



Two new miniature silverside fishes of the genus *Membras* Bonaparte (Atheriniformes, Atherinopsidae) from the Tropical North Atlantic Ocean

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Abstract

Two new species of miniature silverside fishes are described from coastal habitats in the tropical Atlantic: *Membras pygmaea* **sp. nov.**, from Brus Lagoon, Honduras, and *M. procera* **sp. nov.**, from the Gulf of Urabá, Colombia. These new species belong to the *martinica* species-group within the genus *Membras* Bonaparte. The monophyletic *martinica* species-group (see below) contains four additional species, all coastal, marine that extend from the east coast of North America to São Paulo State, Brazil. Within the *martinica* species-group, all but *M. martinica* are miniature species, ranging from 41–60 mm SL. The smallest species, *M. pygmaea* **sp. nov.**, is mature at 24 mm SL. A geometric morphometric analysis shows: (i) each species of the *martinica* species-group occupies its own portion of shape space; and (ii) none of the miniature species possess the shapes of small immature *M. martinica*. While some of the literature suggests that miniaturization may involve paedomorphosis, our results show that the miniatures accelerate to adult body forms.

Key words: miniaturization, geometric morphometrics, Neotropical biodiversity

Resumen

Dos especies nuevas de peces tinicalos pigmeos son descritos provenientes de hábitats costeros del Atlántico Tropical: *Membras pygmaea* n. esp. de la Laguna Brus en Honduras y *M. procera* n. esp. proveniente del Golfo de Urabá, Colombia. Estas nuevas especies pertenecen al grupo-especies *martinica* dentro del género *Membras* Bonaparte. El monofolético grupo-especie *martinica* (ver abajo) incluye cuatro especies adicionales, todos ellos marinos-costeros, cuya distribución se extiende desde la costa este de América del Norte hasta el estado de São Paulo, Brasil. Dentro del grupo-especies *martinica*, todas menos *M. martinica* son especies miniaturas con un intervalo de tallas de 41 a 60 mm LE. La especie más pequeña, *M. pygmaea* n. esp. es adulta madura a los 24 mm LE. Un análisis morfo-geométrico muestra que: (i) cada especie del grupo-especie *martinica* ocupa su propia porción en el morfo-espacio; y que (ii) ninguna de las especies miniaturas posee la forma mostrada por ejemplares inmaduros pequeños de *M. martinica*. Mientras que algunos trabajos publicados sugieren que la miniaturización puede implicar pedomorfosis, nuestros resultados muestran que la miniaturas aceleran a las formas de cuerpo del adulto.

Introduction

The genus *Membras* Bonaparte 1836 has five described species (Chernoff 1986b): *M. martinica* (Cuvier & Valenciennes 1835), *M. gilberti* (Jordan & Bollman 1889), *M. analis* (Schultz 1948), *M. argentea* (Schultz 1948) and *M. dissimilis* (Carvalho 1956). These occupy coastal estuarine and marine habitats discontinuously from Long Island, New York, USA to the area of Cananéia, São Paulo, Brasil in the Atlantic and from Jiquilisco Bay, El Salvador to Tumbes, Peru in the Pacific (Chernoff 1986b, 2002; Lavenberg & Chernoff 1995). Campanella *et al.* (2015) in a molecular study of atherinopsids confirmed the monophyly of the genus.

M. gilberti, the lone Pacific member, is sister to the remaining species (Chernoff 1986b, Campanella *et al.*, 2015). The Atlantic clade, including the two new species described herein, comprise the monophyletic *M. martinica* species-group (Chernoff 1986b). Among other uniquely derived traits, the *M. martinica* species-group possesses two unique synapomorphies among atherinopsids: a rostral sensory system with four enlarged pits at the anterior margin of the frontal bones; and an ossified submaxillary meniscus or submaxillary bone (Chernoff 1986b, 2002).

Within the *M. martinica* species-group are five miniature species that are coastal in the tropical and South Atlantic (Figs. 1,2): *M. analis* from Lake Maracaibo, Venezuela; *M. argentea* from off Sabanilla, Colombia; *M. dissimilis* from coastal southern São Paulo State, Brazil; *M. procera* **sp. nov.**, from the Gulf of Urabá, Colombia; and *M. pygmaea* **sp. nov.**, from Brus Lagoon, Honduras. These species are each known from one or at most a few collections. *M. analis* is the largest of the group attaining almost 60 mm SL. The other species are less than 45 mm SL and are sexually mature.

The purpose of this paper is to describe the two new species, provide a key to the species of the genus, and analyze shape variation within the *martinica* species-group to examine the effects of miniaturization. The comparative meristic and morphometric character differences between the new species and the other species of *Membras* are given in the key.

Methods

All counts and measurements are as per Chernoff (1986a) with the following clarification: meristic counts for second dorsal and anal fins enumerate the rays only and do not include the single spine at the origin of the fins. In the frequencies of meristic counts the values for the holotypes are indicated by asterisks. Mensural differences (Table 1) were determined from 24 morphometric characters measured with digital calipers with replaceable steel-pin tips to the nearest 0.1 mm.

For analysis of geometric morphometrics within the *martinica* species-group, with the exception of *M. dissimilis*, landmarks of specimens were pinned with 0000 insect pins. Although 17 landmarks were identified at the outset of the study, two proved to be unreliable, and a scheme of 15 landmarks was analyzed (Fig. 4). The pinned specimens were placed in a shallow cradle with a scale bar on a flat-bed Epson Perfection scanner and scanned at 3200 dpi in color.

The landmarks for *M. dissimilis* were digitized from radiographs. We tested digitizing landmarks from radiographs by pinned samples of *M. martinica* (N=30) and *M. pygmaea* (N=20) and found no discernable differences in distances among landmarks (MANOVA's P 's > 0.7).

