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Prionotus pictus, a new endemic species of searobin from the Galapagos Islands, Ecuador (Teleostei: Triglidae)

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Abstract

A new endemic searobin, Prionotus pictus n. sp., is described from the Galapagos Archipelago in Ecuador. The prior literature generally assumed that all *Prionotus* searobins in the archipelago were *Prionotus miles*, discovered by Charles Darwin on San Cristobal (Chatham Island) and described as endemic by Jenyns (1842). However, almost all underwater photographs from the islands, and surprisingly few museum specimens (three out of dozens), prove to be a quite different-appearing and colorful species. The new species is the island sister species to *Prionotus albirostris* which is found on deeper trawling grounds along the continental shelf, from Baja California to Peru. The second species found in the Archipelago, Darwin's *Prionotus miles*, is uncommonly observed, rarely photographed underwater, and so far accounts for only a handful of the hundreds of searobins photographed in Galapagos. The COI mtDNA sequence (DNA barcode) of P. miles shows that it is an island sister species of continental *Prionotus stephanophrys* (4.87% sequence divergent), which it resembles in a number of basic features, in particular the smooth and gently sloping head and body shape and relatively shorter pectoral fins. A review of the original P. miles holotype and other museum specimens show that P. miles has been inadequately described and guidebooks typically amalgamate and combine characters of the two species, and almost all use photographs of P. pictus to illustrate P. miles. Prionotus pictus is distinguished from P. miles (and *P. stephanophrys*) by a concave, sharply sloped, duck-billed head profile with more prominent head spines; longer, colorful, and prominently spotted pectoral fins; a triangular spinous dorsal-fin outline with the second spine longest following a stout and serrated first spine of almost the same length; no black blotches on the distal fourth or fifth dorsal-spine membranes; thicker, prominently banded, free pectoral (walking) rays; and a variety of head, fin, and body markings. The new species differs from continental P. albirostris in having a rounded snout (vs. squared off) and distinctive colorful and contrasting patterns (hence pictus meaning "painted"). It is notable that a large, conspicuous, and relatively common new endemic fish species has eluded recognition for this long.

Key words: taxonomy, ichthyology, tropical eastern Pacific Ocean, coral-reef fishes, marine biogeography, gurnard, Painted Searobin, DNA barcoding, Charles Darwin, Leonard Jenyns

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Introduction

The fishes of the Galapagos Archipelago have been of particular interest since Charles Darwin visited the islands and collected 15 fish specimens, each of which was subsequently described as a new species by Jenyns in 1842 (Grove & Lavenberg 1997, McCosker & Rosenblatt 2010). Since then, the fish fauna has been closely examined and documented, most exhaustively in the 1997 book by Jack Stein Grove and Robert Lavenberg, and the species list reviewed by McCosker & Rosenblatt (2010). Recently, a thorough evaluation of species records has removed a number of species and added a set of new records (Grove et al. 2022, Victor et al. 2024). As one of the more well-documented island fish faunas, the Galapagos provides an interesting case of island endemism. McCosker & Rosenblatt (2010) estimated 14.8% of the resident shallow non-pelagic shorefishes were limited to Galapagos, and 19.4% limited to the Galapagos plus the other isolated islands of the central tropical eastern Pacific Ocean. Allen (2007) ranked the Galapagos as having the fourth highest rate of endemism (estimated at 11.7%) in his review of the Indo-Pacific hotspots of reef fish diversity. In the analyses of Victor et al. (2024), the varying methods and denominators were assessed and the endemism rate for the Galapagos shallow shorefish fauna (not including vagrants in the denominator) was calculated as 12.7%.

DNA barcoding, or the systematic sequencing of the COI mtDNA marker, has been useful in tropical marine fishes for identifying unknown specimens, uniting different life-stages and genders of species, assessing species-character boundaries, and providing evidence of gene flow (recent or continuing) as part of the evaluation of species status (Victor 2015). Another use of mtDNA sequencing is revealing evolutionary relationships among species, typically including additional markers and nuclear sequences and, more recently, genomes. In this study, a DNA-barcoding result, part of collating the DNA-barcode library for the Galapagos ichthyofauna by the East Pacific Corridor Alliance (EPCA) fish-DNA project, affiliated Darwin's endemic searobin *Prionotus miles* Jenyns, 1842 with its continental sister species, *Prionotus stephanophrys* Lockington, 1881, and that result led to a more complete forensic-type analysis of the searobin species present in the Galapagos.

The investigation revealed the surprising result that among the more than 100 underwater photographs of searobins taken in the archipelago, all but a handful are not the species collected by Darwin, but a different-looking species from a different subgroup of searobins. Photo guidebooks and most divers mistook these searobins for Darwin's species. The misconception was reinforced by erroneous records, inadequate or incorrect keys, and amalgamated descriptions of the species, often using Jenyns' original characters but intermixed with features adopted directly from photographs of the new species. The new species has a variety of colorful and contrasting patterns, warranting a common name of Painted Searobin. Thus, a large, conspicuous, and relatively common new species of fish, endemic to the Galapagos Archipelago, has eluded recognition until now.

Materials and Methods

Type specimens are deposited at the Marine Vertebrate Collection at the Scripps Institution of Oceanography, La Jolla, CA, USA (SIO) and the Canadian Museum of Nature, Ottawa, Canada (CMN). Musuem abbreviations follow Sabaj (2025).

Measurements follow Ginsburg (1950) and Teague (1951) and spine names broadly follow Gruchy (1970), and since head spines are difficult to measure because of no discrete beginning to a spine and much variation with fish length, they are described herein as absent, indistinct, small, medium, and large. The length of the pectoral fin is often cited as an important feature for identifying searobins, however there is much variation within species and between size classes (Ginsburg 1950); often fin length is described in relation to where the fin ends compared to the dorsal or anal fins; however, that is sensitive to the angle of the fin observed. Here pectoral-fin length is the length of the longest ray, and pelvic-fin length is from the insertion of the spine to the tip of the longest ray. Scale-row counts are somewhat variable and counts not consistently repeatable (Ginsburg 1950), due to crowding anteriorly and pored scales can be enlarged and alternating irregularly with unpored scales.

A 652-bp segment was amplified from the cytochrome c oxidase (COI) gene using a variety of primers (Ivanova et al. 2007). DNA extractions, PCR, and sequencing follow procedures described in Victor & Wellington (2013). Specimen information and barcode sequences were compiled using the Barcode of Life Data Systems (Ratnasingham & Hebert 2007, Ward et al. 2009). The sequence data is publicly accessible on BOLD and GenBank. Sequence divergences were calculated using BOLD with the Kimura 2-parameter (K2P) model.



Figure 1. Prionotus pictus, n. sp., Tagus Cove, Isla Isabela, Galapagos Archipelago, Ecuador (Carlos J. Estape).

Prionotus pictus, n. sp.

