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Etmopterus lailae sp. nov., a new lanternshark (Squaliformes: Etmopteridae) from the Northwestern Hawaiian Islands

DAVID A. EBERT[1,2,3,7], YANNIS P. PAPASTAMATIOU[4],
STEPHEN M. KAJIURA[5] & BRADLEY M. WETHERBEE[6]

[1]*Pacific Shark Research Center, Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA. E-mail: debert@mlml.calstate.edu*
[2]*Research Associate, South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown, 6140, South Africa*
[3]*Research Associate, Department of Ichthyology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA, 94118, USA*
[4]*Department of Biological Sciences, Florida International University, North Miami, Florida 33181, USA*
[5]*Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33431, USA*
[6]*Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island 02881, USA and Guy Harvey Research Institute, Nova Southeastern University, Ft. Lauderdale, FL., USA*
[7]*Corresponding author*

Abstract

A new species of lanternshark, *Etmopterus lailae* (Squaliformes: Etmopteridae), is described from the Northwestern Hawaiian Islands, in the central North Pacific Ocean. The new species resembles other members of the "*Etmopterus lucifer*" clade in having linear rows of dermal denticles, and most closely resembles *E. lucifer* from Japan. The new species occurs along insular slopes around seamounts at depths between 314–384 m. It can be distinguished from other members of the *E. lucifer* clade by a combination of characteristics, including a longer anterior flank marking branch, arrangement of dermal denticles on the ventral snout surface and body, flank and caudal markings, and meristic counts including number of spiral valve turns, and precaudal vertebrate. A key to species of the *Etmopterus lucifer*-clade is included.

Key words: Chondrichthyes, elasmobranch, *E. lucifer* clade, new species, central North Pacific Ocean

Introduction

The genus *Etmopterus* Rafinesque, 1810 (Squaliformes: Etmopteridae) is one of the most species rich shark genera with approximately 38 valid species, of which 11 have been described since 2002 (Ebert, 2015; Ebert *et al*., 2013, 2016). Most of these new *Etmopterus* species have been from the western Indo-Pacific and southern African regions (Ebert *et al*. 2013). In the central North Pacific four *Etmopterus* species have been reported, all from the Hawaiian Islands and associated seamounts (Crow & Crites, 2002; Mundy, 2005). These include *E. bigelowi* Shirai & Tachikawa, 1993, *E. lucifer* Jordan & Snyder, 1902, *E. pusillus* (Lowe, 1839), and the poorly known *E. villosus* Gilbert, 1905.

Records of an *Etmopterus* species tentatively identified as *E. lucifer* from throughout the Hawaiian Islands through the Hancock Seamount are common, but Mundy (2005) commented that the occurrence of this species from this region required confirmation. During the course of examining *Etmopterus* species collected in Hawaiian waters, now in the fish collection at the Bernice P. Bishop Museum (BPBM), it was determined that three individuals previously identified as *E. lucifer* represent a distinctly different species from *E. lucifer* found in Japanese waters. Here we describe this new species, *Etmopterus lailae*, from Hawaiian waters.

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Materials and methods

The holotype and two paratypes were measured externally following Ebert *et al*. (2011) and meristics, including tooth, spiral valve, and vertebral counts, were taken. Holotype values are followed in parentheses by a range of paratype values. Comparative material was examined from collections at the Australian Museum, Sydney (AMS), Bavarian State Collection of Zoology (ZSM), BPBM, Natural History Museum (BMNH), California Academy of Sciences (CAS), Commonwealth Scientific and Industrial Research Organization, Division of Marine and Atmospheric Research (CSIRO), South African Institute for Aquatic Biodiversity (SAIAB), Iziko-South African Museum (iSAM), United States National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), and Zoological Museum Hamburg (ZMH). Institutional abbreviations follow Sabaj (2016).

Genus *Etmopterus* Rafinesque, 1810

Etmopterus Rafinesque, 1810: 14. Type species: *Etmopterus aculeatus* Rafinesque, 1810 by monotypy.

Etmopterus lailae, new species

Laila's Lanternshark
(Figures 1–3a, 4–5, Table 1)

Holotype. BPBM 40183, 368 mm TL, immature male, R/V *Townsend Cromwell* cruise 8805, leg 2, station 216, Koko Seamount, 35° 16.48′N 171° 17.13′E to 35° 16.55′N 171° 17.20′E, 314–358 m, 13 August 1988.

Paratypes. BPBM 40174, 303 mm TL, immature male, R/V *Townsend Cromwell* cruise 8805, leg 2, station 167, South Kanmu Seamount, 32° 03′N 173° 04′E to 32° 02′N 173° 06′E, 336–338 m, 6 August 1988; BPBM 40182, 265 mm TL, immature male, R/V *Townsend Cromwell* cruise 8805, leg 2, station 218, Koko Seamount, 35° 17.05′N 171° 22.01′E to 35° 17.05′N 171° 21.54′E, 368–384 m, 14 August 1988.

