle, preopercle, cleithrum, postcleithrum, and post-temporal lacking serration.

**Scales.** E1 32(1), 34(5), 35(9); scales between upper lateral line and dorsal fin 6.5–7.5 anteriorly, 2.5 posteriorly. Scales between lateral lines 2. Scales on upper lateral line 21(1), 22(4), 23(5), 24(3), 25(2) and lower lateral line 13(1), 14(5), 15(5), 16(2). Anterior 1/3 to 1/2 of cheek naked, remainder with ctenoid scales; cheek scale rows 7–8. Opercle and subopercle covered with ctenoid scales; interopercle naked except caudo-dorsal region with ctenoid scales. Single postorbital column of mostly ctenoid scales. Occipital and flank scales ctenoid. Circumpeduncular scale rows 7 above upper, 9 below lower lateral lines, ctenoid.

**Fin scales.** Anal, pectoral and pelvic fins naked. Dorsal fin scaled in spinous and soft portions, scales ctenoid, arranged in double or triple columns along interradial membranes.
to $\frac{1}{4} - \frac{1}{2}$ of fin height. Scaly pad at base of dorsal fin formed by irregularly arranged, small, ctenid scales extending from 2nd or 3rd spine to 5th or 6th ray. Reduced scaly pad on anterior portion of base of anal fin, from second spine to second or third ray, scales small, ctenid. Caudal fin scaled in its entire surface, except the tip of rays, and membranes between D2 and V2, scales ctenid. Accessory caudal fin extensions of lateral line between D3–D4 and V4–V5.

Fins. Dorsal XVIII-10(1), XVIII-11(4), XVIII-12(2), XIX-10(2), XIX-11(5), XIX-1(1); anal III-7(2), III-8(13). Dorsal spines increasing in length from first to sixth, equal length to ninth, then slightly shorter; lappets acutely pointed, up to $\frac{1}{2}$ the length of spines. Soft portion pointed, reaching the base of caudal fin, except for rays 4–5, reaching about $\frac{1}{2}$ of caudal-fin length; specimens smaller than 76.3 mm SL with rounded soft portion, not quite reaching caudal-fin insertion. Anal fin with 3rd soft ray moderately produced, reaching about $\frac{1}{4}$ of caudal-fin length, otherwise scarcely reaches base of caudal fin. Caudal fin emarginate with lobes of approximately the same length and without filaments in studied specimens. Pectoral fin elongate, more or less triangular, longest at 4th ray, reaching 1st or 2nd anal-fin soft rays, then progressively shorter ventrally. Pelvic fin triangular, first ray produced into a filament reaching 1/3 of caudal peduncle length; in one specimen 149.0 mm SL reaching 1/3 of caudal-fin length; specimens 45.5 mm SL or less without produced rays, not reaching base of anal fin.

Teeth. Outer row of upper jaw with 19–31, slightly recurved, unicuspid teeth; slightly larger than in inner rows, extending along most of premaxillary length. Three to four inner rows with no clear gap separating them from outer row; teeth unicuspid, very thin, pointy, straight or slightly recurved. Inner rows parallel to outer on all its length, not forming a pad. Outer row of lower jaw with 7–28 unicuspid, blunt, slightly recurved, unicuspids; outer row restricted to median 1/3 of dentary length in holotype and large specimens, but extending farther in specimens 118.0 mm SL and smaller. Inner rows 3–4, separated from outer row by distinct gap; teeth long, thin, straight or slightly recurved unicuspids, smaller than outer row, and forming a pad on median region of dentary.

Gills. External rakers on first gill arch; 9(2), 10(4), 11(4) on epibranchial lobe, 1 in angle and 11(1), 12(6), 13(3) on ceratobranchial, none on hypobranchials. Microbranchiospines on the outer face of second to fourth arches; gill filaments with narrow basal skin cover.

