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Etmopterus benchleyi n. sp., a new lanternshark (Squaliformes: Etmopteridae) from the central eastern Pacific Ocean

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Abstract

A new species of lanternshark, *Etmopterus benchleyi* n. sp., is described from eight specimens collected off the Pacific coast of Central America at depths ranging between 836 and 1443 meters. The new species is placed in the *Etmopterus spinax* clade by a lack of flank markings and the moderately short, slender, hook-like, conical dermal denticles distributed over the body. It can be distinguished from its closest congeners based on a combination of coloration, proportional body measurements, meristic counts, arrangement of dermal denticles, and size at maturity. The dorsal fins of the new species are either similar in size or the second dorsal fin is slightly larger than the first vs. the second dorsal fin distinctly larger than the first in *E. granulosus*, *E. princeps*, and *E. litvinovi*.

The pre-oral length is shorter in the new species (6.9–9.0% TL) than in its closest congeners, *E. granulosus* (7.9−11.3% TL) and *E. princeps* (9−10% TL). The tooth count in the lower jaw is higher in *E. benchleyi* (30–36) than in *E. granulosus* (28), but lower than in *E. litvinovi* (40–50) and *E. princeps* (40–50). Photophores in *E. benchleyi* are sparse compared to other etmopterids and difficult to identify due to its uniform black color. This new species is also distinct from other members of the *E. spinax* clade in having dense concentrations of dermal denticles closely surrounding the eyes and gill openings. *E. benchleyi* is the only *Etmopterus* species presently known from the Pacific coast of Central America.

Key words: new species, taxonomy, systematics, elasmobranch, ichthyology, Central America, fishes, Chondrichthyes

Introduction

The genus *Etmopterus* (Chondrichthyes: Etmopteridae) is one of the most species-rich genera of sharks with 37 valid species to date (Ebert *et al*. 2013, Eschmeyer & Fricke 2015). The genus has been subdivided into four major clades, i.e. the *E. gracilispinis*, *E. lucifer*, *E. pusillus*, and *E. spinax* clades, based on the arrangement of dermal denticles, concentrated photophores forming lateral flank and tail markings when present, and phylogenetic analyses based on molecular data (Straube *et al*. 2010). Since 2002, ten new *Etmopterus* species have been described (Last *et al*. 2002, Schaaf-Da Silva & Ebert 2006, Ebert *et al*. 2011, Knuckey *et al*. 2011, Straube *et al*. 2011), with four species each being assigned to the *E. lucifer* and *E. pusillus* clades, and two species to the *E. spinax* clade (Straube *et al*. 2010, 2011). Most of these new *Etmopterus* species were from the Indian and western Pacific Oceans and southern Africa (Ebert *et al*. 2013).

Records of *Etmopterus* species from the eastern Pacific Ocean are generally few and scattered, with possibly eight species occurring in the southeastern Pacific Ocean off Chile, but no species confirmed for the central or northern part of the eastern Pacific Ocean (Ebert *et al*. 2013, Bustamante *et al*. 2014). Recently, however, a survey conducted by the Spanish research vessel *Miguel Oliver* off the Pacific coast of Central America in 2010 collected several *Etmopterus* specimens that appeared distinct from all other known species of this genus and are described here as a new species.

Materials and Methods

The holotype and four paratypes were measured, counted, and described following other recent descriptions of new *Etmopterus* species (Schaaf-DaSilva & Ebert 2006, Ebert *et al*. 2011, Knuckey *et al*. 2011, Straube *et al*. 2011). Meristic counts, including spiral valve and vertebral counts, were taken from the type series and from additional voucher specimens not included in the type series. Estimation of dermal denticle density was calculated from one of the paratypes from a 3-mm^2 area on the body just below the second dorsal fin.

All type specimens were deposited into the fish collection at the United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). The X-ray image of USNM 163365 for *E. princeps* was accessed from the online fish collection database of the USNM. Comparative material for *E. granulosus* was deposited into the fish collection at the California Academy of Sciences (CAS). Images of two *E. litvinovi* paratypes (ZMH 24993 & 24994) were provided by Nicolas Straube (Bavarian State Collection of Zoology). Institutional abbreviations follow Sabaj Pérez (2014).

Genus *Etmopterus* Rafinesque 1810

Etmopterus Rafinesque 1810: 14.

Type species. *Etmopterus aculeatus* Rafinesque 1810, by monotypy

Etmopterus benchleyi, new species

Ninja Lanternshark

Figures 1–3, Table 1.

Holotype. USNM 423195, 458 mm TL, adult female, Costa Rica, 8°13 ′42” N, 83°09 ′47” W, bottom trawl at depth 1157–1260 m, R/V *Miguel Oliver*, D.R. Robertson, Nov. 22, 2010.