Painted Searobin Gallineta Pintada

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Figures 1–12

Prionotus albirostris (*non* Jordan & Bollman) Gruchy 1970: 526, text; Grove & Lavenberg 1997: 297, only line drawing in fig. 153a (not photographs figs. 155 & 156 on p. 300 which are *P. miles*); Ruiz et al. 2011: 58, listing.

Prionotus miles (*non* Jenyns) Allen & Robertson 1994: 103, middle fig; Humann & DeLoach 2003, 2011: 154, middle fig. & text (but amalgamated features), 155 middle fig. only; Constant 2002: 100, fig. 117; Banks et al. 2016: 51, photograph.

Prionotus stephanophrys (non Lockington) McCosker 1998: 810; Richards & McCosker 1998: 940, text; McCosker & Rosenblatt 2010: 191, listing; Ruiz et al. 2011: 58, listing; Tirado-Sanchez et al. 2016: 81, listing; Robertson et al. 2017: 80, listing; Grove et al. 2022: 21, listing; Robertson & Allen 2024: listing; Victor et al. 2024: 44, listing.

Holotype. SIO 15-2202 (ex-UCLA W53-315), 191 mm SL, Ecuador, Galapagos Archipelago, Isla Fernandina, Punta Mangles, -0.496°, -91.432°, 5 m, G.J. Fitzgerald, 1 February 1953.

Paratypes. CMNFI 1969-0078.3, 89.9 mm & 171.5 mm SL, Ecuador, Galapagos Archipelago, Isla Isabela, Tagus Cove, mouth of cove into Canal Bolivar, -0.496°, -91.432°, 31–68 fathoms (Michel Anctil, pers. comm.), otter trawl in the mouth of Tagus Cove, R/V *Te Vega*, station 91 of Stanford Oceanographic Expedition 17 (https://seaside.stanford.edu/tv17), L. Barr et al., 8 March 1968.

Diagnosis. Dorsal-fin rays X,12; anal-fin rays 11; pectoral-fin rays 14 plus three ventral free rays; pelvic-fin rays I,5; first dorsal fin nearly triangular, first three spines about equal in length, second spine longest, first spine slightly shorter, third spine slighly shorter than second, anterior margin of first spine with pronounced serrations; membranes without a black spot or ocellus specifically on fourth or fifth membranes; pectoral fins fan-shaped semicircular when expanded and long, usually reaching to last third of second-dorsal-fin base or beyond when flat (but variable); snout concave, sharply rising, duck-billed profile, eyes protruding well above profile, snout broadly rounded from dorsal view, no prominent rostral extensions or spiny edges to lachrymal plate; nasal cirrus present, about twice length of nasal opening, no supraocular cirrus; mouth relatively small, lower jaw subterminal and without a knob; head with prominent bony plates, ridges and granulations; head spines comprising preocular, postocular, sphenotic, pterotic, parietal, nuchal, opercular, preopercular (without a supplemental spine), and a cleithral (humeral) spine over pectoral fin (rostral, preorbital, and suborbital spines absent and no postfrontal groove); scales ctenoid and small, about 48 pored lateral-line scales, about 94 vertical rows of lateral scales, nuchal and opercular-flap scales present, ventral scales extend forward just past level of anterior insertion of pelvic fins. Color pattern from common brownish orange pattern to blotched in colors varying from brown to red, to a darker, almost black-and-white pattern; often bright orange ventrally; white patches like splashed paint on head and body in individual unique patterns; a line of prominent white spots highlighting some of the pored lateral-line scales; lip markings a variety of spots and bars (not a simple three dark bands on a white background, at front, middle and corner of jaw); pectoral fin with irregular spot pattern, clearest on common color form, with small rounded spots concentrated on fifth through tenth membranes, becoming reticulations on distal lowermost rays; a thick blue margin on lower 10 rays; pectoral-fin base around origin of rays with an irregular pattern (not discrete rounded spots); caudal fin with dark bars, one at base and a distal wide bar often splitting into two (dark fish can have a black striped pattern); free pectoral-fin rays thick and prominently banded. Juvenile with brown mottled color pattern and relatively longer pectoral fins, reaching past end of second dorsal fin. Newly settled juvenile uniform orangish with two prominent black-edged white saddles along dorsal midline in front of and behind soft-dorsal-fin base: gill rakers short spiny tubercles in two rows of 11, inner and outer, on lower limb of first arch.

Description. (morphometrics for holotype, larger paratype in parentheses) Dorsal-fin elements X,12; anal-fin elements 11; pectoral-fin rays 14 plus three ventral free rays; pelvic-fin rays I,5; caudal fin with 13 segmented rays (11 branched), and 8 to 10 procurent rays; about 46 lateral-line pored scales and about 94 lateral scale rows. Vertebrae (including preural centrum) 10+16=26.

Body stout and elongate, body depth at dorsal-fin origin 20 (24)% SL, body width at dorsal-fin origin 24 (26)% SL; predorsal length, 32 (36)% SL; prepelvic length 25 (29)% SL; preanal length 54 (61)% SL; caudal-peduncle length 15 (16)% SL, caudal-peduncle depth 7 (8)% SL.

Head large 35 (33)% SL, with bony plates and ridges with extensive striated or granular surfaces; head width



Figure 2. Prionotus pictus, n. sp., holotype, SIO 15-2202, 191 mm SL, Isla Fernandina, Galapagos Archipelago, Ecuador (BCV).



Figure 3. *Prionotus pictus*, n. sp., paratypes, CMN 69-0078, 171.5 mm SL (upper lateral & dorsal) & 89.9 mm SL (lower lateral & dorsal), mouth of Tagus Cove into Canal Bolivar, Isla Isabela, Galapagos Archipelago, Ecuador (courtesy ©Marie-Hélène Hubert, Canadian Museum of Nature).

(at midpoint of orbit) 58 (69)% HL; snout short and blunt, sloping sharply downward in front of eye, snout profile from dorsal view broadly rounded without rostral extensions or serrations, snout length 48 (52)% HL; short, finger-like nasal cirrus about twice width of opening or more, no supraorbital cirrus; eyes relatively small and placed high on head protruding above profile, orbit diameter 17 (19)% HL; bony interorbital relatively narrow 13 (16)% HL and deep, vertical distance from trough to top of orbit 7 (9)% HL; mouth relatively small, upper-jaw ending well before vertical at anterior orbital rim, oblique length 42 (43)% HL; lower jaw slightly subterminal, no knob at tip. Head spines short and stout: preocular a ridge with largest peak a blunt spine at upper end of ridge, postocular a serrated ridge with a stout short spine at posterior end, pterotic and sphenotics stout ridges, parietal a stout serrated ridge with the last point a spine, nuchal a ridge ending in a blunt spine, opercular spine medium with an oblique upper branch over opercular flap ending bluntly, preopercular spine medium and wide, with no supplemental spine, no suborbital (cheek plate), anterior preorbital, or rostral spines along lower snout profile; cleithral spine flattened, short, wide, and blunt.