The landmarks for each specimen were digitized from the images or radiographs in tpsDIG2.1 (Rohlf 2006). The digitized screen coordinates were scaled to the scale bar. Landmark configurations were processed using Procrustes superimposition in MorphoJ version 1.07a (Klingenberg 2011) from which the covariance matrix was calculated. Because of the dramatic range of sizes of individuals in the *martinica* species-group, from 27 mm SL to more than 100 mm SL, it was not surprising that the principal component analysis (PCA) of the covariance matrix was dominated by ontogenetic shifts in size and shape among the species. Thus, an allometric correction was necessary to compare shapes of specimens of different ages and sizes (Bookstein *et al.* 1985, Sidlauskas *et al.* 2011). We used the method of Sidlauskas *et al.* (2011) as follows: 1) a pooled-within group allometric regression using log centroid size was performed on the on the Procrustes coordinates in MorphoJ; and 2) PCA on the covariance matrix of the residuals from step 1 resulted in a size-standardized morphospace. The latter is critical to be able to analyze shape differences across large variation in sizes of the species. The PCA scores from step 2 were plotted using the 99% confidence ellipses for each species and the displacement grids for the PC's were calculated in MorphoJ. To test

species differences in shape, individual scores of species on the first two PC's were analyzed with a MANOVA with multiple post-hoc Hotelling T^2 in PAST version 4.0 (Hammer et al. 2001). A Bonferroni procedure corrected the table of significance levels for multiple species comparisons.

The following sample sizes (meristics, linear measurements, geometric morphometrics) were used for comparisons as shown in the key and geometric morphometrics: *M. analis* (30, 30, 25); *M. argentea* (4, 4, 4); *M. dissimilis* (5, 5, 5); *M. gilberti* (57, 35, 0); *M. martinica* (200, 225, 130); *M. procera* **sp. nov.** (4, 4, 4); *M. pygmaea* (30, 30, 30). The meristic and standard morphometric comparisons of the new species to the described taxa are shown in the following key:

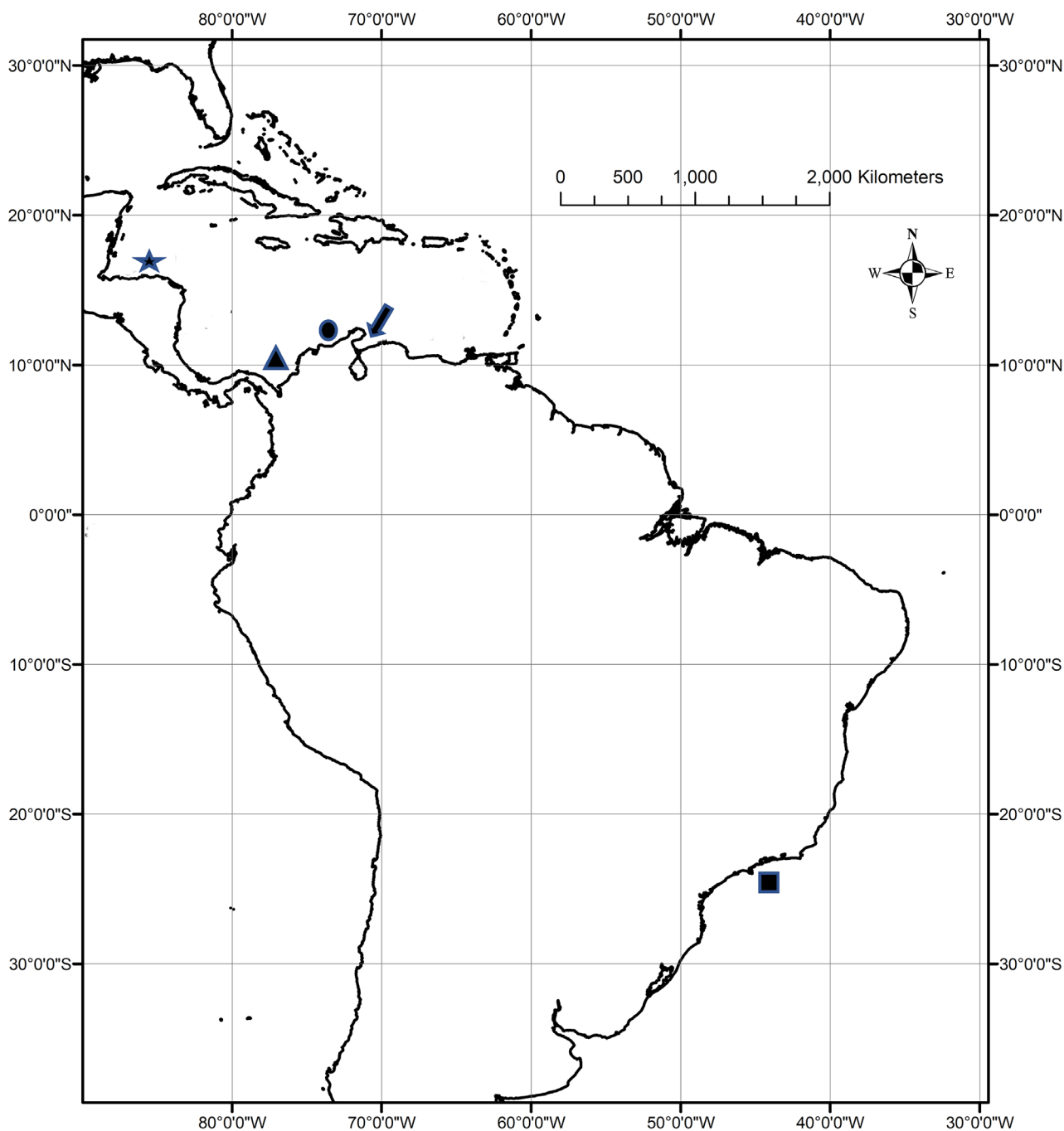


FIGURE 1. Map of southern Central America and South America showing the distribution of the miniature species of the *Membras martinica* species-group as follows: (i) star—*M. pygmaea* **sp. nov.**, Brus Lagoon, Honduras; (ii) triangle—*M. procera* **sp. nov.**, Gulf of Urabá, Colombia; (iii) circle—*M. argentea*, off Sabanilla, Colombia; (iv) arrow—*M. analis*, off Lago Maracaibo, Venezuela; and (v) square—*M. dissimilis*, off Cananéia, Brazil.

