

Taxonomic status of the atherinid fish genus *Melaniris* in lower Central America, with the description of three new species

by

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Abstract: Seven species of *Melaniris* from southern Central America are discussed, their distributions are given, and a key to their identification is provided. *Melaniris guatemalensis* inhabits Pacific coastal lagoons and estuaries between Guatemala and southern Costa Rica. *M. beani*, known only from Colón, Panamá, and *M. milleri*, n. sp. from Atlantic Nicaragua and Costa Rica are principally brackish water forms, but the latter also frequents the Río San Juan basin a great distance from the sea. *M. hubbsi*, n. sp. occurs in the Río Escondido and San Juan drainages and is replaced in rivers to the south by *M. chagresi* which reaches to central Panamá. *M. sardina* is a lacustrine species found in several Nicaraguan lakes and in the Río Sapoá, Costa Rica. *M. jiloesensis*, n. sp. is endemic to Lake Jilóá, Nicaragua.

The small, silvery "sardinas" of the fresh and brackish waters of Middle America are not generally common fishes in rivers, but some species may occur in large shoals in lakes and coastal lagoons or estuaries. Zaret (1972) observed in Gatún Lake, Panamá, that all but the largest individuals of *Melaniris chagresi* are planktivores and this may explain why this and other species are most abundant in standing waters.

Miller and Carr (1974) clarified the distribution and characteristics of four species of Guatemalan and Honduran *Melaniris* and commented on the taxonomic status of southern Central American forms. The need for a morphometric analysis, identification key and delimitation of the geographic distribution of the southern *Melaniris* was obvious. I have confined my analysis to fishes collected between southern Nicaragua and western Panamá in an effort to clarify the taxonomic status of Costa Rican species. It is clear, except for the lake endemics perhaps, that future studies will expand the known ranges of the species of *Melaniris* studied here.

MATERIAL AND METHODS

Meristic counts and measurements were made in accordance with Hubbs and Lagler (1958) as modified by Barbour (1973). The measurement for body depth was consistently taken along a vertical line passing through the origin of the anal

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fin. Counts of the anal and second dorsal-fin rays include the first element which is actually a flexible spine. A transverse scale count as defined by Miller and Carr (1974) was found useful: the number of "...scales between the middle of the anal fin base (excluding crowded scales) and the midline row between the dorsal fins..." The measurement of body width was taken as the widest point below the origin of the first dorsal fin. Body measurements were made and Meristic Index (MI) values calculated only on specimens larger than 35 mm SL to reduce allometric variation in body proportions and gill raker counts, the latter an important component of the MI. The MI is the sum of the number of anal-fin rays, rays of one pectoral fin, median lateral scales, predorsal scales and total gill rakers of the first gill arch on one side of the head.

Length measurements are expressed in standard length (SL) in millimeters (mm). Meristic counts are summarized in Tables 1 to 5 and the MI for four species of *Melaniris* is given in Table 6. Ranges of variation of selected proportional measurements for specimens larger than 35 mm SL are presented in Tables 7 and 8. Body proportions are expressed as times divided into SL or head length (HL).

Collections are listed by country and drainage basins in the following way: catalog number, number of specimens and size range of type material in parentheses, general locality with the elevation in meters (m).

The specimens used in this study are deposited at the Academy of Natural Sciences of Philadelphia (ANSP), the Natural History Museum of Los Angeles County (LACM), the Museo de Zoología, Universidad de Costa Rica (UCR), the University of Florida, Florida State Museum (UF/FSM), the Museum of Zoology, University of Michigan (UMMZ) and the National Museum of Natural History (USNM) and are listed at the end of each species account.

KEY TO LOWER CENTRAL AMERICAN *MELANIRIS*

This aid to identification is designed for specimens larger than 35 mm SL. Identifications should be confirmed by consulting the species accounts and accompanying tables and figures.

- A. Transverse scale rows usually 6, rarely 7. B
- AA. Transverse scale rows usually 7, occasionally 6 or 8. C
- B. Pectoral fin long, 3.2-3.8 times in SL; Pacific coast of Central America.
 *M. guatemalensis*
- BB. Pectoral fin shorter, 3.8-4.5 times in SL; Atlantic coast of Panamá.
 *M. beani*
- C. Body nearly round in cross section, not highly compressed, body width 8.4-10.8 times in SL; scales extremely thin, deciduous; height of anal fin 1.55-1.84 times in HL; orbit length 3.4-3.9 times in HL; length of pectoral fin 4.4-5.2 times in SL; endemic to Lake Jiloá, Nicaragua *M. jiloaensis*
- CC. Body compressed, 10.1-19.5 times in SL; scales normal, not deciduous; height of anal fin 1.16-1.67 times in HL; orbit length 2.5-3.7 times in HL; length of pectoral fin 3.5-4.8 times in SL. D
- D. Total gill rakers on first arch 18-25; predorsal scales with smooth or finely crenate margins; caudal fin without a black distal margin; Atlantic slope rivers from Nicaragua to Panamá E

- DD. Total gill rakers 22-29, usually 23-27; predorsal scales usually with prominent lobes on margins; caudal fin frequently with a narrow black posterior margin F
- E. Body depth 4.6-5.5 times in SL; preanal distance 1.63-1.83 times in SL; median lateral scales 38-43 (\bar{x} = 40.1); predorsal scales 19-23 (\bar{x} = 20.9); pelvic fin usually reaching to vent, rarely beyond it; MI 112-123 (\bar{x} = 17.6) *M. hubbsi**
- EE. Body depth 5.2-6.9 times in SL; preanal distance 1.7-2.03 times in SL; median lateral scales 41-46 (\bar{x} = 43.5); predorsal scales 21-27 (\bar{x} = 23.4); pelvic fin usually reaching beyond vent; MI 117-131 (\bar{x} = 25.9) *M. chagresti**
- F. Preanal distance 1.76-1.94 times in SL; greatest body depth 5.2-6.5 times in SL; length of anal-fin base 2.9-3.4 times in SL; anal-fin rays 23-27; Atlantic coast, rarely rivers, from Nicaragua to Costa Rica *M. milleri*
- FF. Preanal distance 1.65-1.79 times in SL; greatest body depth 4.3-5.3 times in SL; length of anal-fin base 3.2-3.9 times in S; anal-fin rays 19-25; Lakes Nicaragua, Managua, Masaya, Jiloá and tributaries *M. sardina*

MELANIRIS GUATEMALENSIS (GÜNTHER)

(Fig. 1A)

Atherinichthys guatemalensis Günther 1864, *Proc. Zool. Soc. Lond.*, 1864: 151.
(type: Lakes of Huamuchal, Pacific coast of Guatemala).

Description: *M. guatemalensis* is a large, moderate to deep-bodied (body depth 4.6-6.1 times in SL) *Melaniris* with long pectoral fins (3.2-3.8 times in SL), usually six transverse scale rows, low median lateral scale counts (39-43, \bar{x} = 40.7) and high gill raker counts (24-28, \bar{x} = 25.6). The scales are crenate; the notching on the posterior border of the predorsal scales is especially pronounced, resulting in a regular toothed border in specimens larger than 50 mm SL. The pectoral fins usually reach the vent, but may fall short or extend slightly beyond the vent. The pelvic fins reach at most to the vent, but often fall short of it. The caudal fin is generally clear, but occasional large individuals have a dusky caudal fin with a slightly darkened posterior margin. The largest specimen at hand is 85 mm SL.