Teeth small and villiform, densely packed in an outer band along upper jaw with a similar inner band of palatine teeth, a single band along lower jaw with fine spiny teeth covering thick wide tongue. Gill rakers in two rows on lower limb of first arch, inner and outer, each short stout tubercles (about one tenth length of gill filament), often finely spiky, about 11 elevated projections in each row on lower limb (including rudiments), becoming flattened bumps on upper limb.

Spinous dorsal fin about triangular, base 23 (22)% SL, first spine prominently serrated along anterior aspect; first three spines about same in length, second spine longest 50 (54)% HL, first spine slightly shorter 48 (51)% HL (over 90% of second spine), third spine slightly shorter than second 49 (49)% HL (over 90% of second spine), fourth through tenth spine gradually declining 44 (45)%, 35 (42)%, 32 (36)%, 22 (25)%, 17 (16)%, 11 (11)%, and 3 (4)% HL; soft dorsal fin immediately following tenth spine, base 31 (32)% SL, first element a stiff ray



Figure 4. *Prionotus pictus*, n. sp., smooth rounded snout, Tagus Cove, Isla Isabela, Galapagos Archipelago, Ecuador (Allison Morgan Estape).



Figure 5. Prionotus pictus, n. sp., colorful pattern, Galapagos Archipelago, Ecuador (Roger Uzun, shutterstock.com).



Figure 6. *Prionotus pictus*, n. sp., contrasted pattern, Isla Isabela, Galapagos Archipelago, Ecuador (William Bensted-Smith).



Figure 7. Prionotus pictus, n. sp., brown and white pale phase, Galapagos Archipelago, Ecuador (© Paul Humann).



Figure 8. *Prionotus pictus*, n. sp., brick-red and black pattern, Punta Vicente Roca, Isla Isabela, Galapagos Archipelago, Ecuador (courtesy @Salome Buglass).



Figure 9. *Prionotus pictus*, n. sp., dark phase, Cabo Douglas, Fernandina, Galapagos Archipelago, Ecuador (courtesy Carlos Alfredo Delgado Ibarra, Plongée Aqua-Mundo Inc., Sherbrooke, Quebec, Canada).



Figure 10. *Prionotus pictus*, n. sp., dark phase, Mosquera, Galapagos Archipelago, Ecuador (courtesy @spritelightkrayon YouTube videos).

38 (41)% HL, longest soft ray about second 42 (45)% HL; last ray split to base, distance to caudal-fin base 41 (45)% HL; caudal fin slightly rounded to truncate 28 (31)% SL; anal-fin base 30 (29)% SL, first anal-fin element unsegmented but flexible, 17 (21)% HL, second ray 33 (35)% HL, longest about ninth 41 (45)% HL, last ray split to base, distance to caudal-fin base 15 (16)% SL; pectoral fin fan-like, semicircular, long, when flat reaching past mid-soft-dorsal fin, often to last ray, sometimes beyond, fifth ray longest 57 (53)% SL, first ray shorter 49 (36)% SL, second through last ray branched once midway out, last contiguous ray shortest 21 (22)% SL; free rays stout, first free ray longest 23 (25)% SL, second 20 (24)% SL, third 18 (21)% SL; pelvic-fin length 31 (32)% SL, pelvic-fin spine 14 (15)% SL, longest pelvic-fin ray fourth 29 (29)% SL, distance between pelvic-fin-spine origins 17 (17)% SL.

Scales small and ctenoid, head scaleless except scales covering opercular flap; nuchal scales present and crowded, ventral scales cover abdomen and chest, extending forward just past level of pelvic-fin-spine insertion, lateral scales extend onto base of caudal fin. Pored lateral-line scales irregular, enlarged anteriorly and with intervening unpored scales posteriorly, about 43 before caudal-fin base, vertical scale rows beyond level of dorsal-fin origin about 96 (crowded anteriorly), about 7 rows between spinous-dorsal-fin origin and lateral line.

Color in life. (Figs. 1 & 4–12) Variable color patterns, each with reticulations of white on head and splashes of white on body in a unique individual pattern (like a fingerprint), with a few lateral irregular to rounded large dark blotches; a common color palette is basic brown with bright orange tints and a prominent blue margin on pectoral fins; less frequent patterns are bright red and orange, washed-out tan or pale (on white sand) with muted blue, dark brown markings with a red ventral wash, or mostly black-and-white. In all cases, a row of prominent white spots highlight pored lateral-line scales. Lip markings in an individual pattern of irregular red, brown, or purple spots and bars (not three discrete dark bands on a white background, at front, middle and corner of jaw). Spinous dorsal fin with anterior margin of first spine banded white and dark, irregular brown to black blotches on fin membranes, becoming a thick, radiating, spoke pattern on dark individuals; soft dorsal and anal fins with a variable, usually broken, stripe along middle of fin. Caudal fin on common form with a pale bar after a dark base followed usually by two alternating dark bands, or one wide band with some indication of splitting, followed by a thin white posterior margin: in contrast, dark phases can have prominent, black, radiating spokes. Pectoral fin on common form spectacular when fanned out, with a thick bright-blue margin on membranes of lower 10 rays; upper portion of fin lighter and prominently showing three or 4 indistinct broad dark bands with intervening mottling (bands show more clearly when fin folded), large area on lower portion of fin, from fifth to tenth membranes, with distinct orange-brown circles outlined in bluish, becoming smaller and fading into bright distal reticulations; in



Figure 11. Prionotus pictus, n. sp., juvenile, Tagus Cove, Isla Isabela, Galapagos Archipelago, Ecuador (Frank Krasovec).



Figure 12. *Prionotus pictus*, n. sp., newly settled juvenile, Tagus Cove, Isla Isabela, Galapagos Archipelago, Ecuador (William Bensted-Smith).

darker forms, distal portion of fin becomes darkened, even to black. Free pectoral-fin rays thick with prominent, equal-width, broad bands, with dark or orange alternating with white or yellow. Large juveniles apparently show a similar pattern to adults (Fig. 11). Newly settled small juveniles have bright contrasting markings against an orangish background, with especially prominent two black-outlined white saddles along dorsal midline, placed in front of and just behind base of soft dorsal fin, with an array of bluish spots along margins of pectoral fins that later develop into bright blue rims of adult pectoral fins (Fig. 12).

Color in preservative. (Figs. 2 & 3) Adults and larger juveniles with a tan to dark-brown background and faded dark-brown patterns on body and brown-to-black, indistinctly spotted pectoral fins. Median fins mostly unmarked and free pectoral-fin rays pale with indistinct darker bands.

Etymology. The species name *pictus*, Latin for painted, refers to the variegated patterns and colors and individual distribution of colors, with white markings as if splashed with paint. The epithet is considered a masculine adjective.