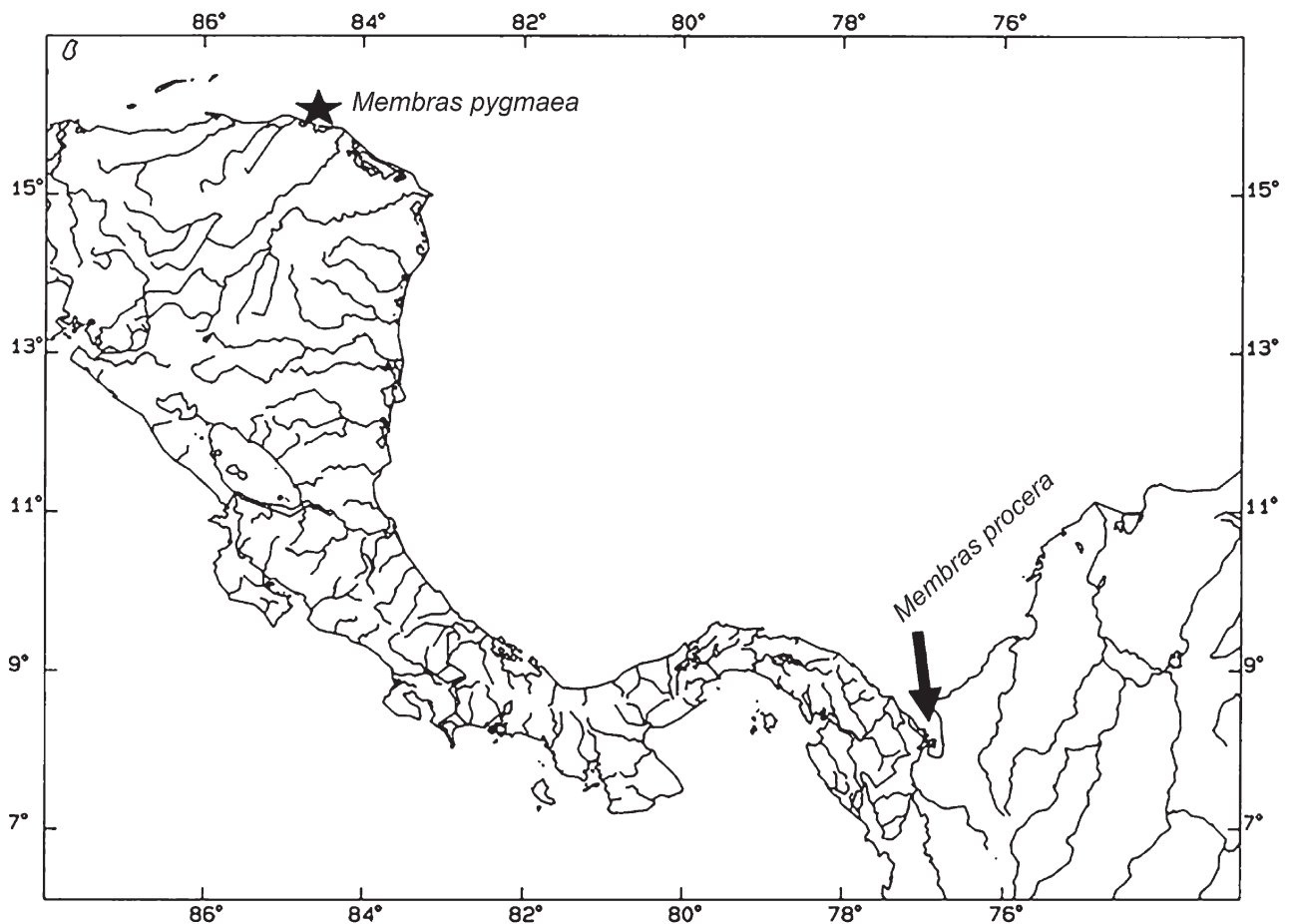


FIGURE 2. Map of Honduras to northern Colombia showing the localities for *Membras pygmaea* sp. nov., Brus Lagoon, Honduras and *M. procera* sp. nov., Gulf of Urabá, Colombia.

Key to the Genus *Membras* Bonaparte

- 1A. Rostral sensory system 4+2, without four large pits at margin of frontal bones; scales around body 20–27, modally 22 *M. gilberti*
- 1B. Rostral sensory system 4+2+4, with four large deep pits at margin of frontal bones (in largest specimens the two intermediate pits may fuse with the two posterior pits); scales around body 13–19, modally 16. 2
- 2A. Anus located just anterior to origin of anal fin; tips of pelvic fins not reaching anterior margin of vent; predorsal scales 21–26, modally 23–24; posterior margins of scales laciniate *M. martinica*
- 2B. Anus positioned closer to base of pelvic fin than to origin of anal fin; tips of pelvic fins reaching or extending beyond anterior margin of vent; predorsal scales 16–21, modally 19–20; posterior margins of scales smooth or laciniate 3
- 3A. Posterior margins of predorsal and lateral scales strongly laciniate. 4
- 3B. Posterior margins of predorsal and lateral scales smooth or irregular. 5
- 4A. Lateral scales 38–39; predorsal scales 16–18, modally 18; length of spinous dorsal fin 6.4–6.9% SL, mean = 6.8%; least depth of caudal peduncle greater than 9.2–9.5% SL, mean = 9.4%. *M. argentea*
- 4B. Lateral scales more than 40; predorsal scales 20–21, modally 21; length of spinous dorsal fin 8.8–9.0% SL, mean = 8.8%; least depth of caudal peduncle 7.4–8.6% SL, mean = 8.2%. *M. procera* sp. nov.
- 5A. Precaudal vertebrae 17–18; pre-anal-fin length 6.3–6.4% SL, mean = 6.3%; orbit diameter 6.5–6.7% SL, mean = 6.6%; lateral stripe becomes diffuse at base of caudal fin, lacking a distinctive mark *M. dissimilis*
- 5B. Precaudal vertebrae 14–16, modally 15; pre-anal-fin length 5.6–6.2% SL, mean = 6.0%; orbit diameter 6.8–8.5% SL, mean = 7.7%; lateral stripe ends distinctly before hypural base there can be a diffuse spot or crescent mark present 6
- 6A. Least depth of caudal peduncle 8.5–10.5% SL, mean = 9.7%; body depth 15.7–18.1% SL, mean = 16.9%; total gill rakers, first arch 15–18, modally 16–17 *M. analis*
- 6B. Least depth of caudal peduncle 6.7–8.5% SL, mean = 7.7%; body depth 13.5–15.9% SL, mean = 14.8%; total gill rakers, first arch 16–20, modally 18 or 19. *M. pygmaea* sp. nov.