Tooth plates. Lower pharyngeal tooth plate elongate (Fig. 12); width of bone 84% of length; dentigerous area 76% of width; 30 teeth in posterior row, 11 in median row. Anteriormost teeth subconical, erect, laterally compressed; cusps on caudal half, slightly curved anteriorly, small rostral edge ridge; lateral marginal teeth as anteriorly on rostral edge, gradually flatter and smaller caudally; posteromedial teeth much larger, nearly round in circumference, medial or slightly posterior cusps, almost blunt. Ceratobranchial 4 with 5 toothplates with 4, 14, 6, 6 and 2 teeth.

Vertebrae. 14+19=33(1), 14+20=34(1), 15+19=34(13); 11–13 epihemal ribs.
**Color pattern in alcohol** (Fig. 10). Base color grayish yellow; nape, snout and upper lip dark gray, fading caudally to base color towards cheek; lower lip yellowish white. The only marking on the head is a vertical, dark mark in the corner of the preopercule, roughly parallel to its caudal edge, fading ventrally but continued into the interopercule in large specimens; indistinguishable or faded in specimens smaller than 70 mm SL. Gill cover slightly darker than base color. Flanks with four, broad, ventro-caudally directed, yellowish-gray bars running from dorsal to ventral regions and disappearing below the lower lateral line (Fig. 2c). Bar 1 expands from the 4th or 5th scale, anterior to dorsal-fin origin, to the base of the 5th or 6th dorsal-fin spine, extends over the anterior portion of the flank and disappears in the region caudal to the pectoral-fin insertion. Bar 2 extends from the 7th or 8th to the 11th or 12th dorsal-fin spine, runs parallel to bar 1 and disappears approximately at the level of H1. A blackish medial spot coincides with bar 2, extending rostro-caudally between the scales 10 and 13 of E3 and dorso-ventrally between the lower half of E3 and E1, such that the upper lateral line borders the dorsal edge of the spot. Bar 3 extends between the 13th or 14th dorsal-fin spine to the 1st or 2nd soft ray, and runs parallel to bar 2 to H1 or H2, where it fades. Bar 4 extends between the base of the 3rd and the last dorsal-fin ray, and disappears in H1; in some specimens bar 4 can start at the base of the 1st or 2nd dorsal-fin ray and then appears merged with bar 3 at its base, but it is clearly separated ventrally (Figs. 1, 2c). A fifth, faded vertical bar can generally be distinguished covering the caudal-most 4 or 5 columns of scales of the caudal peduncle, but this bar tends to turn into a grayish colored area in larger specimens.

Dorsal fin hyaline to smoky, lappets dark gray or blackish; soft portion with white spotting on the interradial membranes, forming a more or less parallel pattern of horizontal stripes; in specimens 149.0 mm SL and smaller, 3 longitudinal, parallel, grayish stripes alternate with hyaline stripes along most of the dorsal fin, fading into an increasingly indistinguishable pattern rostrally. Anal fin dusky to grayish; two longitudinal, parallel darker stripes along soft portion of fin. Caudal fin dusky, with indistinct pattern ranging from round spots to longitudinal, whitish stripes, or a combination of both; specimens 45.5 mm SL and smaller with 2 or 3 blackish, vertical bands. Pectoral fin immaculate. Pelvic fin dusky to dark gray, spine and first ray whitish to slightly dusky.

**Live colors** (Fig. 11). Live specimens show the same dark markings as described for preserved individuals. Snout gray turning bluish gray in the cheek, gill cover yellow with iridescent blue spots on each scale, lips yellowish white. Flanks are bluish silver with five longitudinal yellow stripes between base of dorsal fin and H1. Dorsal and anal fins brownish red with iridescent blue longitudinal banding; pelvic fin bright red with iridescent blue banding, first ray white; caudal fin red, with large iridescent blue to white spots. An aquarium picture in Weidner (2000: 125, Fig. 3: *Geophagus* sp. “Rio Negro I”) shows unpaired fins and pelvic with a much brighter red than specimens photographed shortly after capture in the wild (HLF pers. obs.).
FIGURE 11. *Geophagus winemilleri*. AMNH 233638, adult paratype immediately after capture at comunidad Punta de Barbosa, Río Negro headwaters, Amazonas State, Venezuela. 1.9844°N, 67.1183°W.

