



## *Apristurus manocheriani* (Carcharhiniformes: Pentanchidae), a new species of catshark from the Southwest Indian Ocean

JUSTIN A. CORDOVA


*Pacific Shark Research Center, Moss Landing Marine Laboratories,  
Moss Landing, CA 95039, USA*

 <https://orcid.org/0000-0002-5138-8629> E-mail: [jcordova@mlml.calstate.edu](mailto:jcordova@mlml.calstate.edu)

DAVID A. EBERT

*Pacific Shark Research Center, Moss Landing Marine Laboratories,  
Moss Landing, CA 95039, USA*

*Research Associate, Department of Ichthyology, California Academy of Sciences,  
55 Music Concourse Drive, San Francisco, CA. 94118, USA*  
*Research Associate, South African Institute for Aquatic Biodiversity,  
Private Bag 1015, Grahamstown, 6140, South Africa*

 <https://orcid.org/0000-0003-4604-8192> E-mail: [debert@mlml.calstate.edu](mailto:debert@mlml.calstate.edu)

### Abstract

A new species of catshark, *Apristurus manocheriani* n. sp., is described from 8 specimens collected from seamounts in the southwest Indian Ocean (SWIO). The new species is placed in the *Apristurus spongiceps* subgroup and is only the second known species in this subgroup occurring in the western Indian Ocean. Geographically, *A. manocheriani* is known only from the SWIO, while its two closest congeners are from distant locations: *Apristurus albisoma* Nakaya & Séret, 1999 occurs in the southwest Pacific Ocean and *Apristurus aphyodes* Nakaya & Stehmann, 1998 in the northeast Atlantic.

**Key words:** taxonomy, ichthyology, Chondrichthyes, elasmobranch, seamounts, Southwest Indian Ridge.

**Citation:** Cordova, J.A. & Ebert, D.A. (2021) *Apristurus manocheriani* (Carcharhiniformes: Pentanchidae), a new species of catshark from the Southwest Indian Ocean. *Journal of the Ocean Science Foundation*, 38, 13–26.

**doi:** <https://doi.org/10.5281/zenodo.5081131>

**urn:** [lsid:zoobank.org/pub:AC333F16-ACC8-47DD-8FA6-BB8030C7DBE4](https://lsid.zoobank.org/pub:AC333F16-ACC8-47DD-8FA6-BB8030C7DBE4)

**Date of publication of this version of record:** 7 July 2021

## Introduction

The genus *Apristurus* Garman, 1913 (Chondrichthyes: Pentanchidae) comprise one of the most species-rich shark genera with 39 valid species (Weigmann 2016, White et al. 2017). The genus is divided into three subgroups based on morphological and meristic characters (Nakaya & Sato 1999), egg case morphology (Flammang et al. 2007), and molecular data (Sato 2000, Iglesias et al. 2005). The three subgroups are referred to as the *longicephalus*, *brunneus* and *spongiceps* subgroups. The *longicephalus* subgroup can be distinguished from the other two subgroups by a very long, narrow, and slender snout; its length from snout tip to anterior nostrils is greater than 6.4% total length (TL). The other two subgroups, referred to as the *spongiceps* and *brunneus* subgroups, have relatively shorter snouts, with their lengths being less than 6.4% total length (TL). The *spongiceps* subgroup is separable from the *brunneus* subgroup by having a more stout vs. slender body, lower labial furrows equal to or longer than the uppers, lower spiral valve counts (7–12 vs. 13–22), and a continuous vs. discontinuous supraorbital sensory canal (Nakaya & Sato 1999). Also, the egg cases of the *spongiceps* group lack tendrils at their corners, while those of the *brunneus* subgroup have long coiled tendrils (Flammang et al. 2007).

Members of the genus *Apristurus* are found in all oceans, including Arctic, but not Antarctic, waters, mostly at depths from about 200–2200 m, and on continental and insular slopes, deep-sea ridges, seamounts, and trenches (Ebert & Winton 2010, Kawauchi et al. 2014). Many *Apristurus* species appear to be endemic, while others appear to have a wider distribution. The majority of species are found in the western Pacific (at least 20 species), followed by the western Atlantic with 8 species (Ebert et al. 2021a). The western Indian Ocean (WIO) is reasonably well represented, with 6 *Apristurus* species, including: *A. longicephalus* Nakaya, 1975; *A. breviventralis* Kawauchi, Weigmann & Nakaya, 2014; *A. indicus* (Brauer, 1906); *A. melanoasper* Iglésias, Nakaya & Stehmann, 2004; *A. microps* (Gilbert, 1922); and *A. saldanha* (Barnard, 1925). Of these 6 species, the only *spongiceps* subgroup representative is *A. microps*, whose distribution extends just into the southwest Indian Ocean (SWIO) off the south coast of South Africa (Ebert 2013, Kawauchi et al. 2014, Ebert et al. 2021b).

During two surveys conducted in 2012 and 2014 along the Southwest Indian Ridge (SWIOR), specimens of an *Apristurus* species were collected with characteristics associated with the *spongiceps* subgroup. Upon closer examination, it was found to be distinct from all other known *spongiceps* subgroup species and we describe it here. This paper is part of a series describing new species and revising chondrichthyan taxa from the SWIO.

## Materials and Methods

Morphometric measurements were taken in full on the holotype and 7 paratypes following the methodology and terminology proposed by Nakaya et al. (2008) for the genus *Apristurus*. Morphometric values to the nearest millimeter (mm) are presented as ratios of the total length (TL). Meristics, including tooth and vertebral counts, were taken from the type series.

To identify differences between the new species and its two closest congeners, morphometric measurements expressed as %TL were assessed using non-metric multidimensional scaling (nMDS) ordination (Clarke & Gorley 2006). In this analysis, similar morphometric characters are plotted on a graph close together in ordination space, while dissimilar ones fall far apart (Gotelli & Ellison 2013, White et al. 2013). The different assemblages identified using nMDS represent different species. To assess if there was a statistical difference in the multivariate morphometric data collected for each group, a Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted. No additional transformations were necessary before calculation of the resemblance matrix since morphological data were expressed as percentages. Data were visually inspected for normality using a Normal Quantile-Quantile plot with 95% Confidence intervals and this assessment indicated that the morphometric data were normally distributed. Similarity Percentages (SIMPER) analysis associated with the nMDS was conducted to provide insight into which traits most contributed to differences among groups using the Vegan package in R (Oksanen et al. 2020).

All type specimens are deposited into the fish collection at the California Academy of Sciences Ichthyology (CAS-ICH). Comparative material was examined from the Commonwealth Scientific and Industrial Research Organization, Division of Marine and Atmospheric Research (CSIRO), Moss Landing Marine Laboratories (MLML), Museum of Comparative Zoology (MCZ), South African Institute for Aquatic Biodiversity (SAIAB),

Iziko South African Museum (SAM), Muséum national d'Histoire naturelle, Paris (MNHN), Scripps Institution of Oceanography (SIO), United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), University of Washington (UW), and the Zoological Museum Hamburg (ZMH). Institutional abbreviations follow Sabaj (2019).

**A**



**B**



**Figure 1.** *Apristurus manocheriani*, n. sp., holotype, lateral view, adult male, 558 mm TL (CAS-ICH 247255) before preservation (A) and after preservation (B); scale bar = 5 cm.

## Genus *Apristurus* Garman, 1913

### *Apristurus* Garman, 1913: 96

Type species. *Scyliorhinus indicus* Brauer, 1906, by original designation.

### *Apristurus manocheriani*, new species

Manocherian's Catshark

urn:lsid:zoobank.org:act:61EB269F-189D-4367-A3DF-F85CA05F82AA

Figures 1–7, Table 1

**Holotype.** CAS-ICH 247255, mature male, 558 mm TL, SWIOR, Indian Ocean,  $-35.133^{\circ}$ ,  $53.700^{\circ}$ , 89–1240 m, 30 April 2014 (taken as bycatch in deep-sea trawl for Alfonsino (*Beryx* spp.) and Orange Roughy (*Hoplostethus atlanticus*)).