Distribution and habitat. The new species is endemic to the Galapagos Archipelago and underwater photographs show fish from most of the islands, with many records from the western side, at Fernandina and Isabela. They are found on rocky or reef substrates as well as adjacent open sandy patches in shallow and medium diving depths, although the paratypes were reportedly trawled at about 50 m depth at the mouth of Tagus Cove.

Comparisons. This species is the island sister species of the continental *Prionotus albirostris* Jordan & Bollman, 1890, sharing basic morphology and the spiny features of the head and serrated dorsal-fin spines. It differs most prominently morphologically in the shape of the snout, where the dorsal view of the snout profile is rounded and smooth in *P. pictus* vs. squared off with spiny rostral flanges and a dark midline indentation in *P. albirostris* (Fig. 13).

The color patterns differ, as might be expected between a deeper continental shelf species and a relatively shallow, clear-water, reef-associated species. In contrast to the bright colors and variegated patterns of *P. pictus*, freshly caught *P. albirostris* are either relatively uniformly reddish brown or countershaded dark with a white

ventrum (Fig. 14). No underwater photographs are known of *P. albirostris*, not surprising given that most specimens are trawled in places divers do not frequent. Among series of photographs of specimens captured in mainland Ecuador (many photographs on iNaturalist), including off Salango (Fig. 15), there are three prominent dark bands on the lips: at the tip, about halfway along and at the corner of the mouth, contrasting conspicuously with the white lips and throat, leading to the common name Whitesnout Searobin. Brown fish often have reddish free pectoral-fin rays and pelvic fins and the pale area around the base of the pectoral fin typically has small rounded spots instead of reticulations. The pectoral-fin pattern, especially clear on the specimen from Baja California (Fig 16), shows small and large brown circles over the first 4 membranes, becoming a dusky blotchy pattern interspersed with a network of blue lines and a thin blue edge. The unusual prominent markings on the tiny juvenile *P. pictus* are not present on preserved specimens of the same stage of *P. albirostris*, which are well represented in museum collections.

The new species can easily be distinguished from *P. miles*, the other species present in the Galapagos Archipelago, which has a less sloped snout profile, a shallow interorbital with the eyes barely protruding above the profile, less-developed head spines, a dorsal fin not quite triangular (a more sloping arc), the first dorsal-fin spine not prominently serrated and well shorter than the second, the third spine longest, discrete black patches on the distal membranes of the fourth and fifth dorsal-fin spines, a shorter pectoral fin (usually not extending past mid-soft-dorsal fin) that is mostly black with a white margin, and a different pattern of spots and speckles on the body.

Remarks. The differences between the island *P. pictus* and the continental *P. albirostris* likely reflect a different habitat and lifestyle: the continental shelf is deep, silty, and dark, and specimens of *P. albirostris* are typically captured by deep trawling on soft bottoms. The holotype was dredged at 33 fathoms off the coast of Colombia. Fresh specimens are either red or dark with limited color and reduced patterning. In contrast, the Galapagos provides a large area of relatively shallow reef and rock shore habitat with relatively clear water and clean substrate, due to the volcanic rock geology and the absence of rivers, streams, and runoff. The open bottom is mostly coarse clean sand without much sediment. Species characteristic of deep soft substrate are either absent or limited to the rare deep mud bottoms in the Archipelago; for example, the flatfishes *Citharichthys gnathus* and *Hippoglossina bollmani* have been captured at only a single deep muddy location (Victor & Wellington 2013).



Figure 13. *Prionotus albirostris* (left), SIO 64-878, 175 mm SL, Isla Santa Margarita, Baja California Sur, Mexico vs. *P. pictus* (right), SIO 15-2202, 191 mm SL, Isla Fernandina, Galapagos Archipelago, Ecuador (BCV).



Figure 14. Prionotus albirostris, Manta region, Ecuador (courtesy Enrique Laaz, Instituto Nacional de Pesca).

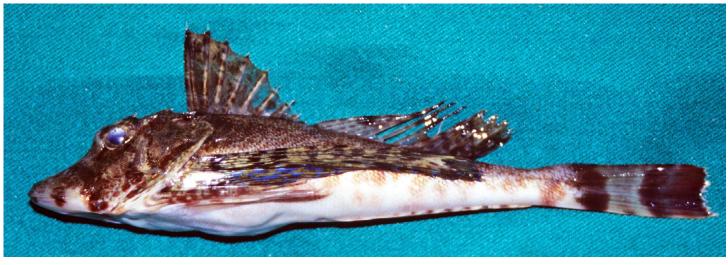


Figure 15. *Prionotus albirostris*, MNHN-IC-2002-1063, Salango, Ecuador (courtesy Philippe Bearez, Muséum National d'Histoire Naturelle).



Figure 16. Prionotus albirostris, San Jose del Cabo, Baja California, Mexico (courtesy John Snow).

Prionotus miles Jenyns, 1842

Galapagos Searobin Gallineta de Galapagos

Figures 17–24

Prionotus albirostris (*non* Jordan & Bollman) Grove & Lavenberg 1997: 300, figs 155 & 156; Humann & DeLoach 1993: 132, middle photograph on p. 133; Constant 2002: 100, text as "whitemargin searobin")

Holotype. BMNH 1917.7.14.75, 202 mm SL, Ecuador, Galapagos Archipelago, Isla San Cristobal (Chatham), approx -0.81°, -89.5°, Charles Darwin et al. on the *Beagle*, 18–22 September 1835.