Paratypes. (from bottom trawls by D.R. Robertson aboard the R/V *Miguel Oliver*) USNM 423209, 515 mm TL, adult female, Costa Rica, 9°01 ′10” N, 84°34 ′54” W, collected at 1359–1443 m, Nov. 24, 2010; USNM 422645, 325 mm TL, immature male, Central America; USNM 422639, 290 mm TL, immature male, Panama, 7°04 ′52” N; 81°22 ′55” W, collected at 1113–1126 m, Nov. 18–19, 2010; USNM 421539, 292 mm TL, immature

Figure 1. *Etmopterus benchleyi,* n. sp., holotype, USNM 423195, adult female, 458 mm TL, fresh specimen.

male, Nicaragua, 12°07′59″ N; 88°16′27″ W, collected at 1353–1389 m, Dec. 9, 2010; USNM 421389, 212 mm TL, immature male, Panama, 6°56′30″ N, 81°45′21″ W, collected at 1033–1214 m, Nov. 19, 2010; USNM 421394, 177 mm TL, immature female, Costa Rica, 8°45′19″ N, 84°16′06″ W, collected at 836–1030 m, Nov. 23, 2010; USNM 422489, 180 mm TL, immature female, Costa Rica, 9°08′27.1″ N, 84°32′59.1″ W, collected at 902–924 m, Nov. 24, 2010.

Diagnosis. A moderately large species of *Etmopterus* with the following combination of characteristics: snout short with pre-narial length 2.9% TL (2.9–4.0%) and pre-oral length 7.8% TL (6.9–9.0%); mouth broad and strongly arched, mouth width 1.2 (1.0–1.5) times into pre-oral length; dentition exhibits strong disjunct dignathic heterodonty with upper teeth comprised of single median cusp, flanked by 1–2 pairs of lateral cusplets, lower teeth with low, distally-inclined cusps lacking serrations and a low posterior blade; dermal denticles short, slender, with slightly hook-like conical crowns; denticles below second dorsal fin arranged in irregular patch densities and align into rows along the ceratotrichia of the fins; denticles dense around eyes and gill openings, sparse to bare on ventrum of snout tip and around mouth; first dorsal fin similar in size to second dorsal fin; second-dorsal-fin spine 1.7 (1.6–2.3) times longer than first-dorsal-fin spine; second-dorsal-fin spine height greater than second-dorsal-fin apex; interdorsal-fin space moderately long, 23.1% TL (19.2–21.4%); color uniformly black with antero-posteriorly oblong narrow pineal window apparent.

Description. Proportional measurements expressed as a percentage of total length (TL) are reported for the holotype followed by the range of paratype values in parentheses.

Body fusiform, trunk sub-cylindrical, width 0.8 (0.8–1.5) in trunk height; body narrows posteriorly with trunk width 0.8 (0.7–0.9) times into head width, tail width 0.4 (0.4–0.5) times into abdomen width. Head not depressed,

Figure 2. *Etmopterus benchleyi,* n. sp., paratype, USNM 421539, immature male, 292 mm TL, fresh specimen.

TABLE 1

Morphometric data for the holotype and ranges for four paratypes of *Etmopterus benchleyi* n. sp. (as percent of the total length)

	holotype	4 paratypes	
	USNM 423195	min	max
Total length (mm)	**458**	**290**	**515**
Pre–caudal length	75.8	73.2	77.7
Pre–narial length	2.9	2.9	4.0
Pre–oral length	7.8	6.9	9.0
Pre–orbital length	6.2	4.4	6.7
Pre–spiracle length	12.3	9.3	14.1
Pre–branchial length	17.6	16.0	20.1
Head length	22.5	21.7	26.8
Pre–pelvic fin length	53.5	49.2	55.3
Snout–vent length	57.0	52.5	59.2
Pre–first dorsal fin length	34.5	34.2	36.4
Pre–second dorsal fin length	61.8	57.9	62.2
Interdorsal space	23.1	19.2	21.4
Dorsal–caudal fin space	10.0	9.4	10.7
Pectoral–pelvic space	24.6	22.5	25.8
Pelvic–caudal space	14.3	14.2	15.4
Eye length	5.0	4.1	9.1
Eye height	0.8	1.3	2.1
Inter-gill length	6.9	5.1	6.2
Interorbital length	8.6	7.2	10.4
Nostril width	2.5	2.5	7.5
Internarial space	3.0	2.8	3.8
Anterior nasal-flap length	0.3	0.3	0.5
Spiracle length	1.4	1.8	2.6
Eye–spiracle space	2.7	2.3	3.2
Mouth length	1.8	1.5	2.5
Mouth width	9.6	9.1	10.9
Upper labial furrow	1.3	1.3	1.6
Lower labial furrow	2.5	0.6	2.3
First gill height	1.7	2.6	4.6
Second gill height	2.0	2.7	4.1
Third gill height	1.4	2.4	4.4
Fourth gill height	1.4	2.4	4.0
Fifth gill height	1.3	1.8	3.3
Head height	9.2	11.0	15.0
Head width	12.4	14.4	15.6
Abdomen width	10.8	9.6	11.9
Trunk height	12.1	9.4	13.2
Trunk width	9.9	11.2	14.3