Remarks: Günther (1864) described this species from presumably freshwater lakes near the Pacific coast of Guatemala. Miller and Carr (1974) reported on additional specimens from brackish biotopes on the Pacific coast of Guatemala and also from Puntarenas, Costa Rica. Günther (1864) also described *Atherinichthys pachylepis* (= *Melaniris pachylepis*) from Panamá and it has subsequently been reported from Perú (Chirichigno, 1969). Literature descriptions reveal conflicting differences in lateral scale counts and in condition of scale margins between *M. guatemalensis* and *M. pachylepis*. Dr. Robert R. Miller (pers. comm.) reported that the best difference he had found to distinguish the two species was that *M.*

guatemalensis has from 35 to 39 vertebrae, whereas *M. pachylepis* has from 42 to 44 vertebrae. Radiographs of 65 specimens of *Melaniris* from brackish waters of Nicaragua and Costa Rica reveal vertebral counts of 37 to 40 (Table 5), and on this basis our specimens are referred to *M. guatemalensis*. No geographic variation is apparent in the specimens at hand, which also suggests that a single species is involved. Thus, *M. guatemalensis* is the only species inhabiting the Pacific coast of Costa Rica and is apparently replaced by *M. pachylepis* somewhere south in Panamá.

Distribution: The species occurs on the Pacific coast of Central America from Guatemala to southern Costa Rica, perhaps reaching Panamá and is found principally in brackish waters (Fig. 2).

Material examined: NICARAGUA: **Río Tamarindo drainage:** UCR 52-4 (4) Río Tamarindo, ≤ 50 m. **Río La Flor drainage:** UCR 482-3 (5) Río La Flor at Cásares, sea level. COSTA RICA: **Puntarenas:** UCR 36-14 (2) Estero Chacarita, sea level. **Caldera:** UCR 53-3, 320-10 and 420-7 (48) Estero Mata Limón, sea level. **Río Rincón drainage:** UCR 262-3 and 598-14 (14) mouth of Río Rincón, sea level.

MELANIRIS SARDINA MEEK

(Fig. 1B)

Melaniris sardina Meek 1907, *Field Col. Mus. Publ.* 121, *Zool. Ser.* 7: 114-116.
(type: Lake Managua, Nicaragua).

Description: *M. sardina* is a small deep-bodied (body depth 4.3-5.3 times in SL) species with large head (3.4-4.3 times in SL) and orbit (2.5-3.5 times in HL), rather long pectoral fins (3.5-4.3 times in SL), low predorsal-scale counts (18-25, \bar{x} = 21.4), low median lateral scale counts (39-43, \bar{x} = 40.4) and low caudal vertebral counts (17-19, \bar{x} = 18.3). The scales are crenate, but with only a few shallow notches; predorsal scales have a few, usually irregular, lobes on specimens larger than 40 mm SL. The pectoral fins usually fall short of the vent of Lake Masaya specimens, whereas on material from Lake Nicaragua the pectoral fins frequently extend beyond the vent. The pelvic fins usually reach to or beyond the vent. Melanophores are usually concentrated along the posterior margin of the caudal fin in specimens collected in the littoral zone of lakes, or in one case, in a river. Material collected in the offshore waters of Lake Nicaragua and in Lake Masaya reveal no such dark border to the caudal fin.

The maximum and average length is greatest in specimens from Lake Masaya; the largest specimen is 57 mm SL. The largest specimen from Lake Nicaragua is 54 mm SL.

Remarks: Meek (1907) based his description of *M. sardina* on material from both of the Great Lakes. Specimens from Lake Masaya show minor meristic and proportional differences (Tables 1 to 5, 7 and 8) which are not of specific importance. Three specimens of *M. sardina* were collected with a large series of *M. jiloaensis* in Lake Jiloá by Jaime Villa. These specimens exceed the range of variation of the above mentioned fish only with respect to the dorsal-fin ray count: two have 8 rays, one has 9 rays. Two specimens of *M. sardina* from the Río Sapoa, an affluent of Lake Nicaragua are indistinguishable from typical lacustrine individuals. In the Sapoa, and presumably other tributaries of Lake Nicaragua, *M. sardina* is syntopic with *M. hubbsi*. The former were conspicuous in their paler

pigmentation; *M. hubbsi* had a much more intense lateral stripe and dorsal melanophore pattern.

Distribution: *M. sardina* is an Atlantic slope lacustrine species which inhabits Lakes Managua and Nicaragua and tributaries (Villa, 1971) as well as the crater lakes Masaya and Jiloá. The Río Sapoa locality represents the first occurrence of the species in Costa Rica. *M. sardina* is sympatric with *M. jiloensis* in Lake Jiloá and with *M. hubbsi* in the Río Sapoa and probably other tributaries of Lake Nicaragua (Fig. 2).

Material examined: NICARAGUA: **Lake Nicaragua:** 31 m elevation: UCR 24-14 and 62-1 (43) Isletas de Granada; UCR 61-5 (8) near Asese; UCR 536-2 (100) beach at Granada; UCR 547-2 (21) Estero Guayabo at N end of lake; UCR 551-4 (6) W side of Cerro Menco; UCR 553-3 (11) mouth of Río Mayales. **Lake Jiloá:** UCR 596-3 (3) 50 m. **Lake Masaya:** UCR 597-1 (97) 135 m. COSTA RICA: **Lake Nicaragua drainage:** UCR 122-23 (2) Río Sapoa, 40 m.

MELANIRIS MILLERI n. sp.

(Fig. 1C)

Melaniris chagresi (Meek and Hildebrand), in part, Gilbert and Kelso, 1971, *Bull. Florida State Mus.*, 16:30 (misidentification).

Diagnosis: The species is large, slim-bodied (body depth 5.2-6.5 times in SL), small-headed (4.0-4.7 times in SL) with a long anal-fin base (2.9-3.4 times in SL), high anal-fin ray count (23-27, \bar{x} = 24.7), high predorsal-scale count (23-28, \bar{x} = 25.4), high gill-raker count (23-29, \bar{x} = 25.2) and high total vertebral count (38-41, \bar{x} = 39.5).

Description: The counts of the holotype are followed by the range for 33 paratypes in parentheses: Dorsal-fin rays IV-9 (III to V-8 to 10); anal 25 (23-27); pectoral 13 on each side (13-15); pelvic 6 (6); median lateral scales 42 (41-45); predorsal scales 28 (23-28); transverse scales 7 (6-7); interdorsal scales 6 (5-7); scales around caudal peduncle 14 (12); total gill rakers 25 (23-29).