Other material examined. MCCDRS 3945, 230 mm SL, Ecuador, Galapagos Archipelago, Isla Fernandina, Cabo Hammond, 0.4805°, -91.6135°, G. Merlen, 1 April 2009; MCCDRS 10771, 190 mm SL, Ecuador, Galapagos Archipelago, Isla Santa Cruz, Bahia Ballena, -0.528°, -90.490°, B. Schreyer of the *Beagle III*, circa 1970; MCCDRS 10866, 215 mm SL, Ecuador, Galapagos Archipelago, Isla Santa Cruz, Isla Eden, -0.558°, -90.534°, B. Schreyer, 1 November 1963; MCCDRS 11532, 60 mm SL, Ecuador, Galapagos Archipelago, Isla Rabida, -0.398°, -90.71, F. Angermeyer, March 1966; USNM 322076, 191 mm SL, Ecuador, Galapagos Archipelago, Isla Fernandina, -0.27°, -91.43°, D.R. Robertson, R. Steene, G. Allen, G. Wellington & B. Victor, 3 April 1990; SIO 50-80, 185 mm SL, Ecuador, Galapagos Archipelago, D. Maestro, 1950; SIO 15-2169 (ex-UCLA W53-21), 223 mm SL, Ecuador, Galapagos Archipelago, Isla San Cristobal, Wreck Bay, -0.895°, -89.62°, H. Clemens & W. Baldwin, 13 November 1952; SIO 15-2161 (ex-UCLA W56-329), 69 mm SL, Ecuador, Galapagos Archipelago, -1.37°, -90.7°, H. Hoover & R. Miller, 19 March 1955; SIO 79-51, 238 mm SL, Ecuador, Galapagos Archipelago, K. Kuronuma, 1960; SIO 25-32, 39 mm SL, Ecuador, Galapagos Archipelago, Isla Isabela, Tagus Cove, -0.265°, -91.373°, B. Victor, G. Wellington & C. Caldow, 28 May 1998 (https://www.ncbi.nlm.nih.gov/nuccore/PO628526); SIO 11-349, 80 mm SL, Ecuador, Galapagos Archipelago, Isla Isabela, Tagus Cove, -0.265°, -91.373°, G. Wellington, 30 May 1999; LACM 43857, (2) Ecuador, Galapagos Archipelago, North Seymour, -0.4°, -90.283°, 15 m depth, J. Grove, 7 July 1982; LACM 43883 (1) Ecuador, Galapagos Archipelago, North Seymour, -0.4°, -90.283°, 15 m depth, J. Grove, 20 October 1982; LACM 44019, (1), Ecuador, Galapagos Archipelago, North Seymour, -0.4°, -90.283°, 18 m depth, J. Grove, 4 August 1984; LACM 44021, (1), Ecuador, Galapagos Archipelago, Isla Floreana, Punta Cormorant, -1.215°, -90.426°, J. Grove, 8 August 1994; LACM 44025, (2), Ecuador, Galapagos Archipelago, Isla Rabida, North side, -0.4°, -90.717°, 22–25 m, J. Grove, 24 August 1994; LACM 44309, (4), Ecuador, Galapagos Archipelago, North Seymour, -0.4°, -90.283°, J. Grove, no date; CAS-SU 7008, <20 mm SL (dried), Ecuador, Galapagos Archipelago, Isla Isabela, Tagus Cove, -0.265°, -91.373°, Hancock Expedition, 13

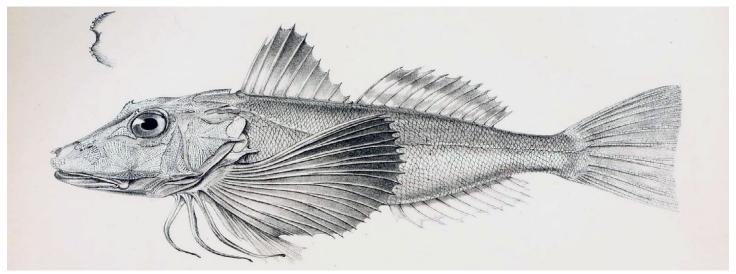


Figure 17. Prionotus miles, syntype, engraving from Jenyns (1842), image reversed.

January 1934; CAS-SU 368, (4), Ecuador, Galapagos Archipelago, Isla Santa Maria, R/V *Albatross*, U.S. Fish Commission, prob. 1891; CAS-SU 24411, (1), Ecuador, Galapagos Archipelago, Isla Santa Maria, Post Office Bay, -1.236°, -90.450°, Albert Herre Expedition, 15 January 1929; (additional R/V *Albatross* specimens from Isla San Cristobal in CAS-SU 10719, 10753 & 10754 are presently missing from the collection).

Diagnosis. Dorsal-fin elements X,12; anal-fin elements 11; pectoral-fin rays 13 plus three ventral free rays; pelvic-fin rays I,5; first dorsal fin an arc skewed rearward, peaking at third spine and sloping down to last spine, first spine distinctly shorter, less than 90% of second, second spine slightly shorter than third spine, spines smooth and slender, anterior margin of first spine smooth; membranes with a black blotch on fourth and usually fifth membranes; pectoral fins fan-shaped and semioval when expanded and medium length, seldom reaching past middle of second-dorsal-fin base; snout smoothly rising, eyes barely above profile, shallow interorbital; snout squared off and indented midline from dorsal view, prominent rostral spines on lachrymal plate; no significant nasal cirrus, no supraocular cirrus; mouth medium, reaching about level of anterior orbital rim, lower jaw subterminal and without a knob; head with smooth bony plates, minimal ridges and granulations; head spines comprising only small preocular and medium opercular, preopercular, and cleithral (humeral) spines; no emergent spines at postocular, sphenotic, pterotic, parietal, nuchal, rostral, preorbital, or suborbital locations, and no postfrontal groove; scales ctenoid and small, about 52-57 pored lateral-line scales, about 86-98 vertical rows of lateral scales, nuchal scales present, opercular flap with a few small scales, an unscaled area on body along dorsalfin base, small embedded ventral scales extend forward onto isthmus well past level of first free-pectoral-finray origin. Body with a brown freckled pattern on a pale background with a few larger darker brown blotches. notably a bar below rear soft dorsal fin and a few large rounded spots on sides, speckles merge to become a fine reticulate pattern over head and snout with a prominent dark bar across interorbital. No prominent line of white spots along lateral-line. Pectoral-fin membranes from tan brown to mostly black between paler rays with a thin pale or bluish margin (when on dark sand) to light brown membranes with white rays and broad white bands (on pale sand backgrounds); free pectoral-fin rays thin and pale with at most wide indistinct dusky bands, swollen at tips. Spinous dorsal fin black, or pale with black blotches on fourth and fifth membranes. Caudal fin with a wide dark band across middle of fin, flanked by wide bands of white at base and rear margin. Juvenile with a similarly spotted pattern and medium-length, dark pectoral fins and a dark blotch on distal fourth dorsal-fin-spine membrane. Two rows of gillrakers on first arch, outer row long and slender, about twice length of gill filaments, two on upper limb and 12 along lower limb of first arch, inner row of gill rakers short and finely spiny tubercles, three on upper limb and 11 on lower limb of first arch. Vertebrae (including preural centrum) 10+16= 26.

Description. (morphometrics only for matched size to holotype of *Prionotus pictus*, i.e. 4 specimens 185–202 mm SL, from MCCDRS 10771, SIO 50-80, USNM 322076, BMNH 1917.7.14.75) Dorsal-fin rays X,12; anal-fin rays 11; pectoral-fin rays 13 plus three ventral free rays; pelvic-fin rays I,5; caudal fin with 11 branched rays (9 in juvenile), 15 segmented rays, 9 or 10 dorsal and 8 or 9 ventral procurrent rays; about 52–57 lateral-line pored scales and about 86–98 lateral scale rows. Vertebrae (including preural centrum) 10+16= 26.

Body stout and elongate, body depth at dorsal-fin origin 20–28% SL, body width at dorsal-fin origin 19–25% SL; predorsal length 38–45% SL; prepelvic length 27–36% SL; preanal length 60–64% SL; caudal-peduncle length 12–13% SL, caudal-peduncle depth 6% SL.