TABLE 1 continued

Tail width	4.6	4.3	5.7
Caudal peduncle height	2.7	2.4	3.4
Caudal peduncle width	1.5	1.7	2.3
Pectoral fin length	6.8	8.2	9.8
Pectoral fin anterior margin length	8.0	7.1	8.2
Pectoral fin base length	4.5	4.3	5.2
Pectoral fin height	4.9	4.5	5.4
Pectoral fin inner margin length	2.9	3.7	4.8
Pectoral fin posterior margin length	4.3	3.8	5.4
Pelvic fin length	10.2	8.7	12.3
Pelvic fin anterior margin length	4.5	5.2	6.0
Pelvic fin base length	6.1	5.7	8.6
Pelvic fin height	3.5	3.2	4.2
Pelvic fin inner margin length	4.0	3.1	5.0
Pelvic fin posterior margin length	6.8	5.0	7.0
Clasper outer length	NA	1.2	1.7
Clasper inner length	NA	1.3	4.2
Clasper base width	NA	0.2	0.7
First dorsal fin length	10.0	9.5	10.1
First dorsal fin anterior margin length	8.2	6.5	11.1
First dorsal fin base length	4.9	4.6	5.5
First dorsal fin height	3.6	3.0	3.4
First dorsal fin inner margin length	4.8	4.1	5.1
First dorsal fin posterior margin length	3.4	2.7	4.2
Second dorsal fin length	10.5	11.3	11.7
Second dorsal fin anterior margin length	8.5	7.5	9.5
Second dorsal fin base length	6.0	5.5	6.7
Second dorsal fin height	3.4	3.0	3.8
Second dorsal fin inner margin length	4.9	3.8	6.2
Second dorsal fin posterior margin length	4.5	3.8	5.4
Dorsal-caudal fin margin length	19.8	19.4	22.9
Caudal fin fork width	4.8	3.4	5.6
Pre-ventral caudal fin margin	10.7	8.3	12.1
Lower post-ventral caudal fin margin	2.7	3.0	4.5
Upper post-ventral caudal fin margin	7.2	6.8	10.4
Sub-terminal caudal fin margin	3.1	3.2	4.7
Terminal caudal fin margin	2.8	2.6	4.0
Terminal caudal fin lobe	4.3	2.2	6.6
Caudal fin fork length	9.6	6.7	12.5
First dorsal fin midpoint – pectoral fin insertion	10.1	7.9	10.7
First dorsal fin midpoint – pelvic fin origin	15.5	11.7	18.1
Pelvic fin midpoint – first dorsal fin insertion	17.4	14.2	19.1
Pelvic fin midpoint – second dorsal fin insertion	5.0	2.7	5.3
First dorsal fin spine length	3.6	3.3	3.8
First dorsal fin naked spine length	2.5	2.2	2.7
Second dorsal fin spine length	5.8	6.1	7.1
Second dorsal fin naked spine length	4.1	4.2	5.1

width 1.4 (1.0–1.4) times head height; head long 22.5% TL (21.7–26.8%). Snout conical in lateral view and triangular in dorsal view, relatively short, with pre-narial length 2.9% TL (2.9–4.0%) and pre-oral length 7.8% TL (6.9–9.0%). Eyes elliptical, moderately large, orbits with anterior and posterior notches; eye length 4.5 (2.4–5.7) times into head length, eye height 11.1 (5.8–9.3) times into head height. Nostrils large, oblique, width 1.7 (1.0–3.2) times spiracle length; nasal flaps small, triangular, with anterior tip extending across width of nasal opening. Spiracles semicircular, anterior margin extending to and above dorsal margin of eye; distance between eye and spiracle 2.7% TL (2.3–3.2%); spiracle diameter 3.5 (2.0–4.9) into eye length. Gill openings relatively large, first gill opening 1.7% TL (2.6–4.6%), opening decreases posteriorly, first gill opening 1.3 (1.0–1.5) times longer than fifth gill opening. Mouth broad and strongly arched, width 1.2 (1.0–1.5) times into pre-oral length.

Jaws of all eight specimens examined and showed similar dental morphology. No adult males available to determine sexual dimorphism. Teeth dignathic between upper and lower jaws (Fig. 3A); upper teeth (Fig. 3B) with stout, erect pointed median cusp with an acute apex showing no distal inclination flanked by a single (occasionally a double) pair of lateral cusplets, distal pair much smaller than medial pair; mesial denticles extend to less than one-half length of primary cusp; labial crown face smooth and weakly convex, lingual crown face smooth and moderately convex; upper teeth arranged in one or two functional series with about three posterior replacement teeth; root lobes acutely pointed forming a chevron-shaped attachment at base; labial root face strongly convex and forming a round pit; crown foot showing a row of vertical, short ridges at base of primary cusp; longest teeth anteriormost, length of primary cusp decreasing in size distally; lower-jaw teeth (Fig. 3C) labiolingually thin, mesodistally wide, and vertically tall with very low distally inclined crown lacking serrations and with a low and poorly-developed posterior blade, arranged in one functional row with three to four reserve rows; labial face of root with low central bulge, 3–4 small foramen, and basal root margin with a short central notch, usually with a small foramen; lower teeth progressively decrease in size from most mesial to most distal; tooth count in first row of upper jaw 25 (26–30), first row of lower jaw 34 (30–36).