Diagnosis. *Etmopterus lailae* is a moderately large, slender species of linear–denticled *Etmopterus* that can be separated from most of its congeners within the *E. lucifer* clade by the length of its anterior flank marking branch being much longer relative to its posterior branch; all other members of this genus, except for two species, have a posterior branch that is equal to or longer than the anterior branch. The only two species with an anterior branch relatively longer than the posterior branch, *E. lucifer* Jordan & Snyder, 1902 and *E. sculptus* Ebert, Compagno, & De Vries, 2011, can be separated from the new species by a lower spiral valve count (8–9 vs 14–16 for *E. lailae*), a slightly higher precaudal vertebral count (55–64 vs 53–57), and a higher number of teeth on the lower jaw (30–43 vs 26–28). *Etmopterus lailae* lacks dermal denticles between the nostrils on the ventral snout surface and on the dorsal fins, while the other two species have denticles present on the snout and dorsal fins.

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

Body fusiform, trunk sub-cylindrical, width 1.2 (0.7–1.0) in trunk height; head sub-conical, moderate-sized, length 14.9 (13.9–16.2)% TL, slightly depressed, height 1.6 (1.3–1.6) times width. Snout moderately long, triangular–shaped becoming rounded at snout–tip in dorsal view, slightly depressed in lateral view, head width 11.1 (9.2–10.9)% TL. Eyes oval-shape, large, length 2.9 (2.6–3.3) in head, 1.9 (1.6–1.8) times width of eye; orbits with anterior and posterior notches; inter–orbital space 1.6 (1.3–1.5) in width of head; eye length 1.3 (1.4–1.5) times in inter–orbital distance. Spiracles small, greatest diameter 1.9 (1.3–1.5)% TL, 2.7 (3.3–4.0) times into length of eye, distance to eye 2.4 (2.6)% TL, eye–spiracle length 0.9 (0.9) times into height of eye. Nostrils large, oblique, length 1.4 (1.5–1.6) times into internarial width, 2.7 (2.6–2.7) times eye diameter; anterior nasal flap well developed, triangular, anterior tip extending across nasal opening, length 0.6 (0.5) times into spiracle length. Gill openings small, slightly oblique, in horizontal series, height decreasing progressively posteriorly, first two openings noticeably larger than last three openings, fifth opening just in front of pectoral fin origin; height of first gill slit 1.8 (1.3–1.8) in height of fifth gill opening; inter-gill length about equal, 1.1 (1.2–1.3) times, to length of eye. Mouth broad, length 4.0 (3.0–3.3) times width, slightly arched, width 0.7 (0.6) in preoral length.

TABLE 1. Morphometrics and meristics of *Etmopterus lailae* holotype (BPBM 40183) and two paratypes (BPBM 40174; BPBM 40182). Values expressed as percent TL.

Measurement	Holotype	Paratypes
Total length (mm)	368	265–303
Precaudal length	80.4	75.5–78.5
Prenarial length	2.4	2.3–2.3
Preoral length	10.6	10.9–11.2
Preorbital length	6.5	5.3–5.9
Prespiracle length	13.0	12.8–13.9
Pregill length	19.0	18.1–18.8
Head length	14.9	13.9–16.2
Prepectoral length	23.9	21.8–22.6
Prepelvic length	53.3	48.3–50.8
Snout–vent length	57.6	52.1–54.5
Pre–first dorsal fin length	35.1	32.8–33.3
Pre–second dorsal fin length	61.4	56.6–57.4
Interdorsal fin length	22.0	18.1–20.1
Dorsal–caudal length	12.0	10.6–10.9
Pectoral–pelvic length	22.3	21.5–24.4
Pelvic–caudal length	17.1	16.2–19.2
Eye length	5.2	4.9–5.3
Eye height	2.7	3.0–3.0
Interorbital length	6.8	7.2–7.3
Nostril width	1.9	1.9–2.0
Internarial length	2.7	3.0–3.0
Anterior nasal flap length	1.1	0.7–0.8
Spiracle length	1.9	1.3–1.5
Eye–spiracle length	2.4	2.6–2.6
Mouth length	1.9	2.0–2.3
Mouth width	7.6	6.6–6.8
Upper labial furrow	1.6	2.3–2.3
Lower labial furrow	1.6	1.3–1.9
First gill height	1.9	1.9–2.3
Second gill height	1.6	1.5–2.0
Third gill height	1.1	1.5–1.7
Fourth gill height	1.1	1.3–1.5
Fifth gill height	1.1	1.3–1.5
Head height	7.1	6.8–6.9
Head width	11.1	9.2–10.9
Pectoral fin length	9.0	8.3–8.3
Pectoral fin anterior margin length	7.9	8.3–8.6
Pectoral fin base length	4.6	4.3–4.9
Pectoral fin height	6.8	4.6–7.2
Pectoral fin inner margin length	5.2	4.5–5.0
Pectoral fin posterior margin length	6.5	4.6–7.2
Pelvic fin length	11.1	8.6–10.6
Pelvic fin anterior margin length	4.9	5.3–6.0
Pelvic fin base length	6.5	5.3–6.8
Pelvic fin height	1.9	2.0–2.6
Pelvic fin inner margin length	5.4	3.3–4.2
Pelvic fin posterior margin length	6.0	4.0–6.4
First dorsal fin length	9.0	7.9–8.6
First dorsal fin spine length	Broken	3.0–3.4
First dorsal fin spine exposed length	Broken	1.7–1.9
First dorsal fin anterior margin length	3.8	4.5–4.6
First dorsal fin base length	5.2	5.3–5.3
First dorsal fin height	2.4	1.5–2.6