Body proportions in permillage of SL of the holotype are followed by the range for 10 paratypes in parentheses: Standard length (mm) 102.4 (48.0-88.7); head length 222 (215-237); orbit diameter 60 (62-77); postorbital distance 96 (89-98); snout length 73 (67-76); length of upper jaw 73 (70-80); bony interorbital distance 69 (62-69); body depth at vertical through origin of anal fin 186 (154-188); body width at vertical through first dorsal fin 68 (62-84); least depth of caudal peduncle 80 (69-82); length of caudal peduncle 163 (153-183); predorsal (first) distance 621 (572-611); predorsal (second) distance 756 (701-750); preanal distance 546 (517-556); prepectoral distance 236 (232-244); prepelvic distance 390 (368-399); length of dorsal-fin base 94 (88-112); length of anal-fin base 311 (302-334); height of dorsal fin 117 (118-147); height of anal fin 166 (173-192); length of pectoral fin 241 (235-259); length of pelvic fin 111 (101-127); length of upper lobe of caudal fin 220 (221-238); length of lower lobe of caudal fin 249 (236-263).

TABLE 1

Frequency distribution of second dorsal and pectoral fin-ray and transverse scale counts in *Melaniris*. Drainage basin is indicated for populations of *M. sardina* and *M. chagresi*

	Dorsal rays						Pectoral rays					Transverse scales			
	7	8	9	10	11	\bar{x}	12	13	14	15	\bar{x}	6	7	8	\bar{x}
<i>M. sardina</i> (L. Masaya)			10	13	7	9.9	2	4	17	7	14.0	1	29		7.0
<i>M. sardina</i> (L. Nicaragua)			13	16	1	9.6	2	20	8		13.2		30		7.0
<i>M. hubbsi</i>		3	19	26	3	9.6	6	37	10		13.1	13	40		6.8
<i>M. chagresi</i> (Matina)		4	21	6		9.1	5	17	9		13.1		31		7.0
<i>M. chagresi</i> (Sixaola)			7	15	3	9.8	6	18	1		12.8		25		7.0
<i>M. chagresi</i> (Guarumo)			1	2	1	10.0			4		14.0		4		7.0
<i>M. chagresi</i> (Chagres)		2	19	7	1	9.2	1	17	11		13.3		27	2	7.1
<i>M. beani</i>	1	2	6	1		8.7		8	2		13.2	10			6.0
<i>M. milleri</i>		5	21	7		9.1		8	21	4	13.9	1	32		7.0
<i>M. guatemalensis</i>		12	12	4		8.7	2	16	12		13.3	29	1		6.0
<i>M. jilolaensis</i>	1	6	16	7	1	9.0	3	22	6		13.1		18	13	7.4

The scales are weakly crenate, those of the predorsal series have a few long lobes on specimens over 50 mm SL. The pectoral fins usually reach the vent, but may fall short or extend slightly beyond it. The pelvic fins usually extend beyond the vent, but may fall slightly short of, or just reach it. Large specimens consistently, and specimens as small as 25 mm SL, often have a concentration of melanophores on the extreme border of the caudal fin. The largest specimen available measures 120.5 mm SL.

Remarks: Since some individuals of *M. milleri* penetrate well up the San Juan drainage, it is critical in faunal studies to distinguish it from the very similar *M. hubbsi*. Where the two species are syntopic, the dark caudal-fin border and slimmer body of *M. milleri* readily distinguish it. Since *M. milleri* has higher average meristic counts than *M. hubbsi*, a Meristic Index (MI) was prepared to confirm preliminary separation of these species. No overlap in MI occurs between the two species in the San Juan drainage (Table 6). A shift in average MI between the San Juan and Matina populations of *M. milleri* (Table 6) is due to several slightly higher mean counts in the Matina population compared to the San Juan fish: median lateral scales (43.2 vs 42.5), predorsal scales (25.8 vs 24.9), pectoral rays (14.2 vs 13.6) and total gill rakers (26.0 vs 24.7). Both populations are very similar in body proportions. The southward increase in MI of *M. milleri* suggests that it would be especially useful in distinguishing it from *M. beani* when further collecting is done in western Panamá.

A conspicuous hiatus occurs on our distribution maps due to the paucity of fish collections from the Atlantic slope and coast of western Panamá. In spite of this discontinuity, I believe the trenchant differences between *M. milleri* and *M. beani* are such that it is reasonable to assume that distinct species are involved, and that future collecting will reveal replacement or overlap of the two rather than intergradation of subspecific populations.

Distribution: *M. milleri* is known from brackish waters along the Atlantic coast of Nicaragua from Pearl Lagoon south to Quebrada Westfalia, Costa Rica (Fig. 2). Some individuals ascend tributaries of the Río San Juan a considerable distance from the coast. A single specimen from Corozal, Honduras may also represent this species.

Etymology: This species is dedicated to Dr. Robert R. Miller, foremost authority on Middle American fishes, who first recognized the fish as new to science.

Holotype: LACM 37508-1 (102.3 mm SL) COSTA RICA: Limón Province, coastal lagoon near mouth of Río Colorado, Barra Colorado; sea level; 9 January 1977; collectors W. Bussing *et al.*

Paratypes: NICARAGUA: Pearl Lagoon: UCR 363-11 (51, 29.0-59.6 mm SL), sea level. Río San Juan drainage: UCR 1053-7 (1, 66.0 mm SL) Río Sábalo, 35 m; UCR 1001-6 (1, 42.7 mm SL) Caño Santa Cruz, 40 m; UCR 1055-18 (2, 55.7-56.1 mm SL) Río Santa Cruz, 35 m. COSTA RICA: Río San Juan drainage: UCR 1073-2 (4, 88.0-120 mm SL) Río Colorado, 5 m; UCR 1075-1 (13, 31.8-67.5 mm SL) Río Colorado at "El Hueco", 5 m; UCR 1077-1 (8, 62.1-120.5 mm SL) coastal lagoon at Barra Colorado, sea level; LACM 37508-2 (20, 20.8-56.7 mm SL), UMMZ 202348 (20, 21.3-60.2 mm SL), USNM 218528 (20, 21.1-56.5 mm SL),

UCR 1067-1 (166 and 3 cleared and stained, 18.5-113.3 mm SL) same data as holotype; UCR 992-1 (6, 97.2-111.0 mm SL) Laguna de Atrás near Barra Colorado, sea level. **Río Tortuguero drainage:** UF/FSM 5805 (12, 41.2-76.5 mm SL), 5809 (5, 34.4-59.8 mm SL), 5811 (8, 29.2-101.8 mm SL), 5821 (4, 32.7-74.6 mm SL), 7141 (3, 94.8-98.3 mm SL), 7142 (3, 51.6-89.6 mm SL), 7148 (14, 38.2-82.5 mm SL), 7159 (2, 86.4-92.5 mm SL), 7171 (6, 89.5-105.7 mm SL), 10254 (14, 60.5-90.0 mm SL), 11045 (59, 34.4-91.5 mm SL), 11069 (39, 31.8-79.6 mm SL), 11102 (30, 27.5-69.1 mm SL), 11127 (8, 35.8-57.2 mm SL), 11184 (1, 92.4 mm SL), 11687 (1, 91.1 mm SL), 16402 (1, 81.8 mm SL), 16452 (4, 50.3-64.5 mm SL) Tortuguero Lagoon, sea level; UF/FSM 5786 (20, 41.0-65.2 mm SL), UMMZ 180652 (15, 41-91 mm SL) Río Tortuguero and lagoon, near sea level; UF/FSM 5793 (2, 41.6-50.0 mm SL) Río Tortuguero, 4 km from inlet, near sea level. **Río Matina drainage:** LACM 37510-1 (2, 59.0-68.5 mm SL), UMMZ 202347 (2, 72.2-74.8 mm SL), UCR 804-12 (20, 48.2-89.2 mm SL) canal near mouth of Río Matina, sea level. **Coastal streams S of Limón:** LACM 37509-1 (2, 90.7-103.0 mm SL), UMMZ 202346 (2, 95.6-100.2 mm SL), USNM 218531 (2, 94.0-95.0 mm SL), UCR 376-13 (19, 35.6-105.3 mm SL) Quebrada Westfalia, sea level.