Dermal denticles moderately short, slender, hook-like with conical crowns, anterior face of denticles with low median ridge and two lateral ridges that extend to near apex, denticles embedded into skin with quadrangular base, arranged in irregular patches with some areas aligned in short irregular rows. On head, denticles shortest and thickest, irregularly spaced with some clustering together at interorbital region, closely surrounding eyes and gill openings, sparse to absent on ventrum of snout tip and around and between nostrils, continuing more densely posteriorly to midway area between snout tip and mouth, thin bare patch around mouth at labial furrows. Arrangement of denticles along dorsal fins follows ceratotrichia. Average dermal denticle density below second dorsal fin 37.8 per 3mm^2 with range of 27–51 for six separate counts; denticle density increases towards mid-line, lateral denticles longer and thinner than head denticles with mostly unidirectional curvature, directed postero-ventrally; denticles along ventral side of pectorals fins clustered closer together than other parts of body and in evenly spaced linear pattern, cusp more erect with slight posterior curvature; skin near pectoral and dorsal-fin insertions naked or at most sparse small patches of denticles; caudal fin denticles strongly hooked, directed posteriorly, and widely spaced in prominent rows following axis of ceratotrichia.

Ampullae of Lorenzini conspicuous along dorsal head surface, forming parallel longitudinal rows between spiracles, continuing laterally around pineal window to nostrils, and forming three rows of ampullae on each side (Figs. 1 & 2); ampullae continuing onto ventral surface between nostrils, forming 1-2 rows posterior to nostrils, converging together anterior to eyes; additional ampullae irregularly spaced anterior to mouth, with longitudinal rows extending above first and below fifth gill slits.

Distal margins of all fins primarily covered in skin and denticles, then fringed with naked ceratotrichia. Pectoral-fin origin directly posterior to fifth gill opening, pre-pectoral fin length equals head length. Pectoral fins rounded at free rear-tips and posterior margins, fins short, fin length 6.8% TL (8.2–9.8%), inner margin 2.9% TL (3.7–4.8%). Dorsal fins sub-triangular, prone, each with grooved spine anterior to origin; first-dorsal-fin spine straight, origin behind free rear-tip of pectoral fin; pre-first-dorsal-fin length 34.5% TL (34.2–36.4%); first dorsal fin similar in area (dorsal height times length) to second dorsal fin or slightly smaller than second dorsal fin, area of first dorsal fin 1.0 (0.7–1.0) in the second fin; pre-second-dorsal-fin length 61.8% TL (57.9–62.2%); interdorsal fin space moderate, 0.3 (0.3) times into pre-caudal-fin length; origin of second-dorsal-fin spine slightly behind insertion of pelvic fins; dorsal-to-caudal-fin space 0.7 (0.7) times into pelvic-to-caudal-fin space; second-dorsal-