***Membras pygmaea* sp. nov.**

Fig. 3A, Table 1

Holotype. FMNH 117282 (40.2 mm SL); Honduras: Depto. Gracias A Dios: Brus Lagoon off the town Brus Lagoon; R. K. Johnson and G. Glodek, 10 May 1975.

Paratypes. All lots collected with holotype: FMNH 117283, 240 (23.0–41.3 mm SL). ANSP 153429, 5 (27.4–29.7 mm SL).

Diagnosis. A species of *Membras* belonging to the *M. martinica* species-group, and differentiable from all congeners by the following characters: anus positioned closer to the insertion of pelvic fin than the origin of anal fin and; posterior margins of predorsal and lateral scales smooth or slightly irregular, not lacinate; least depth of caudal peduncle 6.7–8.5% SL; total gill rakers, first arch 16–20, modally 18 or 19.

Description. Morphometric data given in Table 1. A dwarf species, less than 41 mm SL. Individuals ≥ 30 mm SL with large testes or large, apparently ripe eggs. Body elongate in appearance; body tapering posteriorly to slender caudal peduncle. Dorsal fins well separated; spinous dorsal posterior to anus and anterior to origin of anal fin.

Head length $< 9.4\%$ SL, not truncate posteriorly. Eye positioned within anterior 2/3 of head. Snout bullet shaped, almost pointed anteriorly; lower jaw jutting gracefully outward from prominent joint with quadrate. Dorsal profile of head slightly convex. Mouth terminal, opening just dorsal to horizontal line through midpoint of orbit. Premaxilla curves downward below ventral rim of orbit but not beyond anterior margin. Premaxillary teeth in two rows medially, extending laterally as broad patch of small teeth but not as far as labial ligament. All teeth relatively small, conical and recurved but those of outer row slightly larger. Dentary teeth restricted to small anteromesial tooth patch; tooth patch not extending to labial ligament or where premaxilla crosses dentary in open jaw. Labial ligament with well-developed sheath to end of alveolar process posteriorly; anterior arm thickened, extending to dentary symphysis; bulbular thickening in dorsal portion forming cap to sheath; dorsal arm extending only one-third way up premaxilla. Mesopterygoid teeth present. Vomerine teeth absent.



FIGURE 3. **A.** *Membras pygmaea* sp. nov., holotype, FMNH 117282, 40.2 mm SL. **B.** *Membras procera* sp. nov., holotype, ANSP 153427, 36.6 mm SL.

Spinous dorsal with anterior spines longest; extending posterior to vertical from anal-fin origin. Distal margin of second dorsal fin straight to slightly falcate; posterior rays longest in depressed fin. Anal fin falcate; depressed anterior lobe extending beyond midpoint of fin. Ventral margin of pectoral fin straight to slightly falcate; fin extending beyond vertical line from base of pelvic fin. Posterior margin of extended pelvic fin straight, reaching anterior margin of vent.

Predorsal scales slightly wider than long or of equal dimension; posterior margin smooth or slightly irregular; or with well-developed central knob. Lateral scales grade from much wider than deep anteriorly to shield shaped on

caudal peduncle; posterior margin smooth or slightly irregular, never lacinate; anterior margin with well-developed central knob. Circuli restricted to anterior scale field. Radii weak, present only on caudal peduncle scales. Axillary scale of pelvic fin 1/2–1/3 fin length. Interpelvic scale >1/2 length of fin. Modified scales with posterior projections at base of spinous dorsal and along second dorsal fin.

First dorsal fin spines 3(1), 4(10), 5*(18), 6(1). Second dorsal fin rays I,8(4), I,9*(19), I,10(7). Anal fin rays: total I,14(1), I,15(10), I,16*(16), I,17(3); anterior to second dorsal fin 9(1), 10(23), 11*(6). Pectoral fin rays 12(1), 13(20), 14*(7), 15(2). Scales: lateral 41(2), 42(14), 43*(8), 44(5), 45(1); predorsal 19(1), 20(14), 21*(12), 22(3); transverse rows 6*(30); rows around body 14(1), 16*(29); rows around caudal peduncle 12*(30). Gill rakers: total 16(1), 17(3), 18(12), 19*(11), 20(3); upper 3(3), 4*(25), 2(2); lower 13(2), 14(14), 15*(13), 16(1). Vertebrae: total 39(2), 40*(17), 41(8), 42(1); precaudal 15*(24), 16(4); caudal 24(2), 25*(21), 26(5). Vertebral count to origin of: spinous dorsal fin 18(16), 19*(12); second dorsal fin 26(20), 27*(8); anal fin 20(6), 21*(22).

TABLE 1. Mensural data for *Membras pygmaea* (n = 30) and *M. procera* (n=3). Values are in thousandths of SL, except for SL, which is in mm.