.....continued on the next page

TABLE 1. (Continued)

Measurement	Holotype	Paratypes
First dorsal fin inner margin length	4.1	3.4–3.6
First dorsal fin posterior margin length	3.5	2.6–3.3
Second dorsal fin length	13.0	12.5–13.2
Second dorsal fin spine length	Broken	6.9–7.5
Second dorsal fin spine exposed length	Broken	4.2–4.3
Second dorsal fin anterior margin length	7.1	6.3–6.4
Second dorsal fin base length	7.6	7.9–9.4
Second dorsal fin height	4.3	3.3–4.5
Second dorsal fin inner margin length	5.7	5.7–5.9
Second dorsal fin posterior margin length	7.1	4.6–6.0
Caudal fin dorsal margin	17.7	18.5–23.1
Caudal fin fork width	6.8	6.6–7.2
Caudal fin preventral margin	7.6	7.2–8.9
Caudal fin lower postventral margin	2.7	1.3–3.0
Caudal fin upper postventral margin	8.4	6.9–9.4
Caudal fin subterminal margin	3.0	2.6–4.0
Caudal fin terminal margin	3.0	3.4–5.0
Caudal fin terminal margin	3.5	4.5–6.9
First dorsal fin midpoint to pectoral fin insertion	6.3	7.3–8.7
First dorsal fin midpoint to pelvic fin origin	17.7	13.2–15.8
Pelvic fin midpoint to first dorsal fin insertion	15.5	14.7–16.2
Pelvic fin midpoint to second dorsal fin origin	4.6	2.0–3.0
Flank marking anterior branch	11.1	9.6–10.4
Flank marking posterior branch	6.3	6.3–7.9
Flank marking base	1.8	1.9–2.0
Central caudal marking	6.0	6.3–6.8
Upper caudal marking	7.1	6.6–6.8

FIGURE 1. *Etmopterus lailae* new species, immature male holotype (BPBM 40183).

FIGURE 2. Tooth morphology of upper and lower teeth of immature male holotype (BPBM 40183).

Teeth dissimilar in upper and lower jaw (Fig. 2); upper jaw teeth with strong central cusp flanked on each side by two smaller lateral cusplets, less than one-half the height of median cusp, and decreasing in size distally; lower jaw teeth unicuspid, blade-like, oblique, fused into a single row. Tooth count in first row of upper jaw 24 (22–24) and in first row of lower jaw 28 (26–26).

First dorsal fin small, length of first dorsal fin 9.0 (7.9–8.6)% TL, anterior margin slightly curved, rounded at apex, origin slightly behind pectoral fin free rear tip; fin base insertion well forward of pelvic-fin origin; pre–first dorsal length 1.6 (1.7–1.8) in inter–dorsal distance; first dorsal–fin spine nearly straight, short, (0.4–0.9) times into height of first dorsal fin, located posterior to pectoral fin posterior margin. Second dorsal fin noticeably larger than first dorsal fin, length of first dorsal fin 0.7 (0.6–0.7) into second dorsal fin, height of first dorsal fin (0.5–0.6) into second dorsal fin; apex broadly rounded, posterior margin concave, free rear tip elongated, length 13.0 (12.5–13.2)% TL, pre–second dorsal length 2.8 (2.9–3.1) in inter–dorsal distance; second dorsal–fin spine large, height about equal to or slightly higher than fin height, slightly curved near tip towards fin apex; origin behind over or slightly behind pelvic fin free rear tips. Interspace between first and second dorsal fins 2.8 (2.9–3.1) times into pre–pectoral length.

Pectoral fin length 9.0 (8.3)% TL, broadly rounded at free rear tips, base into anterior margin length ratio 1.7 (1.7–2.0), posterior margin nearly straight edged. Caudal peduncle rounded, relatively short, 12.0 (10.6–10.9)% TL, and tapering posteriorly; height slightly greater than width, 1.3 (1.0–1.4) times width; distance less than upper caudal fin length. Caudal fin elongated, slightly greater than head length, sub–terminal notch conspicuous; preventral caudal fin margin 2.4 (3.2–3.0) into dorsal caudal fin margin.

Dermal denticles on dorsal body surface erect, thorn-like, curved rearwards, in distinct longitudinal rows extending from dorsal head surface to caudal fin; distance between rows appear to decrease behind pelvic fin insertions to caudal fin. Ventral snout surface with prominent pores (ampullae of Lorenzini) surrounded by dermal denticles, except for bare patch between nostrils and extending just behind posterior nostril edges; area above upper lip of jaw without dermal denticles (Fig. 3a). Dorsal fins mostly naked, without dermal denticles extending on fin base or ceratotrichia.