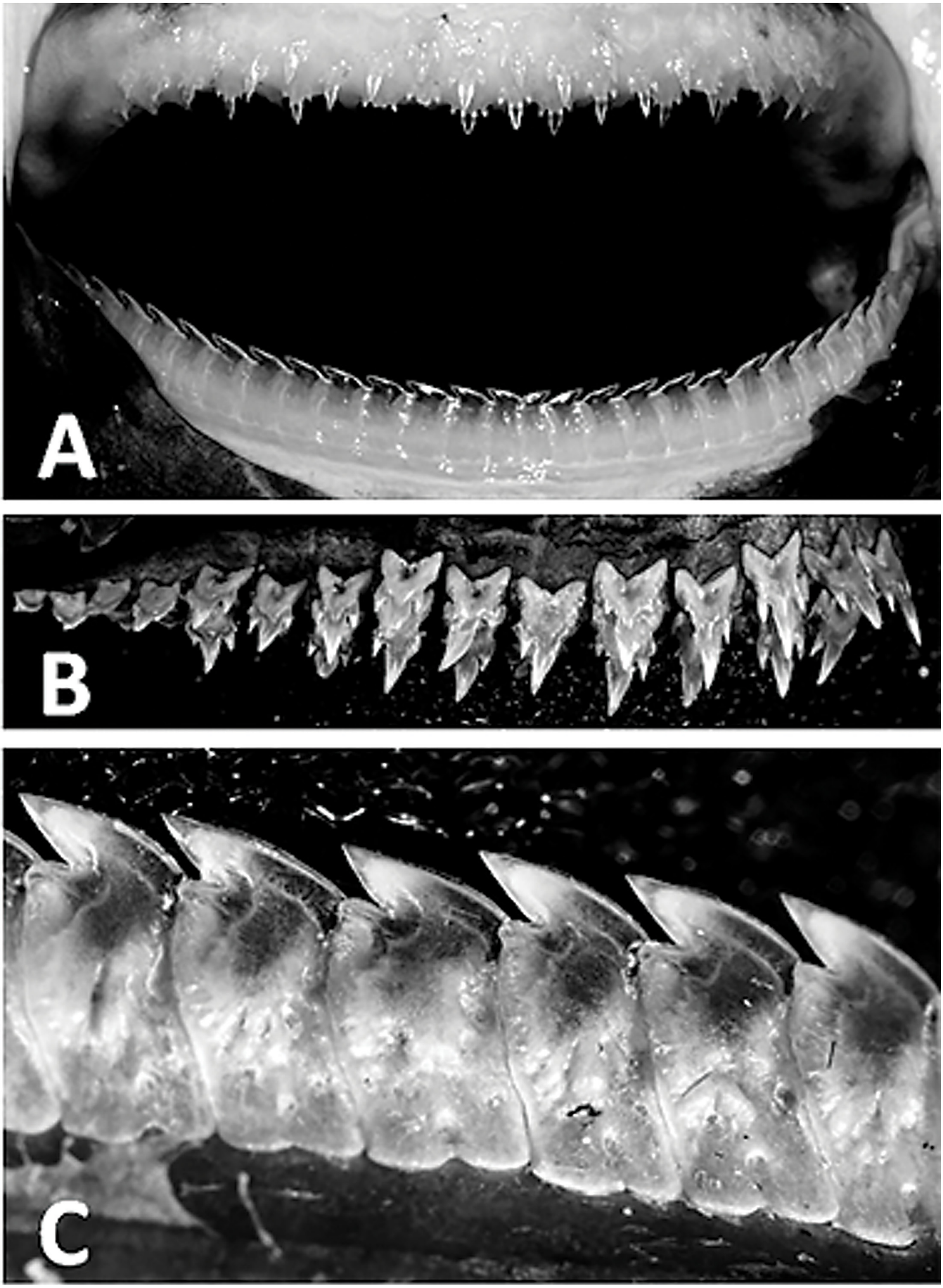

Figure 3. *Etmopterus benchleyi,* n. sp., adult female paratype (USNM 423209): A) Upper and lower *in situ* dentition of specimen before preservation; B) upper right functional tooth row showing the labial face; C) lower right functional tooth row showing labial face of lateral teeth (left), mesial to anterolateral teeth (right).

fin spine 1.7 (1.6–2.3) times longer than first-dorsal-fin spine, curved rearwards, overhanging fin, 1.7 (1.6–2.0) times longer than second dorsal fin. Short and narrow caudal peduncle, width 0.5 (0.6–2.0) into height; dorsal -to-caudal fin space 10.0% TL (9.4–10.7%). Dorsal caudal-fin margin of similar length to head, 19.8% TL (19.4–22.9%, pre-ventral caudal-fin margin much shorter, 1.9 (1.8–2.3) into dorsal caudal-fin margin; sub-terminal notch prominent, terminal caudal-fin margin slightly rounded.

Spiral valve count 8 for paratype (USNM 423209). Vertebral counts for holotype (and two paratypes USNM 423209, 422645) are total 82 (81, 83); precaudal 59 (57, 60); monospondylous 45 (42, 43).

Coloration. (Figs. 1 & 2) Fresh specimens are uniform black, with no apparent flank markings or demarcated clusters of photophores; the antero-posteriorly oblong, narrow pineal window is apparent; a narrow unpigmented posterior margin on pectoral, dorsal, and caudal fins; inner membrane surrounding eye darkly pigmented and narrow; outer membrane wide and unpigmented; pupil pale green. After preservation, head and body are uniformly dark brown to blackish brown with a cream-colored pupil; photophores are mostly indistinguishable, closer inspection of magnified images or by microscopy reveals sparse photophores along the ventral aspect with photophores on snout tip most apparent and dense.

Size. Maximum size is at least 515 mm TL for adult females (USNM 423209); largest male is 325 mm TL, but immature (USNM 422645).

Distribution. The new species has been collected in the eastern Pacific Ocean from Nicaragua south to Panama, with most specimens collected off Costa Rica (Fig. 4). The depth range of collections is from 836–1443 m along the continental slope.

