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A new species of deep-sea catshark (Scyliorhinidae: *Bythaelurus*) from the southwestern Indian Ocean

DAVID A. EBERT
Pacific Shark Research Center, Moss Landing Marine Laboratories, Moss Landing, CA 95039, USA. E-mail: debert@mlml.calstate.edu
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

PAUL J. CLERKIN
Pacific Shark Research Center, Moss Landing Marine Laboratories, Moss Landing, CA 95039, USA. E-mail: pclerkin@mlml.calstate.edu

Abstract

Bythaelurus naylori sp. n. is described based on 41 specimens collected from seamounts in the southwestern Indian Ocean. The new species can be separated from all other *Bythaelurus* species by a combination of distinctly enlarged dermal denticles on the upper caudal-fin margin, lack of papillae on the roof of the mouth and tongue, an anal-fin base length equal to or less than 1.5 times second dorsal-fin base length, and a uniformly plain medium to dark brown body coloration, with light fin edges and a distinct dark dusky-colored snout. No other *Bythaelurus* species has the combination of a caudal crest of prominent, distinctly enlarged, comb-like dermal denticles along the upper caudal margin and lacks oral papillae. *Bythaelurus naylori* sp. n. can be distinguished from its two closest congeners, *B. giddingsi* and *B. lutarius*, by a combination of prominent comb-like dermal denticles along the upper caudal-fin margin, absence of oral papillae, uniform body coloration, and noticeable dark dusky snout; *Bythaelurus giddingsi* has oral papillae present and a variegated color pattern, while *B. lutarius* lacks a caudal crest of enlarged denticles and matures at a much smaller size than the new species.

Key words: taxonomy, systematics, elasmobranch, sharks, *Bythaelurus naylori*, seamounts, deep-water, Southwest Indian Ridge

Introduction

The genus *Bythaelurus* Compagno 1988 (Scyliorhinidae) was first described as a subgenus of *Halaelurus* Gill 1862 based on several morphological characteristics including a soft body with thin skin, a bluntly rounded snout without a pointed, knob-like tip, and eyes not noticeably elevated on dorsal surface of head. In addition, members of this genus are generally found in deep water and have more somber body coloration. This is in contrast to *Halaelurus* species that have a firm body with thick skin, a pointed snout variably with a developed knob-like tip, and eyes noticeably elevated on dorsal surface of head. *Halaelurus* species also generally have an attractive, bold color pattern, and occupy a shallow to moderately deep-water habitat.

Compagno (1988) stated that these two subgeneric groups might eventually prove to merit full generic status, but given the unsettled relationships with other closely related genera (e.g. *Asymbolus*, *Galeus*, and *Parmaturus*), at the time he was reluctant to elevate it. The *Bythaelurus* remained a subgenus within the *Halaelurus* until 1999 when, in two separate publications, Compagno first retained it as a subgenus (Compagno 1999a), but then elevated it, without explanation, to full generic status (Compagno 1999b). Since then, the group has generally been given full generic status. Recent molecular studies have tended to support *Bythaelurus* at full generic rank (Naylor *et al*. 2012a). The subgenus when proposed by Compagno (1988) included six species, tentatively *B. alcockii* (Garman 1913), *B. canescens* (Günther 1878), *B. dawsoni* (Springer 1971), *B. hispidus* (Alcock 1891), *B. immaculatus* (Chu & Meng 1982), and *B. lutarius* (Springer & D'Aubrey 1972). Ebert *et al*. (2013) subsequently listed three additional species: *B. clevai* (Séret 1987), *B. giddingsi* McCosker, Long & Baldwin 2012, and *B. incanus* Last & Stevens 2008.

The distribution of the genus appears concentrated in the Indian Ocean where five species are known to occur; two species occur both in the western Pacific Ocean and southeastern Pacific Ocean (Ebert *et al*. 2013). Of the five Indian Ocean species, two (*B. alcockii* and *B. hispidus*) occur in the northern Indian Ocean and two (*B. clevai* and *B. lutarius*) in the southwestern Indian Ocean, with a fifth species (*B. incanus*) known from the eastern central Indian Ocean (Ebert 2013). The two species known to occur in the southwestern Indian Ocean can be separated by coloration; *B. clevai* has a pattern of large blotches and small spots, while *B. lutarius* generally lacks patterns or spots except for a dark saddle marking at the base of each dorsal fin and the caudal fin.

