



Etmopterus brosei sp. nov.: a new lanternshark (Squaliformes: Etmopteridae) from the southeastern Atlantic and southwestern Indian oceans, with a revised key to the *Etmopterus lucifer* clade

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Abstract

A new species of lanternshark, *Etmopterus brosei* sp. nov. (Squaliformes: Etmopteridae), is described from the southeastern Atlantic and southwestern Indian oceans. The new species resembles other members of the *Etmopterus lucifer* Jordan & Snyder, 1902 clade in having linear rows of dermal denticles, and most closely resembles the conspecific *E. sculptus* Ebert, Compagno, & De Vries, 2011 from the southeastern Atlantic and southwestern Indian oceans. The new species is fairly common along the upper continental slopes off South Africa, Mozambique, and seamounts along the Madagascar Ridge, including Walters Shoal, in 480–1200 m depth. It can be distinguished from other members of the *E. lucifer* clade by a combination of characteristics, including the arrangement of flank and caudal markings, shape and size of flank marking, the arrangement of dermal denticles along the body, and the presence of dermal denticles on the dorsal fin bases. A revised key to the *Etmopterus lucifer* clade is provided.

Keywords Chondrichthyes · Elasmobranch · South Africa · Madagascar Ridge · New species

Introduction

The species-rich genus *Etmopterus* Rafinesque, 1810 (Chondrichthyes: Etmopteridae), with approximately 42 species, is among one of the most diverse shark genera (number updated from Weigmann 2016, 2017; Ebert and van Hees

2018). The genus has four well-defined clades of which the largest is the *E. lucifer* Jordan & Snyder, 1902 clade, whose members are characterized by having prominent flank markings displaying conspicuous anterior and posterior branches, and linear rows of dermal denticles (Straube et al. 2010). In recent years, five additional *Etmopterus* species have been

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described and assigned to the *E. lucifer* clade, bringing the number of species comprising this clade to 14 (Ebert and van Hees 2018). This includes two species from the southern African region, *Etmopterus alphus* Ebert, Straube, Leslie, & Weigmann, 2016 and *Etmopterus sculptus* Ebert, Compagno, & De Vries, 2011.

The morphological descriptions of these two *E. lucifer* clade species, *Etmopterus alphus* and *Etmopterus sculptus*, from the southern African region appeared to have resolved what had been a rather complicated and convoluted taxonomic history for this particular species group (Ebert et al. 2011, 2016). Furthermore, the relative branch lengths of the anterior and posterior flank markings can distinguish these two species from each other (Ebert and van Hees 2018). *Etmopterus alphus* has a much longer posterior branch length, while *E. sculptus* has a longer anterior branch length (Ebert et al. 2016).

During the course of a broader revisionary study on southern African etmopterids, a group of *E. cf. sculptus* specimens we examined revealed a second, cryptic species. Upon closer morphological re-examination of *E. sculptus* specimens from off South Africa and from seamounts in the southwestern Indian Ocean, it was determined that two morphologically similar, ecologically sympatric species are present. Here, we describe this new *Etmopterus* species based on freshly caught and museum preserved specimens. The description of the new species represents contribution no. 22 to the series “Deep-water chondrichthyan fishes of R/V ‘Vityaz’ cruise 17 and other Soviet cruises in the Indian Ocean,” initiated with the description of *Rhinochimaera africana* Compagno, Stehmann, & Ebert, 1990. For a map with all stations of cruise 17 of RV “Vityaz,” see Weigmann et al. (2013) or Weigmann et al. (2015). A key to the species of the *Etmopterus lucifer* clade of lanternsharks is provided.

Material and methods

External morphometric measurements and terminology follow Ebert et al. (2016) and Ebert and van Hees (2018). The base lengths of the first and second dorsal fins were each measured from the unexposed anterior edge of the spine to fin insertion. Meristics including tooth, spiral valve, and vertebral counts were taken for the holotype and 22 paratypes. The holotype and six paratypes of the new species were deposited in the Iziko South African Museum (SAMC), 12 paratypes in the South African Institute for Aquatic Biodiversity (SAIAB), and four paratypes in the Zoological Museum Hamburg (ZMH). Comparative material was examined from collections at the Academia Sinica (ASIZ), Australian Museum, Sydney (AMS), Bavarian State Collection of Zoology (ZSM), Bernice P. Bishop Museum (BPBM), California Academy of Sciences (CAS), Commonwealth Scientific and Industrial Research Organization, Division of Marine and Atmospheric Research

(CSIRO), Museo Nacional de Historia Natural, Santiago (MNHNC), National Taiwan University Museum (NTUM), Natural History Museum, London (NHMUK), Philippines National Museum (PNM), SAIAB, SAMC, United States National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), and ZMH. Institutional abbreviations follow Sabaj (2019).

Comparative material

Etmopterus alphus Ebert, Straube, Leslie & Weigmann, 2016

SAMC MB-F37564 (holotype), 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 Smith & Radcliffe, 1912

USNM 70257 (holotype), male, 186 mm TL, Jolo Island, Philippines. Non-types (23 specimens), CSIRO H 5611-01 (3 specimens), 128–224 mm TL; CSIRO H 5611-09, female 395 mm TL, Ta-Chi fish market, Taiwan, 1 August 2000; CSIRO H 7401-03, female 246 mm TL, Tongkang fish market, Taiwan, 19 March 2012; CSIRO H 7402-01, female 350 mm TL, Tongkang fish market, Taiwan, 20 March 2012; uncatalogued, 17 specimens (eight males, 267–305 mm TL, and nine females, 261–325 mm TL), collected by DA Ebert, Ta-Chi, Taiwan, 24° 53' N, 122° 01' E, April–May 1988.

Etmopterus bullisi Bigelow & Schroeder, 1957

USNM 158186 (holotype), female, 196 mm TL, “Pelican” Sta. 42, off northeast coast of Florida, 30° 02' N, 80° 05' W, 205 fathoms (375 m).

Etmopterus burgessi Schaaf-Da Silva & Ebert, 2006

CAS 223476 (holotype), 355 mm TL, adult male, Ta-Chi, Taiwan, 24° 53' N, 122° 01' E, 11 May 1988; paratypes (3 specimens), CAS 223477, 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, all collected at Ta-Chi, Taiwan, 24° 53' N, 122° 01' E. Non-types (5 specimens); CSIRO H 7395-36, adult male 335 mm TL, CSIRO H 7395-37, juvenile male 230 mm TL CSIRO H 7395-38, female 202 mm TL; CSIRO H 7395-39, juvenile male 210 mm TL; CSIRO H 7395-40, female 215 mm TL, Ta-Chi fish market, Taiwan, 14 March 2012.

***Etmopterus dislineatus* Last, Burgess & Séret, 2002**

CSIRO H 1416-01 (holotype), mature male, 445 mm TL, Queensland Plateau, 17° 00' S, 151° 02' E, December 1985; paratype, CSIRO H 947-2, female, 308 mm TL, Queensland Plateau, 17° 00' S, 151° 02' E, December 1985.

***Etmopterus evansi* Last, Burgess & Séret, 2002**

CSIRO H 3141-06 (holotype), 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. Non-types (4 specimens), NTUM 10312, juvenile male 172 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 520–575 m 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 lailae* Ebert, Papastamatiou, Kajiura & Wetherbee, 2017**

BPBM 40183 (holotype), 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 (2 specimens), 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.

***Etmopterus lucifer* Jordan & Snyder, 1902**

CAS-SU 6863 (syntype), adult male, 278 mm TL, vicinity of Misaki near Sagami Bay, Japan; CAS-SU 23662 (syntype), male, 308 mm TL, vicinity of Misaki near Sagami Bay; CAS-SU 26782, vicinity of Misaki near Sagami Bay. Non-types (8 specimens), CAS 233994 (2 specimens), female, 125 mm TL, male 200 mm TL, M/V *DA-BFAR*, otter trawl, bottom type muddy with pebbles, station BFAR-579, between Luzon Island and Mindoro Island, Philippines, 13° 44' 6.0" to 13° 44' 54.0" N, 120° 45' 22.2" to 120° 45' 21.0" E, 459–496 m, 29 May 2011; USNM 51282 (2 of 10 specimens), both males, Misaki, Japan; USNM 161515, female, Sagami Bay, Japan;

uncatalogued, 3 specimens (1 female, 2 males), Tokyo Bay, Japan, 35° 06' 13.9854" N, 139° 49' 21.9354", 200–250 m.