FIGURE 12. *Geophagus winemilleri*. Lower pharyngeal toothplate in occlusal view, from MCNG 12227, 41.7 mm SL; scale bar 1 mm.
**Distribution and habitat.** *Geophagus winemilleri* is an uncommonly caught species (a revision of nearly 400 lots of *Geophagus* at MCNG resulted in only 6 lots of this species), known only from the black waters of the lower Casiquiare drainage and the headwaters of the Río Negro in southern Venezuela (Fig. 13). The scarcity of collections does not allow determining whether the species reaches the Orinoco main-stem. Individuals of this species are commonly sold in the market at the town of Barcelos, Brazil, in the middle-course of the Río Negro (HLF pers. obs.). An undescribed species known in the German aquarium trade as *G.* sp. “Río Negro I” or *G.* sp. “stripetail” (Weidner 2000) corresponds well with the characters of *G. winemilleri*; according to Weidner’s locality data, the species might extend as south as the Archipelago das Anavilhanas, near the confluence of the Río Negro with the Amazonas.

**FIGURE 13.** Known distribution area of *Geophagus winemilleri* n. sp. (▲), *G. grammepareius* (■), and *G. taeniopareius* (●) in Venezuela. One dot may represent more than one collection locality.

**Etymology.** Named for Dr. Kirk O. Winemiller, who led the field expeditions to the Río Casiquiare region during which most of the type specimens of *G. winemilleri* were collected, and in recognition of his nearly two decades of contributions to ecology and tropical fish biology, many of which have been based on Venezuelan fishes.
Key to the Venezuelan species of *Geophagus*

1  Infraorbital stripe complete (Fig. 1), extending from ventral edge of orbit to edge of preopercule or dorsal half of interopercule .................................................................  2
- Infraorbital stripe absent, or reduced to a dark mark on preopercule (Fig. 1) .............. 3
2  Dorsal fin base with sheath of scales; faint horizontal stripes on flank *G. taeniopareius*  
- Dorsal fin base without sheath of scales; no horizontal markings on flank ...................  

3  Base of gill filaments on first gill arch largely covered by broad flap of skin; no discernible lateral bars on preserved specimens (Fig. 2e); Cuyuni river drainage .............  
- Base of gill filaments on first gill arch narrowly covered with skin at base; 4 to 7 lateral bars on preserved specimens; Orinoco or Río Negro drainages ....................  4
4  Seven dark bars on flank, with bars 4 and 5 forming a “Y” pattern; ventral margin of caudal peduncle contained 1.1 to 1.3 times in dorsal margin of caudal peduncle; subopercule caudoventrally naked (Fig. 2a).................................................. *G. dicrozoster*  
- Fewer than seven bars on flank; ventral margin of caudal peduncle contained 1.5 to 1.6 times in dorsal margin of caudal peduncle; subopercule fully scaled ......................  5
5  Dorsal lobe of caudal fin with accessory lateral line extension between rays D3 and D4; preopercular mark present; four, broad and parallel, caudo-ventrally inclined lateral bars on flank (Fig. 2c) ................................................................. *G. winemilleri*  
- Dorsal lobe of caudal fin without accessory lateral line extension; preopercular mark absent; six, vertical and parallel bars on flank (Fig. 2b) ................................. *G. abalios*

Discussion

We describe three species of *Geophagus* from the “*surinamensis* complex”, elevating the described species in the genus to fourteen, and the known Venezuelan species to six. The new species *Geophagus abalios*, *G. dicrozoster* and *G. winemilleri* are diagnosable from species outside the *G. surinamensis* complex by the lack of a complete infraorbital stripe (Figs. 1, 2), which can be absent (*G. abalios*) or reduced to a preopercular mark (*G. dicrozoster, G. winemilleri*). The combination of coloration and squamation characters distinguishes the three species from each other, and from the other seven described species within the *G. surinamensis* complex (Fig. 2). Lateral bar patterns have been used as diagnostic characters in other genera of Neotropical cichlids, notably *Mesonauta* (Kullander & Silfvergrip 1991; Schindler 1998) and *Apistogramma* (e.g. Kullander 1980). It is clear from the present paper that some species of *Geophagus* present well-defined and stable patterns of lateral bars, and these can be used as diagnostic characters. Color photographs of aquarium specimens suggest that double-bar patterns and the lack of a preopercular mark, as observed in *G. abalios* n. sp., occur together in yet undescribed species (e.g.