Additional material: The following specimen has meristic and proportional characteristics which correspond to *M. milleri*, but I do not include it among the type material because of the lack of a larger study series and great distance from the type locality: UCR 199-3 (1, 71.7 mm SL) HONDURAS: Department of Atlántida, river near Corozal 15 km E of La Ceiba; near sea level.

MELANIRIS BEANI (MEEK AND HILDEBRAND)

Kirtlandia beani Meek and Hildebrand 1923, *Field Mus. Nat. Hist. Publ.* 215, *Zool. Ser.* 15: 270, 271, plate 21 (type: Fox Bay, Colón, Panamá).

Description: *M. beani* is a species of moderate size and body depth (5.2-5.6 times in SL) and moderate head length (3.8-4.2 times in SL) with six transverse scale rows, a low anal-fin ray count (20-23, \bar{x} = 21.1), low median lateral scale count (39-40, \bar{x} = 39.8), low predorsal scale count (19-22, \bar{x} = 20.4), high gill raker count (24-28, \bar{x} = 25.6), a long anal-fin base (3.3-4.2 times in SL) and a high anal fin (1.45-1.59 times in HL). The scales are crenate; those of the predorsal series are deeply and regularly notched, the median lobes are especially long. The pectoral fins fall short of or just reach the vent. The pelvic fins reach the vent or extend beyond it. The fin rays of the type specimens are damaged and it was not possible to determine the pigmentation of the caudal fin. The largest specimen collected by Meek and Hildebrand (1923) had a total length of 100 mm.

Remarks: My counts and measurements of the type specimens correlate well with the original description. However, the paratypes at hand differ from the specimen figured in the original description in two respects: 1) the black lateral stripe does not slope ventrally on the caudal peduncle, but continues equidistant between its dorsal and ventral borders, and 2) the first dorsal fin arises well behind the anal-fin origin (as stated in the text) not over the first few anal rays as pictured. Since the figure is apparently a photograph, these discrepancies may be due to retouching or a distorted or unique specimen.

Distribution: The species has been reported only from the type specimens collected at Colón on the Atlantic coast of Panamá (Fig. 2).

TABLE 2

Frequency distribution of anal fin-ray and median lateral scale counts in *Melaniris**

	Anal rays										\bar{x}	Median lateral scales										\bar{x}
	19	20	21	22	23	24	25	26	27			38	39	40	41	42	43	44	45	46		
<i>M. sardina</i> (L. Masaya)		1	2	14	9	4					22.4		5	13	7	4	1				40.4	
<i>M. sardina</i> (L. Nicaragua)	1	3	8	6	7	4	1				22.0		2	14	13	1					40.4	
<i>M. hubbsi</i>			8	11	19	13	4				22.9	3	14	17	13	5	1				40.1	
<i>M. chagresi</i> (Matina)				3	8	14	4	2			23.8				3	4	6	11	7		43.5	
<i>M. chagresi</i> (Sixaola)			3	11	5	5	1				22.6					4	12	6	3		44.3	
<i>M. chagresi</i> (Guarumo)			1		3						22.5					1	2	1			44.0	
<i>M. chagresi</i> (Chagres)		2	7	11	7	1	1				22.0			4	8	11	6				42.7	
<i>M. beani</i>		4	2	3	1						21.1		2	8							39.8	
<i>M. milleri</i>					4	8	15	5	1		24.7			3	6	18	5	1			42.9	
<i>M. guatemalensis</i>			5	3	12	5	2	3			23.2		2	11	12	4	1				40.7	
<i>M. jilolaensis</i>	6	12	8	2	2	1					20.5			6	9	14	2				41.4	

* See Table 1

Material examined: PANAMA: Colón: USM 79740 (10 paratypes, 41.2-73.3 mm SL) Fox Bay, sea level.

MELANIRIS HUBBSI, n. sp.

(Fig. 1D)

Melaniris chagresi (Meek and Hildebrand), Bussing and López, 1977, *Rev. Biol. Trop.*, 25: 13-37 (misidentification; ecology in Arenal basin).

Diagnosis: *M. hubbsi* is a small, deep-bodied (4.6-5.5 times in SL) species with a large orbit (2.6-3.2 times in HL), long preanal distance (1.63-1.83 times in SL), low median lateral scale count (38-43, \bar{x} = 40.1), low predorsal scale count (19-23, \bar{x} = 20.9), low gill raker count (18-24, \bar{x} = 20.8) and low precaudal vertebral count (17-20, \bar{x} = 18.6).

Description: The counts of the holotype are followed by the range for 53 paratypes in parentheses: Dorsal-fin rays V-9 (III to VI-8 to 11); anal 21 (21-25); pectoral 13 on right side, 14 on left side (12-14); pelvic 6 (6); median lateral scales 41 (38-43); predorsal scales 20 (19-23); transverse scales 7 (6-7); interdorsal scales 5 (5-6); scales around caudal peduncle 11 (11-12); total gill rakers 19 (18-24).

Body proportions in permillage of SL of the holotype are followed by the range for 10 paratypes in parentheses: Standard length (mm) 53.0 (45.3-67.6); head length 245 (240-262); orbit diameter 91 (77-93); snout length 77 (73-83); length of upper jaw 89 (88-97); bony interorbital distance 77 (72-82); body depth at vertical through origin of anal fin 204 (185-215); body width at vertical through first dorsal fin 89 (71-99); least depth of caudal peduncle 83 (76-92); length of caudal peduncle 172 (162-177); predorsal (first) distance 608 (586-621); predorsal (second) distance 734 (725-750); preanal distance 579 (556-593); prepectoral distance 251 (249-262); prepelvic distance 409 (398-427); length of dorsal-fin base 106 (88-108); length of anal-fin base 281 (274-307); height of dorsal fin 117 (105-119); height of anal fin 153 (148-181); length of pectoral fin 240 (222-262); length of pelvic fin 125 (120-135); length of upper lobe of caudal fin 226 (219-244); length of lower lobe of caudal fin 247 (234-263).