**Paratypes.** (7 specimens) CAS-ICH 247256, mature male, 536 mm TL, Indian Ocean, SWIOR,  $-35.167^{\circ}$ ,  $54.283^{\circ}$ , 620–920 m, 1 April 2014; CAS-ICH 247257, female, 476 mm TL, Indian Ocean, Walters Shoal,  $-34.667^{\circ}$ ,  $44.250^{\circ}$ , 1000–1300 m, 8 March 2012; CAS-ICH 247258, Female 467 mm TL, Indian Ocean, SWIOR,  $-35.167^{\circ}$ ,  $53.667^{\circ}$ , 900–1100 m, 8 March 2012; CAS-ICH 247259, female, 485 mm TL, Indian Ocean, Walters Shoal,  $-34.667^{\circ}$ ,  $44.250^{\circ}$ , 89–1240 m, 8 March 2012; CAS-ICH 247260, female, 480 mm TL, Indian Ocean, Walters Shoal,  $-34.417^{\circ}$ ,  $44.333^{\circ}$ , 1200–1300 m, 10 March 2012; CAS-ICH 247261, female, 495 mm TL, Indian Ocean, SWIOR,  $-35.167^{\circ}$ ,  $54.283^{\circ}$ , 620–920 m, 1 April 2014; CAS-ICH 247262, mature male, 491 mm TL, Indian Ocean, SWIOR,  $-39.00^{\circ}$ ,  $46.50^{\circ}$ , 800–1200 m, 4 April 2012.

**Diagnosis.** A new species in *spongiceps* subgroup of *Apristurus*, as defined by Nakaya & Sato (1999), distinguished from all congeners by a combination of characteristics: an overall uniformly whitish “porcelain” colored body with lighter colored anal and caudal-fin margins and a distinct white spot on tail tip vs. a uniform dark brown to grayish, or blackish, body coloration, variably with blotches, flecks, spots, or squiggles, in all other *spongiceps* subgroup species (except *A. albisoma* and *A. aphyodes* with similar light coloration, but subtle differences); clasper hooks present vs. absent; oral papillae absent or sparsely covering oral cavity roof vs. distinct and densely covering oral cavity roof; dorsal caudal margin with widely spaced, non-overlapping dermal denticles vs. closely spaced, overlapping denticles; lower tooth counts, i.e. 46–57 in upper jaw and 44–50 in lower jaw vs. 56–71 and 49–70 respectively.

**Description.** (proportional measurements expressed as percentage of total length (TL) for holotype followed by range for 7 paratypes in parentheses) Body cylindrical, elongate, relatively stout to about pelvic fins, tapering posteriorly (Fig. 1); abdomen relatively long with pectoral–pelvic fin space longer than anal-fin-base length and first and second dorsal-fin origins length; posterior body behind pelvic fins compresses laterally to caudal origin. Head depressed, length about twice maximum head width (Fig. 2). Snout bell-shaped in dorsoventral view, moderately long, tip rounded, tapering evenly. Pre-outer nostril length slightly greater than internarial width and about 0.6 (0.5–0.7) times interorbital width. Pre-oral length less than pre-orbital length, about 1.9 (1.7–2.3) times internarial width, less than mouth width, and about 1.1 (0.9–1.3) times interorbital width. Pre-orbital length about 1.4 (1.3–1.9) times interorbital width and about 3.2 (3.2–4.3) times orbit length. Internarial width about 1.3 (1.3–1.4) times orbit length, about 1.2 (1.2–1.5) times nostril length. Supraorbital sensory canal continuous. Nostrils large, expanding obliquely inwards from snout edge; nostril length about 0.5 (0.4–0.5) times pre-inner nostril length, about 0.8 (0.6–0.8) times internarial width, and about 1.1 (0.9–1.1) times orbit length. Nostril–mouth space about 0.4 (0.3–0.6) times internarial width. Mouth broadly arched in an inverted U-shape, with well-developed labial furrows at mouth corners; upper labial furrows about 1.1 (1.0–1.1) times longer than lower ones. Oral papilla not present (mostly) or poorly developed. Upper labial furrows not reaching midpoint between mouth corner and posterior margin of nostril. Orbits oval, relatively small, without distinct subocular folds; orbit length less than internarial width and about 0.8 (0.7–0.8) times interorbital width. Spiracles small, located closely behind and just below



**Figure 2.** *Apristurus manocheriani*, n. sp., head of holotype, lateral (top), ventral and dorsal views; scale bar = 3 cm.

TABLE 1

Proportional measurements of type specimens of *Apristurus manocheriani*  
n. sp. as percentages of total length