***Etmopterus marshae* Ebert & van Hees, 2018**

PNM 15353 (holotype), 205 mm (213 mm prior to preservation) (TL), maturing male, M/V *DA-BFAR*, otter trawl, bottom type sandy, station BFAR-583, between Luzon Island and Mindoro Island, Philippines, 13° 46' 12.6" to 13° 48' 53.4" S, 120° 50' 54.6" to 120° 50' 40.2" E, 322–337 m, 30 May 2011; paratypes (10 specimens), CAS 234011, males (2 specimens) 234 mm TL, mature, 150 mm TL, immature, females (8 specimens) 97–192 mm TL, maturity undetermined, M/V *DA-BFAR*, otter trawl, bottom type sandy, station BFAR-583, between Luzon Island and Mindoro Island, Philippines, 13° 46' 12.6" to 13° 48' 53.4" S, 120° 50' 54.6" to 120° 50' 40.2" E, 322–337 m, 30 May 2011.

***Etmopterus molleri* (Whitley, 1939)**

AMS 5816 (holotype), female, 295 mm TL, off New South Wales Australia, June 1933. Non-types (8 specimens), CAS-SU 23779, female, 347 mm TL, off Sagami Nada; CAS 11225, female, 293 mm TL; CAS 11225, female, 265 mm TL, off Misaki, Japan; CSIRO H 7030-4, female, 374 mm TL, CSIRO H 7059-2, female, 390 mm TL; uncatalogued, 3 specimens (3 males), Tokyo Bay, Japan, 35° 06' 13.9854" N, 139° 49' 21.9354", 200–250 m.

***Etmopterus pycnolepis* Kotlyar, 1990**

ZMH 24995 (ISH 4-1989) (paratype), Soviet Expedition, Sta. 1964, Nazca Ridge, Chile, SE Pacific, 25° 56.3' S, 88° 32.6' W, 564–580 m, 30 April 1987. Non-types (2 specimens), MNHNC P.6501, female 511 mm TL, Nazca Ridge, Chile, SE Pacific, 21° 08' S, 70° 26' W, 528–708 m, 22 February 1981; MNHNC P.7247, female 508 mm TL, Nazca Ridge, Chile, SE Pacific, 25° 56' 6" S, 84° 25' 6" W, 880 m, 4 February 2003.

***Etmopterus samadiae* White, Ebert, Mana & Corrigan, 2017**

NTUM 10078 (tissue accession GN 17184) (holotype), adult male 265 mm TL, east of Malamal Passage, Madang, Papua New Guinea, 05° 07' S, 145° 50' E, 527–539 m depth, 30 Nov 2012; paratypes (9 specimens), ASIZ P.73777, adult male 230 mm TL; ASIZ P.73778, female 188 mm TL; ASIZ P.73765, pregnant female 277 mm TL, off Lae, Huon Gulf, Morobe Province, Papua New Guinea, 06° 51.841' S, 147° 04.672' E, 395–406 m depth, 22 Aug 2010; NTUM 10313 (tissue accession GN 17195), female 269 mm TL, northern Cape King William, Morobe Province, Papua New Guinea, 06° 00' S, 147° 38' E, 785 m depth, 10 Dec 2012;

NTUM 10314 (tissue accession GN 17197), female 258 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 05° 22' S, 145° 48' E, 420–490 m depth, 14 Dec 2012; NTUM 10315 (tissue accession GN 17198), female 154 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 05° 22' S, 145° 48' E, 340–385 m depth, 14 Dec 2012; NTUM 10316 (3 specimens; tissue accessions GN 17210–2), female 177 mm TL, subadult male 201 mm TL, female 228 mm TL, west of Kairiru Island, East Sepik, Papua New Guinea, 03° 19' S, 143° 27' E, 422–425 m depth, 19 Dec 2012.

Etmopterus sculptus Ebert, Compagno & De Vries, 2011

SAMC 37569 (holotype), 442 mm TL, mature male, R/V *Africana* cruise 060, mesopelagic survey, station A6986 060 01-02B, 33° 22.9' S 17° 29.1' E, 552 m, 4 March 1988. Paratypes (5 specimens), SAMC 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, 5 March 1988; SAMC 37570 (two specimens), 435 and 501 mm TL, mature male/mature female, R/V *Africana* cruise 060, mesopelagic survey, station A6986 060 01-02B, 33° 22.9' S, 17° 29.1' E, 552 m, 4 March 1988; SAMC 37571 (two specimens), 474 and 495 mm TL, mature females, R/V *Africana* cruise 060, mesopelagic survey, station A6990 060 02-02B, 33° 18.6' S, 17° 28.4' E, 480 m, 5 March 1988. Non-types, SAIAB 25309, 400 mm TL, mature male, R/V *Africana* cruise 015, West Coast Demersal Survey, bottom trawl, station A01205 015 009 5144, 35° 20' S, 18° 46' E, 510 m, 8 January 1984; SAIAB 26256, 428 mm TL, mature male, R/V *Africana* cruise 046, West Coast Demersal Survey, bottom trawl, station A04361 046 E12, 31° 59.8' S, 15° 56.2' E, 850 m, 17 July 1986; SAIAB 26258, 442 mm TL, mature male, R/V *Africana* cruise 046, West Coast Demersal Survey, bottom trawl, station A04361 046 E12, 31° 59.8' S, 15° 56.2' E, 850 m, 17 July 1986; SAMC 41924-3, 493 mm TL, mature female, R/V *Africana* cruise 291, West Coast Demersal Survey, bottom trawl, station A3101 291 042 6410, 36° 32' S, 20° 09' E, 616 m, 21 January 2017; SAMC 41924-4, 457 mm TL, mature female, R/V *Africana* cruise 291, West Coast Demersal Survey, bottom trawl, station A3101 291 042 6410, 36° 32' S, 20° 09' E, 616 m, 21 January 2017; ZMH 26196, 276 mm TL fresh / 272.6 mm TL preserved, juvenile female, R/V *Vityaz*, cruise 17, station 2735, Walters Shoals, 33° 36' S, 44° 32' E – 33° 38' S, 44° 34' E, 930–950 m depth, 29 m shrimp trawl, trawl # 68, trawl time 05:25–06:40 am, 19 Dec 1988, collected by Matthias F.W. Stehmann. ZMH 26197 (five specimens), two juvenile females, 230 mm TL fresh / 220.2 mm TL preserved and 245 mm TL fresh / 232.6 mm TL preserved, and three juvenile males, 211 mm TL fresh / 203.2 mm TL preserved, 250 mm TL fresh / 243.9 mm TL preserved and 286 mm TL fresh / 270.0 mm TL preserved, R/V *Vityaz*, cruise 17, station 2765, Walters Shoals, 33° 05.3' S,

43° 41.9' E – 33° 02.6' S, 43° 42.1' E, 870–930 m depth, 29 m shrimp trawl, trawl # 74, trawl time 09:09–09:45 am, 24 Dec 1988, collected by Matthias F.W. Stehmann. Uncatalogued (8 specimens), female, Walters Shoal, Southwest Indian Ocean, 34° 10' S, 45° 05' E, F/V *Will Watch*, bottom trawl, between 800 and 1200 m, 3 March 2012; (2) females, Walters Shoal, Southwest Indian Ocean, 33° 50' S, 44° 20' E, F/V *Will Watch*, bottom trawl, between 700 and 1000 m, 3 March 2012; (5 specimens) adult male (1), 460 mm TL, females (4), 410–555 mm TL, Walters Shoal, Southwest Indian Ocean, 35° 00' S, 44° 15' E, F/V *Will Watch*, bottom trawl, between 800 and 1200 m, 5 March 2012.

Results

Systematic account

Family Etmopteridae

Genus *Etmopterus* Rafinesque, 1810

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

Etmopterus brosei sp. nov. Ebert, Leslie & Weigmann
<http://zoobank.org/4CF96D09-FADE-4B79-94F7-E9E18834D58F>

Barrie's Lanternshark

Figures 1, 2, 3, 4, 5, 6, and 7; Tables 1, 2, and 3

Holotype SAMC-F41923, 426 mm total length (TL), mature male, R/V *Africana*, cruise 291, West Coast Demersal Survey, bottom trawl, station A33101-291-042-6410, 36° 32' S, 20° 09' E, 616 m, 21 January 2017, collector Robin W. Leslie.