Head large 38–42% SL, mostly smooth with bony plates and indistinct ridges and finely striated and granular surfaces; head width (at midpoint of orbit) 48–53% HL; snout medium length, sloping relatively smoothly downward about 45 degrees in front of eye, snout profile from dorsal view squared off with midline indentation and prominent rostral serrations, 5 or 6 sharp points on each side, snout length 39–49% HL; no developed nasal cirrus (can be a fleshy tab shorter than nasal opening), no supraorbital cirrus; eyes medium and placed high on head, protruding only slightly above profile, orbit diameter 19–23% HL; bony interorbital relatively wide 12–19% HL and shallow; mouth medium-length, upper jaw ending about at vertical at anterior orbital rim, oblique length 37–47% HL; lower jaw slightly subterminal, no knob at tip.

Head spines mostly undeveloped, preocular a low ridge with about three points, largest at upper end, slightly raised ridges without spines at postocular (holotype has a tiny spine), undeveloped pterotic, sphenotic, and parietal ridges, and no postfrontal groove, nuchal point not raised above surface, opercular spine medium, preopercular spine medium with no supplemental spine, no suborbital (cheek plate) or anterior preorbital or rostral spines along

lower snout profile, medium cleithral (humeral) spine. Notably, 39 mm SL juvenile has anterior preorbital, rostral, and nuchal spines, lost in maturity.

Teeth small and villiform, densely packed in an outer band along upper jaw with a similar inner band of palatine teeth, a single band along lower jaw, finely toothed relatively slender tongue. Gill rakers in two rows on first arch, inner and outer, outer rakers long and slender, maximally about twice length of gill filaments, two on upper limb and 12 along lower limb, inner row a series of low tubercles, each covered with fine spines, about three along upper limb and 11 on lower limb.

Spinous dorsal fin a skewed arc, peaking at third spine and sloping down to last spine, base 22–28% SL, first spine smooth and slender, shorter than next two spines, 30–41% HL (less than 90% of second and third spine), second spine 36–49% HL, third spine longest 38–51% HL, fourth through tenth spine gradually declining 34–43%, 28–36%, 21–30%, 15–20%, 10–14%, 4–7%, and 2–3% HL; soft dorsal fin immediately following tenth spine, base 25–28% SL, first element a stiff ray 27–35% HL, longest soft ray about second 29–36% HL; last ray split to base; caudal fin slightly rounded to truncate 20–27% SL; anal-fin base 26–32% SL, first anal-fin ray unsegmented but flexible, 8–13% HL, second ray 13–22% HL, longest about ninth 23–28% HL, last ray split to base, distance to caudal-fin base 12–13% SL; medium-length pectoral fin fan-like, semioval, when lying flat on body usually ending before mid-soft-dorsal fin, fifth ray longest 41–45% SL (in adults), first ray shorter 33% SL,

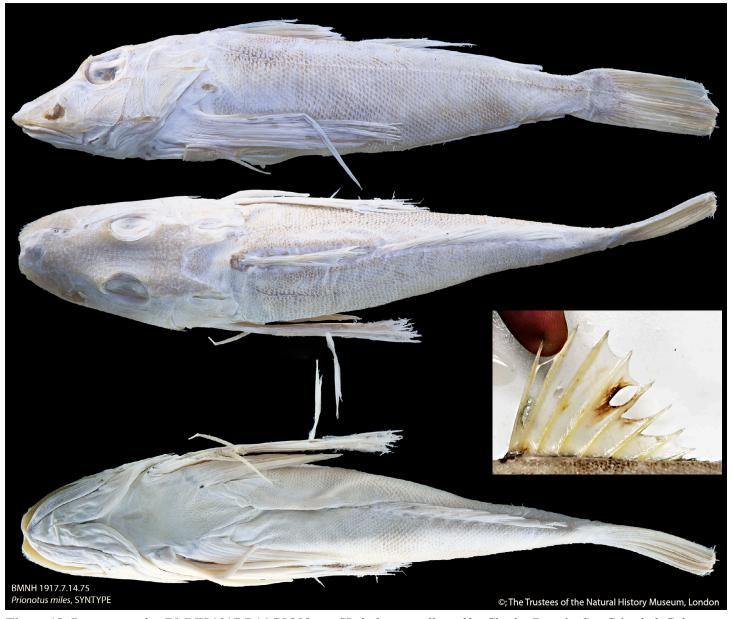


Figure 18. *Prionotus miles*, BMNH 1917.7.14.75 202 mm SL, holotype collected by Charles Darwin, San Cristobal, Galapagos Archipelago, Ecuador, inset is present state of dorsal fin (courtesy James Maclaine, Natural History Museum, London).

second through last ray branched once midway out, last contiguous ray shortest 20–22% SL; free rays slender, expanding to a small bulb at tip, first free ray longest 24–29% SL, second 23–25% SL, third 20–23% SL; pelvic fins long, reaching about to anus level, length 25–32% SL, pelvic-fin spine 11–15% SL, longest pelvic-fin ray fourth 25–26% SL, distance between pelvic-fin spine origins 13–14% SL.

Scales small and ctenoid, head scaleless except for a few small scales on opercular flap (visible on holotype, Fig. 18, middle), nuchal scales present and crowded; in adult, small embedded ventral scales extend forward onto isthmus well past level of first free pectoral-fin-ray origin (juvenile has no scales on chest or abdomen); lateral scales extend onto base of caudal fin. Pored lateral-line scales irregular, enlarged anteriorly and with intervening unpored scales posteriorly, about 52–57 before caudal-fin base, vertical scale rows beyond level of dorsal-fin origin 86–98 (crowded anteriorly), border around dorsal-fin base naked, then about 7 rows between spinous-dorsal-fin origin and lateral line.

Color in preservative. (Figs. 18 & 19) Adults and juveniles are uniformly brownish with prominently black pectoral fins and dark blotches on distal fourth and fifth spinous-dorsal-fin membranes.



Figure 19. *Prionotus miles*, USNM 322076, 191 mm SL, Isla Fernandina, Galapagos Archipelago, Ecuador (courtesy Sandra Raredon and Abigail Reft, Department of Vertebrate Zoology, Smithsonian Institution).



Figure 20. *Prionotus miles*, Isla Santiago, Galapagos Archipelago, Ecuador (by Rino Iubatti, iNaturalist.org, CC-BY-SA 3.0 license).

Color in life underwater. (Figs. 20–25) Basic color shades of pale to brown and black without other colors (except blue edging on pectoral fins), reflecting background color of sand. On light sand (Fig. 20), body is white with brown freckles and irregular spots and bars of light brown with a darker interorbital band; spinous dorsal fin has black blotches on distal fourth and fifth dorsal-fin membranes; pectoral fins are white with tan to brownish membranes, leaving base, shafts, and a short rim white; caudal fin has a white band behind peduncle, often bisected with a brownish bar, followed by a broad brownish bar and a white band at rear fin margin.