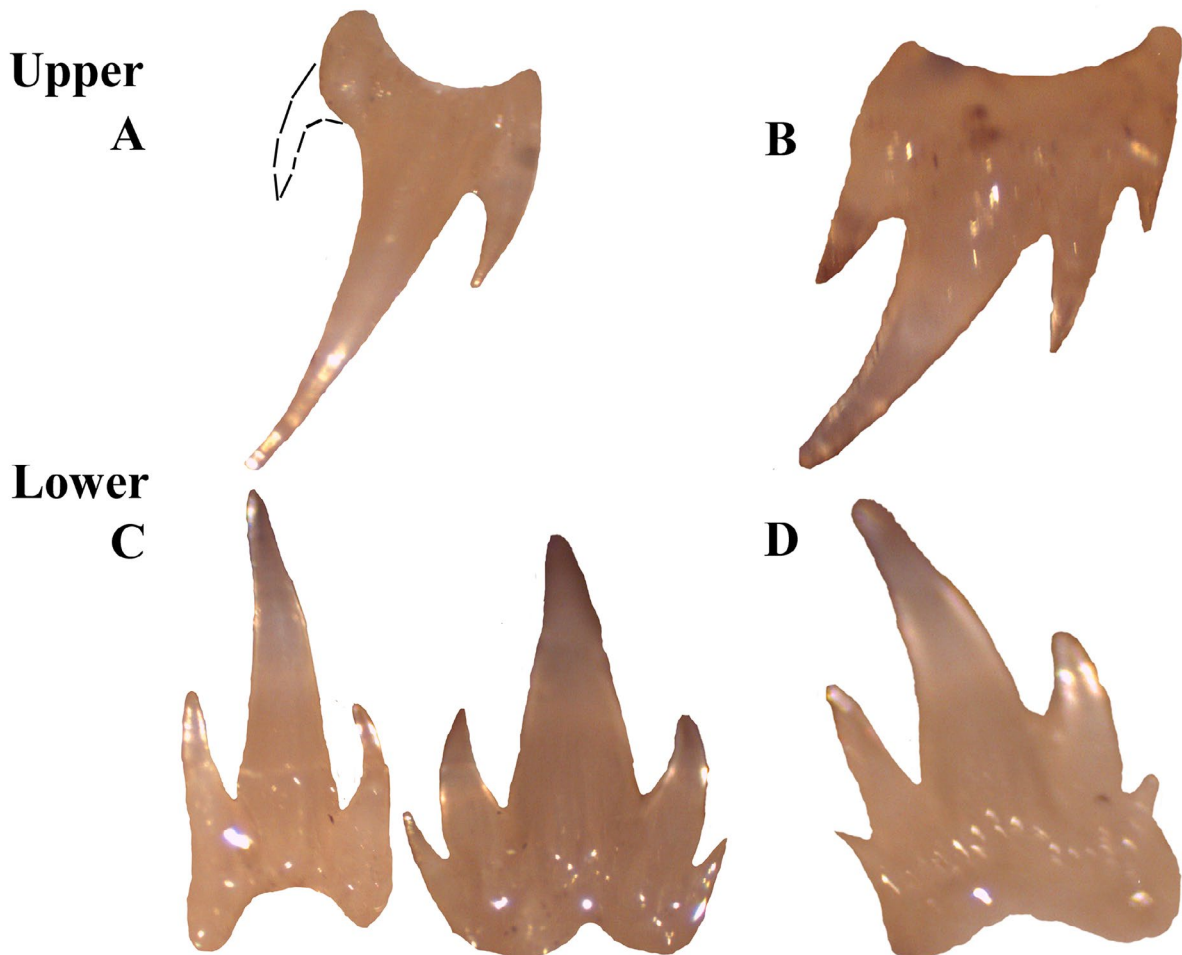
	holotype	paratype max	paratype min		holotype	paratype max	paratype min
Total length (mm)	558	536	467	P1 tip to P2 origin	13.6	15.2	10.8
PreD2–insertion length	73.8	73.7	70.5	P1–P2 origins	25.1	26.3	21.4
PreD2–origin length	67.9	67.9	64.8	P1–P2 insertions	26.9	26.9	23.4
PreD1–insertion length	59.1	59.6	57.8	P2–anal space (ceratotrichia)	7.5	8.8	5.9
PreD1–origin length	53.0	55.9	52.1	P2–anal origins (ceratotrichia)	14.9	16.1	12.8
PreP1 length	22.9	26.4	21.2	D1 length	8.2	9.3	8.0
PreP2 length	48.4	48.1	46.0	D1 base length	5.2	5.9	4.7
Pre–vent length	50.9	50.9	48.3	D1 height	2.2	2.3	1.8
Pre–anal length (ceratotrichia)	61.8	62.3	58.7	D1 free lobe length	3.2	3.5	2.5
Pre–anal length (incl. muscle)	60.8	59.2	56.4	D2 length	9.0	10.9	8.5
Pre–caudal length	73.8	74.5	70.5	D2 base length	5.7	6.1	5.1
Pre–branchial length	18.3	19.0	16.4	D2 height	3.0	2.9	2.1
Pre–spiracular length	13.1	14.7	13.3	D2 free lobe length	3.0	4.7	3.5
Pre–orbital length	9.7	12.9	9.7	P1 base length	6.5	8.1	6.3
Pre–outer nostril length	3.8	5.0	3.7	P1 anterior margin	9.3	11.3	8.4
Pre–inner nostril length	5.9	6.8	5.5	P1 posterior margin	7.3	6.7	5.4
Pre–oral length	7.3	8.5	7.1	P1 inner margin	5.6	7.1	5.2
Head length	22.0	23.8	22.0	P1 width	7.2	6.9	5.6
Head height	9.0	10.1	6.7	P2 anterior margin	2.7	5.4	2.9
Head width (mouth corners)	10.0	10.8	8.7	P2 length	8.2	10.9	8.2
Head width (max)	10.8	11.7	8.9	P2 base length	6.8	8.6	6.9
Mouth width	7.9	9.4	7.6	P2 posterior margin	5.9	6.7	5.0
Mouth length	5.4	6.1	4.6	P2 inner margin	0.9	2.4	0.9
Internarial length	3.9	4.4	3.7	Anal base length (ceratotrichia)	12.5	13.7	9.9
Upper labial furrow	2.7	3.1	2.2	Anal base length (muscle)	14.3	16.2	12.6
Lower labial furrow	2.5	3.1	2.0	Anal anterior margin	7.3	9.7	6.5
Orbit length	3.0	3.4	2.9	Anal posterior margin	7.3	7.9	6.0
Orbit height	1.6	1.9	1.3	Anal height (muscle)	5.2	5.9	4.0
Nostril length	3.2	3.1	2.5	Anal inner margin	0.5	1.3	0.2
Nostril mouth–space	1.4	2.2	1.4	Caudal peduncle height	3.9	4.4	3.5
Interorbital width	6.8	8.0	6.4	Caudal length	27.8	30.7	26.5
First gill height	3.6	3.5	2.6	Caudal height	7.7	8.4	7.4
Third gill height	3.4	3.7	2.8	Caudal preventral margin	9.5	10.1	9.0
Fifth gill height	1.6	2.4	1.9	Caudal postventral margin	15.8	15.5	13.6
D1–D2 space	9.5	9.3	8.1	Caudal terminal lobe height	2.3	2.6	1.7
D1–D2 origins	14.2	14.4	13.3	Caudal terminal lobe length	3.6	5.5	4.3
D1–D2 insertions	15.2	14.4	13.1	Caudal terminal lobe post. margin	2.9	3.9	2.1
P1–P2 space	19.2	19.6	17.6	Clasper outer length	5.4	5.5	5.2
				Clasper inner length	9.0	9.7	9.4

horizontal axis at posterior rim of orbits. Five small gill slits present, first three similar in height; fourth gill slit located above pectoral fin origin, slightly smaller than first three; fifth gill slit smallest. Gill septa visible, without projections, densely covered with fine dermal denticles.

Pectoral fins relatively small, subangular, and broadly rounded posteriorly; length of anterior margin about equal to or less than one-third distance between pectoral–pelvic-fin origins; right and left fins separated by a space nearly equal to mouth width. Pelvic fins moderate in size, length about 1.6 (1.5–2.0) times anal fin height, slightly less than distance between pectoral–pelvic-fin origins. Dorsal fins similar in shape and size. First-dorsal-fin origin slightly posterior to pelvic-fin insertion (axil); insertion slightly anterior to level of anal-fin origin. Second-dorsal-fin origin about mid-point of anal-fin base; insertion slightly anterior to anal-fin insertion; base length about two-thirds pectoral–pelvic space length. Anal fin high, broadly rounded, base length more than twice height; anal and caudal fins separate only by a notch. Caudal fin slender; ventral lobe high; apex of ventral lobe rather angular; subterminal notch distinct; terminal lobe long, about 1.5 (1.9–3.1) times as long as high. Caudal peduncle high, height less than one-half interdorsal space, nearly equal to internarial width.

Teeth numerous and large (Fig. 3); similar in upper and lower jaw; upper anteriors with long, robust, central cusp, flanked by one or two acutely pointed lateral cusps on each side, less than one-half height of central cusp; upper laterals with long central cusp flanked by two successively smaller cusps on each side, about one-half or less than height of preceding cusp; lower teeth similar to uppers, with central cusp of anteriors having one or two lateral cusps on each side, and laterals flanked by two lateral cusps on each side. Sexual dimorphism apparent: adult male jaws more pronounced than adult females, very strongly arched, adult female jaws more weakly arched. Tooth counts in first row of upper jaw 51 (46–57) and in first row of lower jaw 49 (44–50).

Dermal denticles (Fig. 4) on dorsolateral side of body erect, small, overlapping each other, tricuspidate with a long, ridged central cusp flanked on each side by a much smaller lateral cusp; outer surface of denticles structured by reticulations. No observed difference between similar-sized female and male specimens; smaller individuals



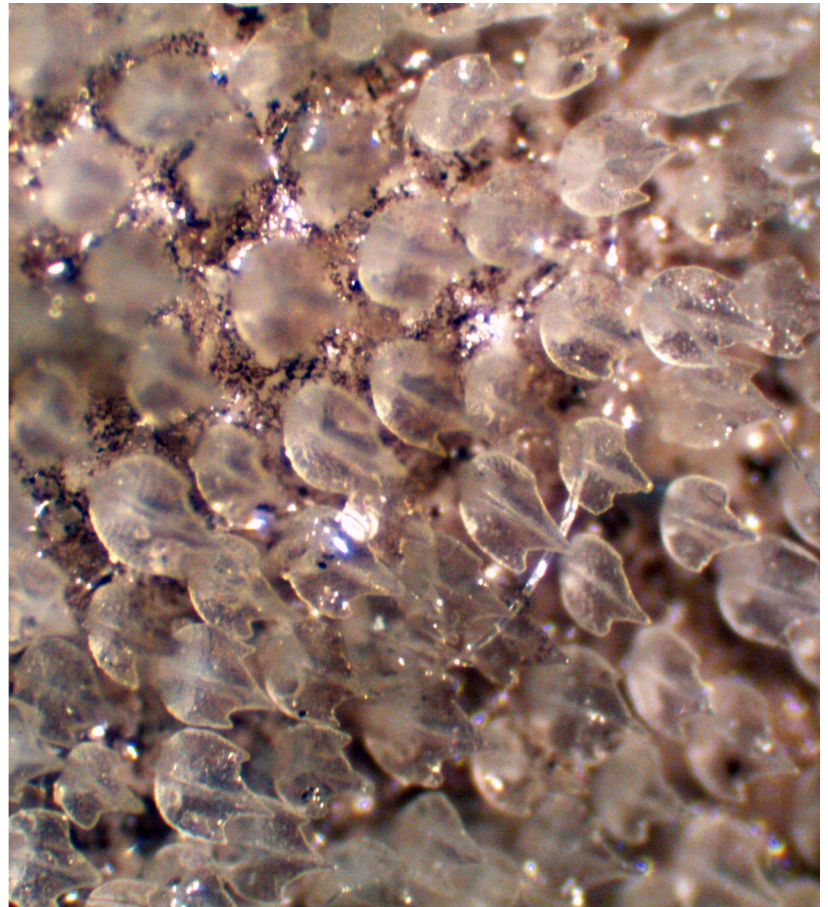
**Figure 3.** *Apristurus manocheriani*, n. sp., teeth of holotype, A: upper anterior tooth, B: upper lateral tooth, C: lower anterior tooth, D: lower lateral tooth.

unavailable. Caudal-fin dorsal margin without enlarged dermal denticles, shape similar to flank denticles, but more widely spaced.