Paratypes (22 specimens) SAMC-F041936, (2 specimens collected with holotype) 400–429 mm TL, all mature male, R/V *Africana*, cruise 291, West Coast Demersal Survey, bottom trawl, station A33101-291-042-6410, 36° 32' S, 20° 09' E, 616 m, 21 January 2017, collector Robin W. Leslie. SAMC-F34407 (3 specimens) 398–437 mm TL, all mature males, R/V *Africana*, cruise 133, West Coast Demersal Survey, bottom trawl, station A18003-133-076-5090, 32° 24' S, 16° 29' E, 500 m, 12 February 1996, collector Robin W. Leslie. SAMC-F037718, 422 mm TL, mature male, R/V *Africana*, cruise 127, West Coast Demersal Survey, bottom trawl, station A17103-127-034-5116, 33° 17' 42" S, 17° 27' 12" E, 480 m, 13 January 1995, collector Robin W. Leslie. SAIAB 25311, 433 mm TL, female, R/V *Africana*, cruise 033, West Coast Demersal Survey, bottom trawl, station A2771-033-027-5150, 35° 58.0' S, 19° 32.0' E, 517 m, 7 July 1985. SAIAB 26254, 433 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04310-046-E01, 34° 25.6' S, 17° 41.2' E, 760 m, 7 July 1986. SAIAB 26255, 432 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom

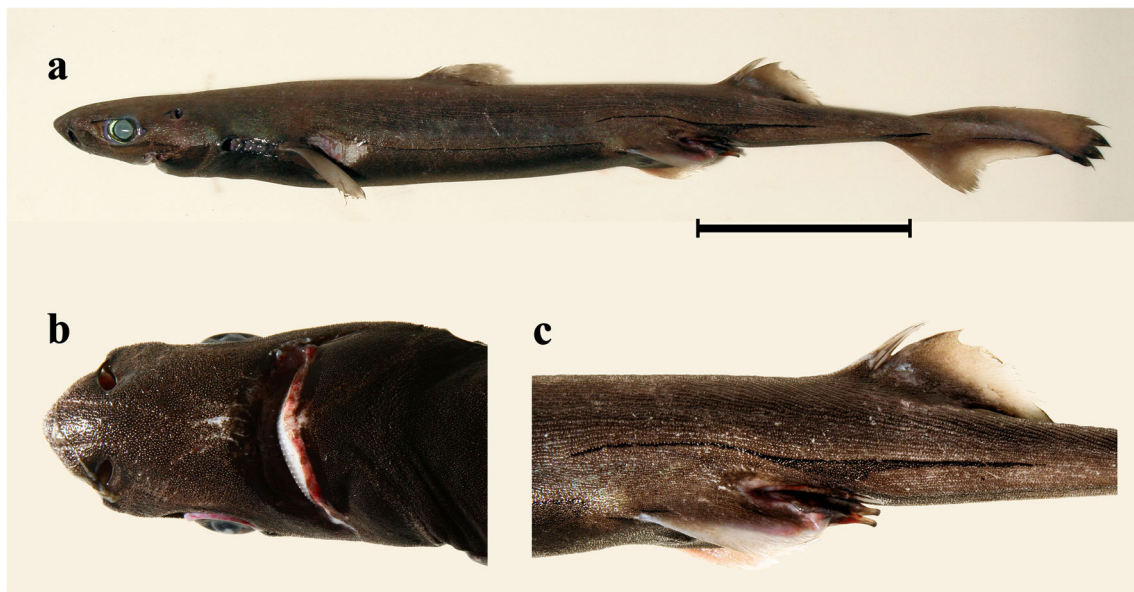


Fig. 1 *Etmopterus brosei* sp. nov., holotype (SAMC-F41923) before preservation in lateral view (a), ventral view of snout (b), and close up view of lateral flank marking (c). Scale bar: 10 cm

trawl, station A04361-046-E12, 31° 59.8' S, 15° 56.2' E, 850 m, 17 July 1986. SAIAB 26257, 420 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04310-046-E01, 34° 25.6' S, 17° 41.2' E, 760 m, 7 July 1986. SAIAB 26259, 390 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04310-046-E01, 34° 25.6' S, 17° 41.2' E, 760 m, 7 July 1986. SAIAB 26260, 425 mm TL, female, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04310-046-E01, 34° 25.6' S, 17° 41.2' E, 760 m, 7 July 1986. SAIAB 26261, 424 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04310-046-E01, 34° 25.6' S, 17° 41.2' E, 760 m, 7 July 1986. SAIAB 26262, 451 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04310-046-E01, 34° 25.6' S, 17° 41.2' E, 760 m, 7 July 1986. SAIAB 26263, 423 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04361-046-E12, 31° 59.8' S, 15° 56.2' E, 850 m, 17 July 1986. SAIAB 26264, 425 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04361-046-E12, 31° 59.8' S, 15° 56.2' E, 850 m, 17 July 1986. SAIAB 26265, 410 mm TL, mature male, R/

V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04310-046-E01, 34° 25.6' S, 17° 41.2' E, 760 m, 7 July 1986. SAIAB 26266, 422 mm TL, mature male, R/V *Africana*, cruise 046, West Coast Demersal Survey, bottom trawl, station A04310-046-E01, 34° 25.6' S, 17° 41.2' E, 760 m, 7 July 1986. ZMH 26194 (3 specimens), two presumably mature females, 378 mm TL fresh / 371 mm TL preserved and 430 mm TL fresh / 420 mm TL preserved, and one mature male, 375 mm TL fresh / 370 mm TL preserved, R/V *Vityaz*, cruise 17, station 2637, off Mozambique, 25° 13' 9" S, 35° 32' 1" E – 25° 18' S, 35° 27' 5" E, 980–1000 m depth, 29 m shrimp trawl, trawl # 35, trawl time 10:44–11:45 pm, 25 Nov 1988, collected by Matthias F.W. Stehmann. ZMH 26195, 408 mm TL fresh / 390 mm TL preserved, mature male, R/V *Vityaz*, cruise 17, station 2707, Walters Shoals, 33° 1.8' S, 44° 23.6' E – 32° 59.8' S, 44° 24.4' E, 910–925 m depth, 19.4 m shrimp trawl, trawl # 60, trawl time 10:00–11:00 am, 15 Dec 1988, collected by Matthias F.W. Stehmann.

Non-types (uncatalogued, 6 specimens) 450 mm TL, mature male, Walters Shoal, Southwest Indian Ocean, 33° 50' S, 44° 20' E, F/V *Will Watch*, bottom trawl, between 700 and 1000 m, 3 March 2012; mature male, Walters Shoal,



Fig. 2 *Etmopterus brosei* sp. nov., holotype (SAMC-F41923) after preservation in lateral view. Scale bar: 10 cm



Fig. 3 *Etmopterus brosei* sp. nov. Tooth morphology of upper and lower teeth of holotype (SAMC-F41923)

Southwest Indian Ocean, 34° 10' S, 45° 05' E, F/V *Will Watch*, bottom trawl, between 800 and 1200 m, 3 March 2012; (2) mature males, Walters Shoal, Southwest Indian Ocean, 35° 00' S, 44° 15' E, F/V *Will Watch*, bottom trawl, between 800 and 1200 m, 5 March 2012; (2) 455–509 mm TL, females, Southwest Indian Ocean Ridge, 36° 50' S, 52° 05' E, F/V *Will Watch*, bottom trawl, between 900 and 1200 m, 20 March 2012.

Diagnosis A relatively large linear-denticled lanternshark was assigned to the *E. lucifer* clade and distinguished from all other clade members, except for three species, by an anterior flank marking branch longer than its posterior branch. The new species is distinguished from its closest congener *E. sculptus* by an indistinct color gradation between the flank and abdomen vs a sharp demarcation between the flank and abdomen, a V-shape arrangement of ampullae on the ventral snout surface with evenly distributed dermal denticles vs a U-shape arrangement with sparse denticle coverage, dorsal fins densely covered with dermal denticles vs sparse or mostly

bare dorsal fins, and higher vertebral (85–88 vs 78–85) and spiral valve turn (11 vs 8–9) counts. The new species can be separated from the other two closest *E. lucifer* clade species, *E. lailae* and *E. lucifer*, by a longer posterior flank marking branch extending to or beyond the end of the second dorsal fin free rear tip vs shorter branch not reaching the rear tip, an upper caudal lobe with a dark terminal band or spot, which is absent in these other two species, and biogeography with the new species occurring in the southern African region vs the central and western Pacific Ocean.

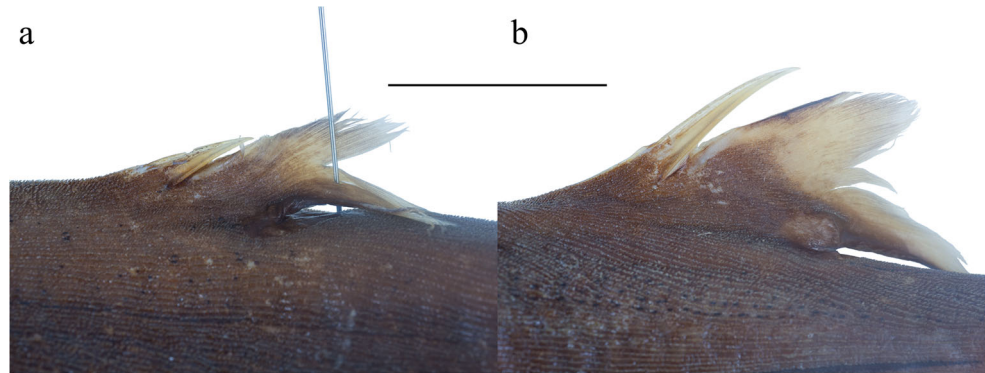
Description of the holotype Values of the 22 paratypes are given in parentheses. Detailed morphometric measurements can be found in Table 1.