Etymology. The species is named in honor of Peter Benchley, author of *Jaws* and subsequently an avid shark conservationist. His legacy, the Benchley Awards, recognizes outstanding achievements in ocean conservation. In line with Mr. Benchley's outreach efforts, the privilege of deciding a common name for this species was bestowed upon four young shark enthusiasts, ages 8 to 14, and relatives of the first author (VEV). The suggested common name, the Ninja Lanternshark, refers to the uniform black coloration and reduced photophore complement used as concealment in this species, somewhat reminiscent of the typical outfit and stealthy behavior of a Japanese ninja.

Biology notes. The largest female paratype contains five ova ranging from 25.6 to 34.2 mm, with no embryos apparent. The holotype appears to be a mature female at 458 mm TL. The immature male paratype has claspers

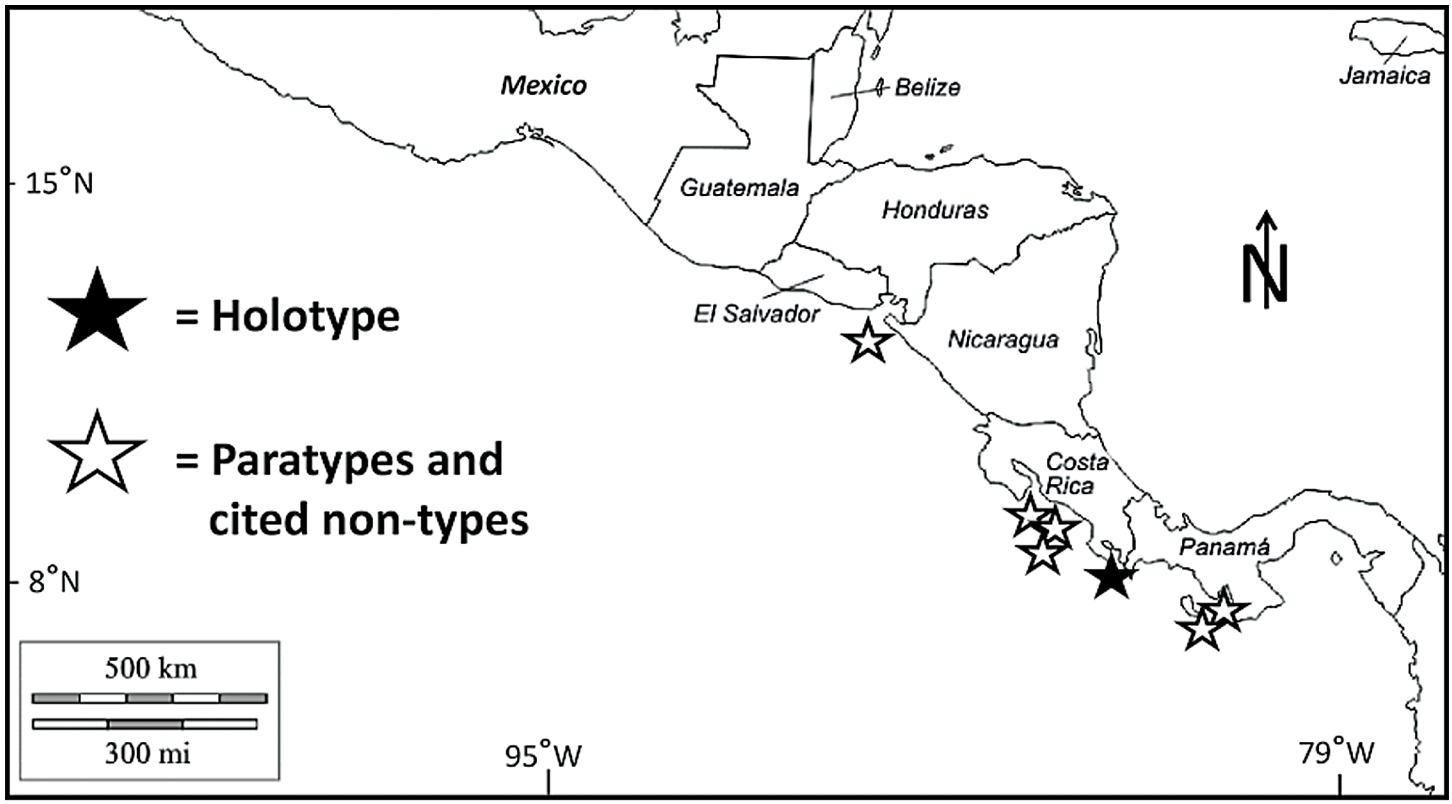

Figure 4. *Etmopterus benchleyi,* n. sp., collection locations along Pacific Ocean coastline of Central America.

at the earliest stage of development, suggesting that maturity for males is attained at a greater size. It is thus unclear if males and females of this new species reach maturity at similar sizes; female *Etmopterus* typically reach maturity at larger sizes than the males (Ebert *et al*. 2013, Jakobsdottir 2001).

Prominent umbilical scars on the two smallest specimens, USNM 421394 (177 mm TL) and USNM 422489 (180 mm TL) confirm yolk-sac viviparity as is typical of the Etmopteridae (Ebert *et al*. 2013). Litter sizes apparently consist of at least 5 pups with post-partum lengths less than 177 mm TL.