The scales have smooth borders or are weakly crenate on the caudal peduncle of larger specimens; the scales of the predorsal series in some specimens over 50 mm SL are weakly crenate and specimens as small as 40 mm SL may have one small produced lobe. The pectoral fins may reach the vent, but usually fall short of it. The pelvic fins usually reach the vent, but may reach slightly short of or slightly beyond this point. The caudal fin is clear or dusky without a concentration of melanophores on the posterior margin.

The largest specimen at hand has a SL of 67.6 mm.

Remarks: Meek and Hildebrand (in Meek, 1914) did not include specimens from the Río San Juan drainage in their description of *M. chagresi*. Bussing and López (1977) considered the population of the upper Arenal basin as conspecific with *M. chagresi*. The new species is distinguished from the similar *M. chagresi* which replaces it to the south, by the characters presented in the key as well as the low anal fin of *M. hubbsi* (Table 8 and Fig. 3). The distinctions between *M. hubbsi* and *M. milleri* are cited under the latter species account.

Distribution: *M. hubbsi* was collected in freshwaters of the Río Escondido drainage, Nicaragua, affluents of Lake Nicaragua, and other tributaries of the Río San Juan system which drain southern Nicaragua and a vast portion of northern Costa Rica. It was taken in tributaries of Lake Nicaragua and was syntopic with *M. sardina* in one of these, but has not been found in the lake proper (Fig. 2).

Etymology: The species is named in honor of Dr. Carl L. Hubbs, who has done so much for ichthyology, including numerous pioneer contributions dealing with Middle American fishes.

Holotype: LACM 37506-1 (53.0 mm SL) COSTA RICA: Alajuela Province, Río Zapote a tributary of Lake Nicaragua, 0.4 km S of Upala; 50 m elevation; 26 April 1968; collectors W. Bussing and Carlos Mata R.

TABLE 3
Frequency distribution of predorsal-scale counts in *Melaniris**

	18	19	20	21	22	23	24	25	26	27	28	29	\bar{x}
<i>M. sardina</i> (L. Masaya)			5	8	8	5	2	1					21.8
<i>M. sardina</i> (L. Nicaragua)	1	1	7	12	5	1	2						21.0
<i>M. hubbsi</i>		3	15	19	12	3							20.9
<i>M. chagresi</i> (Matoma)				1	2	11	5	8	4				23.9
<i>M. chagresi</i> (Sixaola)					4	7	9	3	1	1			23.7
<i>M. chagresi</i> (Guarumo)					2	1	1						22.8
<i>M. chagresi</i> (Chagres)			4	1	8	7	6	3					22.7
<i>M. beani</i>		3	2	3	2								20.4
<i>M. milleri</i>						3	7	7	9	1	5		25.4
<i>M. guatemalensis</i>					5	10	9	6					23.5
<i>M. jiloaensis</i>				1	1	4	8	3	9	2	1	1	24.9

* See Table 1

TABLE 4
Frequency distribution of gill-raker counts in *Melaniris**

	18	19	20	21	22	23	24	25	26	27	28	29	\bar{x}
<i>M. sardina</i> (L. Masaya)					2	11	7	9	1				23.9
<i>M. sardina</i> (L. Nicaragua)						8	9	9	3				24.2
<i>M. hubbsi</i>	2	4	16	18	4	6	1						20.8
<i>M. chagresi</i> (Matina)			1	3	10	13	4						22.5
<i>M. chagresi</i> (Sixaola)					8	6	7	4					23.3
<i>M. chagresi</i> (Guarumo)				1	2	1							22.0
<i>M. chagresi</i> (Chagres)			4	10	10		2	2					22.6
<i>M. beani</i>							3	3		3	1		25.6
<i>M. milleri</i>						1	10	13	4	3	1	1	25.2
<i>M. guatemalensis</i>							6	6	12	5	1		25.6
<i>M. jiloaensis</i>							1	1	10	8	5	5	27.0

* See Table 1

Paratypes: NICARAGUA: **Lake Nicaragua drainage:** UCR 265-10 (12, 20.5-35.5 mm SL) Río Malacatoya near Teustepe, ca. 100 m. **Río Escondido drainage:** UCR 461-4 (2, 35.8-39.0 mm SL) Río Muhán, 100 m. **Río San Juan Drainage:** UCR 1003-7 (2, 23.6-30.0 mm SL) Río Sábalo, 40 m; UCR 1052-11 (2, 48.4-49.5 mm SL) Caño Santa Rosa, tributary of Río Sábalo, 40 m; UCR 1001-4 (8, 36.0-55.2 mm SL) Caño Santa Cruz, 40 m; UCR 1004-13 (6, 28.5-57.2 mm SL) Río Santa Cruz, 40 m; UMMZ 202343 (5, 38.6-47.6 mm SL), USNM 218530 (5, 39.8-51.0 mm SL), UF/FSM 25174 (5, 42.5-47.8 mm SL) UCR 1055-1 (27 and 3 cleared and stained, 30.9-52.6 mm SL) Río Santa Cruz between La Concepción and Las Mercedes, 35 m. COSTA RICA: **Lake Nicaragua drainage:** UCR 122-11 (6, 36.5-55.4 mm SL) Río Sapoá, 40 m; LACM 37506-2 (5, 28.3-53.9 mm SL), UMMZ 202344 (5, 32.1-52.6 mm SL), UCR 247-11 (27, 24.0-56.2 mm SL) same data as holotype; UCR 246-8 (3, 40.4-44.7 mm SL) Laguna Avillán at Los Chiles, 45 m. **Río San Juan drainage:** UCR 1005-4 (2, 40.2-40.7 mm SL) Río Infiernito, 40 m; UCR 836-9 (5, 42.3-52.7 mm SL) Río Mata de Caña, tributary of Lake Arenal, 535 m; LACM 37507-1 (5, 33.6-46.6 mm SL), UMMZ 202345 (5, 38.8-45.3 mm SL), UCR 980-12 (32, 30.8-50.2 mm SL) Río Dos Bocas, trib. of Lake Arenal, 540 m; UCR 981-15 (28, 31.6-52.5 mm SL) Quebrada Rugama, trib. of Lake Arenal, 540 m; UCR 843-15 (78, 17.3-52.4 mm SL) Quebrada Santa Rita, trib. of Río San Carlos, 200 m; USNM 218529 (5, 52.5-59.4 mm SL), UCR 263-13 (24, 47.7-67.6 mm SL) Quebrada Máquina, trib. of Río San Carlos, 90 m; UCR 769-22 (1, 38.7 mm SL) Quebrada Sábalo, trib. of Río Puerto Viejo, 35 m.

MELANIRIS CHAGRESI (MEEK AND HILDEBRAND)

(Fig. 1 E)

Menidia chagresi Meek and Hildebrand, in Meek 1914, *Field Mus. Nat. Hist. Publ.* 174, *Zool. Ser.* 10: 119 (type: Gorgona, Canal Zone, Panamá).