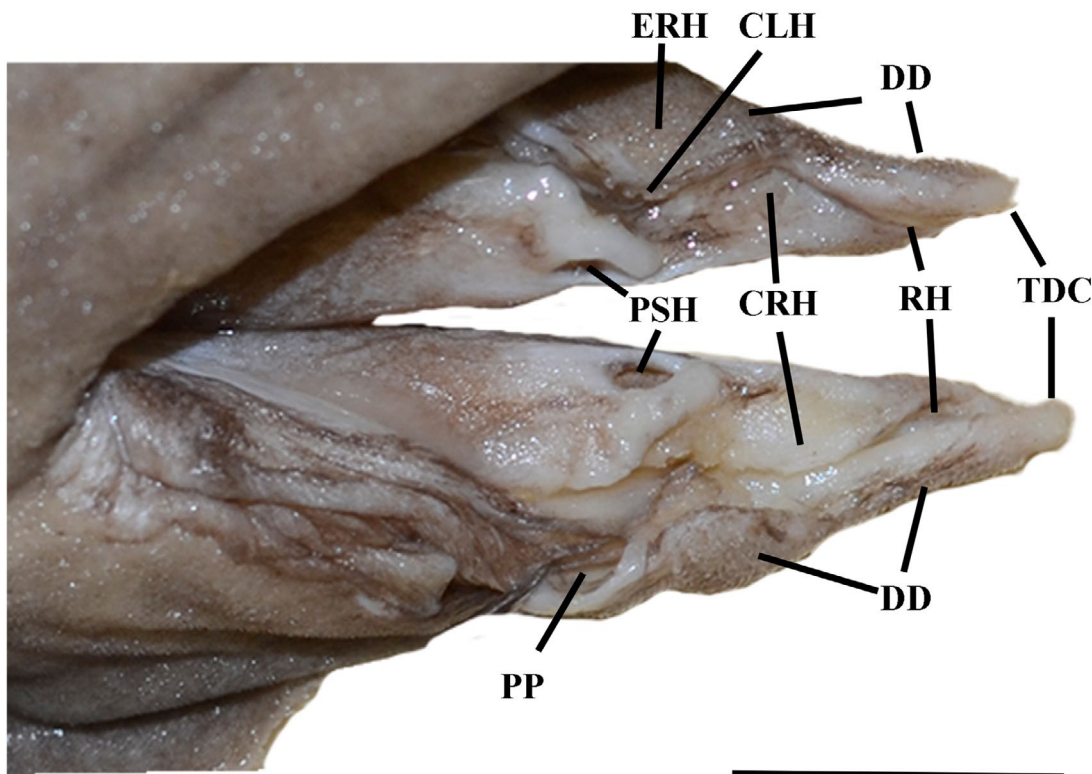
Claspers (Fig. 5) short, robust, tapering posteriorly to tip, nearly reaching anal-fin-muscle origin; dermal denticles cover entire ventral side, partially on dorsal area, and almost entire claspers; clasper hooks present, 5 visible on lateral side of exorhipidon; pseudosiphon distinct, circle-shaped, and deep; rhipidon cover reduced, not covering center of the clasper groove; pseudopera large, deep, only visible if clasper extended; exorhipidon flat, simple oval shaped; terminal dermal cover present at distal tips of clasper.

Vertebral counts: monospondylous pre-caudal (MP) 35 (32–35); diplospondylous pre-caudal (DP) 29 (25–29); total pre-caudal counts 64 (60–64); caudal 52 (49–54); total vertebral counts 116 (112–116).

Meristic features: (following counts are for holotype, then range of paratypes in parentheses, if different) Dorsal-fin elements X,15 (15 or 16, most 16; when 15, a deeply divided last ray); anal-fin elements III,7, all



**Figure 4.** *Apristurus manocheriani*, n. sp., paratype, adult male, 491 mm TL (CAS-ICH 247262); dermal denticles of dorsolateral side.



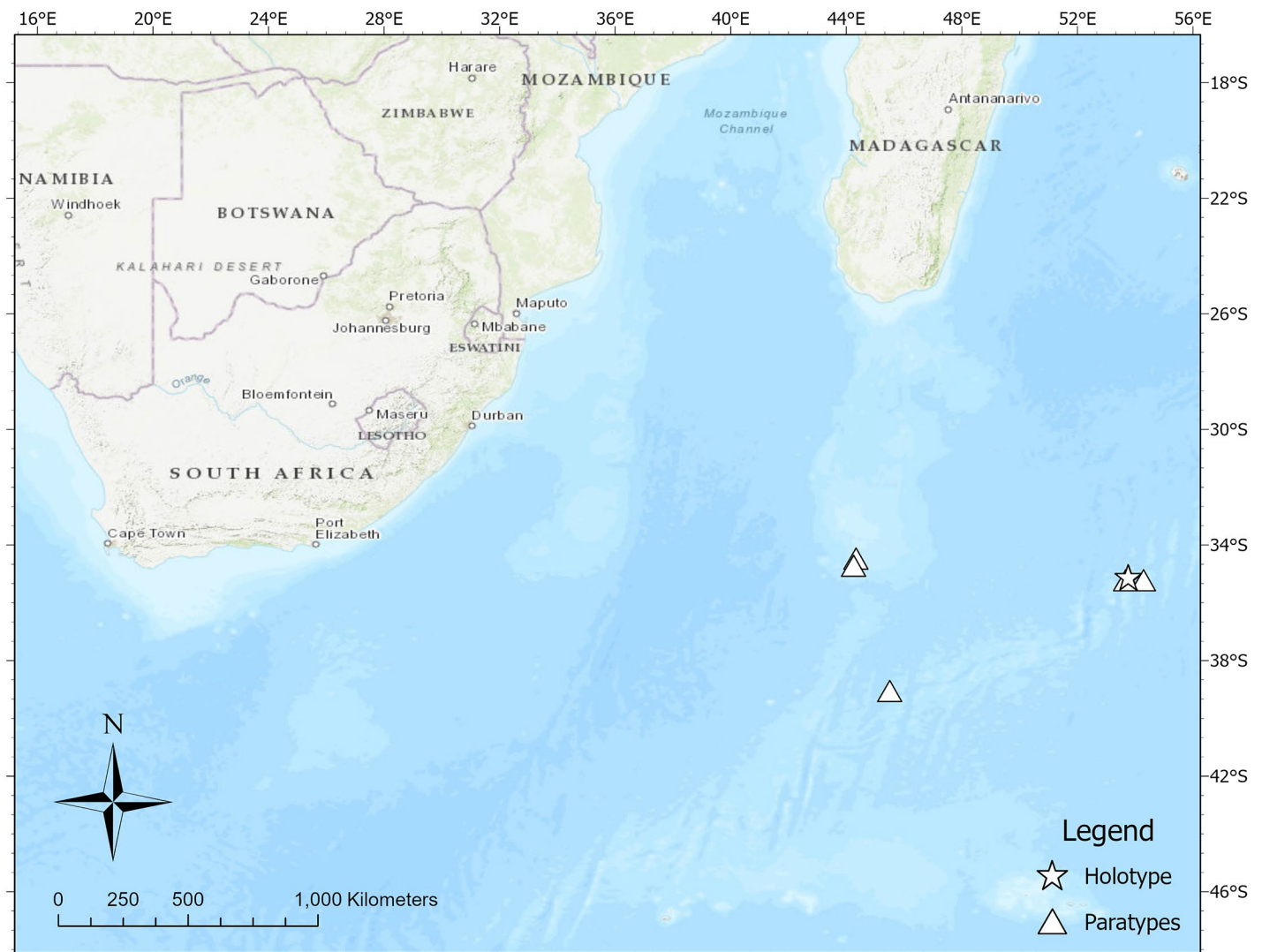
**Figure 5.** *Apristurus manocheriani*, n. sp., dorsal view of left and right claspers of holotype: CRH: cover rhipidon; CLH: clasper hooks; DD: dermal denticles; ERH: exorhipidon; PP: pseudopera; PSH: pseudosiphon; RH: rhipidon; TDC: terminal dermal cover; scale bar = 1 cm.