During a series of surveys conducted along the Southwest Indian Ridge in the southwestern Indian Ocean, that one of us (PJC) participated in during 2012 and 2014, a *Bythaelurus* species was collected that appeared to be distinct from all other known species in this genus. Here we describe this new species. This paper is part of a series describing and revising chondrichthyan taxa from the southwestern Indian Ocean.

Materials and Methods

The holotype and nine paratypes were measured in full and are herein described. Morphometric measurements and terminology generally follow other recent new *Bythaelurus* species descriptions by McCosker *et al*. (2012) and Last & Stevens (2008). Meristics, including spiral valve and vertebral counts, were taken from the type series and from additional voucher specimens. Tissue samples were taken from 41 specimens, with samples from nine paratypes sent to the College of Charleston for sequencing at the mitochondrial DNA NADH dehydrogenase subunit 2 (NADH2) locus that has been shown to be useful for distinguishing elasmobranch species (Naylor *et al*. 2012b). The remaining non-type specimens in good condition were deposited as voucher specimens into museum collections, while damaged specimens were dissected for detailed biological examination and discarded.

Institutional abbreviations follow Sabaj Pérez (2014). Type specimens were deposited into fish collections at the California Academy of Sciences (CAS), South African Institute for Aquatic Biodiversity (SAIAB), Iziko-South African Museum (iSAM MB), and the United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Additional voucher specimens were deposited at the Natural History Museum, London (BMNH), the Museum of Comparative Zoology (MCZ), and the Scripps Institution of Oceanography (SIO).

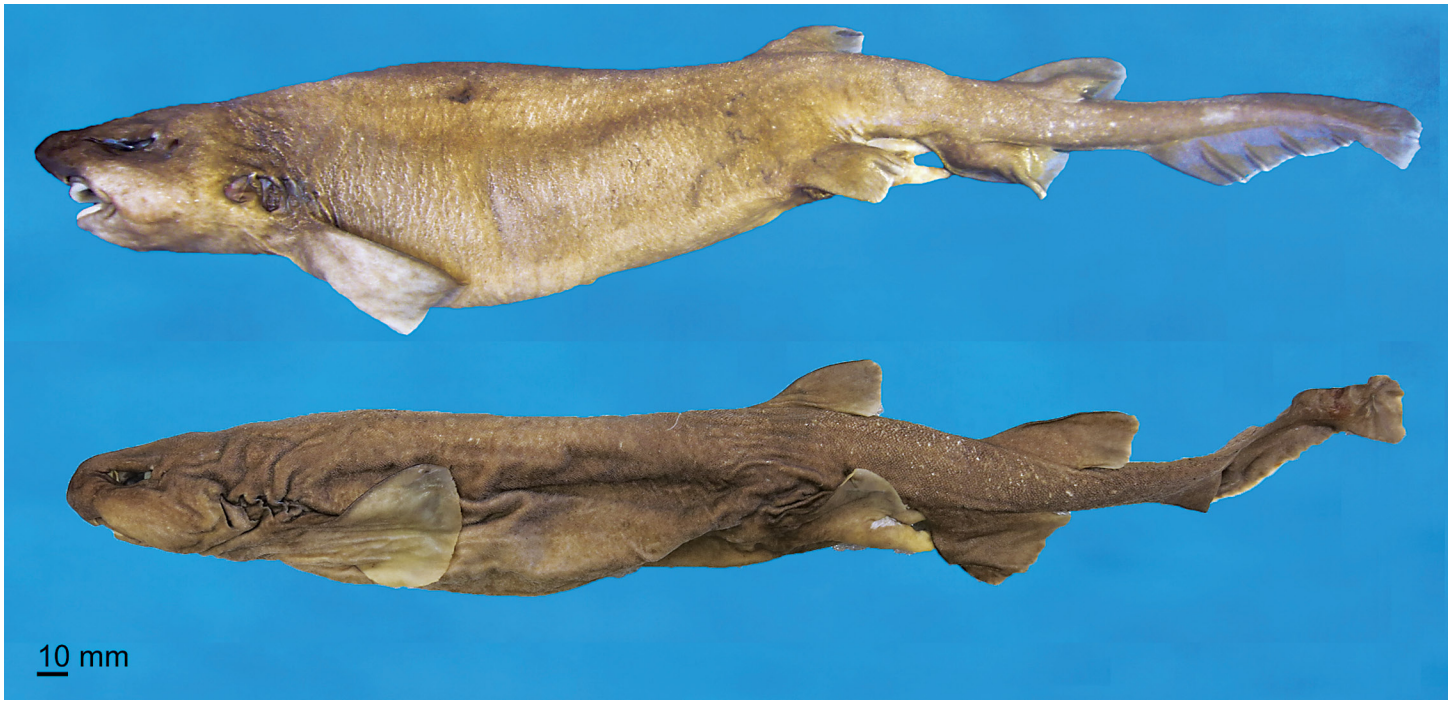

Figure 1. *Bythaelurus naylori* n. sp., holotype, adult male 452 mm TL (CAS 237869), unpreserved specimen (upper), and post-preservation (lower) lateral view.