Description: *M. chagresi* is a moderate-sized, slim-bodied (5.2-6.9 times in SL) species with a short preanal distance (1.71-2.03 times in HL), high anal fin (1.22-1.58 times in HL), short pectoral fin (3.9-4.8 times in SL), high dorsal-fin ray count 8-11, \bar{x} = 9.4), high median lateral scale count (41-46, \bar{x} = 43.5) and high total vertebral count (38-41, \bar{x} = 39.6).

The scales have smooth borders or are weakly crenate on the caudal peduncle of larger specimens; in examples over 50 mm SL some of the predorsal scales are very weakly crenate. The pectoral fins of a few individuals from the Matina and Chagres basins reach the vent, in all other they fall short of it. The pelvic fins of Matina and Sixaola fishes reach the vent (17 specimens) or extend beyond it (39 specimens); the pelvics of the Guarumo specimens reach the vent; the pelvics of the Chagres fishes fall short of the vent (1 specimen), reach the vent (14 specimens), or extend beyond it (7 specimens). The caudal fin is clear or dusky with no darkened posterior margin.

The largest specimen studied has a SL of 85 mm and total length of 107 mm. Meek and Hildebrand (1923) recorded specimens from Panamá which reach 115 mm total length.

Remarks: Meek and Hildebrand (in Meek, 1914) described the type specimens of *M. chagresi* from Panamá, but also assigned Costa Rican material from the Parismina and Matina drainages to the same species. Miller and Carr (1974) referred specimens from the Atlantic versant of Honduras to *Melaniris* c. f. *chagresi*

TABLE 5

Frequency distribution of vertebral counts in *Melaniris**

	Precaudal						Caudal						Total						
	17	18	19	20	21	\bar{x}	17	18	19	20	21	\bar{x}	36	37	38	39	40	41	\bar{x}
<i>M. sardina</i> (L. Masaya)				10		20.0		4	6			18.6			4	6			38.6
<i>M. sardina</i> (L. Nicaragua)			6	3	1	19.5	3	3	4			18.1		4	6				37.6
<i>M. hubbsi</i>	2	10	17	1		18.6			6	15	9	20.1	1	1	13	8	7		38.6
<i>M. chagresi</i> (Matina)			9	2		19.2			1	3	7	20.6				3	8		39.7
<i>M. chagresi</i> (Chagres)		2	5	5	1	19.4			1	10	2	20.1			2	5	6	2	39.5
<i>M. milleri</i>			6	14		19.7			7	11	2	19.8			3	6	10	1	39.5
<i>M. guatemalensis</i>	2	57	3			18.0			3	33	26	19.4		4	34	26	1		38.4
<i>M. jiloensis</i>	4	5				17.6			4	4	1	19.7	2	3	5				37.3

* See Table 1

TABLE 6

Frequency distribution of Meristic Index (MI) for *Melaniris hubbsi*, *chagresi*, *milleri* and *beani* by drainage basins.
The MI is the sum of the number of anal-fin rays, rays of one pectoral fin, median lateral scales, predorsal scales and total gill rakers

	110	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40			
<i>M. hubbsi</i> (San Juan)																																		
<i>M. chagresi</i> (Matina)			1	1	4	3	9	9	7	6	4	2	4	1																				
<i>M. chagresi</i> (Sixaola)											1			3	4	6	3	2	5	5		1												
<i>M. chagresi</i> (Guarumo)														1	1	1				1														
<i>M. chagresi</i> (Chagres)								1	1		2	3	1	7	2	2	6	1	2															
<i>M. milleri</i> (San Juan)																1	1	2	1	1	2	3			4	1						1		
<i>M. milleri</i> (Matina)																						1	2	3	3	2	1	2	1					
<i>M. beani</i> (Chagres)						1		1		2	1	2	2			1																		

and cited several differences between these fish and *M. chagresi* from Barro Colorado Island, Panamá. They indicated the need to examine specimens from localities between Honduras and Panamá to determine the taxonomic status and range of the Honduran species. Among other differences, they found that the Panamá specimens usually have 8 rather than 7 transverse scales, although my material from the Chagres basin, including Gatún Lake, usually has 7 scales in the transverse series (Table 1).

The data obtained from *Melaniris* collected in rivers between southern Nicaragua and the Canal Zone, Panamá reveal considerable variation (see *M. hubbsi* and *M. chagresi*, Tables 1-8). In some characters the variation between adjoining populations is clinal, which suggests gene flow between the populations along the entire transect, but in others no such gradual changes take place. If one considers the highly conservative nature of the species of *Melaniris*, significant distinctions are shown by the Río San Juan populations and to a lesser degree, by the Río Chagres form. Within a distance of about 20 km, between Barra Colorado and the Tortuguero lagoon two consistently different forms, *M. hubbsi* and *M. chagresi*, replace each other. The diagnostic features of *M. hubbsi* are presented under that species heading.

There is evidence that the Lake Gatún and Río Piedras populations of *M. chagresi* should be distinguished taxonomically from the form inhabiting the Matina, Sixaola and perhaps, Guarumo drainages to the north. I hesitate to do this however because it is impossible to establish whether a sharp discontinuity in character traits actually occurs at some point along the 450 km gap between the Sixaola and Gatún populations. Only the four Río Guarumo specimens are available from this collecting hiatus and the data from so few specimens is not conclusive. Additional specimens would clarify for example, if the MI of the Guarumo fishes is intermediate between the Sixaola and Chagres forms or indeed similar to that of the Sixaola form (Table 6). Average proportional differences in head length, orbit diameter, length of anal-fin base, and length of pectoral fin (Tables 7 and 8) of the Chagres populations also distinguish them from the drainages to the north, but these differences are of a lesser degree than those shown by *M. hubbsi*. Future studies based on material from western Panamá will best be able to allocate these populations to their proper taxonomic rank.

Distribution: *M. chagresi* has been collected only in freshwaters between the Río Tortuguero drainage, Costa Rica and the Río Piedras, a short distance NE of Colón, Panamá. (Fig. 2). The identity of similar freshwater forms to the north in Honduras and in eastern Panamá is still undetermined.

Material examined: COSTA RICA: **Río Tortuguero drainage:** UF/FSM 11244 (3) Río Agua Fría, 8 miles upstream from village, 8 m. **Río Matina and Madre de Dios drainages:** UCR 444-15 (3) Quebrada Salsipuedes, 20 m; UCR 1013-4 (8) Río Chirripó, 20 m; UCR 1126-24 (53) Río San Miguel, 12 m. **Río Sixaola drainage:** UCR 1144-1 (26) trib. of Río Telire near Shiroles, 60 m. PANAMA: **Río Guarumo drainage:** ANSP 104003 (4) backwaters of Río Guarumo at Chiriquito, 60 m. **Gatún Lake:** ANSP 104286 (9) Barro Colorado Island, 30 m; UCR 1100-1 and 1101-1 (17) Gatún Lake, 30 m. **Río Piedras drainage:** ANSP 99905 (11) Río Piedras, ca. 4 miles from mouth, near sea level.