Body fusiform, trunk sub-cylindrical, width 1.1 (0.7–1.3) in trunk height; head subconical, long, 21.6 (20.2–22.3)% TL, slightly depressed, height 1.3 (1.0–1.8) times width (Figs. 1 and 2). Snout short, subconical to slightly flattened in lateral view, in dorsal view triangular-shaped becoming rounded at snout tip, head width 9.4 (8.2–10.5)% TL, preorbital snout length sub-equal to distance from posterior orbit to spiracle. Eyes oval-shape, large, length 5.4 (5.2–7.0) in head and 1.1 (1.2–1.6) times height of eye; orbits with anterior and posterior notches; moderately spaced, interorbital space 1.3 (1.2–1.6) in width of head; eye length 1.9 (1.3–2.2) times in interorbital distance. Spiracles small, semi-circular, greatest diameter 1.9 (0.9–2.3)% TL, length 2.1 (1.7–4.0) times into length of eye, distance to eye 1.6 (1.2–2.5)% TL, eye-spiracle length 0.4 (0.3–0.8) in height of eye. Nostrils large, oblique, length less than internarial length, less than eye diameter; anterior nasal flap reasonably developed, triangular, anterior tip extending across nasal opening, length 0.9 (0.3–1.0) times spiracle length. Gill openings small, narrow, slightly oblique, in horizontal series, height decreasing progressively posteriorly, height of first gill slit 1.4 (0.8–2.3) times height of fifth gill opening, intergill length 0.9 (0.7–1.1) times in length of eye.

Fig. 4 Dermal denticle arrangement on ventral snout surface of *Etmopterus brosei* sp. nov. holotype (SAMC-F41923) after preservation. Scale bar: 1 cm



Fig. 5 *Etmopterus brosei* sp. nov., dermal denticle coverage of first (a) and second (b) dorsal fins of paratype ZMH 26194, mature male, 370.0 mm TL. Scale bar: 2 cm



Mouth broad, length 3.1 (2.3–8.1) times in width, slightly arched, width 0.7 (0.5–0.8) times preoral length.

Teeth dissimilar in upper and lower jaw (Fig. 3); upper teeth multicuspid in two or three functional series, functional teeth in lower jaw unicuspid in single series, with about five series of replacement teeth in upper and lower jaw; multicuspid upper teeth small, perpendicular, with strong central cusp flanked by three lateral cusplets on each side, decreasing size distally; teeth in lower jaw fused into single row, blade-like, cusp oblique, semi-erect.

First dorsal fin small, rounded at apex, base scaled, length of first dorsal fin 8.0 (7.2–9.3)% TL, origin well behind pectoral fin insertion; fin base insertion well forward of pelvic fin origin; pre-first dorsal length 1.4 (1.2–1.5) times interdorsal distance; first dorsal fin spine nearly straight, short, 0.8 (0.6–1.7) in height of first dorsal fin, located well behind pectoral fin rear margin. Second dorsal fin conspicuously larger and more erect than first dorsal fin, length of first dorsal fin 0.8 (0.6–0.8) times second dorsal fin, height of first dorsal fin 0.8 (0.4–0.7) times second dorsal fin; apex subangular, posterior margin slightly concave, free rear tip elongated, length 10.6 (10.6–14.5)% TL, pre-second dorsal length 2.6 (2.3–2.7) times interdorsal distance; second dorsal fin exposed spine length 2.6 (1.9–3.8) times first dorsal fin exposed spine length, height greater than fin height, slightly curved near tip towards fin apex; origin behind insertion of pelvic fins, over pelvic fin free rear tips. Interspace between first and second dorsal fins 0.9 (0.8–1.0) times prepectoral length.

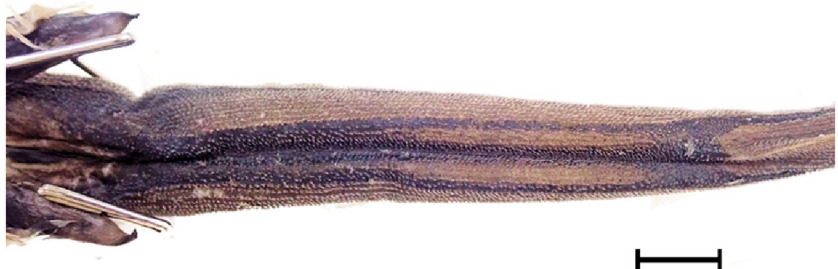
Pectoral fins relatively large, length 8.9 (7.9–10.2)% TL, subangular at free rear tips, base 1.6 (1.5–2.3) in anterior

margin, posterior margin slightly rounded to nearly straight edged. Caudal peduncle relatively long, length from second dorsal fin insertion to caudal origin 12.7 (10.3–13.3)% TL, height about equal to or slightly greater than width, rounded, and tapering posteriorly; less than upper caudal fin length. Caudal fin moderately elongated, slightly less than head length, subterminal notch conspicuous; length of lower preventral caudal fin margin less than one-half upper caudal fin margin.

Dermal denticles on dorsal body surface erect, thorn-like, hook-like, directed rearwards in distinct longitudinal rows extending from dorsal head surface to caudal fin, a characteristic of *E. lucifer* clade members. Distance between lateral rows decreases behind pelvic fin insertions towards caudal fin origin. Ventral snout surface densely and uniformly covered with dermal denticles, except for bare area surrounding mouth region (Figs. 1b, 4); pores (ampullae of Lorenzini) in V-shaped pattern extending from snout tip to bare region of mouth. Dorsal fins dissimilar in dermal denticle coverage; first dorsal fin unevenly covered with denticles present on fin spine base, becoming sparse to absent posteriorly along fin base (Fig. 5a); second dorsal fin strongly covered with dermal denticles (Fig. 5b). Flank mark area denticles less dense and pointed ventrally.

Luminescent markings distinct, covering ventral head surface, extending from snout tip to level of nostrils and descending just anterior to orbital notch below eye level to mouth, then upwards over mouth corners, and encircling mouth; throat with distinct, light chevron originating behind lower jaw and extending to each side of head to just anterior of first

Fig. 6 Ventral flank marking between pelvic fins and lower caudal origin of *Etmopterus brosei* sp. nov. (SAMC-F41923). Scale bar: 1 cm



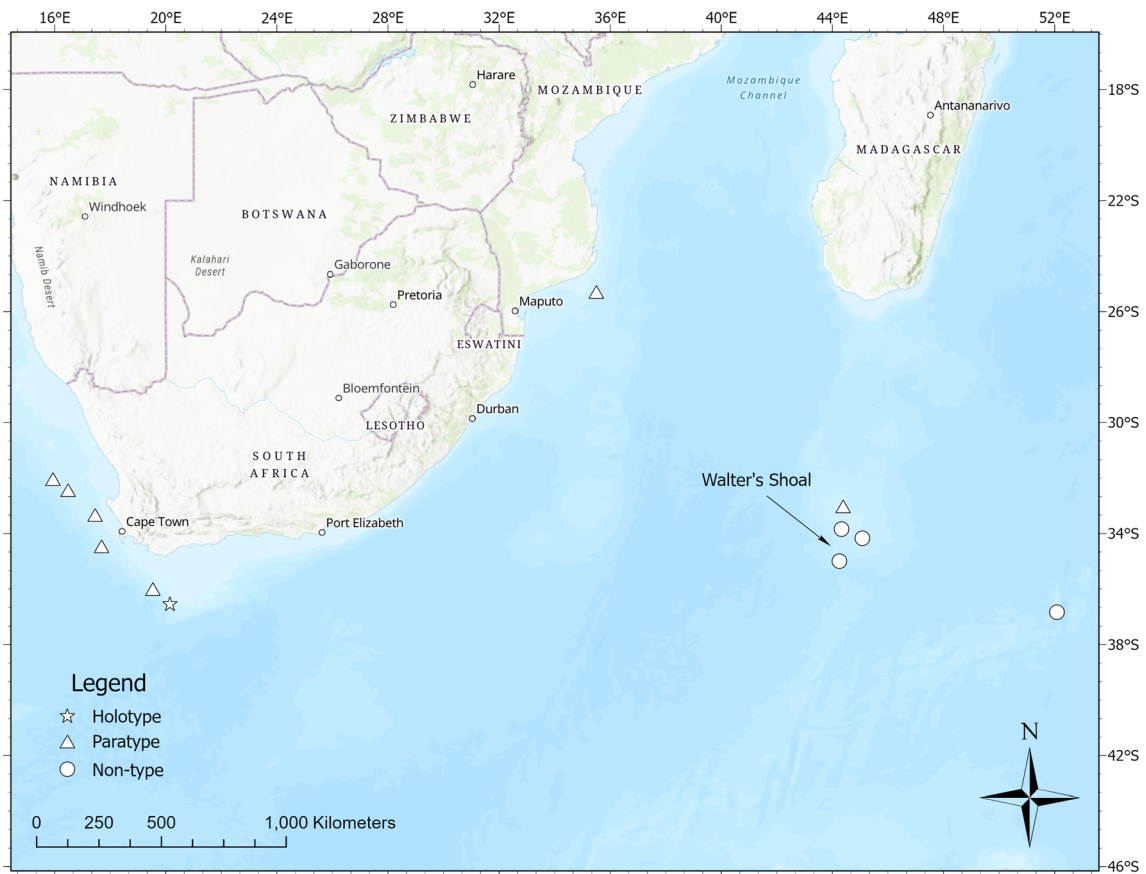


Fig. 7 Distribution map of *Etmopterus brosei* sp. nov. specimens examined from South Africa, southern Mozambique and the Madagascar Ridge. Holotype represented by star, paratypes by triangles, and non-types by circles

gill opening; belly marking posterior to chevron, extending across lower half of gill openings, poorly demarcated. Head dorsal surface photophore pattern faint, indistinct, originating above level of orbits and extending along midline of back and flanked on each side by a row, extending in parallel posteriorly to about upper caudal origin.