Genus *Bythaelurus* Compagno 1988

genus *Halaelurus* Gill 1862
subgenus *Bythaelurus* Compagno 1988: 146

Type species. *Scyllium canescens* Günther 1878, by original designation.

Bythaelurus naylori, new species

Dusky Snout Catshark

Figures 1–5, Table 1.

Holotype. CAS 237869, 452 mm TL, mature male, Southwest Indian Ridge, 35° 10'S, 53° 40'E, bottom trawl between 800–1,300 m, P.J. Clerkin, 21 May 2014.

Paratypes. CAS 237870, 455 mm TL, mature male, Southwest Indian Ridge, 33° 55'S, 55° 16'E, midwater trawl between 1,008–1,190 m, P.J. Clerkin, 28 April 2014; CAS 237872, 506 mm TL, female, Southwest Indian Ridge, 34° 53'S, 54° 23'E, bottom trawl between 811–1,150 m, P.J. Clerkin, 28 April 2014; CAS 237873, 505 mm TL, female, Southwest Indian Ridge, 36° 49'S, 52° 05'E, bottom trawl between 1,438–1,443 m, P.J. Clerkin, 21 May 2014; CAS 237941, 511 mm TL, mature male, Southwest Indian Ridge, 35° 08'S, 53° 42'E, bottom trawl between 861–1,160 m, R. Downie, 11 March 2014; CAS 237942, 548 mm TL, female, Southwest Indian Ridge, 39° 00'S, 46° 30'E, 30'E, bottom trawl between 800–1,200 m, P.J. Clerkin, 17 March 2012; CAS 237943, 450 mm TL, female, Southwest Indian Ridge, 39° 00'S, 46° 30'E, 30'E, bottom trawl between 800–1,200 m, P.J. Clerkin, 17 March 2012; CAS 237944, 491 mm TL, mature male, Southwest Indian Ridge, 35° 10'S, 53° 40'E,

30’E, bottom trawl between 800–1,300 m, P.J. Clerkin, 8 April 2012; CAS 238013, 502 mm TL, mature male, Southwest Indian Ridge, 35° 10’S, 53° 40’E, 30’E, bottom trawl between 800–1,300 m, P.J. Clerkin, 8 April 2012; CAS 238070, 341 mm TL, immature male, Southwest Indian Ridge, 33° 55’S, 55° 16’E, 30’E, bottom trawl between 1,040–1,250 m, P.J. Clerkin, 29 April 2014; CAS 238071, female, Southwest Indian Ridge, 33° 55’S, 55° 16’E, 30’E, bottom trawl between 1,008–1,185 m, P.J. Clerkin, 29 April 2014; SAIAB 200728, 482 mm TL, mature male, Southwest Indian Ridge, 35° 08’S, 53° 42’E, bottom trawl between 861–1,160 m, R. Downie, 11 March 2014; SAIAB 200729, 464 mm TL, female, Southwest Indian Ridge, 33° 55’S, 55° 16’E, midwater trawl between 1008–1,190 m, P.J. Clerkin, 28 April 2014; iSAM MB-F041239, 453 mm TL, female, Southwest Indian Ridge, 35° 08’S, 53° 42’E, bottom trawl between 89–1,240 m, P.J. Clerkin, 30 April 2014; USNM 432400, 465 mm TL, mature male, Southwest Indian Ridge, 35° 08’S, 53° 42’E, bottom trawl between 752–780 m, P.J. Clerkin, 23 April 2014; USNM 432401, 466 mm TL, female, Southwest Indian Ridge, 35° 08’S, 53° 42’E, bottom trawl between 861–1,160 m, R. Downie, 11 March 2014.

Diagnosis. A moderate-sized *Bythaelurus* species with the following combination of characteristics: snout short, bluntly rounded; preoral length 4.2–5.5% TL; oral cavity without papillae on the roof of the mouth and tongue; anal-fin base length equal to or less than 1.5 times second dorsal-fin base length; distinctly enlarged dermal denticles on the upper caudal-fin margin; uniformly plain medium to dark brown body coloration, with light fin edges and a distinct dark dusky-colored snout.