Of the specimens examined in this study, larger individuals were collected at greater depth than smaller specimens. A positive relationship between size and depth has been observed in *E. princeps* (Jakobsdottir 2001).

Comparisons. The new species is part of the *E. spinax* clade based on its short, slender, hook-like, conical dermal denticles and its lack of flank markings (Straube *et al*. 2010). The clade as presently arranged has nine species, with two species lacking flank markings, *E. litvinovi* and *E. princeps*, and the remainder with distinct or indistinct (faded) flank markings (Ebert 2013, Ebert & Stehmann 2013, Ebert *et al*. 2013, Straube *et al*. 2010, 2011, 2015).

Etmopterus benchleyi can be distinguished from the wide-ranging *E. granulosus* by having all fins with thin translucent margins, sparse to bare dermal denticles at fin insertions and base of pectoral fins, the second dorsal fin only slightly larger in area than the first dorsal fin, uniform black with no discernable markings, and a clearly apparent pineal window. In contrast, on *E. granulosus* there is a prominent white posterior margin along all of its fins, the base of all fins are completely bare of dermal denticles, the second dorsal fin is much larger than the first (usually somewhat less than twice the area), the underside is black with conspicuous markings along the caudal fin, there are indistinct flank markings, and the pineal window is not apparent (Yano 1997, Straube *et al*. 2011, Ebert 2013). The snout of *E. benchleyi* is shorter; pre-oral length is 7.8% TL (6.9–9.0%) vs. 7.9–11.3% TL in our *E. granulosus* comparative material listed below (or 9.5–11% TL from Ebert (2013) and 9.7% TL from Straube *et al*. [2011]).

The total number of lower teeth in *E. benchleyi* is higher (30–36) vs. the holotype of *E. granulosus* (28). As compared to *E. granulosus* (Ebert 2013), *E. benchleyi* has fewer spiral valves, 8 vs. 10–13, and fewer monospondylous (42–45) and total vertebrae (81–83) vs. 46–53 and 86–94. *E. benchleyi* has slightly sparser arrangements of dermal denticles below the second dorsal fin (27–51 vs. 34–58; Straube *et al*. 2011). The largest specimen examined of *E. benchleyi* is smaller than the size at maturity for *E. granulosus*, i.e. 605 mm TL for males and 750 mm TL for females (Ebert 2013, Ebert *et al*. 2013). Lastly, *E. granulosus* is restricted to higher latitudes in the southern oceans (Ebert 2013, Ebert *et al*. 2013), whereas the new species was collected in the tropics.

Etmopterus princeps can be distinguished from *E. benchleyi* by a combination of features described in Ebert & Stehmann (2013) and Ebert *et al*. (2013): a whitish margin on the second dorsal fin only, the second dorsal fin much larger than the first, an indistinct pineal window, a longer pre-oral length of 9−10% TL (vs. 6.9−9.0% TL), higher total lower tooth counts 40−50 (vs. 30−36), higher monospondylous vertebral count 44–47 (vs. 42–45), and dermal denticles relatively widely spaced and scattered over the head and trunk and in rows along the caudal peduncle and at the caudal fin base. Females of E. princeps are also larger, reaching maturity at 620 mm TL and maximum size at 890 mm TL. Lastly, *E. princeps* is only found in the North Atlantic Ocean.

Etmopterus litvinovi can be distinguished from *E. benchleyi* by a combination of features described in Kotlyar (1990), Straube *et al*. (2011), and Ebert *et al*. (2013): brighter and wider white posterior fin margins, a second dorsal fin distinctly larger than the first, the second-dorsal-fin spine of similar height to the adjacent fin and only slightly curved, vs. long and overhanging the fin, a flatter head (7.7–8.9% vs. 9.2–15% TL), a longer pectoral-fin anterior margin (11.1−11.9% vs. 7.1−8.2% TL), a longer pelvic-to-caudal fin space (16.9–17.5% vs. 14.2−15.4% TL), more teeth (30−40/40−50 vs. 25−30/30−36), up to 3 lateral cusplets flanking each side of median primary cusp on upper-jaw teeth (vs. 1 or 2 cusplets flanking each side of primary cusp and more robust), and more erect and thinner lower-jaw teeth. Females of *E. litvinovi* are also larger, maximum 610 mm TL. It should be noted that these comparisons are somewhat limited since *E. litvinovi* was described from 32 specimens, but only two specimens were available for morphological comparisons. As a result, intraspecific variability is difficult to assess. *Etmopterus litvinovi* is presently considered endemic to the Nazca and Sala y Gomez ridges in the southern eastern Pacific Ocean.