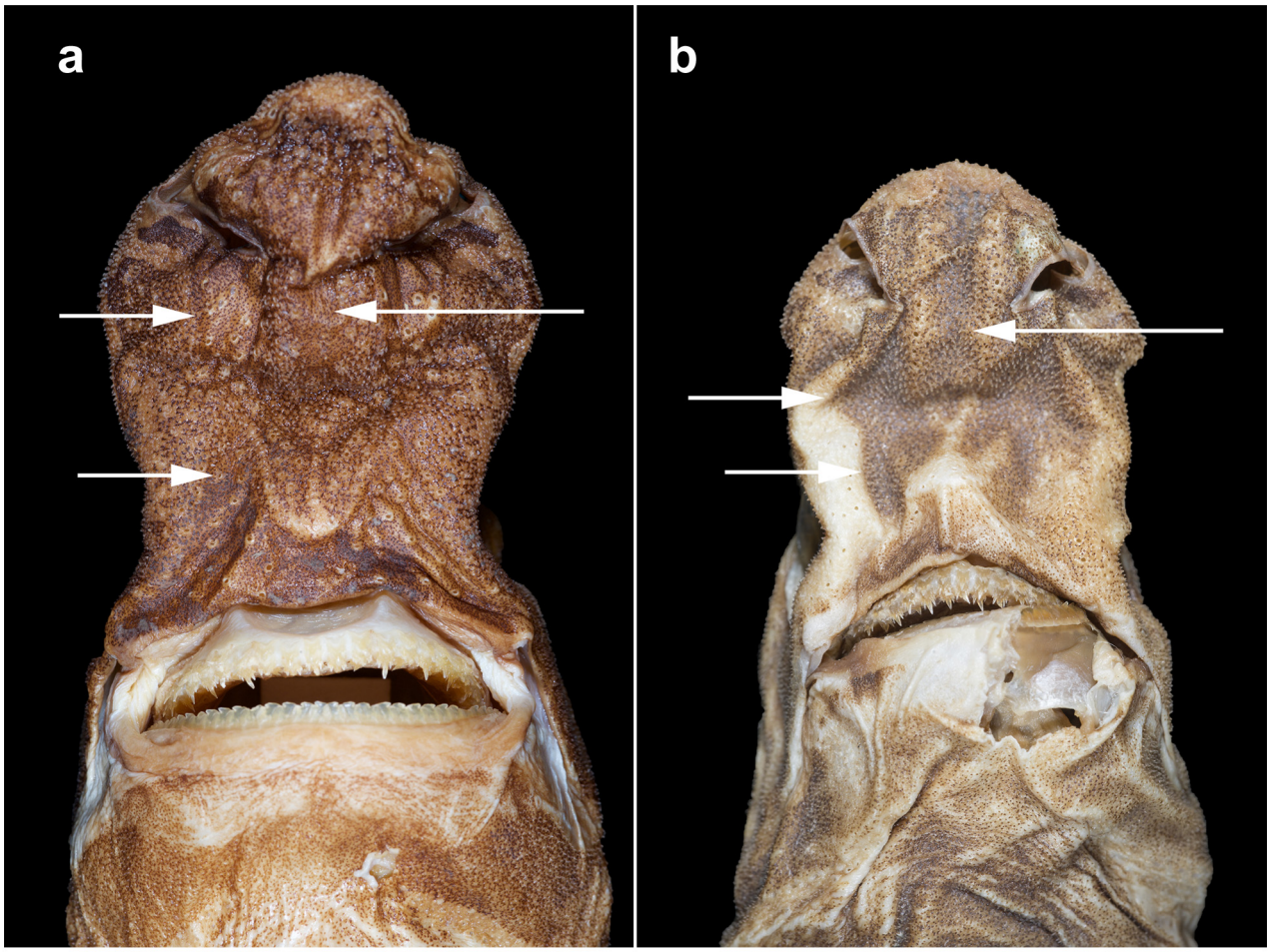

FIGURE 3. Dermal denticle arrangement on ventral snout surface of (a) *Etmopterus lailae* new species (holotype BPBM 40183) and (b) *E. lucifer* (syntype, CAS-SU 6863). Arrows denote areas of presence (*E. lucifer*) or absence (*E. lailae*) of dermal denticles.

Luminescent markings distinct, covering ventral head surface, extending to level of nostrils and at about orbital anterior notch, descending below eye level to mouth, then extending upward over mouth corners, but not encircling mouth; discontinuous with belly marking posterior to mouth at about first gill openings, demarcated by a faint band of transverse dermal folds across throat extending from below lower edges of first and second gill openings on either side.

Belly marking originates behind mouth on posterior portion of transverse dermal folds and extends ventrally along pectoral fin bases slightly extending upwards to about level with fin base insertion, about level with ventral edges of gill openings, and posteriorly to pelvic fin bases; ventral surface of pectoral fin with two very dark lobe-shaped markings, one at fin origin and another at insertion, each extending from fin base to origin of ceratotrichia bisected by distinct lighter band forming a two–prong fork pattern; margin on pectoral–pelvic space clearly demarcated, line extending from rear margin of pectoral–fin insertion nearly to pelvic–fin origin except for lighter space at pelvic–fin origin; dark ventral belly surface terminates under free rear inner margin of second dorsal fin; ventral caudal peduncle surface with darker marking just behind cloaca and extending about halfway to lower caudal origin (Fig. 4).

Flank markings distinctive, with anterior and posterior branches present; anterior branch slender, curving slightly over pelvic fins with a downward concavity, thin proximally near marking base, thickening medially before narrowing to acute tip distally; length relatively long, 11.1 (9.6–10.4)% TL as measured from marking base to tip, extending beyond origin of pelvic–fin; posterior branch nearly straight, relatively thick, length less than anterior branch, 6.3 (6.3–7.9)% TL, extending just beyond second dorsal fin base insertion, terminating below and before midpoint of inner fin margin; base of flank marking relatively narrow, origin posterior to pelvic fin insertion.