Belly marking originates on throat behind chevron, extending dorsally to lower half of gill openings, and encircling the pectoral fin base, followed by a semi-circular bare area just behind the pectoral fin insertion; pectoral-pelvic fin space clearly demarcated with line extending from above pectoral fin insertion to just anterior of pelvic fin origin; dark, slightly curved, finger-like extension just reaching upper pelvic insertion, but not extending over it; dark ventral belly surface continuous, and solidly colored onto caudal peduncle ventral surface to about midpoint, then becoming fork-shaped, and extending to lower caudal origin where it is again solid colored (Fig. 6).

Flank markings (Fig. 1c) well defined, anterior and posterior branch lengths unequal; anterior branch slightly longer, length 10.6 (9.6–12.4)% TL, slender, curving over pelvic fin base, and extending beyond origin of pelvic fin; posterior branch shorter than anterior branch, length 8.0 (6.7–10.6)% TL, straight, not curving, and thick, extending to just before or

under free rear tip of dorsal fin, occasionally extends past; width at level of base end of second dorsal fin 3.5 (2.5–4.0)% TL; base of flank marking narrow, origin posterior to pelvic fin insertion. Caudal base marking distinct, narrow medially, subangular posteriorly, with tip acutely pointed, length 1.8 (1.0–2.7) times longer than base of flank marking. Upper caudal fin marking very narrow, its length 1.7 (1.5–2.7) times caudal base marking.

Vertebral counts: total counts 88 (85–88); total precaudal counts 63 (60–63); monospondylous 44 (43–46); diplospondylous precaudal 19 (16–19); caudal 25 (23–25). Spiral valve turn counts based on paratypes 11 ($n = 3$).

Coloration *Etmopterus brosei* sp. nov. in life is a dark brownish-black dorsally and laterally on body trunk becoming black ventrally, and without a silvery sheen, but with slight bronzy iridescence in strong light; transition between lateral and ventral surfaces poorly demarcated, except for faint line behind pectoral fin insertions extending to pelvic fin origins (Fig. 1a). Eyeball pupil uniform greenish, with blackish iris. Dorsal fins dissimilar in color; first dorsal fin mostly whitish to translucent, except for black anterior and inner margins; second dorsal fin darker brown to blackish with black anterior margin, becoming lighter to translucent posteriorly, inner

Table 1 Morphometric measurements for *Etmopterus brosei* sp. nov. holotype (SAMC-F41923) and ranges for 22 paratypes followed by the mean ($n = 23$). Values expressed as percent total length (TL), except for TL given in mm.

	Holotype	Paratypes		Mean
	SAMC-F41923	Minimum	Maximum	
Total length (TL)	426	370	451	416.3
Precaudal length	78.6	77.2	81.2	79.1
Prenarial length	1.9	1.6	2.3	1.9
Prenarial length (direct)	2.8	2.6	3.8	3.3
Preoral length	9.4	9.2	11.5	9.9
Preorbital length	5.9	4.5	6.5	5.6
Preorbital length (direct)	6.3	5.8	7.1	6.6
Prespiracle length	11.7	11.1	12.6	11.8
Prespiracle length (direct)	12.2	11.6	13.6	12.6
Pregill length	18.3	16.0	18.3	17.1
Pregill length (direct)	17.1	16.8	19.2	17.7
Head length	21.6	20.2	23.3	21.6
Prepectoral length	21.1	19.3	23.2	20.8
Prepelvic length	52.8	50.8	54.6	52.6
Snout-anterior vent length	55.2	54.4	58.2	56.3
Pre-1st dorsal fin length	32.9	29.4	34.0	31.4
Pre-2nd dorsal fin length	62.2	58.3	62.8	60.6
Interdorsal fin length	23.7	22.1	25.9	24.3
2nd dorsal-caudal length	12.7	10.3	13.3	12.1
Pectoral-pelvic length	25.4	24.9	29.5	27.4
Pelvic-caudal length	19.5	15.7	20.8	18.6
Orbit length	4.0	3.1	4.5	3.8
Orbit height	3.3	2.1	3.4	2.7
Interorbital length	7.5	6.0	7.5	6.8
Nostril length	2.1	1.8	2.7	2.3
Internarial length	3.1	2.4	3.2	2.8
Anterior nasal flap length	0.9	0.5	1.0	0.9
Spiracle length	1.9	0.9	2.3	1.4
Eye-spiracle length	1.6	1.2	2.5	1.9
Mouth length	2.1	1.0	2.8	1.8
Mouth width	6.6	5.3	8.2	6.6
Upper labial furrow length	1.4	1.3	2.4	1.6
Lower labial furrow length	1.2	0.9	1.7	1.2
Intergill length	4.5	3.9	5.5	4.6
1st gill height	1.6	1.0	2.8	1.9
2nd gill height	1.4	1.0	2.6	1.7
3rd gill height	1.4	1.1	2.6	1.6
4th gill height	1.4	0.9	2.1	1.4
5th gill height	1.2	0.9	1.8	1.3
Head height	7.3	5.3	9.1	6.6
Head width	9.4	8.2	10.5	9.3
Abdomen width	7.0	4.9	9.6	7.5
Trunk height	8.7	5.2	9.8	7.9
Trunk width	8.0	5.4	9.3	7.9
Tail width	4.2	3.2	6.2	4.1
Caudal peduncle height	2.6	2.0	2.6	2.3
Caudal peduncle width	2.1	1.7	2.6	2.1
Pectoral fin length	8.9	7.9	10.5	8.9
Pectoral fin anterior margin	8.0	7.1	10.4	8.5
Pectoral fin base	4.9	3.7	5.3	4.7
Pectoral fin height	5.2	3.8	6.4	5.2
Pectoral fin inner margin	4.5	3.4	5.3	4.4
Pectoral fin posterior margin	4.7	3.8	6.4	5.1
Pelvic fin length	11.3	9.2	11.3	10.6
Pelvic fin anterior margin	6.1	4.2	10.5	6.0
Pelvic fin base	5.9	4.7	8.5	6.0
Pelvic fin height	2.8	1.7	4.3	2.4
Pelvic fin inner margin	5.2	3.0	5.9	4.8
Pelvic fin posterior margin	4.7	4.2	6.9	5.7
Clasper length outer	6.1	5.9	7.6	5.9
Clasper length inner (taken at cloaca apex)	7.5	6.9	8.8	7.2
Clasper base width	1.9	1.1	2.4	1.6
1st dorsal fin length	8.0	7.2	9.3	8.3

Table 1 (continued)