TABLE 7

Proportional variation in *Melaniris* expressed as head length (HL), orbit diameter (OR), snout length (SN), greatest body depth (BD) and preanal distance (PA) into standard length (SL) or head length (HL)

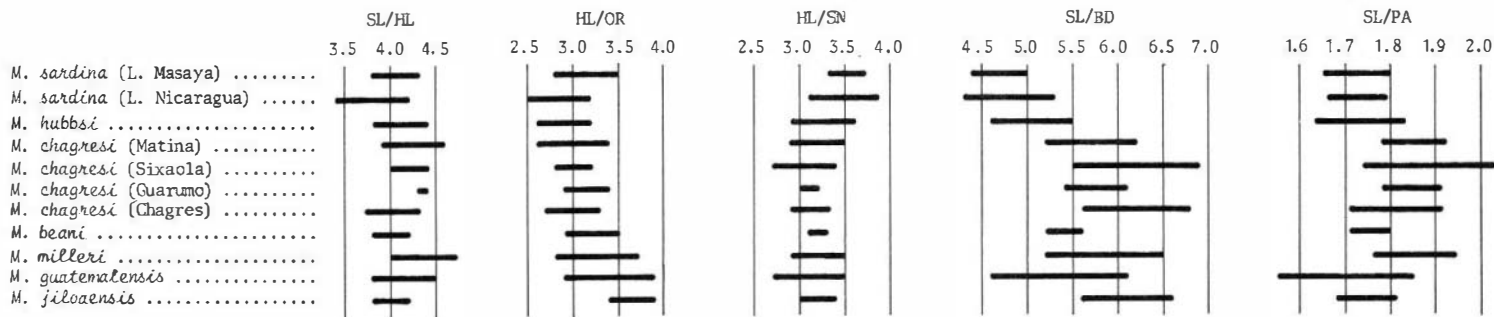
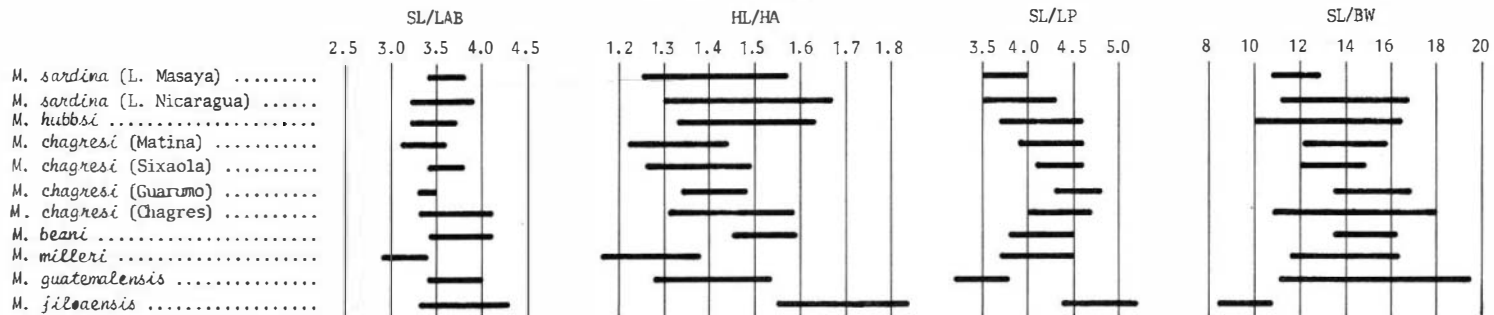


TABLE 8

Proportional variation in *Melaniris* expressed as length of anal-fin base (LAB), height of anal fin (HA), length of pectoral fin (LP) and body width at origin of first dorsal fin (BW) into standard length (SL) or head length (HL)



MELANIRIS JILOAENSIS, n. sp.
(Fig. 1F)

Melaniris c. f. *sardina* Meek, Villa, 1968, *Encuentro: Rev. Univ. Centroamericana*, 1:202-214 (compared to *M. sardina* and *M. chagresi*).

Diagnosis: *M. jiloensis* is a small, slim (body depth 5.6-6.6 times in SL) species which is readily distinguished from its southern Central American congeners in having thin, deciduous scales and a rounded body in cross-section as opposed to the highly compressed body of the other species (body width at first dorsal-fin origin 8.4-10.8 vs. 10.1-19.5 times in SL). The following combination of characteristics is also diagnostic: the small orbit (3.4-3.9 times in HL), short anal-fin base 3.3-4.3 times in SL), low anal fin (1.55-1.84 times in HL), short pectoral fins 4.4-5.2 times in SL), low anal-fin ray counts (19-24, \bar{x} = 20.5), low precaudal vertebral counts (17-18, \bar{x} = 17.6), high predorsal scale counts (21-29, \bar{x} = 24.9), high gill raker counts (24-29, \bar{x} = 27.0) and high transverse scale counts (7-8, \bar{x} = 7.4).

Description: The counts of the holotype are followed by the range for 31 paratypes in parentheses: Dorsal-fin rays IV-10 (III to V-7 to 11); anal 21 (19-24); pectoral 13 on right side, 14 on left side (12-14); pelvic 6 (6); median lateral scales 43 (40-43); predorsal scales 23 (21-29); transverse scales 7 (7-8); interdorsal scales 5 (5-7); scales around caudal peduncle 12 (12-14); total gill rakers 27 (24-29).

Body proportions in permillage of SL of the holotype are followed by the range for 10 paratypes in parentheses: Standard length (mm) 44.1 (41.6-50.6); head length 247 (238-260); orbit diameter 68 (65-70); postorbital distance 113 (113-126); snout length 79 (74-84); length of upper jaw 77 (77-84); bony interorbital distance 63 (59-70); body depth at vertical through origin of anal fin 170 (151-178); body width at vertical through first dorsal fin 104 (86-110); least depth of caudal peduncle 79 (73-81); length of caudal peduncle 175 (163-200); predorsal (first) distance 605 (580-619); predorsal (second) distance 726 (719-756); preanal distance 580 (560-594); prepectoral distance 240 (236-260); prepelvic distance 408 (394-418); length of dorsal-fin base 91 (76-99); length of anal-fin base 272 (240-275); height of dorsal fin 113 (106-113); height of anal fin 145 (142-162); length of pectoral fin 202 (197-223); length of pelvic fin 107 (107-119); length of upper lobe of caudal fin 231 (212-244); length of lower lobe of caudal fin 243 (230-251).

The deciduous scales are weakly crenate; some scales of the predorsal series have several long, irregular lobes in specimens larger than 45 mm SL. The short pectoral fins reach at most to a midpoint between the base and tip of the pelvic fin. The pelvic fins usually fall short of the vent, or at most just reach it. The caudal fin is clear or with a slightly darkened border. The largest specimen at hand is 56 mm SL.

Remarks: Villa (1968) cited differences between the Jiloá *Melaniris* and the species *sardina* and *chagresi*, and concluded that it represented a distinct species or a subspecies presumably of *M. sardina*. Certainly with its thin, tubular body and small eye, it is the most distinctive *Melaniris* in lower Central America. The fact that *M. sardina* also occurs in Lake Jiloá, and no intermediate specimens were collected adds further support to the assumption that *M. jiloensis* has differentiated to the species level and is genetically isolated from its congener.