On darker sand (Figs. 21 & 22), markings are darker brown to black, head has tan to gray fine reticulations with a wide dark brown to black interorbital band over eyes which can extend down cheek; body has large irregular to rounded spots with or without an intervening speckled pattern, large spots occur below spinous dorsal fin, midlateral body, below front and rear soft dorsal fin, and in an oblique bar on caudal peduncle; spinous dorsal



Figure 21. Prionotus miles, Wolf Island, Galapagos Archipelago, Ecuador (©Paul Humann).

fin is mostly black, darker at fourth and fifth membranes, and soft dorsal fin has a thick dark band from distal first ray to base of last ray; pectoral fins are mostly black with a white or pale bluish thin edge, also with fine white streaks along ray shafts, sometimes bands made up of small pale spots or lines and a pale or white patch can develop on distal portion of upper third of fin, thin free rays are either uniformly pale or with a few wide indistinct dusky bands; caudal fin has a white band behind peduncle, often bisected with a dusky bar, followed by a broad prominent dark to black bar and a white band at rear fin margin.

In contrast, fresh or freshly frozen fish are reportedly purple-red, see comment on type below.

Juveniles have a similar but simpler pattern of bars and spots, but also range in color from speckled brown on pale sand (Fig. 23), to almost black and white on dark sand (Fig. 24), to mottled brown and orangish to match orange sand, especially on pectoral fins, which have not yet developed a white rim (Fig. 25). If not all black, spinous dorsal fin has distinct black blotches on distal fourth and fifth membranes.

Comment on holotype. Darwin's specimen at the British Museum is presently pale with the primary dark markings the blotches on the distal fourth and fifth membranes (Fig. 18). Although the membranes are damaged,





Figure 22. Prionotus miles, Galapagos Archipelago, Ecuador (by Helmut Gothal, alamy.com).



Figure 23. Prionotus miles, juvenile, Galapagos Archipelago, Ecuador (by Jan Dekker, Observation.org, CC-BY-NC license).



Figure 24. Prionotus miles, juvenile, Galapagos Archipelago, Ecuador (by Jeff Rotman, alamy.com).



Figure 25. *Prionotus miles*, tiny juvenile, Tagus Cove, Isla Isabela, Galapagos Archipelago, Ecuador (Allison Morgan Estape).

the blotches are clearly apparent, in contrast to Jenyn's plate of the specimen showing the spinous dorsal fin only with some distal shading, but focused in the same location (Fig. 17). The specimen is labeled as a syntype, but it is the only type specimen known, and was called a syntype due to a historical BMNH policy of assigning syntypes if any question at all is raised about the number of type specimens (James Maclaine, pers. comm.). In this case, Jenyns "Long. unc. 10 lin.3", meaning 10 inches and 3 "lines" (twelfths of an inch) TL (about 260 mm), is about the size of the holotype.

Darwin's notes on the color of the specimen are curious: "Above mottled brilliant tile red; beneath silvery white", although Jenyns (1842) adds "Mr. Darwin is rather doubtful whether by the above description, he meant that the entire fish was brilliant red, or only mottled with red upon some obscure ground." Based on the few underwater images of the species, there is no evidence of red on these fishes, but these are not freshly caught specimens. The notes for the collection of SIO 50-80, presumably from a fresh specimen, include "head and body deep purple-red. Anal pink. Branchiostegal pink. Lining of branchial cavity deep orange. Spinous dorsal largely sooty in front of 6th spine except near base, blackest between 4th and 5th spines. Anal with a sooty median stripe and whitish near tips of rays. 2nd dorsal similarly, but less sharply, colored. Pectoral blackish with white edge." This description explains Darwin's color description of a red body, which Jenyns was uncertain about. This corresponds with the phenomenon where many fish that appear pale or brown underwater become reddish when dead or dying on the deck.

Seale (1940, p. 32) documents the original state of CAS-SU 7008 juvenile specimen (that is presently dried) as follows, confirming the identification as *P. miles*: "*Prionotus miles* Jenyns One from Tagus Cove, Albemarle Island, Galapagos, January 13, 1934. Length 34 mm. Dorsal X, 12; anal 10. Color brownish with indistinct bars. Ventral and anal fins white. Pectorals black. Caudal barred. Distal portion of spinous dorsal black".

Etymology. The species name *miles*, Latin for a soldier, as in military, presumably because it is spiny.

Distribution and habitat. *Prionotus miles* is endemic to the Galapagos Archipelago. Although rarely observed, it has been collected at San Cristobal, Floreana, Santa Cruz, North Seymour, Rabida, Isabela, and Fernandina and photographed at Santiago, Isabela (Tagus Cove), and Wolf. Evidently it occurs on open soft subtrates where it is easier to catch by trawl or hook-and-line or net for collections than to observe underwater, given that it accounts for all but three of the about two dozen specimens in museums, yet rarely photographed underwater.

Comparisons. *Prionotus miles* is the island sister species of the continental *Prionotus stephanophrys* (Fig. 26), found on deep trawling grounds (over 100 m) from USA to Chile (Robertson et al. 2017) and sharing basic morphological features such as a relatively smoothly sloping head profile in adults (approaching linear), eyes barely protruding above profile with a shallow interorbital, little development of head spines, relatively smooth



Figure 26. Prionotus stephanophrys, Panama (© D.R. Robertson, Smithsonian Tropical Research Institute).

dorsal-fin spines with the first well shorter and the third longest, with black blotches on the distal fourth and fifth dorsal-fin membranes, and a mostly black pectoral fin of medium length, usually not reaching past mid-soft-dorsal fin level (with exceptions to the rear of the fin, but not past).

DNA barcoding. The mtDNA sequence for *P. miles* was obtained from a juvenile specimen we collected at Tagus Cove more than 25 years ago, during a National Geographic/National Public Radio expedition with the late Peter Benchley. After sequencing technology caught up, many years later, our collections (fortuitously preserved only in ethanol) provided the first sequences for Galapagos fishes in the Barcode of Life program. The COI sequence, GenBank accession number PQ628526, is released as part of the fish-DNA project assembling and collating the DNA barcode lineages for all marine fishes in the region, by the East Pacific Corridor Alliance (EPCA, epcafoundation.org). The sequence is 4.87% divergent from the nearest sister lineage, the continental *P. stephanophrys* (BIN BOLD:AAH7610), sequenced from California, Baja California, El Salvador, Costa Rica, Panama, and Peru. The trans-isthmic Caribbean sister species to the pair, *Prionotus tribulus* (BIN BOLD:AAM3196), is 7.5% divergent from *P. pictus*.

Remarks. In a curious twist, while the photographic guides have routinely used photographs of the new species *P. pictus* to illustrate *P. miles*, Humann & DeLoach (1993) actually used the only photograph known (at the time) of *P. miles* to illustrate the fish they called "*P. albirostris*" in the Galapagos. A clue as to why they may have decided that species identification was their use of the invented common name "white-margined searobin" for their *P. albirostris*, clearly reflecting the prominent white margin to the pectoral fin of *P. miles*. However, the common name of *P. albirostris* is "whitesnout searobin" (based on the Latin translation), not in reference to the pectoral fin.