dorsal-fin and anal-fin rays branched, last sometimes to base; pectoral-fin rays 18 or 19 (usually 19), about two upper and lower rays unbranched; pelvic-fin rays 1,5; principal caudal-fin rays 8+7, middle 13 branched; pored lateral-line scales 50 or 51 (48–54); scales above first lateral-line scale to base of second-dorsal-fin spine 4 1/2; scales above lateral-line apex to base of middle dorsal-fin spines 3 1/2; scales below lateral line to origin of anal fin about 15; circumpeduncular scales about 26; gill rakers 10+26 (9–11 + 24–27); branchiostegal rays 7.

**Color.** (Figs. 1A & B) Prior to preservation, body uniformly “porcelain” whitish with a slight pinkish tinge, fins mostly similar except for white edges along posterior margins of anal and caudal fin and a prominent to faint white caudal-fin tip; anterior margins of dorsal fins thinly blackish, first-dorsal-fin posterior margin and free rear tip white, second-dorsal-fin posterior margin blackish. After preservation, body and fins become dark gray to brownish, except for white fin edges still distinct, but may eventually fade with time.

**Size.** A moderate-sized *Apristurus* species, *A. manocheriani* reaches a maximum total length of at least 558 mm for males and 495 mm for females. All three males were mature, with a minimum mature size of 491 mm TL. Females ranged in size from 467–495 mm TL, but were not examined internally for maturity.

**Distribution.** Based on the available material, the new species is presently known only from the SWIO on the southern end of the Madagascar ridge at Walters Shoal, in an area from approximately -34.417°, 44.333° to -34.667°, 44.250°, and on the SWIOR in an area from approximately -35.133°, 53.700° to -35.167°, 54.283° and at -39.00°, 46.50° (Fig. 6). Specimens were collected from 89–1,300 m deep, although mostly deeper than 620 m, in both bottom and midwater trawls. The shallowest catch record of the new species, possibly at 89 m, came from a midwater trawl.



**Figure 6.** Distribution map of *Apristurus manocheriani* n. sp. specimens collected from the Madagascar ridge at Walters Shoal and on the SWIOR. The holotype is represented by a star and paratypes by circles.



**Etymology.** The new species is named for Greg Manocherian in recognition of his strong commitment to and passion for shark conservation and research. The proposed English common name is Manocherian's Catshark.

**Comparisons.** *Apristurus manocheriani* n. sp. is assigned to the *spongiceps* subgroup as defined by Nakaya & Sato (1999) based upon its relatively stout body, upper and lower labial furrows being approximately equidistant in length, a pre-outer nostril length shorter than interorbital width, a continuous sensory canal, and the low number of spiral valve turn counts ranging from 7–12. Presently, there are 13 species represented in the *spongiceps* subgroup including *A. albisoma* Nakaya & Séret, 1999; *A. ampliceps* Sasahara et al., 2008; *A. aphyodes* Nakaya & Stehmann, 1998; *A. bucephalus* White et al., 2008; *A. fedorovi* Dolganov, 1985; *A. kampa* Taylor, 1972; *A. manis* Springer, 1979; *A. microps* Gilchrist, 1922; *A. pinguis* Deng, Xiong & Zhan, 1983; *A. profundorum* Goode & Bean, 1896; *A. riveri* Bigelow & Schroeder, 1944; *A. spongiceps* Gilbert, 1905; and *A. stenseni* Springer, 1979.

The new species can be separated from all but two *spongiceps* subgroup species based on its overall whitish body coloration, lighter anal and caudal-fin margins, and distinct white spot on its tail tip. Nakaya & Séret (1999) stated that white to light grayish coloration in fresh specimens is not found in many species within the *spongiceps* subgroup. Furthermore, they found that coloration was a useful characteristic to separate most *spongiceps* subgroup species. In fact, most members of this subgroup have a uniform dark brown to grayish or blackish body coloration, including *A. ampliceps*, *A. bucephalus*, *A. fedorovi*, *A. kampa*, *A. manis*, *A. microps*, *A. pinguis*, *A. profundorum*, *A. riveri*, *A. spongiceps*, and *A. stenseni*. In addition, 6 of these species (*A. fedorovi*, *A. microps*, *A. profundorum*, *A. riveri*, *A. spongiceps*, and *A. stenseni*) have no distinct markings such as blotches, flecks, spots, squiggles or lighter fin edges. In addition to their dark body coloration, three species (*A. ampliceps*, *A. bucephalus*, and *A. pinguis*) have blotches, flecks, spots, or squiggles, while two species have lighter fin edges (*A. kampa* and occasionally *A. manis*). Only *A. albisoma* and *A. aphyodes* have light body coloration most similar to *A. manocheriani*.

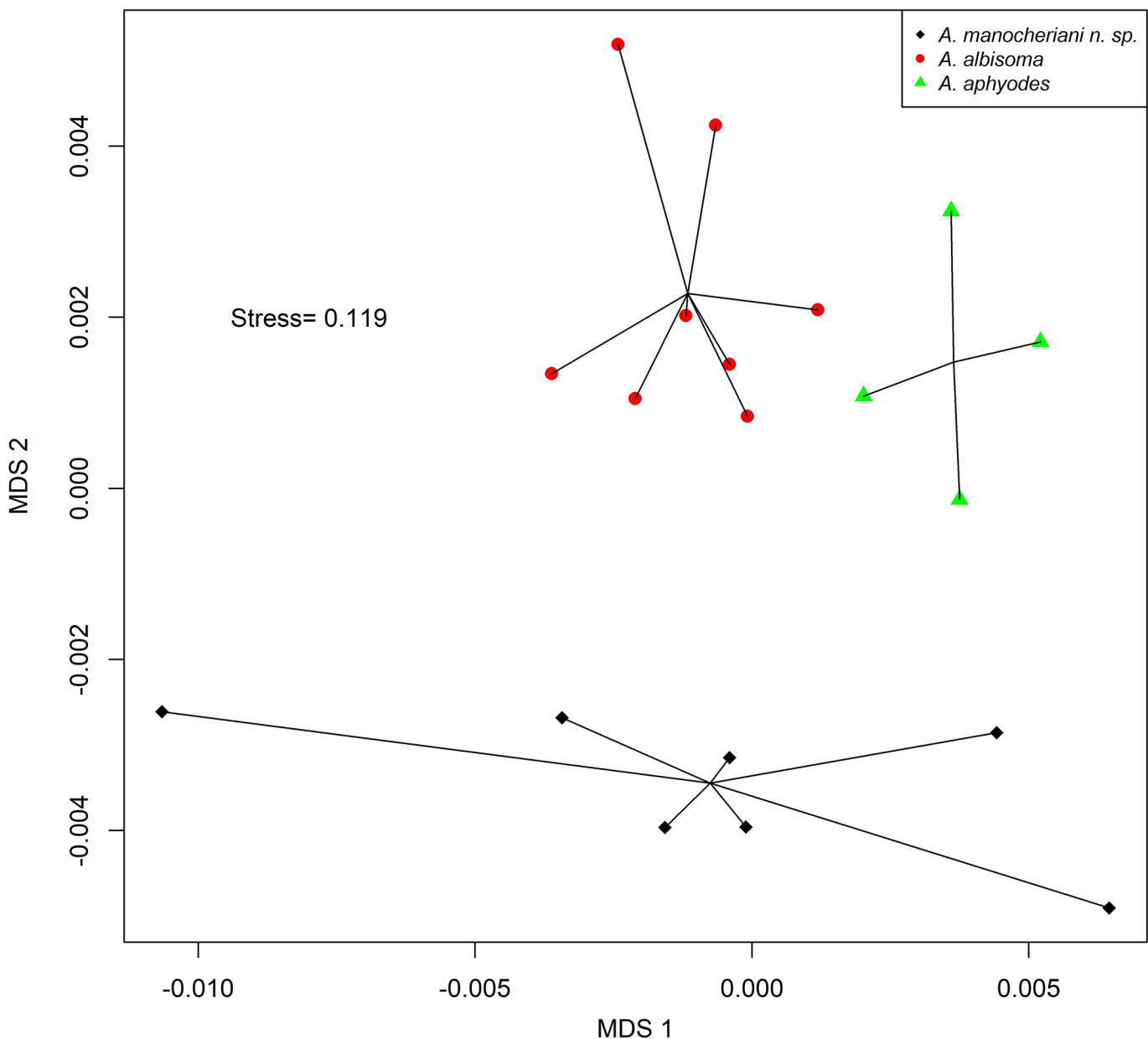
Geographically, 4 *spongiceps* subgroup species occur in the Indian Ocean, with three (*A. ampliceps*, *A. bucephalus*, and *A. pinguis*) occurring in the eastern Indian Ocean, and only *A. microps* found the SWIO off South Africa. All 4 species can be separated from the whitish *A. manocheriani* by their darker body coloration. Furthermore, the closest biogeographic *spongiceps* subgroup congener, *A. microps* has a crest of enlarged dermal denticles along the upper caudal margin, while *A. manocheriani* lacks a crest of enlarged denticles. The two closest congeners to *A. manocheriani* based on their whitish body coloration both occur outside the Indian Ocean. *Apristurus albisoma* is found in the southwest Pacific Ocean along the Norfolk and Lord Howe Ridges extending from off New Caledonia to the Australian exclusive economic zone (Nakaya et al. 2015), while *A. aphyodes* is known from the northeast Atlantic from Iceland to the northern Bay of Biscay (Ebert & Dando 2020).