Variables	<i>M. pygmaea</i>			<i>M. procera</i>		
	Holotype	Range	Mean	Holotype	Range	Mean
SL, mm	40.2	28.7–43.1	32.8	36.6	34.0–36.6	35.8
PreD1 length	587	539–612	561	568	562–568	565
PreD2 length	746	695–746	721	713	706–713	709
Preanal length	619	561–626	605	587	587–609	595
Prepelvic length	400	371–404	389	393	386–410	396
Prepectoral length	231	214–245	226	232	232–241	238
Head length	219	211–233	221	221	221–238	232
Head depth	109	101–120	108	115	107–119	157
Interorbital width	80	64–88	77	79	79–83	81
Orbit diameter	80	68–82	76	74	74–86	78
Snout length	62	47–62	54	60	60–66	62
Body depth	114	135–159	148	153	153–163	157
Body width	72	46–84	59	68	68–72	71
Caudal peduncle						
length	197	197–241	216	210	198–210	205
width	27	18–35	26	30	28–30	29
depth	80	67–85	77	82	74–86	82
PostD2 length	187	176–216	192	191	187–194	191
Anal fin-D1	162	126–162	152	150	146–155	150
Anal fin-D2	199	167–199	184	197	196–197	196
Anal fin base	184	167–218	190	202	202–212	206
D2 fin base	92	81–131	104	93	91–102	95
D1 spine length	85	74–86	76	90	88–90	88
Pectoral fin length	177	155–185	172	180	172–187	180
Pelvic fin length	119	102–139	118	120	119–124	95

Pigmentation in alcohol. Overall, a lightly pigmented species, most pigment contained on lateral stripe.

Top of head with posterior heart-shaped brain pigment with deeply incised central notch; anterior portion with a few large melanophores; remainder of frontals immaculate. Ethmoid region irregularly pigmented with a few scattered flecks. One or two dark spots under nasal bones. Premaxila with relatively dense pigment dorsally, contrasting with light anterior border, becoming sparser laterally, not extending to labial ligament. Dentary with large scattered flecks, largest under labia ligament, extending to joint with quadrate. Gular region immaculate. Infraorbital series, opercular bones and branchiostegals with small scattered melanophores.

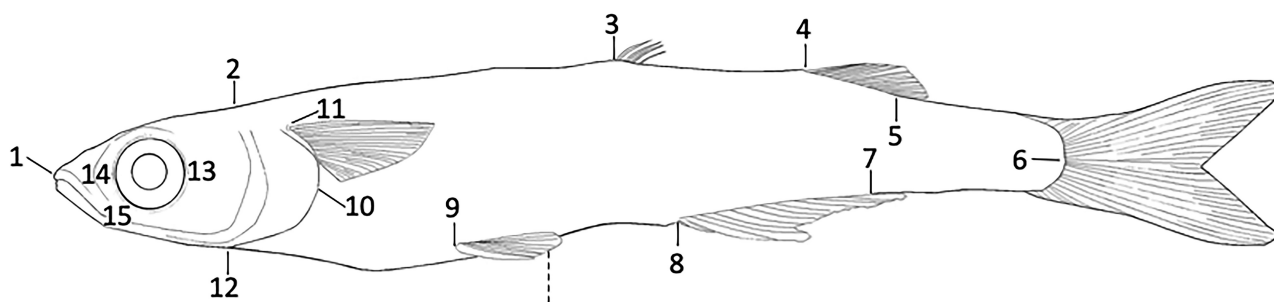


FIGURE 4. Outline of *Membras pygmaea* sp. nov., showing the landmarks that were digitized. The dashed line on the ventral side indicates the location of the anal pore. The digitized landmarks: 1 tip of snout; 2 posterior margin of occiput; 3 origin of spinous dorsal fin; 4 origin of second dorsal fin; 5 terminus of second dorsal fin; 6 posterior margin of hypural plate; 7 terminus of anal fin; 8 origin of anal fin; 9 insertion of pelvic fin; 10 posterior bony margin of head; 11 insertion of pectoral fin; 12 posterior extent of gular region; 13 posterior margin of orbit; 14 anterior margin of orbit; 15 posterior margin of upper jaw.

Depth of lateral stripe 1/2–3/4 of orbit, bearing several rows of distinct melanophores, constricted slightly on caudal peduncle. Usually two rows of melanophores between upper edge of lateral stripe and dorsum; scale margins not outlined or crosshatched. Predorsal and interdorsal stripes with one row of melanophores; postdorsal stripe with one or two rows. Body below lateral stripe and breast without pigment. Row of melanophores from posterior margin of anus along sides of anal fin and under caudal peduncle to caudal fin.

Spinous dorsal fin with only a few scattered flecks along spines or immaculate. Second dorsal fin with melanophores along rays, especially proximally, not on membranes; small specimens lacking pigment. Anal fin and pelvic fins immaculate. Pectoral fin with melanophores present only on basal part of rays; fleshy base of fin with at most a few pigment spots, not freckled.

Distribution and Habitat. The species is only known from Brus Lagoon, Depto. Gracias a Dios, Honduras (Fig. 2). The habitat for the collections was a salt marsh with channels bordered by reeds and saw grass. The bottom was peaty. The channel in which the species was collected was on the coastal edge of the lagoon-salt marsh complex.

Etymology. The species-group name, *pygmaea*, an adjective derived from the Latin meaning little or dwarf, referring to the diminutive size of the species.

Membras procera sp. nov.

Fig. 3B, Table 1

Holotype. ANSP 153427 (36.6 mm SL); Colombia: Gulf of Urabá, 8 17.0° N, 76 49.5° W; R.V. Pillsbury, 11 July 1966.

Paratypes. All lots collected with holotype. ANSP 153428 (36.1 mm SL); UMML 30095, 2(34.0–36.3 mm SL).

Diagnosis. A species of *Membras* belonging to the *martinica* species-group, distinguishable from all congeners by the following characters: anus between anal fin origin and pelvic fin insertion; tips of pelvic fins reaching anterior margin of vent; posterior margins of predorsal and lateral scales strongly lacinate; lateral scales 42–44; predorsal scales 20–22; length of spinous dorsal fin 8.5–9.5% SL; least depth of caudal peduncle 7.3–8.6% SL.

Description. Morphometric data given in Table 1. Values for holotype indicated by asterisks; number of examined specimens with a given count in parentheses.

A dwarf species, known from specimens less than 40 mm SL, yet specimens with large testes and large eggs. Body slender, elongate with belly curving gracefully to slender, elongate caudal peduncle. Anus almost midway between pelvic fin insertion and anal fin origin. Spinous dorsal fin just anterior to origin of anal fin and posterior to anus. Dorsal fins well separated. Base of second dorsal fin terminates posterior to anal fin.