Key to the Species of the Genus *Etmopterus* in the *E. spinax* clade

1a. Lateral flank marking present with long, thin, linear anterior branch, posterior branch absent or truncated...2

1b. Lateral flank markings absent 8

2a. Flank markings distinct, contrasting sharply with background 3

2b. Flank markings indistinct, barely visible, but faded 6

3a. Body pink .... ***E. dianthus***

3b. Body brownish with black underside 4

4a. Dermal denticles stout, bristle-like and strongly bent .... ***E. compagnoi***

4b. Dermal denticles elongate and slender with conical crown 5

5a. Length from pelvic–fin insertion to lower caudal-fin origin about half of pectoral-to-pelvic–fin space; no conspicuous photolines on body .... ***E. spinax***

5b. Length from pelvic–fin insertion to lower caudal-fin origin 2/3 or more of pectoral-to-pelvic–fin space; horizontal photolines of dashes & individual photophores present on back and dorsal flanks ... ***E. hillianus***

6a. Denticles on flanks, caudal peduncle, and caudal-fin bases in linear rows .... ***E. granulosus***

6b. Denticles on sides of body scattered, not in linear rows 7

7a. Distinct elongate caudal markings; dermal denticles densely arranged, bristle–like; matures relatively large, over 530 mm TL, with a maximum of about 790 mm TL .... ***E. unicolor***

7b. No markings on tail; dermal denticles not densely arranged, not bristle–like; matures relatively small, under 500 mm TL, with a maximum of about 580 mm TL .... ***E. viator***

8a. First and second dorsal fins similar in size; second-dorsal-fin spine overhanging second dorsal fin apex .... ***E. benchleyi,* n. sp.**

8b. Second dorsal fin well larger than first; second-dorsal-fin spine similar height to second dorsal fin 9

9a. Wide white posterior margin on all fin edges .... ***E. litvinovi***

9b. Light posterior margin on second dorsal fin only .... ***E. princeps***

Other material examined:

Etmopterus compagnoi
Holotype: SMNS 8999, male, 327 mm TL, off Cape Town, South Africa, 34°41' S, 18°37' E. Paratypes: (3 specimens) SMNS 9000, collection data same as for holotype.
Etmopterus granulosus
Holotype: BMNH 1879.5.14.460, 267 mm TL, male, Chile, 47°48' S, 74°47' W, collected at 219 m, R/V *HMS Challenger* Expedition, 1 January 1876. Ten specimens all collected by P.J. Clerkin, F/V *Will Watch*: CAS 238757, 774 mm TL, pregnant female, Southwestern Indian Ocean, 39°20' S, 46°00' E, bottom trawl collected between 700–1100 m, 13 March 2012; CAS 238758, 685 mm TL, pregnant female, Southwestern Indian Ocean, 35°10' S, 53°40' E, collected between 900–1300 m, 22 March 2012; CAS 238759, 722 mm TL, pregnant female, Southwestern Indian Ocean, 34°30' S, 44°05' E, collected between 800–1000 m, 7 March 2012; CAS 238758, 736 mm TL, pregnant female, Southwestern Indian Ocean, 35°10' S, 53°40' E, bottom trawl collected between 900–1300 m, 22 March 2012; CAS 238760, 832 mm TL, pregnant female, Southwestern Indian Ocean 40°40' S, 43°20' E, collected between 500–600 m, 12 March 2012; CAS 238761, 705 mm TL, pregnant female, Southwestern Indian Ocean, 34°10' S, 45°05' E, collected between 800–1000 m, 12 March 2012; CAS 238762, 340 mm TL, female, Southwestern Indian Ocean, 35°55' S, 44°15' E, bottom trawl collected between 1200–1300 m, 5 March 2012; CAS 238763, 445 mm TL, female, Southwestern Indian Ocean, 34°30' S, 44°05' E, bottom trawl collected between 800–1300 m, 10 March 2012; CAS 238764, 355 mm TL, immature male, Southwestern Indian Ocean, 34°40' S, 44°15' E, bottom trawl collected between 1000–1300 m, 7 March 2012; CAS 238765, 377 mm TL, immature male, Southwestern Indian Ocean, 35°00' S, 44°15' E, bottom trawl collected between 900–1100 m, 7 March 2012.
Etmopterus litvinovi
Paratypes: Two specimens collected aboard the R/V *Professor Shtokman*, Nazca Ridge, Southeastern Pacific. ZMH 24993, 519 mm TL, male, 25°21' S, 85°8' W, collected 720 m, 24 April 1987; ZMH 24994, 445 mm TL, male, 25°56.3' S, 88°32.6' W, collected between 564–580 m, 24 April 1987.
Etmopterus princeps
USNM 163365, New Jersey, 40°10' N, 68°16' W, collected by W.C. Schroeder, 896 m, R/V *Captain Bill II*.
Etmopterus viator
Holotype: MNHN 2008-1899, pregnant female, 525 mm TL, Kerguelen Plateau, Indian Ocean, 49°39′29" S, 72°45′00" E, depth 1111–1023 m, October 2006.

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