In addition to biogeography, *A. manocheriani* can be separated from the two light-colored *spongiceps* subgroup species by a combination of morphological and meristic characteristics. Morphologically, *A. manocheriani* have clasper hooks present vs. absent in *A. albisoma* and *A. aphyodes*; widely-spaced dermal denticles along the dorsal caudal margin vs. closely packed denticles; oral papillae mostly absent or if present greatly reduced and sparsely covering the oral cavity roof vs. distinct, finger-like, papillae densely covering the oral cavity roof; tooth counts for upper (46–57) and lower (44–50) jaws slightly lower vs. higher counts for *A. albisoma* upper (56–71) and lower 61 (54–70) jaws, and for *A. aphyodes* upper (56–68) and lower (49–64) jaws; and monospondylous precaudal counts are slightly lower (32–35) vs. *A. albisoma* (34–36) and *A. aphyodes* (34–37).

*Apristurus manocheriani* can further be separated from *A. albisoma* by subtle differences in body coloration. *A. manocheriani* is uniformly “porcelain” whitish with a pinkish tinge, with ventral head, body, and gill area coloration similar to dorsal surface vs. uniform white without a pinkish tinge, with ventral head, body, and gill area noticeably darker than the dorsal surface; fin margins distinctly white along anal fin margins vs. dark margins along anal fin; caudal-fin margins white with a prominent white spot at tip vs. no distinct lighter or blackish fin margins or prominent white spot at caudal-fin tip. Morphologically, *A. manocheriani* has a slightly longer pre-orbital length times inter-orbital width 1.3–1.9 vs. 0.9–1.4 for *A. albisoma*; a slightly longer caudal terminal lobe length times its height 1.9–3.1 vs. 1.4–2.1; shorter head width at mouth corners 8.7–10.8 vs. 11.8–13.7; slightly longer orbit length 2.9–3.4 vs. 2.3–3.1; slightly shorter interorbital width 6.4–8.0 vs. 8.1–8.7; longer interdorsal space 8.1–9.5, pectoral–pelvic space 17.6–19.6, and pelvic–anal space 5.9–8.8 vs. 6.7–8.4, 13.5–17.7, and 4.1–6.6, respectively.

*Apristurus manocheriani* can be distinguished from *A. aphyodes* by differences in body coloration. The body coloration of *A. aphyodes* is a uniform whitish to lead or pale gray, with distinctly darker fins distally and no white spot at the caudal tip. This is in contrast to the light “porcelain” colored *A. manocheriani* with its distinct white posterior anal and caudal-fin margins and prominent white spot on its caudal tip. *A. manocheriani* differs from *A. aphyodes* morphologically by having a noticeably smaller second dorsal fin vs. similar-sized dorsal fins; anal fin being more broadly rounded vs. angular; mouth strongly arched vs. broadly rounded; mouth width wider 7.6–9.4 vs. 6.7–7.7 and length longer 4.6–6.1 vs. 4.1–4.4; upper labial furrows extending past lower symphysis of mouth vs. not extending past lower mouth symphysis; head width slightly smaller 8.9–11.7 vs. 11.1–12.6; shorter pre-orbital length times inter-orbital width 1.3–1.9 vs. 2.9–3.1; caudal terminal lobe longer, its length times its height 1.9–3.1 vs. 1.7–1.9.

The MDS analysis of *A. manocheriani* with its two closest morphological congeners *A. albisoma*, and *A. aphyodes* showed clear differences between species, visualized as three distinct clustered groups (Fig. 7). The PERMANOVA output showed a modest percentage of variation in distances is explained by species grouping (df=2, F statistic=3.8693, p=0.001), which rejects the null hypothesis and concludes that there are differences between these three species. The data met assumptions that the variance in measures was homogenous among



**Figure 7.** Non-metric multi-dimensional scaling (nMDS) plot comparing the morphological traits of *Apristurus manocheriani* n. sp., *A. aphyodes*, and *A. albisoma*.

groups, so the differences are due to differences in their centroids rather than from differences in variances of the measurements ( $df=2$ ,  $F$ -statistic=1.4184,  $p=0.271$ ). SIMPER analysis revealed the measurements most responsible for differences between *A. manocheriani* compared to *A. albisoma*, in order of importance, is pectoral–pelvic-fin origins length, head width at maximum length, head width at mouth corners, interorbital length, and interdorsal fin space. SIMPER analysis of *A. manocheriani* compared to *A. aphyodes* revealed, in order of importance, that pre-first dorsal-fin origin length, head height, pre-vent length, mouth length, and mouth width were the most significant values.

### Key to the Western Indian Ocean genus *Apristurus*

(modified from Ebert (2013) and Kawauchi et al. (2014))

- 1a. Snout very slender and elongate; length of pre-outer nostril much greater than interorbital width (Seychelles, Mozambique, and Western Pacific) (***longicephalus* subgroup**)..... *A. longicephalus*
- 1b. Snout relatively wide and short; length of pre-outer nostril length much shorter than interorbital width ..... 2
- 2a. Body relatively slender; upper labial furrows longer than lowers; supraorbital sensory canals discontinuous; spiral valve counts high (13–22) (***brunneus* subgroup**)..... 3
- 2b. Body relatively stout; upper labial furrows as long as or shorter than lower ones; supraorbital sensory canals continuous; spiral valve counts low (7–12) (***spongiceps* subgroup**)..... 6
- 3a. First dorsal-fin origin behind pelvic-fin insertion (Socotra Islands, Gulf of Aden) ..... *A. breviventralis*
- 3b. First dorsal-fin origin above pelvic-fin base ..... 4
- 4a. Pectoral–pelvic space about as long as anal-fin base (ceratotrichia) (Somalia, Gulf of Aden, Oman) ..... *A. indicus*
- 4b. Pectoral–pelvic space about as long as anal-fin base (ceratotrichia) ..... 5
- 5a. Interdorsal space very long, about equal to prespiracular head; 13–16 spiral valves (South Africa, SE Atlantic) ..... *A. saldanha*
- 5b. Interdorsal space shorter, much less than prespiracular head, 19–23 spiral valves (Madagascar Ridge, North and SE Atlantic, Eastern Indian Ocean, southwest Pacific Ocean) ..... *A. melanoasper*
- 6a. Body coloration uniformly dark brown, brownish gray, to purplish-black, no distinctive lighter or darker fin margins; enlarged crest of dermal denticles along upper caudal margin (South Africa, SE Atlantic, North Atlantic) ..... *A. microps*
- 6b. Body coloration uniformly whitish, with lighter anal and caudal posterior margins; no enlarged crest of dermal denticles along upper caudal margins (Madagascar Ridge) ..... *A. manocheriani* n. sp.