Description. Proportional measurements expressed as a percentage of total length (TL) are given for the holotype and the range for the nine paratypes in Table 1.

Body stout, flabby, slightly depressed anteriorly, quickly tapering posteriorly from about first dorsal fin and vent towards caudal-fin origin (Fig. 1). Head short and broad (Fig. 2), length 13.6–18.7% TL, width 11.9–14.0% TL; moderately depressed, narrowly rounded in lateral view, height 5.6–8.6% TL. Snout short, pre-narial length 2.2–2.9% TL; bluntly rounded in dorsal view, without pointed knob-like tip. Eyes dorsolateral on head, slit-like, not elevated, at about lateral midline; interorbital width 2.6–3.9 times snout length, 1.6–2.4 in head length; suborbital groove well developed. Spiracles minute, suboval, length about equal to distance behind eyes, and set behind and just below posterior eye notch. Gill openings slightly curved rearwards, filaments not visible externally; first three openings slightly larger than fourth (1.8–3.0% TL vs. 1.6–2.2%TL), and much larger than fifth opening (1.8–3.0% TL vs. 0.9–1.9% TL).

Nostrils with angular anterior nasal flaps, narrowly rounded at tips, partially overlapping posterior margin, but not reaching mouth; nostrils above level with mouth. Mouth broadly rounded, length 2.1–3.0 times in width; lower symphysis not reaching upper symphysis; roof of mouth and tongue lack papillae. Labial furrows present along upper and lower jaws, moderately long, ending well behind level of upper mouth symphysis; uppers 1.4–2.4 times lower labials. Teeth similar in upper and lower jaws, with a single, strong erect cusp, flanked laterally on each side by a single cusplet; tooth row counts number more than 70 on each jaw.

Pectoral fins large, broadly rounded, anterior margin convex, apices narrowly rounded, posterior margin and free rear tips broadly rounded, and inner margin slightly convex; origin about below fourth gill openings. Pelvic fins broadly triangular; pelvic anterior margins 1.3–2.0 in pectoral fin anterior margins; area subequal to anal fin area. Adult claspers stout (Fig. 3), extending beyond origin of pelvic fins, tapering distally to slender point; denticles covering dorsal surface, mostly absence from ventral surface; juvenile claspers not developed, slightly depressed, not reaching pelvic inner margin free rear tips.

Dermal denticles (Fig. 4) along flanks, below dorsal-fin bases, erect, posteriorly convex, tapering abruptly to a single cusp, flanked with a smaller cusplet on each side; denticles closely spaced, but not overlapping. Dorsal caudal upper margin with prominent caudal crest of distinctly enlarged, overlapping denticles originating from just posterior to second dorsal-fin base insertion, below inner fin margin, and extending more than halfway along margin; similar to those found in *B. giddingsi* and some *Parmaturus* species (McCosker *et al*. 2012); similar enlarged crest-like denticles also found between anal-fin base insertion and lower caudal fin insertion.

Dorsal fins subequal, first smaller than second. First dorsal fin high, narrowly rounded at apex, origin about over pelvic fin origin; anterior margin about equal to length; posterior margin relatively straight, length less than one-half anterior margin length; free rear tip narrowly rounded, inner margin straight. Second dorsal fin high, anterior margin nearly straight, narrow at apex, origin posterior to anal origin; posterior margin slightly convex,

Figure 2 (below). *Bythaelurus naylori* n. sp., dorsal (top), lateral (middle), and ventral (bottom) views of head.