Although little is known of the ecology of *Geophagus abalios* and *G. dicrozoster*, it appears that they share many essential aspects of their biology. Field observations in the Río Cinaruco (south-western Venezuelan llanos) indicate that both species are mouth-brooders (HLF unpubl.). Both species are among the most abundant in samples from lagoon, or to a lesser extent, channel habitats over bare sandy bottoms, although they can be abundant in structured habitats with submerged wood or rocks (Arrington, 2002). On at least one occasion, *G. dicrozoster* was captured in rapids near the headwaters of the Río Negro (K. Winemiller et al. unpubl.). Preliminary diet analyses indicate that, at least qualitatively, both species share a diet of benthic insect larvae dominated by chironomids (Diptera), trichopterans and ephemeropterans (HLF unpubl.). Given the great similarity of these species in overall morphology, color patterns, feeding modes, and probably reproductive behavior, it is remarkable that they seem to share the same habitats in an extensive manner. The ecology of *G. winemilleri* is almost entirely unknown: all of our available records and observations indicate that it inhabits black waters with sandy bottoms, and it probably is a “larvophilous” mouth brooder (Weidner 2000).

*Geophagus abalios* and *G. dicrozoster* are sympatric in most of their known distribution, and frequently are found in the same habitats, particularly in the Cinaruco river, southern Apure State (HLF unpubl.). Their syntopy will probably be shown to be more extensive once they are distinguished in collections, where they are commonly referred to as *G. surinamensis* or *G. altifrons* (e.g. Mago-Leccia 1970; Machado-Allison 1987; 1993; Royero et al. 1992). The broad distribution of both species in the Orinoco basin suggests they should be as common in Colombia as they are in the Venezuelan portion of the basin. It is not clear from our current distributional knowledge whether the range of *G. abalios* and *G. dicrozoster* extends further south than the headwaters of the Río Negro. The known distribution of *G. winemilleri* is restricted to the lower Casiquiare and the upper Río Negro, but the species may be present in the Río Ventuari drainage of the middle Orinoco basin (DCT and C. Montaña unpubl.). The fish diversity of the middle Orinoco and its tributaries is poorly known, and further collections are needed to clarify whether *G. winemilleri* is present in the upper Casiquiare and upper-middle Orinoco region. *G. winemilleri* is known to occur in the middle Río Negro (HLF pers. obs.). Weidner (2000) indicates that all aquarium imports come from the Río Negro and refers to a case in which the species was caught in the Archipelago das Anavilhanas, just north of Manaus. Further taxonomic, phylogenetic and distributional studies in the Río Negro will be necessary before a fruitful discussion of the biogeographic history of *Geophagus* in this region is possible.
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Appendix

Catalogue numbers from MCNG used to draw the distribution maps in Figures 9 and 13. Details on each locality are given with each species description and/or are available at the Neodat project website (http://www.neodat.org).

*Geophagus abalios*. MCNG 6111, 6660, 7023, 7681, 7827, 9390, 10118, 10195, 11413, 12359, 13220, 15892, 20631, 24241, 24303, 24757, 25952, 27197, 27962, 28076, 28081, 28139, 28158, 29781, 29866, 29880, 29939, 29959, 29987, 30680, 30714, 30728, 30745, 30769, 30801, 30855, 30882, 30921, 30939, 31010, 31018, 31027, 31061, 31073, 31096, 31182, 31221, 31231, 31255, 31288, 31326, 31342, 31349, 31364, 31366, 32668, 32682, 32836, 33153, 33157, 33173, 33197, 33211, 33269, 33851, 33976, 35209, 36769, 37650, 38232, 38317, 38707, 38735, 40385, 40591, 40878, 40976, 41368, 43979, 44865, 44866, 44867, 45025, 45028, 45029, 45034, 45040, 44690.