	Holotype	Paratypes		Mean
	SAMC-F41923	Minimum	Maximum	
1st dorsal fin anterior length	5.9	5.0	8.0	6.2
1st dorsal fin base length	4.9	4.0	5.6	4.7
1st dorsal fin height	2.1	1.4	3.0	2.1
1st dorsal fin inner margin	3.1	2.4	4.7	3.5
1st dorsal fin posterior length	2.6	1.4	4.0	2.7
2nd dorsal fin length	10.6	10.6	14.5	12.2
2nd dorsal fin anterior margin	6.6	7.8	10.4	9.1
2nd dorsal fin base length	6.3	5.9	8.5	6.9
2nd dorsal fin height	2.6	2.6	4.6	3.9
2nd dorsal fin inner margin	4.2	4.0	6.4	5.3
2nd dorsal fin posterior length	4.5	3.8	6.8	5.2
Caudal fin dorsal margin length	20.0	18.8	22.1	20.2
Caudal fin lower pre-ventral margin length	9.6	7.2	11.1	9.4
Caudal fin fork width	6.6	6.5	8.3	7.3
Caudal fin fork length	9.6	7.3	10.5	9.4
Caudal fin lower post-ventral margin length	2.1	1.6	3.5	2.5
Caudal fin upper post-ventral margin length	7.5	6.4	8.7	7.6
Caudal fin subterminal margin length	3.8	2.4	4.6	3.7
Caudal fin terminal margin length	2.8	2.3	4.5	3.4
Caudal fin terminal lobe length	4.2	4.2	6.6	5.1
DPI = 1st dorsal fin midpoint pectoral fin insertion	9.4	6.9	10.0	8.7
1st dorsal fin midpoint pectoral fin free rear tip	5.2	3.0	6.0	4.4
DPO = 1st dorsal fin midpoint pelvic fin origin	16.2	17.3	21.0	18.6
PDI = pelvic fin midpoint 1st dorsal fin insertion	15.7	18.3	20.7	18.9
PDO = pelvic fin midpoint 2nd dorsal fin origin	8.0	2.7	7.6	5.0
1st dorsal fin spine length	2.6	1.2	3.3	2.1
1st dorsal fin spine naked length	1.2	0.9	1.8	1.2
2nd dorsal fin spine length	4.7	3.7	6.2	4.7
2nd dorsal fin spine naked length	3.1	2.8	3.8	3.2
Flank marking anterior branch length	10.6	9.5	12.4	10.7
Flank marking posterior branch length	8.0	6.7	10.6	8.6
Posterior marking width at level D2 base end	3.5	2.5	4.0	3.3
Total flank marking length	21.4	19.8	23.8	21.6
Flank marking base length	2.3	1.6	3.1	2.4
Caudal base marking length	4.2	2.6	4.9	4.0
Central caudal marking length	7.3	5.9	9.8	8.0

margin black. No blotch or spot on caudal peduncle. Caudal fin mostly brownish, with distinct black tip, lower and upper post-ventral margins becoming whitish, with a distinctly lighter lower lobe. Ventral surface similarly a dark brown to black around mouth, belly, between pelvic fin origins and lower caudal origin. Upper lip with a clear median groove appearing as a white line flanked by one or two lines on either side (Fig. 1b), clearly visible in fresh material but becoming progressively less noticeable over time in preserved specimens. After preservation coloration is mostly a uniform black to dark charcoal gray, and with eyeball uniformly black (Fig. 2). Although the new species and *E. sculptus* are easily distinguished by color in life and in freshly preserved specimens, they become nearly indistinguishable by coloration with increased preservation time.

Size Maximum length attained by males 451 mm TL, with minimum maturity of 375 mm TL. Females attained a maximum length of 509 mm TL, but size at maturity undetermined.

Distribution *Etmopterus broseii* sp. nov. is known to be sympatric with *E. sculptus* and most currently known specimens of *E. broseii* sp. nov. from South Africa were captured together with *E. sculptus*. Based on confirmed specimens in the present study *E. broseii* sp. nov. occurs from the west coast of South Africa to the western Agulhas Bank from 480–850 m depth, off southern Mozambique in 980–1000 m depth and on the southern end of the Madagascar Ridge, southwestern Indian Ocean and at Walters Shoal from about 896–1200 m depth (Fig. 7). Its range may be more extensive, and with improved differentiation between these two species, it can be expected to occur further east along the south coast of South Africa and possibly over a wider area.

Etymology The species is named after the late Barrie Rose, friend and colleague for many years, an excellent naturalist who made a life-long study of vertebrate diversity and a love of chondrichthyans, and affectionately known as “Brose” to

Table 2 Nominal *Etmopterus* species within each of the four recognized clades after Straube et al. (2010), but modified and updated (present study).

<i>E. gracilispinis</i> clade
<i>Etmopterus gracilispinis</i> Krefft, 1968
<i>Etmopterus perryi</i> Springer & Burgess, 1985
<i>Etmopterus polli</i> Bigelow, Schroeder, & Springer, 1953
<i>Etmopterus robinsi</i> Schofield & Burgess, 1997
<i>Etmopterus schultzi</i> Bigelow, Schroeder, & Springer, 1953
<i>Etmopterus virens</i> Bigelow, Schroeder, & Springer, 1953
<i>E. lucifer</i> clade
<i>Etmopterus alphus</i> Ebert, Straube, Leslie, & Weigmann, 2016
<i>Etmopterus brachyurus</i> Smith & Radcliffe, 1912
<i>Etmopterus brosei</i> sp. nov. Ebert, Leslie, & Weigmann
<i>Etmopterus bullisi</i> Bigelow & Schroeder, 1957
<i>Etmopterus burgessi</i> Schaaf-Da Silva & Ebert, 2006
<i>Etmopterus decacuspoidatus</i> Chan, 1966
<i>Etmopterus dislineatus</i> Last, Burgess, & Séret, 2002
<i>Etmopterus evansi</i> Last, Burgess, & Séret, 2002
<i>Etmopterus lucifer</i> Jordan & Snyder, 1902
<i>Etmopterus marshae</i> Ebert & van Hees, 2018
<i>Etmopterus mollerii</i> (Whitley, 1939)
<i>Etmopterus pycnolepis</i> Kotlyar, 1990
<i>Etmopterus samadae</i> White, Ebert, Mana, & Corrigan, 2017
<i>Etmopterus sculptus</i> Ebert, Compagno, & De Vries, 2011
<i>E. pusillus</i> clade
<i>Etmopterus bigelowi</i> Shirai & Tachikawa, 1993
<i>Etmopterus carteri</i> Springer & Burgess, 1985
<i>Etmopterus caudistigmus</i> Last, Burgess, & Séret, 2002
<i>Etmopterus fusus</i> Last, Burgess, & Séret, 2002
<i>Etmopterus jounji</i> Knuckey, Ebert, & Burgess 2011
<i>Etmopterus pseudospualiolus</i> Last, Burgess, & Séret, 2002
<i>Etmopterus pusillus</i> (Lowe, 1839)
<i>Etmopterus sentosus</i> Bass, D'Aubrey, & Kistnasamy, 1976
<i>Etmopterus splendidus</i> Yano, 1988
<i>Etmopterus villosus</i> Gilbert, 1905
<i>E. spinax</i> clade
<i>Etmopterus benchleyi</i> Vásquez, Ebert, & Long, 2015
<i>Etmopterus compagnoi</i> Fricke & Koch, 1990
<i>Etmopterus dianthus</i> Last, Burgess, & Séret, 2002
<i>Etmopterus granulosus</i> (Günther, 1880)
<i>Etmopterus hillanus</i> (Poey, 1861)
<i>Etmopterus litvinovi</i> Parin & Kotlar, 1990
<i>Etmopterus parini</i> Dolganov & Balanov, 2018
<i>Etmopterus princeps</i> Collett, 1904
<i>Etmopterus spinax</i> (Linnaeus, 1758)
<i>Etmopterus unicolor</i> (Engelhardt, 1912)
<i>Etmopterus viator</i> Straube, 2011
Unassigned clade
<i>Etmopterus sheikoi</i> (Dolganov, 1986)

his friends. The proposed English common name is Barrie's Lanternshark.

Discussion

The *E. lucifer* clade is the largest of the four *Etmopterus* clades with 15 species, followed by the *E. pusillus* and *E. spinax* clades with 10 and 11 species each, respectively, and the *E. gracilispinis* clade with six species (Table 2). The *E. lucifer* clade has shown the highest increase in the number of species with eight species added over the past two decades,

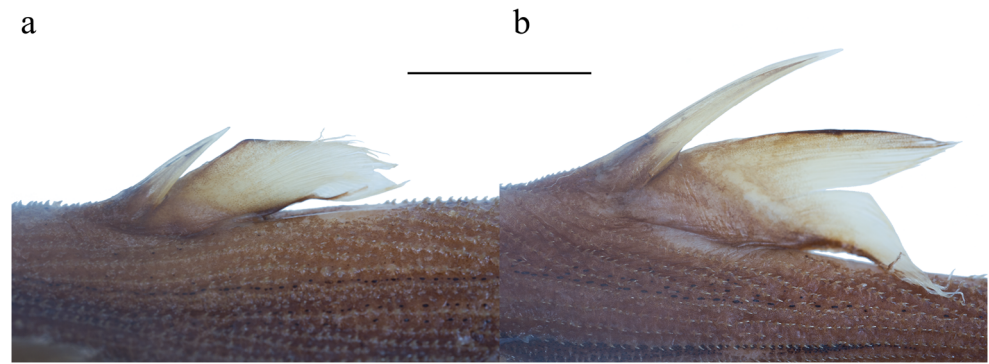
Table 3 Nominal *Etmopterus* species within each *E. lucifer* subclade based on relative flank marking branch, anterior and posterior, lengths (modified from Ebert and van Hees 2018).