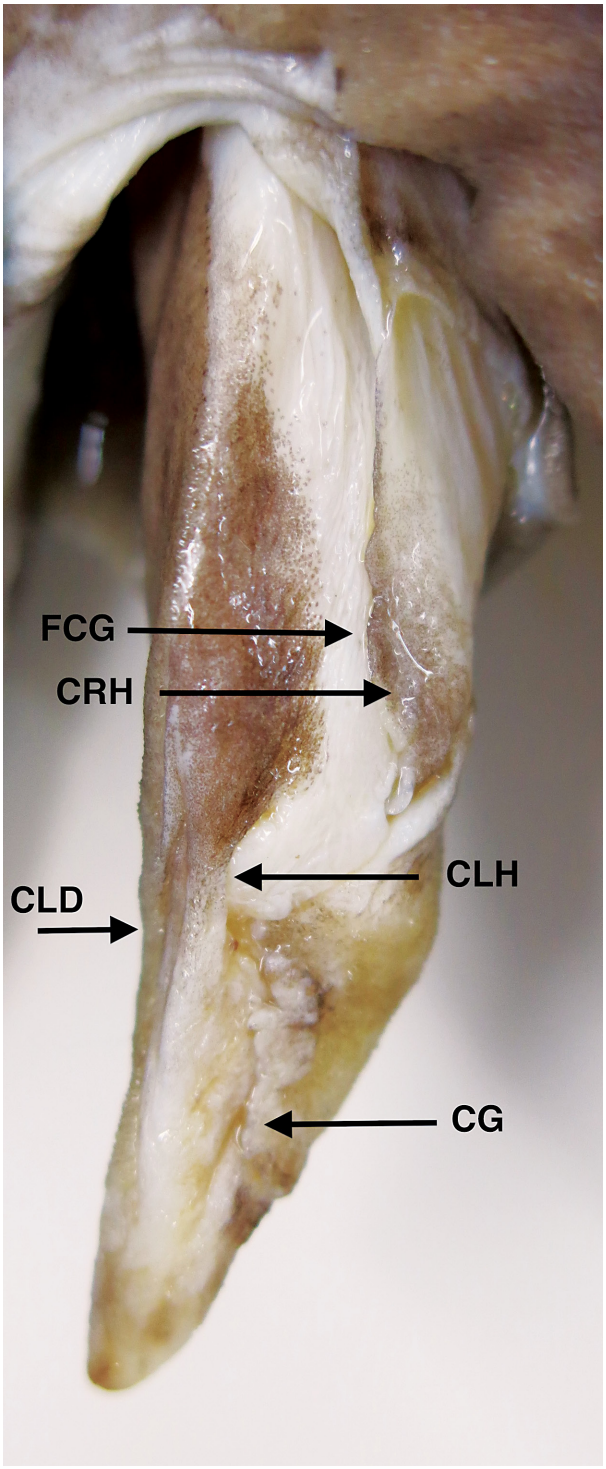

Figure 3 (above). *Bythaelurus naylori* n. sp., paratype, adult male, 465 mm TL (USNM 432400). Abbreviations: CG: clasper groove; CLD: clasper denticles; CLH: clasper hooks; CRH: cover rhipidon; FCG: fused clasper groove.

free rear tip rounded, inner margin straight. Anal fin broadly rounded, anterior margin convex, rounded at apex, posterior margin slightly convex; inner margin short, mostly straight; base length 1.5 times or less second dorsal-fin base length. Caudal fin elongate, upper margin about one-quarter body length, ventral lobe not well developed; terminal lobe well developed, terminal margin broad, weakly convex.

Total vertebral counts 122 (114–128), monospondylous precaudal (MP) vertebrae 39 (36–41), precaudal

TABLE 1

Morphometric data for the holotype and ranges for nine paratypes of *Bythaelurus naylori* n. sp. (as percent of the total length)

	holotype	9 paratypes	
	CAS 237869	min	max
Total length (mm)	**452**	**453**	**511**
Pre–caudal length	74.3	72.5	75.9
Pre–narial length	2.4	2.2	2.9
Pre–oral length	5.1	4.2	5.5
Pre–orbital length (horizontal)	6.2	4.7	5.7
Pre–orbital length (direct)	7.3	5.8	8.1
Pre–spiracle length	12.8	10.3	13
Pre–gill length (horizontal)	15.5	12.8	15.4
Pre–gill length (direct)	16.2	14.2	17.2
Head length	15.5	13.6	18.7
Pre–pectoral fin length (direct)	18.1	15.3	21.5
Pre–pelvic fin length	49.8	47	51.6
Snout–vent length	53.1	49.9	54.7
Pre–anal fin length	61.5	58.6	63
Pre–first dorsal fin length	48.7	46.6	49.5
Pre–second dorsal fin length	65.3	63.8	67.2
Interdorsal fin length	10.6	9	11.5
Dorsal–caudal length	1.3	1	2
Pectoral–pelvic length	27.2	23.5	31.3
Pelvic–anal space	5.5	4.8	9.4
Anal–caudal space	6.6	6	8.6
Eye length	4	3.9	4.7
Eye height	1.1	0.8	1.3
Interorbital length	7.7	6.9	8.8
Nostril width	2.4	2.4	3.4
Internarial length	2.7	2.1	2.8
Anterior nasal flap length	1.3	1	1.8
Spiracle length	0.9	0.7	1.5
Eye–spiracle length	1.1	0.7	1.2
Mouth length	4.6	2.5	4
Mouth width	8.8	7.2	9.2
Upper labial furrow	1.5	1	1.7
Lower labial furrow	2.4	1.5	2.8
First gill height	2.4	1.8	3
Second gill height	2.4	1.8	2.9
Third gill height	2	1.9	2.9
Fourth gill height	2	1.6	2.2
Fifth gill height	1.3	0.9	1.9
Head height	8.2	5.6	8.6