## Other material examined:

*Apristurus albisoma* (9 specimens): Holotype: MNHN 1997-3366, male, 573 mm TL, off New Caledonia, 25° 47' 77" S, 167° 11' 52" E to 25° 50' 65" S, 167° 12' 47" E, 1317–1383 m. Paratypes: (8 specimens) MNHN 1997-3359, male, 595 mm TL, MNHN 1997-3361, female, 566 mm TL, MNHN 1997-3365, male, 582 mm TL, all off New Caledonia, 25° 47' 77" S, 167° 11' 52" E to 25° 50' 65" S, 167° 12' 47" E, 1317–1383 m; MNHN 1997-3368, male, 540 mm TL, MNHN 1997-3370, male, 592 mm TL, off New Caledonia, 25° 34' 29" S, 167° 25' 08" E to 25° 34' 48" S, 167° 21' 74" E, 1132–1160 m; MNHN 1997-3360, female, 548 mm TL, off New Caledonia, 25° 41' 99" S, 167° 25' 60" E to 25° 42' 98" S, 167° 22' 43" E, 1230–1268 m; MNHN 1997-3383, male, 547 mm TL, off New Caledonia, 23° 56' 56" S, 161° 53' 14" E to 23° 58' 96" S, 161° 55' 15" E, 1034–1056 m; MNHN 1997-3358, male, 376 mm TL, off New Caledonia, 23° 40' 02" S, 168° 03' 15" E to 23° 40' 04" S, 168° 05' 33" E, 935–1100 m.

*Apristurus ampliceps* (4 specimens): Paratype: CSIRO H 1009-05, male, 821 mm TL, north-west of Sandy Cape, Tasmania, Australia, 41° 12'–16' S, 143° 56'–58' E, 1110–1190 m, 11 August 1987. Non-types: CSIRO H1009-04, adult male, northwest of Sandy Cape, Tasmania, 41° 16.05' S, 143° 58' E, 1110–1190 m, 11 August 1987; CSIRO H1009-06, adult female, northwest of Sandy Cape, Tasmania, 41° 16.05' S, 143° 58' E, 1110–1190 m, 11 August 1987; CSIRO H5220-01, adult female, South Tasman Rise, Tasman Sea, 47° 09' S, 148° 43' E, 1100 m, 16 February 1999.

*Apristurus aphyodes* (7 specimens): Holotype: ZMH 24878 [ex ISH 71-1981], adult male, 521 mm TL, Lousy Bank, Eastern North Atlantic, 58° 42.8' N, 13° 37.6' W, 1200–1240 m. Paratypes (6 specimens): ZMH 24877 [ex ISH 49-1981], female, 494 mm TL, Lousy Bank, Eastern North Atlantic, 60° 20.5' N, 14° 44' W, 1800 m; ZMH 24870 [ex ISH 124-1981], male, 478 mm TL, northern Bay of Biscay, Eastern North Atlantic, 49° 37.7' N, 12° 35.1' W, 1740–1750 m; ZMH 24872 [ex ISH 17-1974], adult female, 532 mm TL, Lousy Bank, Eastern North Atlantic, 60° 42' N, 12° 57' W, 1014–1024 m; ZMH 24874 [ex ISH 187-1983], female, 408 mm TL, Porcupine Seabight, Eastern North Atlantic, 49° 31.9' N, 12° 34.6' W, 1487–1491 m; ZMH 24880 [ex ISH 807-1974], male, 315 mm TL, Porcupine Seabight, Eastern North Atlantic, 51° 30' N, 12° 48' W, 1500–1525 m; ZMH 24875 [ex ISH 24-1981], juvenile female, 209 mm TL, Bill Bailey Bank, Eastern North Atlantic, 59° 56.8' N, 10° 03.8' W, 1138–1140 m.

*Apristurus fedorovi* (2 specimens): H3994-01 female, east of Iwate Prefecture, Japan, 40° 04.5' N, 142° 43.5' E, 1095–1100 m, 25 September 1978; H3995-01 adult male, east of Aomori Prefecture, Japan, 40° 47.6' N, 142° 16.7' E, 920–948 m, 11 September 1978.

*Apristurus kampae* (14 specimens): Holotype: SIO70-248, female 340 mm TL, Gulf of California, Mexico, 27° 22.4' N, 111° 20.5' W to 27° 10.1' N, 111° 29.6' W, 1830–1888 m, 14 June 1970. Non-types (13 specimens): SIO70-299, juvenile male, 189 mm TL, Galapagos Islands, Isla San Salvador 0° 7.5' S, 90° 54.0' W, 490 m, 25 October 1970; SIO88-98, adult male, 562 mm TL, S of Morro Bay, 1 35° 12.9' N–121° 40.4' W, 109–1106 m, 29 March 1988; SIO92-133, adult female, 540 mm TL, 35° 26.8' N–121° 40.8' W, 1092 m, 31 March 1988; SIO85-70, adult male, 560 mm TL, Monterey Co., Point Sur, 36° 22.1' N–122° 13.4' W, 988–1006 m, 13 March 1985; CAS 58482, adult female, 543 mm TL, 1381–1408 m, 36° 115' 18" N, 122° 122' 54" W, 8 December 1985; CAS 58771, adult female, 559 mm TL, 1008–1171 m, 35° 144' 36" N, 122° 103' 48" W, 7 December 1985; UW 045629, adult female, 37° 115' 1.5" N, 123° 108' 25.89" W, 31 October 1997; UW 045634, adult female, 528 mm TL, 1253 m, 37° 113' 22.3" N, 123° 110' 30.3" W, 24 September 1997; UW045634, adult female, 550 mm TL, 1253 m, 37° 113' 22.3" N, 123° 110' 30.3" W, 24 September 1997; UW046041, adult female, 539 mm TL, 1132 m, 34° 131' 31.4" N, 121° 114' 54.9" W, 7 November 2001; MLML uncatalogued (AK015) adult female, 555 mm TL, 1005–1010 m, 34° 141' 52" N, 121° 129' 59" W, 26 July 2002; MLML uncatalogued (AK016) adult female, 589 mm TL, 1110–1155 m, 36° 114' 53" N, 122° 117' 13" W, 15 September 2002; MLML uncatalogued (AK018) adult female, 548 mm TL, 1044–1054 m, 37° 115' 13" N, 123° 107' 32" W, 14 September 2002.

*Apristurus microps* (5 specimens): ZMH105158, female 356 mm TL Southwestern Coast of South Africa; SAIAB 26318, 465 mm TL, R/V *Africana* cruise 046, West Coast Demersal Survey, bottom trawl, station A4361 046 E12, 31° 59.8' S, 15° 56.2' E, 850 m, 17 July 1986; SAIAB 26319, 504 mm TL, R/V *Africana* cruise 046, West Coast Demersal Survey, bottom trawl, station A4361 046 E12, 31° 59.8' S, 15° 56.2' E, 850 m, 17 July

1986; SAIAB 26320, 511 mm TL, R/V *Africana* cruise 046, West Coast Demersal Survey, bottom trawl, station A4361 046 E12, 31° 59.8' S, 15° 56.2' E, 850 m, 17 July 1986; SAIAB 27439, 545 mm TL, R/V *Africana* cruise 054, West Coast Demersal Survey, bottom trawl, station A5867 054 E01, 35° 44.4' S, 19° 12.2' E, 763 m, 20 June 1987.