Head length <25% SL, not truncated posteriorly. Orbit positioned within anterior 2/3 of head. Snout blunt with bullet-shaped lateral profile. Lower jaw angling upwards obliquely from prominent quadrate-angular joint. Dorsal profile of snout curved broadly not pointed; top of head slightly convex. Mouth terminal, opening above midpoint

of orbit. Closed lower jaw included within upper jaw. Premaxilla curved downward but not extending below ventral margin of orbit. Teeth in both jaws minute, conical and recurved slightly; largest in premaxilla. Premaxillary teeth generally in two rows, though additional teeth added to series forming wider patch laterally on inner surface of alveolar arm; largest on outer row; teeth extending up to but not beyond labial ligament. Dentary teeth in two uneven rows near symphysis becoming a single row laterally extending up to coronoid process. Labial ligament with well-developed sheath, thickened and extending to distal edge of alveolar process; anterior dentary arm of ligament thickened and extending to symphysis; dorsal arm with base above sheath thickened and bulbous, extending to midpoint of premaxilla. Mesopterygoid teeth present; vomerine teeth absent.

Spinous dorsal elongate and slender, not near base of second dorsal when depressed. Second dorsal fin with falcate posterior margin. Anal fin falcate with pronounced anterior lobe extending beyond midpoint of fin when depressed. Distal margin of pectoral fin straight to slightly falcate extending beyond vertical from base of pelvic fin. Pelvic fin with almost straight distal margin; tip of fin reaching or just extending beyond anterior margin of vent, not covering anus.

Shape of scales varies by region of body. Predorsal scales as wide or slightly wider than long. Lateral scales grade from much wider than long on anterior scales to shield shaped or as long as wide on caudal peduncle scales. Posterior margins of scales notched deeply or lacinate; best developed on predorsal scales. Predorsal scales with one or sometimes two well-developed anterior knobs, remainder of margins irregular, wavy or somewhat lacinate. Lateral scales with a single anterior knob on a straight margin. Circuli restricted to anterior scale field of all scales, posterior field naked. One or two weakly developed radii on caudal peduncle scales only. Axillary scale of pelvic fin triangular, pointed posteriorly reaching from 1/3–1/2 length of fin. Interpelvic scale pointed posteriorly, reaching midpoint of fin. Modified scales with single posterior projection along bases of both dorsal fins.

First dorsal fin spines 3(1), 4*(3). Second dorsal fin rays I,9*(4). Anal fin rays: total I,16(1), I,17*(3); anterior to second dorsal fin I,10*(3), I,12(1). Pectoral fin rays 12(2), 13*(2). Scales: lateral 42(1), 43*(2), 44(1); predorsal 20(1), 21*(2); transverse rows 6*(4); rows around body 16*(4); rows around caudal peduncle 12*(4). Gill rakers: total 18(1), 20*(2), 21(1); upper 4*(2), 5(2); lower 14(1), 15(1) 16*(2). Vertebrae: total 41*(3), 42(1); precaudal 15*(4); caudal 26*(3), 27(1). Vertebrae count to origin of: spinous dorsal fin 19(3), 20*(1); second dorsal fin 27*(4); anal fin 20(2), 21*(2).

Pigmentation in alcohol. Overall, a lightly pigmented species, most pigment contained on lateral stripe.

Top of head with posterior heart-shaped brain pigment with deeply incised central notch; anterior portion with a blotch of pigment; remainder of frontals almost immaculate. Ethmoid region irregularly pigmented with a few scattered flecks. One or two large melanophores under nasal bones. Premaxilla dusky dorsally becoming sparser laterally, not extending to labial ligament. Dentary with a row of dark, large melanophores, largest under labia ligament, extending to joint with quadrate. Gular region immaculate. Infraorbital series, opercular bones and branchiostegals with relatively few scattered pigment specks.

Lateral stripe less than a scale width anteriorly expanding to 1.5 scales at mid-body and decreasing to less than a scale on the caudal peduncle. Lateral stripe with several rows of distinct melanophores, the darkest and largest along the dorsal margin. Usually two rows of melanophores between upper edge of lateral stripe and dorsum; scale margins not outlined or crosshatched. Predorsal and interdorsal stripes with a single file of melanophores; postdorsal stripe with one or two rows. Body below lateral stripe and breast without pigment. Row of melanophores from posterior margin of anus along sides of anal fin and under caudal peduncle to caudal fin.

Spinous dorsal fin with a few large melanophores along anterior spines. Second dorsal and anal fins with melanophores along rays not on membranes. Pelvic fin immaculate. Pectoral fin with melanophores present only on inner surface of basal part of rays; fleshy base of fin lacking pigment spots.

Distribution and Habitat. The species is only known from the Gulf of Urabá in eastern Colombia. It was collected in open water about 1 km offshore. The species was captured at night when lights were submerged below the surface waters to 1 m off the R.V. Pillsbury.

Etymology. The species-group name, *procera*, an adjective derived from the Latin, meaning long or slender, in reference to the overall shape of this species.

Geometric Morphometrics of the *martinica* species-group

Each of the species of the *martinica* species-group occupied its own section of the size-corrected shape space (Fig. 5); there were no overlaps of the 99% confidence ellipses. Individuals of *Membras martinica* demonstrated an allometric trend so that larger individuals had different shapes (higher PC2 scores) than smaller individuals (Fig. 5, ellipse 1). The lack of such a trend in the other species was most likely due to their small sizes-ranges. The overall MANOVA was significant ($P < .0001$) as were all of the species-by-species post-hoc comparisons with Bonferroni corrections ($.000 < P < .001$).