TABLE 1 continued

Head width	12.6	11.9	14
Trunk height	10.2	6.1	13.8
Trunk width	10	11.9	15.6
Caudal peduncle height	3.5	3.4	3.7
Caudal peduncle width	2	2	2.3
Pectoral fin length	11.5	9.1	11.2
Pectoral fin anterior margin length	11.7	8.5	11.4
Pectoral fin base length	5.1	4	6.1
Pectoral fin height	8.8	7.7	10.3
Pectoral fin inner margin length	6.4	4.5	6.7
Pectoral fin posterior margin length	8.6	7.1	10.1
Pelvic fin length	9.7	9.8	12.1
Pelvic fin anterior margin length	5.8	6.3	8.2
Pelvic fin base length	5.8	6	8.4
Pelvic fin height	4.4	3.7	5.3
Pelvic fin inner margin length	2.7	1	4.1
Pelvic fin posterior margin length	6.6	5.6	8.2
First dorsal fin length	10	9.9	11.1
First dorsal fin anterior margin length	10.4	9.8	11.4
First dorsal fin base length	7.1	6.4	8.9
First dorsal fin height	4.2	3.3	6.3
First dorsal fin inner margin length	3.1	2.2	3.2
First dorsal fin posterior margin length	4.4	2.9	5.1
Second dorsal fin length	11.7	9.8	13
Second dorsal fin anterior margin length	12.2	9.1	12.5
Second dorsal fin base length	7.5	6.8	8.6
Second dorsal fin height	4.9	4	5.7
Second dorsal fin inner margin length	2.9	2.2	3.7
Second dorsal fin posterior margin length	4.6	4.4	5.4
Anal fin length	11.9	11.2	12
Anal fin anterior margin length	8.4	7.3	9.3
Anal fin base length	10.4	9.1	10.8
Anal fin height	6.2	4	6.7
Anal fin inner margin length	2	1.6	2.4
Anal fin posterior margin length	8.6	6.5	7.8
Caudal fin dorsal margin	25.2	24.3	26.5
Caudal fin preventral margin	6.6	6.1	7.3
Caudal fin upper postventral margin	14.2	11.6	14.9
Caudal fin subterminal margin	4.4	3.8	4.5
Caudal fin terminal margin	5.1	3.1	6.2
Second dorsal origin – anal fin origin	3.8	3.3	5.9
Second dorsal insertion – anal fin insertion	1.3	0.9	1.8