<i>E. lucifer</i> subclade (anterior branch longer)
<i>Etmopterus brosei</i> sp. nov. Ebert, Leslie, & Weigmann
<i>Etmopterus lailae</i> Ebert, Papastamatiou, Kajiura & Wetherbee, 2017
<i>Etmopterus lucifer</i> Jordan & Snyder, 1902
<i>Etmopterus sculptus</i> Ebert, Compagno & De Vries, 2011
<i>E. mollerii</i> subclade (posterior branch longer)
<i>Etmopterus alphus</i> Ebert, Straube, Leslie & Weigmann, 2016
<i>Etmopterus brachyurus</i> Smith & Radcliffe, 1912
<i>Etmopterus bullisi</i> Bigelow & Schroeder, 1957
<i>Etmopterus decacuspoidatus</i> Chan, 1966
<i>Etmopterus dislineatus</i> Last, Burgess & Séret, 2002
<i>Etmopterus mollerii</i> (Whitley, 1939)
<i>Etmopterus samadae</i> White, Ebert, Mana & Corrigan, 2017
<i>E. burgessi</i> subclade (branch lengths equal)
<i>Etmopterus burgessi</i> Schaaf-Da Silva & Ebert, 2006
<i>Etmopterus evansi</i> Last, Burgess & Séret, 2002
<i>Etmopterus marshae</i> Ebert & van Hees, 2018
<i>Etmopterus pycnolepis</i> Kotlyar, 1990

while the *E. pusillus* and *E. spinax* clades have each added four species during this same timeframe. Most of the new species described were from the western and central Pacific ($n = 10$), followed by two species each from the northeastern Indian Ocean and southern African region (i.e., southeastern Atlantic and southwestern Indian oceans); a single new species was described from the southern Indian and southeastern Pacific oceans, respectively. The two new species described from southern Africa (*E. alphus*, *E. sculptus*) were both assigned to the *E. lucifer* clade.

The *E. lucifer* clade, as defined by Yamakawa et al. (1986), included those *Etmopterus* species with dermal denticles arranged in longitudinal rows along the flanks. The group originally included seven nominal species: *E. lucifer* Jordan & Snyder, 1902; *E. abernathyi* Garrick, 1957 (a junior synonym of *E. lucifer*); *E. brachyurus* Smith & Radcliffe, 1912; *E. bullisi* Bigelow & Schroeder, 1957; *E. granulosus* (Günther, 1880); *E. mollerii* (Whitley, 1939); and *E. villosus* Gilbert, 1905. Five additional species were later assigned to this group, including *E. burgessi* Schaaf-Da Silva & Ebert, 2006; *E. decacuspoidatus* Chan, 1966; *E. dislineatus* Last, Burgess, & Séret, 2002; *E. evansi* Last, Burgess, & Séret, 2002; and *E. pycnolepis* Kotlyar, 1990 (Straube et al. 2010). However, some species were found to be inconsistent with molecular and morphological data as reported by Straube et al. (2010). The prominent flank markings displaying conspicuous anterior and posterior branches similar to those found in *E. lucifer* were found to be a suitable character to unite this group. This finding was further supported by molecular data (Straube et al. 2010). Therefore, *E. granulosus*

Fig. 8 *Etmopterus sculptus*, dermal denticle coverage of first (a) and second (b) dorsal fins of non-type ZMH 26197, juvenile male, 203.2 mm TL (both images reversed). Scale bar: 1 cm



and *E. villosus* were removed from the *E. lucifer* clade, with the former being reassigned to the *E. spinax* clade and the latter being left unassigned to a clade due to missing information and a lack of morphological and molecular data (Straube et al. 2010), but with subsequent assignment to the *E. pusillus* clade. In recent years, five additional *Etmopterus* species have been described and assigned to the *E. lucifer* clade (Ebert and van Hees 2018), including *E. alphus*; *E. lailae* Ebert, Papastamatiou, Kajiura, & Wetherbee, 2017; *E. marshae* Ebert & van Hees, 2018; *E. samadiae* White, Ebert, Mana, & Corrigan, 2017; and *E. sculptus*. In addition to morphological data, molecular data further supported the assignment of *E. alphus*, *E. samadiae*, and *E. sculptus* (Ebert et al. 2016; White et al. 2017) to this clade; molecular data were unavailable for *E. lailae* and *E. marshae*.

Presently, there are eight species of *Etmopterus* recognized in the southern African region (Ebert and van Hees 2015; Ebert et al. 2016), including *E. alphus*, *E. bigelowi* Shirai & Tachikawa, 1993; *E. compagno* Fricke & Koch, 1990; *E. granulosus*; *E. pusillus* (Lowe, 1839); *E. sculptus*; *E. sentosus* Bass, D'Aubrey, & Kistnasamy, 1976, and *E. viator* Straube, 2011. In addition to the two *E. lucifer* clade species, three species each can be placed in the *E. pusillus* clade (*E. bigelowi*, *E. pusillus*, *E. sentosus*) and *E. spinax* clade (*E. compagno*, *E. granulosus*, *E. viator*). The placement of these

species into their respective clades is supported by molecular and morphological data (Straube et al. 2010, 2011, 2015).

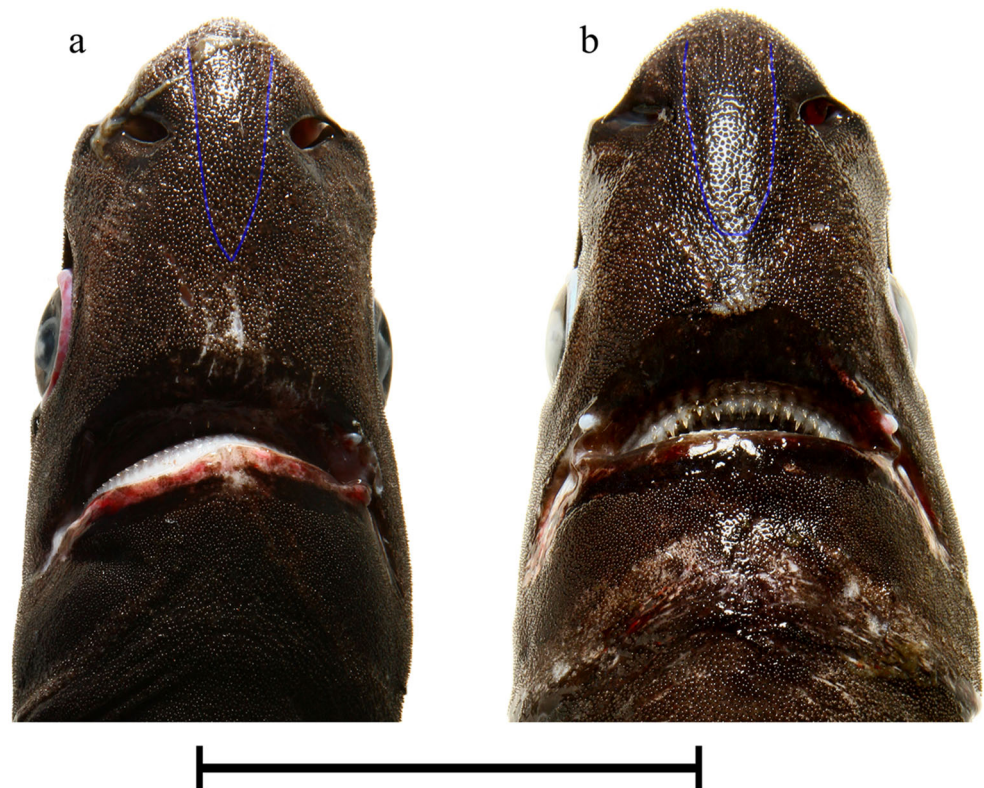
Recently, Ebert and van Hees (2018) examined and revised the *E. lucifer* clade redefining it into three subclades based on the relative branch lengths of the anterior and posterior flank markings (Table 3). These three subclades as defined by Ebert and van Hees (2018) are as follows: (1) *E. lucifer* subclade with the anterior branch of the flank marking being relatively longer than the posterior branch, (2) *E. molleri* subclade with the anterior branch of the flank marking being shorter than the posterior branch, and (3) *E. burgessi* subclade with the anterior and posterior branches of the flank markings being subequal in length. Examination of 14 of 15 *E. lucifer* clade holotypes, paratypes, syntypes, and non-types supports this arrangement. Although no molecular studies have directly addressed this classification, molecular results from several studies have shown support for this arrangement (Straube et al. 2010, 2013; Naylor et al. 2012; Ebert et al. 2016; White et al. 2017). Clades V and VI from Straube et al. (2010), in particular, show support for the separation of the *E. lucifer* and *E. molleri* subclades. Furthermore, Straube et al. (2013) found that *E. burgessi* formed a distinct cluster that was sister to the clade comprising *E. lucifer*.