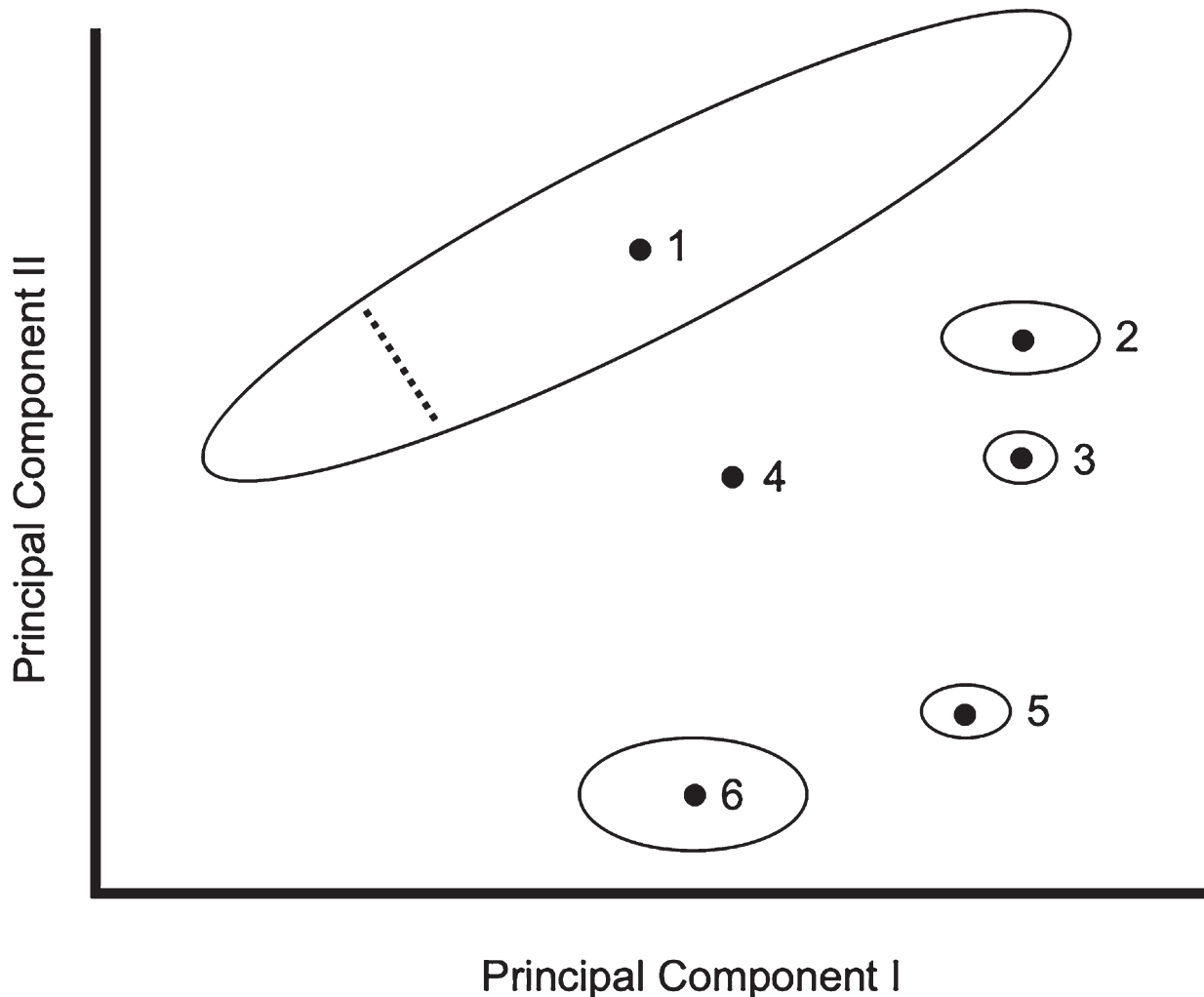


FIGURE 5. Shape space: principal components of Procrustes-aligned, scale-adjusted shape space (= relative warps); 99% confidence limits shown for each species, the dots indicate the centroid value for each species; the dashed line in the *Membras martinica* ellipse demarcates the area of the ellipse occupied by individuals less than 45 mm SL. The ellipses are: 1 *Membras martinica*; 2 *M. analis*; 3 *M. dissimilis*; 4 *M. procera* sp. nov.; 5 *M. argentea*; 6 *M. pygmaea* sp. nov.

The deformation grids (Fig. 6) illustrate the change in morphology, that is the movement of landmarks described by each of the PC's. The vectors coming off the grids indicate: (i) the magnitude of the changes such that individuals with higher scores (to the right of PC1 or the top of PC2) are enlarged morphologically; and (ii) the directions of the displacement of the landmarks. PC1 shows that *M. analis*, *M. argentea*, *M. dissimilis* and larger specimens of *M. martinica* have: (i) longer snouts that open slightly more dorsally; (ii) elongation of the posterior part of the head and pectoral girdle; and (iii) a deepening of the body in the region of the pelvic fin. All of the small species have shapes on PC1 that extended beyond the median shape to the shapes described by the upper end of the ellipse for *M. martinica*. The small species were quite a bit shorter than the comparable shapes for *M. martinica*. For example, *M. analis* (Fig. 5, number 2) is less than 60 mm SL and had scores equivalent for individuals of *M. martinica* 85-110 mm SL.