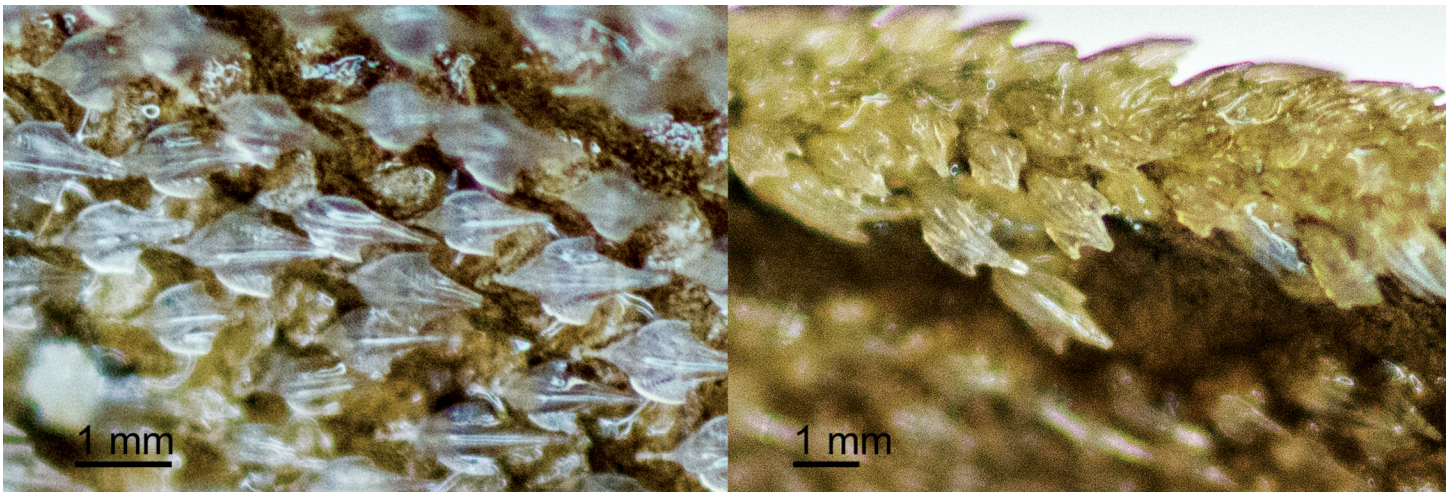

Figure 4. *Bythaelurus naylori* n. sp., close-up of denticles on flank (left) and upper caudal ridge (right).

vertebrae 69 (64–78). Transition between monospondylous and diplosondylous centra (DP) behind pelvic fin girdle and over clasper shafts. Last few centra before MP–DP transition not greatly enlarged, not forming a "stutter zone" of alternating long and short centra. Spiral valve turn counts for six non-type specimens 7–8.

Egg cases. (Fig. 5) The reproductive mode was determined to be oviparous based on egg cases found in two adult non-type females that were dissected. Each female had a single fully developed egg case per uterus. The egg cases are small, 68–70 mm long, excluding horns, relatively broad, and thick, anterior case width about 30.9–32.9% of case length and greatest case height about 15.7–20.6% of case length and 38.6–39.7% of posterior case width. Egg case surface with very fine striations, relatively smooth to the touch. Lateral flanges of case narrow, about 1 mm wide, flat, and without T-shaped lateral surface, extending length of the egg case. The anterior border of case is narrow and concave, with horns narrow, very short, and curved inwards, overlapping slightly, and without any evidence of tendrils being present. The posterior border of case is slightly concave, broad, and with horns not apparent, unless egg cases not quite fully developed in the present examples. The egg cases removed from the preserved females were light brown with a greenish tinge.

Coloration. (Figs. 1 & 2) Body uniform medium to dark brown, occasionally very dark brown almost blackish on dorsal and lateral surfaces, but fading to a light brownish ventrally; no saddle markings or other color patterns except for light edges to pectoral, pelvic, anal, and dorsal fins; caudal fin with lighter color at terminal margin. Dorsal, pectoral, pelvic, and anal fins similar in color although may be slightly darker to grayish on fin surfaces. The most prominent color feature on this shark is the dusky to blackish dorsal and ventral surfaces of the snout;

Figure 5. *Bythaelurus naylori* n. sp., egg case removed from a non-type female 452 mm TL.

dorsal and lateral dusky coloration extends to about anterior orbits, and ventrally to about narials and upper mouth symphysis. After preservation in ethanol coloration is similar, although general body coloration may lighten, with dusky snout and lighter fin edges appearing more prominent.

Size. *Bythaelurus naylori* is a moderately large *Bythaelurus* species reaching a maximum total length of at least 54.8 cm for females and 51.1 cm for males. Females are mature at 48.1 cm TL and immature at 43.0 cm TL, while males are mature at 45.2 cm and immature at 38.0 cm TL. The only *Bythaelurus* species that exceed it in total length are *B. immaculatus* at 76 cm TL and *B. canescens* at 70 cm TL (Ebert *et al*. 2013). Based on the only known specimen, an immature male of 45.4 cm TL (Last & Stevens 2008), *B. incanus* is likely a relatively larger species attaining a size greater since similar sized male *B. naylori* are fully mature.

Distribution. The new species at present is known only from the Southwest Indian Ridge, southwestern Indian Ocean in an area approximately from 33° 55'S, 52° 05'E to 36° 49'S, 55° 16'E. The specimens were collected from 89–1,443 m depth in both bottom trawls and midwater trawls. The shallowest catch record of the new species, possibly at 89 m, came from a midwater trawl.

Etymology. The new species is named in recognition of our colleague Gavin Naylor, College of Charleston, for his contributions and innovative molecular research into the higher classification of chondrichthyans and for his support of this project. The proposed common name Dusky Snout Catshark is in reference to the prominent dusky to dark coloration on the snout of this catshark.