Caudal central marking distinct, thick, ovoid-shaped, length 6.0 (6.3–6.8)% TL, longer than base width of flank marking. Caudal fin upper marking very narrow, its length 1.2 (1.0–1.1) times central caudal marking.

Vertebral counts: total vertebral counts 86 (79–82); monospondylous 40 (40); diplospondylous 17 (13–15); total precaudal 57 (53–55); caudal 29 (26–27). Spiral valve count is 16 (14–16).

FIGURE 4. Ventral flank marking between pelvic fins and lower caudal origin of *Etmopterus lailae* new species (holotype BPBM 40183).

Coloration. After preservation dorsal and lateral surface a light to medium brown, except for prominent dark brown lateral and caudal markings, ventral surfaces also a dark brown; transition between lateral and ventral surfaces sharply demarcated. Body with 1 to 3 rows of prominent dark photophores extending from head posteriorly along flanks to about upper caudal origin; an irregular row of dark photophores also extending between pectoral and pelvic fins. Ventral surface a dark brown to blackish around mouth, belly, between pelvic fin origins and lower caudal origin; area around mouth distinctly dark brownish, sharply contrasting the lighter brown snout; area across throat slightly lighter than area anterior and posterior to this region. Gills and area just below darker than lighter brown area above. Pectoral and pelvic fin bases light brown above, darker below, and with blackish posterior and inner margins; remainder of fins becoming translucent. Dorsal fins light brown at base, becoming lighter to translucent. Lateral and caudal flank markings prominent, sharply demarcated, but without lighter colored lateral flanks. Caudal fin after preservation lacks vertical dark bar or any noticeable markings except for upper caudal marking.

Size. Maximum length is at least 370 mm TL (holotype: BPBM 40183) for an immature male, both paratypes are immature males; females were not available for examination.

Distribution. The new species presently is known only from the Koko and South Kanmu seamounts, Northwestern Hawaiian Islands, and at a depth range of 314–384 m (Fig. 5).

Etymology. The new species is named after Laila Mostello-Wetherbee, shark enthusiast and daughter of co-author Brad Wetherbee. The proposed common name is Laila's Lanternshark.

Comparisons. *Etmopterus lailae* can be assigned to the "*E. lucifer* clade" as defined by Straube *et al*. (2010) with its predominant lateral flank markings displaying conspicuous anterior and posterior branches. The members

of this group are also referred to as linear denticle etmopterids due to the characteristic arrangement of distinct linear rows of denticles on the dorsal head surface that also extends to the flanks, caudal peduncle and caudal base. The "*E. lucifer* clade" can further be subdivided into three distinct subgroups based on the relative lengths of the lateral flank marking branches (Ebert *et al*., 2016); anterior flank marking branch longer than posterior, anterior branch shorter than posterior, and anterior and posterior branches relatively equal in length. Eleven *Etmopterus* species are currently recognized to fall within the "*E. lucifer* clade", of which six species (*E. alphus* Ebert, Straube, Leslie & Weigmann, 2016, *E. brachyurus* Smith & Radcliffe, 1912, *E. bullisi* Bigelow & Schroeder, 1957, *E. decacuspidatus* Chan, 1966, *E. dislineatus* Last, Burgess, & Séret, 2002, and *E. molleri* Whitley, 1939) have an anterior flank branch that is shorter than the posterior, and three species (*E. burgessi* Schaaf-DaSilva & Ebert, 2006, *E. evansi* Last, Burgess, & Séret, 2002, and *E. pycnolepis*, Kotlyar, 1990) have anterior and posterior branch lengths that are about equal in length (Ebert *et al*., 2011, 2016). The remaining two species, *E. lucifer* and *E. sculptus* Ebert, Compagno, & De Vries, 2011, each has an anterior branch length that is longer than the posterior, and appear to be closest to *E. lailae* based on the relative branch lengths of flank markings (Ebert *et al*. 2011).