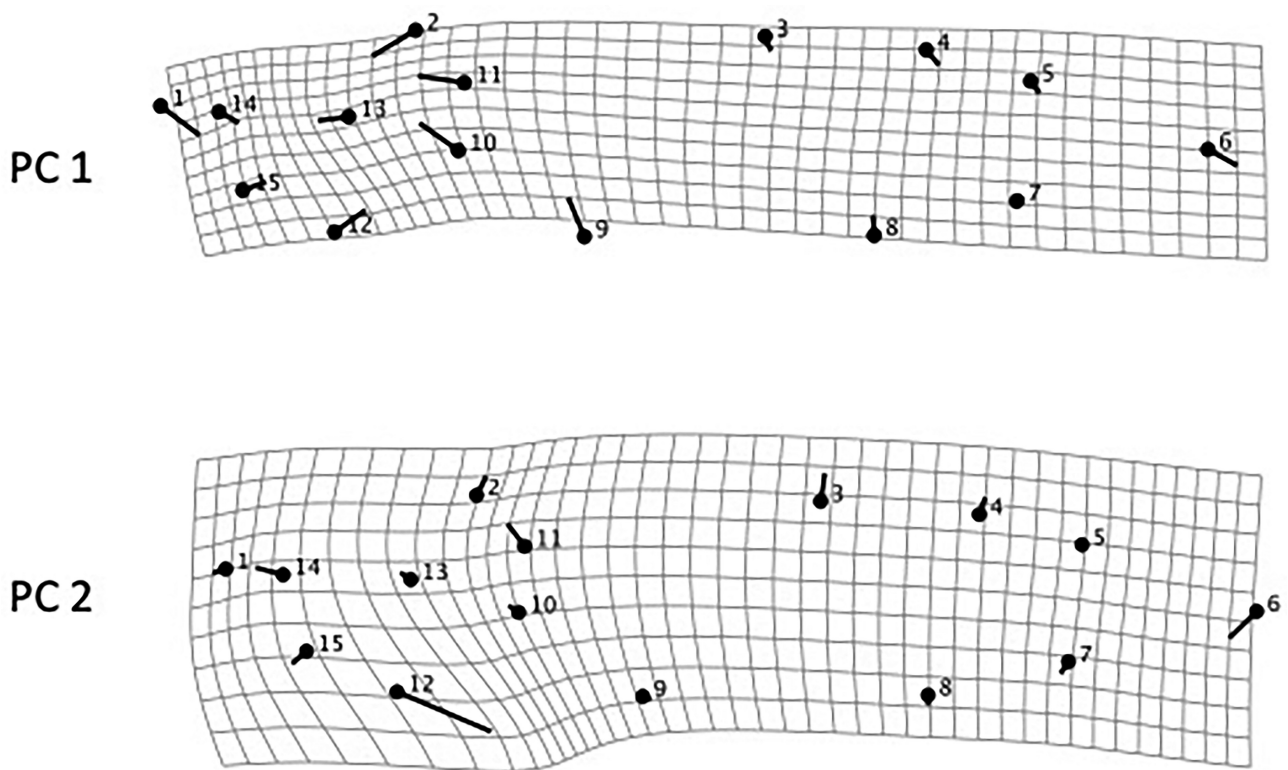


FIGURE 6. Deformation grids among landmarks for the shape space in Figure 5. The vectors coming off the grids indicate: i) the magnitude of the changes such that individuals with higher scores (to the right of PC1 or the top of PC2) are enlarged morphologically; and ii) the directions of the displacement of the landmarks.

PC2 defined a morphospace with the shortest species, *M. pygmaea*, at the bottom and the longest species, *M. martinica*, at the top. *M. martinica*, *M. analis*, and *M. procera* have: (i) slightly shorter eyes; (ii) posteroventral elongation of the ventral portion of the head and the gular area; and (iii) a slightly longer caudal peduncle.

The morphospace defined by PC1 and PC2 highlight that none of the small or dwarf species occupy the space of short, sexually immature *M. martinica* (Fig. 5). Much has been written about miniaturization and miniaturization in fishes (e.g., Weitzman & Vari 1988; Hanken & Wake 1993; Bloom *et al.* 2019). By the definition of Weitzman & Vari (1988), none of the miniature species of *Membras* qualifies as a true dwarf for which they suggested a limit of 26 mm SL. Hanken & Wake (1988) concluded that reduction in body size often, but not always, included morphological simplification. From the perspective of body shape, the small species of *Membras* are not simplified in the sense that simplified could mean pedomorphic. The four miniature species express mature, adult shapes. This result accords well with the study on sardines by Bloom *et al.* (2019) in which they found that the miniature species occupied their own portion of shape space. Furthermore, the miniature species of *Membras* demonstrate that relative to change in standard length the miniatures accelerate (*sensu* Bookstein *et al.* 1985) the ontogenetic transformation to adult body shape and morphology.

Comparative materials. *Adenops analis*: USNM 121824, Holotype, 59.2 mm SL; Paratypes, USNM 121823, (66: 9–53), Venezuela, Lago Maracaibo. *Adenops argenteus*: USNM 121848, Holotype, 42.4 mm SL; USNM 121849, Paratype, (1: 41.7), Colombia, off Sabanilla. *Membras argentea*: Colombia: USNM 211310 (2: 35–39). *Adenops dissimilis*: MZUSP 9401, Holotype, 59 mm SL; MZUSP 9402–9405, Paratypes, (4: 55.1–60.2), Brazil, Sao Paulo State, Cananéia. *Membras gilberti*: El Salvador: UMMZ 202405 (9: 70–126); UMMZ 406 (16: 64–93); USNM 220671 (17: 50–75); USNM 367952 (2: 45–67). Costa Rica: LACM 22327 (9: 54–86); LACM 8880-4 (1: 72); LACM 49316-2 (1: 58); UMMZ 190235 (2: 70–89); UMMZ 190295 (2: 67–70). Panama: USNM 79748 (130: 42–97); USNM 82065 (153: 37–106); USNM 128555 (25: 48–92). Colombia: CAS 47312 (3: 54–71). *Membras martinica*: New York: CU 24048 (94: 61–66) CU 47947 (12: 72–82); UMMZ 86192 (27: 40–48). New Jersey: CU 22054 (1: 66); CU 32196 (1: 44). Maryland: UMMZ 136043 (2: 87–90); UMMZ 157104 (4: 76–88). Virginia: CU

28622 (36: 49–84); UMMZ 2020672 (8: 34–75). South Carolina: UMMZ 139425 (68: 34–47); UMMZ 143264 (7:72–28). Georgia: CU 88587 (72:24–50). Florida: UMMZ 136588 (127: 33–80); UMMZ 155005 (17:84–102); UMMZ 168705 (17: 47–69). Alabama: UMMZ 163584 (73: 54–80). Louisiana: TU 160244 (1073: 17–109); TU 164268 (599: 23–118); UMMZ 167355 (1362:55–88). Texas: UMMZ 170336 (13: 35–83); UMMZ 199183 (38: 59–81). Mexico: Veracruz, UMMZ 184424 (8: 44–49); Campeche, UMMZ 184648 (7: 30–89).

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