Comparisons. The new species can be separated from all other *Bythaelurus* species by a combination of a crest of prominent, distinctly enlarged, comb-like dermal denticles along the upper caudal margin, the lack of papillae on the roof of the mouth and tongue, body coloration, and oviparous reproductive mode. The only other *Bythaelurus* species with a prominent clump of comb-like dermal denticles that forms a caudal crest is *B. giddingsi* (McCosker *et al*. 2012). However, *B. giddingsi* differs from *B. naylori* by the presence of oral papillae and by its variegated color pattern. Geographically, the new species is only known from seamounts in the southwestern Indian Ocean while *B. giddingsi* is known only from the Galápagos Islands (McCosker *et al*. 2012).

The two closest geographic congeners, *B. clevai* and *B. lutarius*, both lack a prominent ridge of dermal denticles on the upper margin of the dorsal fin. Furthermore, the anal-fin base length of *B. clevai* and *B. lutarius* is more than 1.5 times the second dorsal-fin base length while in the new species it is 1.5 times or less (Springer & D'Aubrey 1972, Séret 1987). The number of MP vertebrae is not very informative when comparing *B. naylori* (36 – 41) to *B. clevai* (39–43) and *B. lutarius* (38–42), but the approximate number of total vertebrae is much lower (114–128) relative to *B. clevai* (127–142) and *B. lutarius* (129–142) (Springer & D'Aubrey 1972, Séret 1987). The spiral valve turn count was lower in *B. naylori* (7–8) compared to *B. lutarius* (10) (Springer & D'Aubrey 1972). The body color patterns are also diagnostic since *B. clevai* has a variegated pattern of large blotches and small spots, while *B. lutarius* has saddle markings at the base of each dorsal fin and the caudal fin; neither species has the prominent dusky to dark colored snout found in *B. naylori*. In addition, *B. naylori* has a maximum total length of 51 cm while *B. lutarius* and *B. clevai* both have a maximum length of 39 cm (Séret 1987, Ebert *et al*. 2013). The new species can also be distinguished from its geographically closest congeners by its reproductive mode; *B. naylori* is oviparous while *B. clevai* and *B. lutarius* is viviparous. Francis (2006) reviewed the reproductive modes of *Bythaelurus* species and commented that some species, e.g. *B. canescens* and *B. dawsoni*, were oviparous, while others in the genus were viviparous species. Geographically, *B. clevai* is only known from Madagascar and *B. lutarius* from Mozambique and Somalia, while *B. naylori* is presently known only from seamounts along the Southwest Indian Ridge (Ebert *et al*. 2013).

Remarks. The relationship between the genus *Bythaelurus* and other closely related genera, particularly *Apristurus*, *Galeus* and *Parmaturus* remains unresolved (Naylor *et al*. 2012a & b). The presence (in some *Galeus* and *Parmaturus*) or absence (in some *Galeus* and *Bythaelurus*) of a crest of enlarged denticles along the upper caudal margin has been one of the primary characteristics used to separate these genera (Séret & Last 2007). However, the placement of *B. giddingsi* and *B. naylori*, both *Bythaelurus* species with enlarged denticles along the upper caudal margin, raises questions on the separation of these genera. Further compounding the issue is some recently described Indo-Pacific *Parmaturus* species are known to lack enlarged denticles along the upper caudal margin (Séret & Last 2007). In addition, some *Apristurus* species have an enlarged crest of denticles along the upper caudal margin. In fact, the *Parmaturus* subgenus *Compagnoia* was proposed by Springer (1979) for

two new species, *P. manis* and *P. stenseni*, based on the presence of a crest of enlarged denticles along the upper caudal margin; both species were later transferred to the genus *Apristurus* (Compagno 1988). Therefore, since the presence or absence of an enlarged crest of dermal denticles along the upper caudal margin appears to be variable at best within these genera, the morphological separation of these genera requires further investigation.

Molecular evidence by comparison supports the separation of *Bythaelurus* from *Parmaturus* at the generic level based on recent studies by Naylor *et al*. (2012a & b). Furthermore, molecular data from the new species, *B. naylori*, indicates that it nests within the genus *Bythaelurus*, between *B. canescens* and *B. dawsoni* (G. Naylor, College of Charleston, pers. comm.).

Although beyond the scope of this study, the relationship and separation of many catshark genera remains somewhat enigmatic. This is due to a number of issues, but not in the least that many of these species are very poorly described and/or are known from fewer than five specimens, and, in some instances, from only a single specimen. The collection of additional specimens across all genera, improved morphological descriptions, and inclusion of molecular data at the generic and species levels will be required to clarify and resolve these relationships.

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