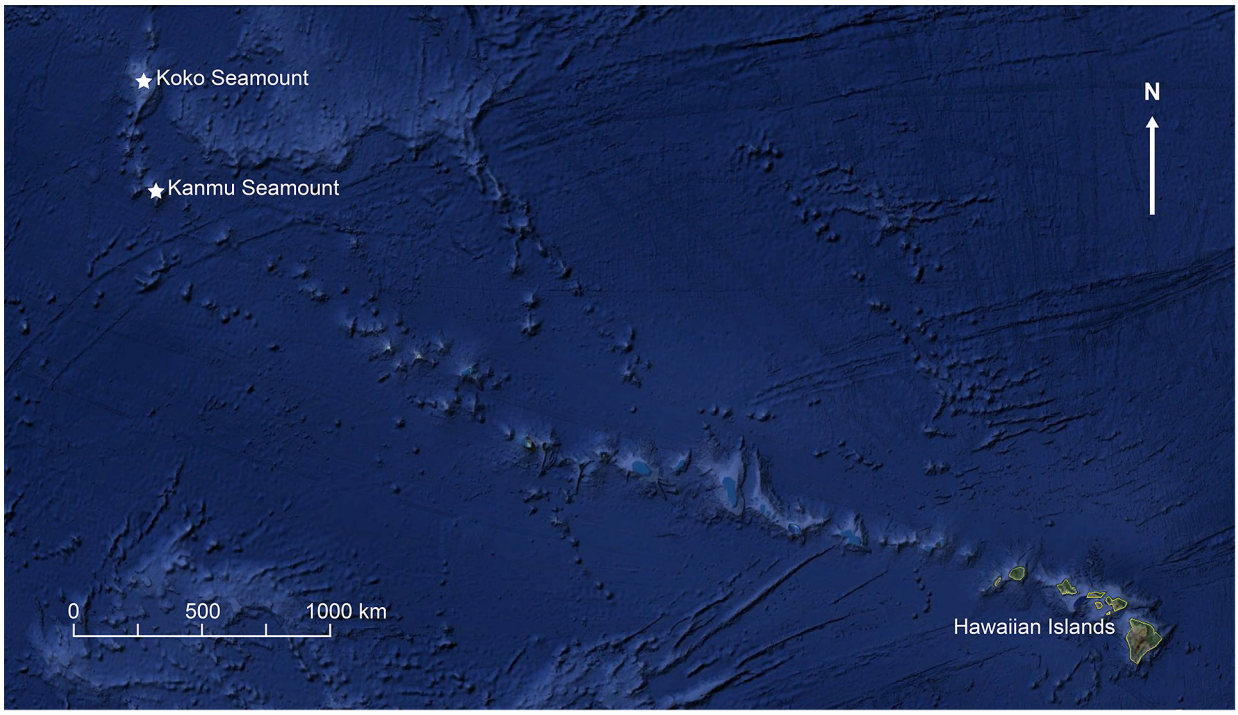

FIGURE 5. Distribution map of Hawaiian *Etmopterus* species.

Etmopterus lailae can be separated from its two closest congeners by a combination of external morphological and internal meristic characteristics. Externally, *E. lailae* can be separated from *E. sculptus* by a shorter posterior flank branch marking (6.3–7.9 vs 7.5–8.6)% TL; a longer central caudal marking (6.0–6.8 vs 3.4–5.0)% TL; central caudal marking length 3.3–3.6 vs 1.4–1.9 times flank base marking width; and a shorter upper caudal marking (1.1–1.2 vs 2.0–2.5) relative to the central caudal marking. The ventral snout surface of *E. lailae* between the nostrils is bare, but posteriorly has dermal denticles surrounding tiny pores (ampullae of Lorenzini), while *E. sculptus* is rather uniformly covered with dermal denticles, with small naked patches along the upper lips, and around and between the nostrils. Internally, *E. lailae* compared to *E. sculptus* has a higher spiral valve turn count (14–16 vs 8–9), a lower precaudal vertebral count (53–57 vs 60–64), and a lower tooth count on the lower jaw (26–28 vs 36–43). The biogeography is also informative since *E. lailae* is only known from the north central Pacific Ocean, while *E. sculptus* occurs from off Namibia to southern Mozambique in the southern hemisphere (Ebert *et al*., 2011).

The closest congener geographically and morphologically to *E. lailae* is the Japanese *E. lucifer*, but these two species can be separated by a combination of meristic and external morphological characteristics. *Etmopterus lailae* can be separated meristically from Japanese *E. lucifer* by having a higher spiral valve turn count (14–16 vs 8–9), a lower tooth count on the lower jaw (26–28 vs 30–39), and an overlapping although slightly lower precaudal

vertebral count (53–57 vs 55–63) and a lower total vertebral count (79–86 vs 85–90), although it should be noted that precaudal and total vertebral counts vary widely depending on the region and within some regions (Last & Stevens, 2009; Last & Stewart, 2015). For example, Yamakawa *et al*. (1986) based on 65 Japanese *E. lucifer* specimens reported a range of 55–62 precaudal vertebral, while we found the range for five Japanese *E. lucifer* to be 59–63. Although Yamakawa *et al*. (1986) did not report on the number of total vertebrae from their study, we found this number to range from 85–90 based on five Japanese *E. lucifer* specimens, while *E. lailae* had a range of 79–86.

Etmopterus lailae can be separated from *E. lucifer* by the following body ratios: mouth width shorter (6.6–7.6 vs 7.4–10.1)% TL; pre-pectoral length slightly shorter (21.8–22.6 vs 22.6–25.3)% TL; pectoral pelvic space shorter (21.5–24.4 vs 24.2–33.2)% TL; anterior pectoral fin length shorter (7.9–8.6 vs 8.8–11.0)% TL; first dorsal fin length longer (7.9–9.0 vs 5.4–8.0)% TL; second dorsal fin height relatively low, its height 26.3–34.3 vs 34.5–41.9% TL of its overall length. The flank markings are also informative in separating these two species: *E. lailae* when compared to *E. lucifer* has a shorter anterior flank marking branch (9.8–12.6% vs 12.7–14.0)%; a lateral flank marking base width that is slightly narrower (1.8–2.0% vs 2.1–2.5%); a slightly narrower flank base width 9.2–9.3 vs 9.6–13.9; a longer central caudal marking (6.0–6.8% vs 2.8–5.1%); central caudal marking length 3.3–3.6 vs 2.5–2.7 times flank base marking width.