Literature corrections in chronological order:

- Jordan & Bollman (1890, p. 168) in the description of *P. albirostris* report the gill rakers as "rather long and slender, longer than interspaces, about equal to one-third of eye, five most strongly developed". My examination of specimens show short stubby gill rakers and a higher number, similar to those found on *P. pictus* (Fig. 27).
- Jordan & Evermann (1898, p. 2172) list *Prionotus horrens* as present in the Galapagos without explanation, but it is not.
- Teague (1951, p. 26) reports that the type specimens of *Prionotus quiescens* (Jordan & Bollman, 1889) (a junior synonym of *P. stephanophrys*) were "taken off the Galapagos", but they were trawled off Panama at *Albatross* stations 2800 (USNM 41152, 8.85°, -79.525°, 13 m); 2802 (USNM 41195 & 41386, 8.6333°, -79.525°, 29 m); 2804 (USNM 41135 & 41139 & 41153 "holotype" & 41163, 8.275°, -79.6292°, 86 m); and 2805 (USNM 41196 & 41241, 7.9333°, -79.6917°, 94 m). He also mistakenly concludes *P. miles* has no opercular-flap scales, resulting in the species ending up in the couplet with *Bellator brachychir* (p. 5).
- Gruchy (1970, p. 526) states that only one species of *Prionotus* had been reported from the Galapagos by all the pre-1970 literature (except Jordan & Evermann's error for *P. horrens*), and he then adds two additional species from the 4 CMN 69-78 (ex-NMC) specimens collected from the mouth of Tagus Cove in 1968, i.e. two specimens of "*Prionotus loxias*" (now type specimens of *Bellator farrago* Richards & McCosker, 1998) and two specimens of "*Prionotus albirostris*", later assigned to "*P. stephanophrys*" by Richards & McCosker (1998), and now paratypes of *Prionotus pictus*.
- Humann & DeLoach (1993, pp. 132 & 133) have a rare true *P. miles* photograph ("white-margined searobin") as well as a text description, both incorrectly titled "*P. albirostris*". Text stating there are three additional species in Galapagos that are difficult to distinguish and that the endemic *P. miles* is a deepwater species is not correct.
- Allen & Robertson (1994, p. 103) illustrate *P. miles* with a photograph of *P. pictus*.
- Bussing (1995, p. 1647) has a range map incorrectly showing *P. albirostris* present in Galapagos and a distorted line drawing of *P. stephanophrys* with a pectoral fin extending beyond the end of the soft dorsal fin (but it should be shorter than that of *P. albirostris* and *P. pictus*).
- Grove & Lavenberg (1997, pp. 296–301) treat both *P. miles* and *P. albirostris* as Galapagos fishes, but the text description of *P. miles* is an amalgam of features of *P. miles* and *P. pictus*. The description of "*P. albirostris*"

is also an amalgam of features mostly based on the misidentified photograph placed under the heading "P. albirostris", of a specimen that is really P. miles from Baltra Channel (LACM 44019).

McCosker (1998, p. 810) in his review of the book, discusses Grove & Lavenberg's (1997) listing of two "P. albirostris" specimens collected at Tagus Cove (CMN 69-78), presumably following Gruchy (1970), as "Gruchy's misidentification of P. stilbostigma" (McCosker must have intended to say P. stephanophrys, note that Prionodes stilbostigma [i.e. not Prionotus] is an old name for Serranus stilbostigma).

Richards & McCosker (1998, p. 940) changed the identification of the two specimens of "*P. albirostris*" in CMN 69-78 to "*P. stephanophrys*".

Constant (2002, reprinted 2011, p. 100) lists "*Prionotus albirostris*" as the "white margin searobin" (i.e. *P. miles*), following Humann & DeLoach (1993), adding that it is the second species in Galapagos with *P. miles*.

Humann & DeLoach (2003, reprinted 2011, p. 154) describe *P. miles* with an amalgam of features of *P. miles* and *P. pictus*; the upper photograph is true *P. miles*, but the middle photographs on pp. 154 & 155 of putative *P. miles* are *P. pictus*.

McCosker & Rosenblatt (2010, p. 191) follow Richards & McCosker (1998) and erroneously list *P. stephanophrys* in the Galapagos species list (in addition to *P. miles*).

Ruiz, Chiriboga & Banks (2011, p. 58) follow multiple sources and erroneously list both *P. albirostris* and *P. stephanophrys* in the Galapagos species list (in addition to *P. miles*).



Figure 27. *Prionotus albirostris* gill rakers (upper), SIO 64-878, Santa Margarita, Baja California Sur, Mexico; *Prionotus pictus*, gill rakers (lower), holotype, SIO 15-2202, Isla Fernandina, Galapagos Archipelago, Ecuador (BCV).

Portnoy et al. (2016, Fig. 1 tree) switch the COI mtDNA sequence of Atlantic *Prionotus punctatus* for their "*P. ruscarius*" (a species from the tropical eastern Pacific), i.e. GenBank accession number KX811030; and use the COI sequence of *Prionotus ruscarius* for their "*P. punctatus*" (a species from the Atlantic) i.e. GenBank accession number KX811023.

Tirado-Sanchez et al. (2016); Robertson et al. (2017); Grove et al. (2022); Robertson & Allen (2024); and Victor et al. (2024) all follow Richards & McCosker (1998) and erroneously list *P. stephanophrys* in the Galapagos species list (in addition to *P. miles*).

Other material examined.

Prionotus albirostris: SIO 15-300, 3, 45–47 mm SL, Mexico, Baja California Sur, Isla Angel de la Guarda, 29.537°, -113.582°, 22 April 1953; SIO 15-974, 37 mm & 78 mm SL, Mexico, Baja California Sur, Isla Angel de la Guarda, 29.537°, -113.582°, 22 April 1953; SIO 62-563, 26 mm SL, Mexico, Baja California Sur, Bahia Magdalena, 24.583°, -112.00°, 2 November 1951; SIO 64-270, 43 mm & 51 mm SL, Mexico, Baja California Sur, Bahia Ballena, 26.633°, -113.208°, 1 December 1963; SIO 64-878, 175 mm SL, Mexico, Baja California Sur, 3.3 miles SW of Isla Santa Margarita, 26.317°, -111.802°, 13 November 1964; SIO 64-890, 166 mm & 177 mm SL, Mexico, Baja California Sur, 14 Miles SE of Punta Abrejos, 26.548°, -113.380°, 17 November 1964; SIO 84-79, 5, 150–161 mm SL, Mexico, Baja California Sur, off La Tinaja Point, 23.128°, -110.140°, 16 July 1984; mtDNA COI sequence from SIO 09-293, 220 mm SL, Mexico, Baja California Sur, Todos Santos Commercial Beach, 23.410°, -110.230°, J. Snow, 2 June 2009.

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