*Apristurus pinguis* (1 specimen): H3101-03 male adult, southwest of Cape Leeuwin, Western Australia, 35° 00' S, 114° 29' E, 1100-1120 m, 27 May 1992.

*Apristurus riveri* (1 specimen): USNM 201760, adult female, 09° 20' N, 81° 24' W, 860–915 m, 25 May 1962.

*Apristurus spongiceps* (1 specimen): Holotype: USNM 51590, adult female, 514 mm TL, 572–1462 m, off Bird Island near Laysan Atoll in the NW Hawaiian Islands, 5 August 1902.

## Acknowledgements

The following individuals are sincerely thanked for their assistance and support: Dave Catania and Jon Fong (California Academy Sciences), Angus Paterson, Paul Cowley, Roger Bills, Nkosinathi Mazungula, Mzwandile Dwani, Vuyani Hanisi, and the fish collection staff (SAIAB), Ben Frable (Scripps Institution of Oceanography), Ralf Thiel, Victoria Sarrazin, Irina Eidus, Björn Kullmann (Center of Natural History Universität Hamburg-Zoologisches Museum, Department of Ichthyology), Zouhaira Gabsi and Jonathan Pfliger (Muséum national d'Histoire naturelle Ichthyology collection), Gavin Naylor (University of Florida, Shark Research Program), Will White (CSIRO), Rachel Aitchison, Amber Reichert, Stephanie Schneider, Vivian Ton, Felicia Miller, and Paul Clerkin (Pacific Shark Research Center, Moss Landing Marine Laboratories) for facilities, logistical, photo- and radiography support. We are grateful to Ross Shotton, Southern Indian Ocean Deepsea Fishers Association, Sealord Corporation of New Zealand, the captains, officers, and crew of the F/V *Will Watch*, Daroomalingum Mauree, Director of Fisheries (retired), Republic of Mauritius, and Boodhun Ramcharrun, Scientific Officer, Mauritius Ministry of Fisheries for their kind facilitation of our work at the Albion Fisheries Research Centre. The manuscript was reviewed by two anonymous reviewers. Funding support for the Pacific Shark Research Center's Lost Sharks project was graciously provided by Andy Sabin, a National Science Foundation grant (DEB 1132229) to G. Naylor, the Discovery Channel, Save Our Seas Foundation, and the Food and Agriculture Organization (United Nations).

## References

- Clarke, K.R. & Gorley, R.N. (2006) *PRIMER v6: user manual/tutorial, Primer E: Plymouth*. Plymouth Marine Laboratory, Plymouth, UK, 192 pp.
- Ebert, D.A. (2013) *Deep-sea Cartilaginous Fishes of the Indian Ocean. Volume 1. Sharks*. FAO Species Catalogue for Fishery Purposes. No. 8, Vol. 1. FAO, Rome, Italy, 256 pp.
- Ebert, D.A. & Dando, M. (2020) *Field Guide to Sharks, Rays, & Chimaeras of Europe and the Mediterranean*. Princeton University Press, Princeton, New Jersey, USA, 383 pp.
- Ebert, D.A., Dando, M. & Fowler, S. (2021a) *Sharks of the World: A complete guide*. Princeton University Press. Princeton, New Jersey, USA, 607 pp.
- Ebert, D.A., Wintner, S.P. & Kyne, P.M. (2021b) An annotated checklist of the chondrichthyans of South Africa. *Zootaxa*, 4947 (1), 1–127. <https://doi.org/10.11646/zootaxa.4947.1.1>
- Ebert, D.A. & Winton, M.V. (2010) Chondrichthyans of high latitude seas. In: Carrier, J.C., Musick, J.A. & Heithaus, M.R. (Eds.), *The Biology of Sharks and their Relatives, Vol. 2*, CRC Press, Boca Raton, Florida, USA, pp. 115–158.
- Flammang, B.E., Ebert, D.A. & Cailliet, G.M. (2007) Egg cases of the genus *Apristurus* (Chondrichthyes: Scyliorhinidae): phylogenetic and ecological implications. *Zoology*, 110, 308–317. <https://doi.org/10.1016/j.zool.2007.03.001>
- Gotelli, N.J. & Ellison, A.M. (2013) *A Primer of Ecological Statistics*. Sinauer Associates, Sunderland, Massachusetts, USA, 614 pp.

- Iglésias, S.P., Lecointre, G. & Sellos, D.Y. (2005) Extensive paraphyly within sharks of the order Carcharhiniformes inferred from nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution*, 34, 569–583. <https://doi.org/10.1016/j.ympev.2004.10.022>
- Kawauchi, J., Weigmann, S. & Nakaya, K. (2014) *Apristurus breviventralis*, a new species of deep-water catshark (Chondrichthyes: Carcharhiniformes: Scyliorhinidae) from the Gulf of Aden. *Zootaxa*, 3881 (1), 1–16. <https://doi.org/10.11646/zootaxa.3881.1.1>
- Nakaya, K. & Sato, K. (1999) Species grouping within the genus *Apristurus* (Elasmobranch, Scyliorhinidae). In: Séret, B. & Sire, J.-Y. (Eds.), *Proceedings of the 5th Indo-Pacific Fish Conference, Nouméa, 3–8 November 1997*. Société Française d’Ichtyologie & Institut de Recherche pour le Développement, Paris, France, pp. 307–320.
- Nakaya, K., Sato, K., Iglésias, S.P. & White, W.T. (2008) Methodology for the taxonomic description of members of the genus *Apristurus* (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). In: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Australian Chondrichthyans*. CSIRO Marine & Atmospheric Research Paper, No. 022, pp. 49–60.
- Nakaya, K. & Séret, B. (1999) A new species of deepwater catshark, *Apristurus albisoma* n. sp. from New Caledonia (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). *Cybium*, 23, 297–310.
- Nakaya, K. & Stehmann, M. (1998) A new species of deep-water catshark, *Apristurus aphyodes* n. sp., from the Eastern North Atlantic (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). *Archives of Fishery and Marine Research*, 46, 77–90.
- Nakaya, K., Sato, K., Kawauchi, J. & Stewart, A.L. (2015) Family Scyliorhinidae, Catsharks. In: Roberts, C.D., Stewart, A.L. & Struthers, C.D. (Eds.), *The Fishes of New Zealand, Systematic Accounts, vol. 2*, Te Papa Press, Wellington, NZ, pp. 75–89.
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O’Hara, R. B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E. & Wagner, H. (2020) Vegan: Community Ecology Package. Version 2.5-7 (28 November 2020). Ordination methods, diversity analysis and other functions for community and vegetation ecologist. Available at <https://github.com/vegandevs/vegan> [accessed 12 March 2021]
- Sabaj, M.H. (Ed.) (2019) *Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 7.1* (21 March 2019). American Society of Ichthyologists and Herpetologists, Washington, DC. Available at <http://www.asih.org/> [accessed 19 January 2021]
- Sato K. (2000) *Phylogenetic systematics of the deep-water catsharks genus Apristurus (Chondrichthyes, Carcharhiniformes, Scyliorhinidae)*. Unpublished PhD thesis, Faculty of Fisheries, Hokkaido University, Sapporo, Japan, 132 pp.
- Weigmann, S. (2016) Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. *Journal of Fish Biology*, 88(3), 837–1037. <https://doi.org/10.1111/jfb.12874>
- White, W.T., Ebert, D.A., Naylor, G.J.P., Ho, H.-C., Clerkin, P.J., Verissimo, A. & Cotton, C.F. (2013) Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 1- redescription of *Centrophorus granulosus* (Bloch & Schneider), a senior synonymy of *C. acus* Garman and *C. niaukang*. *Zootaxa*, 3752, 35–72. <https://doi.org/10.11646/zootaxa.3752.1>
- White, W.T., Mana, R.R. & Naylor, G.J.P. (2017) Description of a new species of deepwater catshark *Apristurus yangi* n. sp. (Carcharhiniformes: Pentanchidae) from Papua New Guinea. *Zootaxa*, 4320 (1), 25–40. <https://doi.org/10.11646/zootaxa.4320.1.2>