The arrangement of the dermal denticles, including their presence or absence, is informative when separating *E. lailae* from *E. lucifer*. The ventral snout surface of *E. lailae* has a naked patch between, and extending just posterior to, the space between the inner nostrils (Fig. 2a). Also, beginning just posterior to the inner nostril opening is a bare patch, absent dermal denticles, extending rearwards to the upper lip except for small patch of denticles bisecting it about one-third the distance from the inner nostril opening to the upper lip; this area has several large pore openings. The area just anterior to the upper lip of the jaw, and traversing its length, also has a bare area with a few large scattered pores. Distinct pores cover the remainder of the snout ventral surface. In contrast, the snout ventral surface of *E. lucifer* is densely and relatively evenly covered by dermal denticles, but has no bare patches, except along the upper lip (Fig. 2b); some small pores are apparent, but scattered. The dorsal fins of *E. lailae* are mostly naked, without dermal denticles extending onto the dorsal fins, while *E. lucifer* has linear rows of denticles present on the bases and extending onto the dorsal fins, including the ceratotrichia. The lateral dermal denticles extending the length of the body on *E. lailae* appear more sculpted than observed in *E. lucifer*.

In addition to the above parameters these two species differ significantly in the size at maturity. All three known specimens of *E. lailae* are immature males, with the largest measuring 368 mm TL after preservation (370 mm TL before preservation), while *E. lucifer* from Japanese waters is a much smaller species with males maturing (before preservation) at a minimum length of 278 mm TL, with a maximum of 310 mm TL, based on the individuals examined in this study.

The separation of "*E. lucifer* clade" etmopterids, including the new species *E. lailae*, is complicated due to the inadequate original description of *E. lucifer* from Japan and the convoluted taxonomic history of this species from Japanese waters and elsewhere. The original description and type series of *E. lucifer* was based on a combination of two different etmopterid species, one form with an anterior branch longer than the posterior, and the other with the posterior branch being longer than the anterior. Examination of several of the syntypes by DAE and J.A. Schaaf-Da Silva (California Department Fish & Wildlife) confirms that two different species are among the type series. Furthermore, a lectotype has never been designated for the species, thus leaving open the question of what species exactly constitutes true *E. lucifer*, and leaves unresolved the status of the other species comprising the type series. Resolution to, and a description of, true *E. lucifer* with a lectotype designation are currently under investigation by DAE and N. Straube (Bavarian State Collection of Zoology).

Key to the *Etmopterus lucifer*-clade of Lanternsharks:

1a. Lateral flank marking anterior and posterior branches nearly equal in length . . . . . 2.
1b. Lateral flank marking anterior and posterior branches dissimilar in length . . . . . 4.
2a. Caudal fin without dark band at fin tip . . . . . *E. burgessi*. (Western North Pacific: Taiwan)
2b. Caudal fin with dark band at fin tip. . . . . 3.
3a. Caudal peduncle with dark saddle; caudal fin with dark band across middle of upper lobe and at fin tip. . . . *Etmopterus evansi*. (Eastern Indian Ocean: off northern Western Australia, Arafura Sea and Timor Sea)

3b. Caudal peduncle without dark saddle; caudal fin without dark band across middle of upper lobe and at fin tip. . . . . *Etmopterus pycnolepis*. (Southeastern Pacific: Nazca and Sala y Gomez submarine ridges)

4a. Lateral flank marking anterior branch noticeably shorter than posterior branch in length. . . . . 5.

4b. Lateral flank marking anterior branch noticeably longer than posterior branch in length . . . . . 10.

5a. Posterior branch of lateral flank marking extends past second dorsal fin free rear tip. . . . . 6.

5b. Posterior branch of lateral flank marking extends does not past second dorsal fin free rear tip. . . . . 8.

6a. Flanks with elaborate pattern of conspicuous rows of dark dots and dashes. . . . . *Etmopterus dislineatus* (Southwestern Pacific: off northern Queensland, Australia).

6b. Flanks without elaborate pattern of conspicuous rows of dark dots and dashes. . . . . 7.

7a. Anterior (6.0–10.6%) and posterior (9.3–12.7%) flank branches relatively shorter. . . . . *Etmopterus alphus* (Southwestern Indian Ocean).

7b. Anterior (8.0–11.5%) and posterior (11.0–15.4%) flank branches relatively longer. . . . . *Etmopterus molleri* (Western Pacific: eastern Australasia to New Zealand).

8a. Upper teeth with 4 or 5 pairs of cusplets on each side; dermal denticles not arranged in rows.. . . . . *Etmopterus decacuspidatus* (Western North Pacific: South China Sea).

8b. Upper teeth with less than 4 or 5 pairs of cusplets on each side; dermal denticles arranged in rows. . . . . 9.

9a. Color light above and conspicuously dark below. Caudal and flank photomarks conspicuous. Denticles closely spaced with low, hooked conical crowns. . . . . *Etmopterus brachyurus* (Western Pacific: Japan to Philippines, possibly Australia).

9b. Color uniformly dark. Caudal and flank photomarks obscure. Denticles widely spaced with high, hooked conical crowns. . . . . *Etmopterus bullisi* (Western Atlantic).

10a. Body slender; ventral snout surface between nostrils bare, without dermal denticles; central caudal marking length 6 %TL or more. . . . . *Etmopterus lailae* n. sp. (Central North Pacific: Hawaiian Islands).