The flank mark of *E. brose* sp. nov. has the anterior branch longer than the posterior branch, which places it into the

Fig. 9 Comparison of coloration of *Etmopterus brose* sp. nov. (a) and *E. sculptus* (b) fresh specimens prior to preservation. Scale bars: 10 cm



Fig. 10 Comparison of ampullae arrangement on ventral snout shape of *Etmopterus broseii* sp. nov. (**a**) and *E. sculptus* (**b**). Scale bar: 5 cm



E. lucifer subclade along with *E. lailae* from the central North Pacific Ocean, *E. lucifer* from the western North Pacific, and *E. sculptus* from the southern Africa region (Table 3). *Etmopterus broseii* sp. nov. is very similar morphologically to *E. sculptus* and until now has been misidentified with it. *Etmopterus broseii* sp. nov. can be separated from *E. sculptus* by the dorsal fin bases being densely covered in dermal denticles (Fig. 5) vs bare to few scattered denticles (Fig. 8) and by a combination of external morphological characteristics including body trunk showing very little contrast between the brownish-black dorso-lateral surfaces and blacker belly vs strong contrast (Fig. 9); although the contrast between dorso-lateral and ventral surfaces in *E. sculptus* fades over time with preservation making older preserved specimens of the two species virtually indistinguishable by color alone. In life, the dorsal trunk has a bronze sheen in strong light vs silvery sheen with purplish iridescence. Additionally, the ventral snout is evenly covered by dermal denticles and with ampullae arranged in a V-shape vs bare patch around nostrils and upper lip with ampullae arranged in a U-shape (Fig. 10). *Etmopterus broseii* sp. nov. further differs in the presence of three to five grooves on the upper lip, clearly visible as white lines in life and freshly preserved specimens, but becoming difficult to see over time with preservation vs absence of grooves. Also, the distance from snout tip to nasal opening is shorter in *E. broseii* sp. nov. than in *E. sculptus*, which accentuates the larger orbit of the former species, the pectoral fin ending is well short of the perpendicular line from the base

of the first dorsal fin spine vs free rear tips reaching or extending beyond, which gives the impression that the first dorsal fin is situated further back (posteriorly) in *E. broseii* sp. nov. than in *E. sculptus*. Meristic characteristics separating *E. broseii* sp. nov. from *E. sculptus* include slightly higher total vertebral (85–88 vs 78–85) and spiral valve turn (11 vs 8–9) counts.

Etmopterus broseii sp. nov. can be separated from the other two *E. lucifer* subclade species, *E. lailae* and *E. lucifer*, by geography (southeastern Atlantic and southwestern Indian Ocean vs central and northwestern Pacific Ocean) and a combination of characteristics, including posterior branch of the flank marking extends to about the end of, or beyond, the second dorsal-fin free rear tip, whereas in *E. lailae* and *E. lucifer* this branch does not reach the rear tip. Furthermore, the upper lobe of the caudal fin has a dark terminal band or spot, which is lacking in *E. lailae* and *E. lucifer*, and the number of spiral valve turns in *E. broseii* sp. nov. (11) is lower compared to *E. lailae* (14–16) and higher than in *E. lucifer* (8–9).

Conservation and research

The IUCN Red List of Threatened Species has assessed 36 of 42 lanternshark species as either least concern (22) or data deficient (14), with the remaining six species listed as not evaluated (IUCN 2020). All eight of the valid species known to occur in southern African waters are currently assessed as least concern. Most species' depth ranges extend beyond current bottom trawl and

longline fisheries in southern Africa, which gives them some refuge from these fisheries. However, all of these species are still a common bycatch component in the offshore demersal trawl fishery, and possibly in deep-sea longline fisheries (Da Silva et al. 2015).

Despite their common occurrence in bycatch of deep-sea fisheries, lanternsharks are poorly known and catch data are rarely recorded. Furthermore, species-specific identification and information are often not recorded due to a lack of identification guides. This lack of information inhibits governing

bodies from making informed conservation and management decisions. In order to implement more effective conservation and management policies, proper identification of non-targeted species is imperative. An updated regional taxonomic guide to deep-sea chondrichthyans would aid fishery observers in identifying non-retained, non-targeted species, which should help in monitoring population trends. Such identification tools will only come about by greater support for chondrichthyan taxonomic research into poorly known taxa such as the lanternsharks.

Key to the species of the *Etmopterus lucifer* clade of lanternsharks (modified after Ebert and van Hees 2018)

- 1 Lateral flank marking anterior and posterior branches nearly equal in length2 (*E. burgessi* subclade)
 - Lateral flank marking anterior and posterior branches dissimilar in length 5
- 2 Caudal fin without dark band at fin tip *E. burgessi* (Western North Pacific: Taiwan)
 - Caudal fin with dark band at fin tip 3
- 3 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)
 - Caudal peduncle with dark saddle; caudal fin with dark band across middle of upper lobe and at fin tip..... 4
- 4 Caudal fin ventral lobe and upper post-ventral margin mostly white to translucent
 - *Etmopterus evansi* (Eastern Indian Ocean: off northern Western Australia, Indonesia, Papua New Guinea)
 - Caudal fin ventral lobe and upper post-ventral margin mostly black
 - *Etmopterus marshallae* (Western North Pacific: Philippines)
- 5 Lateral flank marking anterior branch noticeably shorter than posterior branch in length 6 (*E. molleri* subclade)
 - Lateral flank marking anterior branch noticeably longer than posterior branch in length..... 12 (*E. lucifer* subclade)
- 6 Posterior branch of lateral flank marking extends past second dorsal fin free rear tip7
 - Posterior branch of lateral flank marking does not extend past second dorsal fin free rear tip 9
- 7 Flanks with elaborate pattern of conspicuous rows of dark dots and dashes
 - *Etmopterus dislineatus* (Southwestern Pacific: off northern Queensland, Australia)
 - Flanks without elaborate pattern of conspicuous rows of dark dots and dashes 8
- 8 Anterior (6.0–10.6%) and posterior (9.3–12.7%) flank branches relatively shorter
 - *Etmopterus alphas* (Southwestern Indian Ocean: off Mozambique, Madagascar Ridge)
 - Anterior (8.0–11.5%) and posterior (11.0–15.4%) flank branches relatively longer.....
 - *Etmopterus molleri* (Western Pacific: eastern Australasia to New Zealand)
- 9 Caudal fin lacks a band or spot 10
 - Caudal fin with a band or spot 11
- 10 Upper teeth with 4 or 5 pairs of cusplets on each side; dermal denticles not arranged in rows
 - *Etmopterus decacuspидatus* (Western North Pacific: South China Sea)
 - Upper teeth with less than 4 or 5 pairs of cusplets on each side; dermal denticles arranged in rows
 - *Etmopterus bullisi* (Western Atlantic)
- 11 Length of posterior flank marking 11.4–12.6% TL, flank marking base length 2.8–3.4% TL, and length of caudal base marking length from tip of anterior finger to tip of posterior finger 7.0–7.9% TL
 - *Etmopterus brachyurus* (Western Pacific: Japan to Philippines, possibly Australia)
 - Length of posterior flank marking 9.1–11.2% TL, flank marking base length 3.5–4.9% TL, and length of caudal base marking length from tip of anterior finger to tip of posterior finger 10.6–14.1% TL
 - *Etmopterus samadidae* (Western Pacific: Papua New Guinea)
- 12 Body slender; ventral snout surface between nostrils bare, without dermal denticles; central caudal marking length 6%TL or more
 - *Etmopterus lailae* (Central North Pacific: Hawaiian Islands)
 - 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..... 13

- 13 Flank marking anterior branch nearly twice the length of the posterior branch; area between nostrils without small bare patches *Etmopterus lucifer* (Western North Pacific: Japan to Philippines)
- Flank marking anterior branch only slightly longer than posterior branch; area between nostrils with small bare patches 14
- 14 Color (before preservation) of flank silvery with purplish sheen, sharply demarcated from black abdomen; ventral snout surface with ampullae arranged in U-shape and sparsely covered with dermal denticles; dorsal fins mostly bare of dermal denticles *Etmopterus sculptus* (Southeast Atlantic and Southwest Indian Ocean: Namibia to southern Mozambique, and Madagascar Ridge)
- Color (before preservation) of flank dark blackish brown, not demarcated from black abdomen; ventral snout surface with ampullae arranged in V-shape and evenly covered with dermal denticles; dorsal fins densely covered with dermal denticles *Etmopterus brosei* sp. nov. (Southeast Atlantic and Southwest Indian Ocean: South Africa, southern Mozambique and Madagascar Ridge)

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for animal testing, animal care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability All data generated or analyzed during this study are included in this published article.

Author contribution DAE and RWL conceived and designed the research; DAE, RWL, and SW conducted examinations; DAE and RWL wrote the initial version of the manuscript; and DAE, RWL, and SW revised and approved the manuscript.

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