Distribution: The species is endemic to Lake Jiloá, Nicaragua from which its name *jiloensis* is derived (Fig. 2).

Holotype: LACM 37350-1 (44.1 mm SL) NICARAGUA: Department of Managua, Lake Jiloá on Chiltepe Peninsula which extends into Lake Managua; 50 m elevation; 20 June 1972; collector Jaime Villa.

Paratypes: LACM 37350-2 (20, 38.8-50.9 mm SL), UCR 596-1 (60 and 3 cleared and stained, 40.9-56.1 mm SL), UMMZ 201962 (6, 41.9-49.1 mm SL), USNM 218374 (6, 43.0-48.0 mm SL) same data as holotype.

Additional material: A small collection of *M. jiloensis*, now in poor condition, was not used in preparing the species description: UCR 185-5 (10 and 3 cleared and stained, 35.0-55.7 mm SL) NICARAGUA: Lake Jiloá; 10 July 1967; collector Jaime Villa *et al.*

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RESUMEN

Se presenta un análisis morfométrico de siete especies de sardinas del género *Melaniris* en el sur de Centroamérica, datos sobre su distribución geográfica y claves para su identificación.

Melaniris guatemalensis habita lagunas costeras y esteros del Pacífico entre Guatemala y el sur de Costa Rica. *M. beani*, conocida únicamente de Colón, Panamá, y *M. milleri*, n. sp. de la costa atlántica de Nicaragua y Costa Rica, son principalmente sardinas de aguas salobres; esta última habita los tributarios del río San Juan a muchos kilómetros del mar. Las demás especies viven en las aguas dulces de la vertiente atlántica. *M. hubbsi*, n. sp. vive en las cuencas del río Escondido, Nicaragua y río San Juan; *M. chagresi*, muy parecida a la especie anterior, habita los ríos más al sur hasta el centro de Panamá. *M. sardina* es una especie lacustre que habita varios lagos de Nicaragua y se le encontró por primera vez en Costa Rica en el Río Sapoá. *M. jiloensis*, n. sp. es indígena de la Laguna Jiloá, Nicaragua.

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Fig. 1. Species of lower Central American *Melaniris*. A, *M. guatemalensis*, UCR 420-7, 84.0 mm SL, from Estero Mata Limón, Costa Rica; B, *M. sardina*, UCR 536-2, 40.2 mm SL, from Lake Nicaragua; C, *M. milleri*, UCR 1067-1, 59.1 mm SL, from lagoon at Barra Colorado, Costa Rica; D, *M. hubbsi*, LACM 375061, holotype, 53.0 mm SL, from Río Zapote, Costa Rica; E, *M. chagresi*, UCR 1126-24, 56.9 mm SL, from the Río Matina drainage, Costa Rica; F, *M. jiloensis*, UCR 596-1, 49.4 mm SL, from Lake Jiloá, Nicaragua.



A



B



C



D



E



F

Fig. 2. Map showing collecting localities of seven species of *Melaniris* treated in this study. *M. jiloesensis* is endemic to the crater lake Jilóá. *M. beani* is known only from the types collected at Colón, Panamá. Each symbol represents one to several collections.

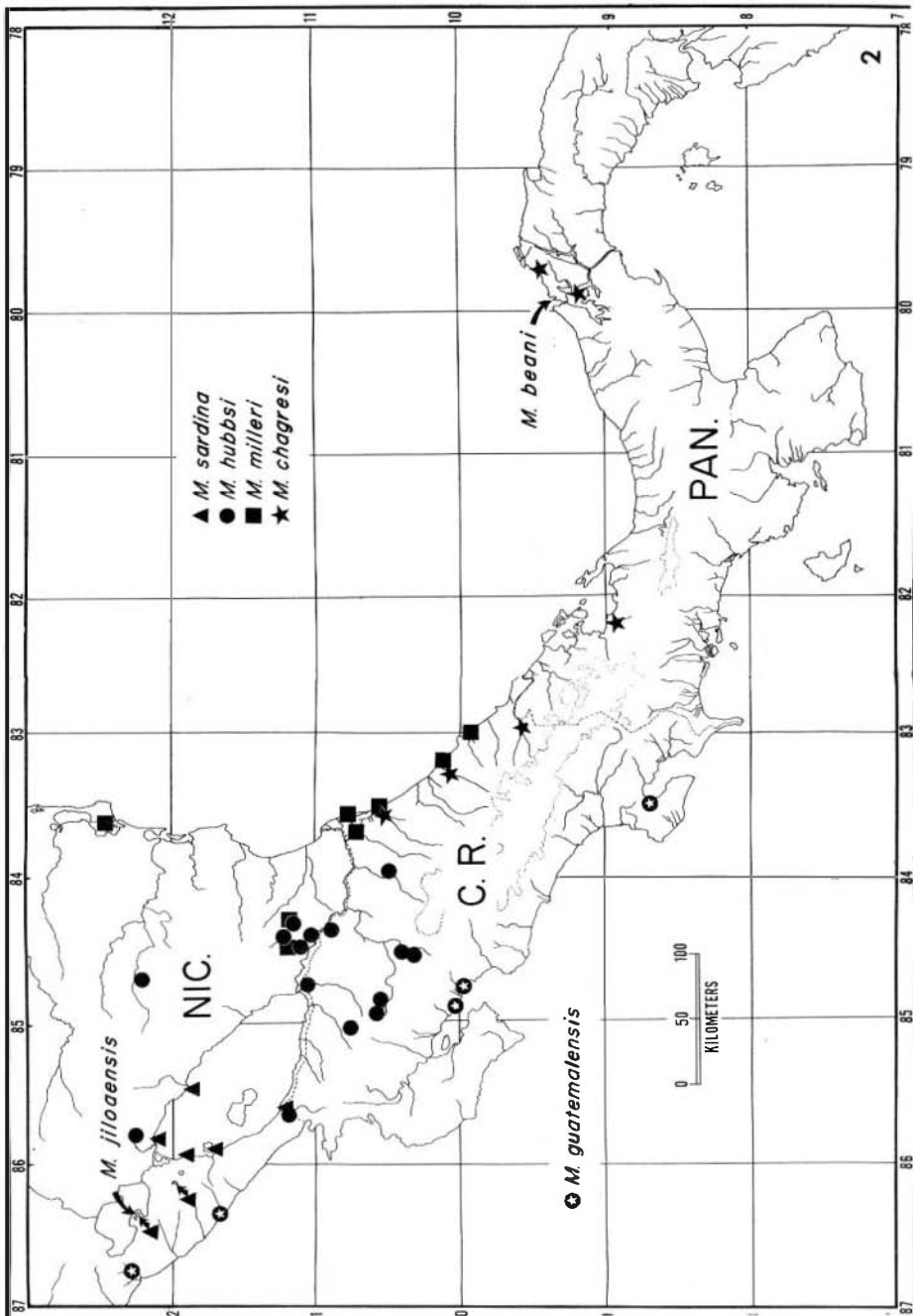


Fig. 3. Two characters, height of anal fin and body depth, which permit separation of *Melaniris chagresi* and *M. hubbsi*.