10b. Body stout; ventral snout surface between nostrils uniformly covered with dermal denticles, and depending on the species may or may not have small bare patches; central caudal marking length less than 5.1 %TL. . . . . 11.

11a. Flank marking anterior branch nearly twice the length of the posterior branch; area between nostrils without small bare patches. . . . . *Etmopterus lucifer* (Central North Pacific: Hawaiian Islands).

11b. Flank marking anterior branch only slightly longer than posterior branch; area between nostrils with small bare patches. . . . . *Etmopterus sculptus* (Southeast Atlantic and Southwest Indian Ocean: Namibia to southern Mozambique).

Comparative material examined

Etmopterus alphus—Holotype, iSAM MB-F37564, adult male 325 mm TL, 18°14'S, 37°31'E, 472 m, 17 July 1994. Material information for 28 paratype specimens is listed in Ebert *et al*. (2016).

Etmopterus brachyurus—Holotype, USNM 70257, male, 186 mm TL, Jolo Island, Philippines; 17 specimens (8 males, 267–305 mm TL and 9 females, 261–325 mm TL), collected by David A. Ebert, Ta–Chi, Taiwan (24° 53' N, 122° 01' E), April–May 1988.

Etmopterus burgessi—Holotype, CAS 223476, 355 mm TL, adult male, Ta-Chi, Taiwan, 24° 53' N, 122° 01' E, collected by David A. Ebert, 11 May 1988; Paratypes (3 specimens), all collected at Ta-Chi, Taiwan, 24° 53' N, 122° 01' E. CAS 223477 (Fig. 2), adult female, 406 mm TL, 22 May 2005; CAS 223478, juvenile female, 241 mm TL, 23 May 2005; CAS 223479, juvenile female, 239 mm TL, 21 May 2005.

Etmopterus dislineatus—Holotype, CSIRO H 1416-01, mature male, 445 mm TL; Paratype, CSIRO H 947-2, female, 308 mm TL.

Etmopterus evansi—Holotype, CSIRO H 3141-06, female 270 mm TL, Rowley Shoals, Western Australia, 29 February 1992; Paratype, CSIRO H 3143-02, adult male 262 mm TL, north of Dampier Archipelago, Western Australia, 10 March 1992; NTUM 10312, juvenile male 172 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 520–575m depth, 14 December 2012; NTUM 10317, male 299 mm TL, east of Cape Croisiles, Madang, Papua New Guinea, 680–689 m depth, 16 December 2012; ASIZ P. unreg (BIOPAPUA field code CP3689-1), adult male 343 mm TL, west of Manus Island, Papua New Guinea, 679–685 m depth, 29 September 2010; ASIZ P. unreg (BIOPAPUA field code CP3713), female 177 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 608–610 m depth, 5 October 2010.

Etmopterus lucifer—Syntype, CAS-SU 6863, adult male, 278 mm in total length (TL), Misaki, Japan; CAS-SU 23662, male, 308 mm TL, off Sandai, Japan; CAS-SU 26782; USNM 51282 (2 of 10 specimens), both males, Misaki, Japan; USNM 161515, female, Sagami Bay, Japan.

Three specimens catalogued as *Etmopterus lucifer* at the CAS were examined and determined to have a longer posterior flank marking relative to anterior flank marking. These specimens are CAS-SU 23779 (1 specimen),

female, 347 mm TL, off Sagami Nada, Japan, collector A. Owston, 21 March 1906; CAS-SU 11225 (2 specimens), both female, 265–293 mm TL, off Misaki, Japan, collectors D.S. Jordan & J.O. Synder.

Etmopterus molleri—Holotype, AMS 5816, female, 295 mm BL, off New South Wales Australia; CSIRO H 7030-4, female, 374 mm TL, CSIRO H 7059-2, female, 390 mm TL.

Etmopterus sculptus—Holotype, SAM 37569, 442 mm TL, mature male, R/V *Africana* cruise 060, mesopelagic survey, station A 6986 060 01-02B, 33° 22.9′S 17° 29.1′E, 552 m, 04 March 1988; Paratypes, SAM 33011, 498 mm TL, mature female, R/V *Africana* cruise 060, mesopelagic survey, station A6987 060 01-03B, 33° 34.6′S 17° 23.6′E, 718 m, 05 March 1988; SAM 37570 (2 specimens), 435 and 501 mm TL, mature male/mature female, R/V *Africana* cruise 060, mesopelagic survey, station A 6986 060 01–02B, 33° 22.9′S 17° 29.1′E, 552 m, 04 March 1988; SAM 37571 (2 specimens), 474 and 495 mm TL, mature females, R/V *Africana* cruise 060, mesopelagic survey, station A 6990 060 02-02B, 33° 18.6′S 17° 28.4′E, 480 m, 05 March 1988. ZMH uncatalogued, 10 specimens, R/V *Vityaz*, cruise 17, stations 2637 (3 specimens), 2707 (1), 2735 (1), and 2765 (5).

Etmopterus villosus—Holotype, USNM-51583, 170 mm TL immature male, *Albatross* sta. 3824, off S. coast of Molokai, Lae-o Ka Laau Light, 35° N, 6.1' W, 406–911 m.

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