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Description of a new lanternshark species from the South China Sea, with additional description of *Etmopterus sheikoi* from Taiwanese waters (Squaliformes: Etmopteridae)

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Abstract. A new species of the lanternshark genus *Etmopterus* Rafinesque, 1810 is described based on 23 specimens collected from the South China Sea. The new species, *Etmopterus lii*, being assigned to the *E. lucifer* group, differs from all other congeners, except *E. sheikoi*, by having a combination of the following morphological characters: dermal denticles frustum-shaped, giving a smooth texture of skin; pelvic-fin flank marking consists of anterior and posterior branches; and lower-jaw teeth multicuspid in mature males. It differs from *E. sheikoi* by having a shorter snout, a more anterior position of second dorsal fin relative to the pelvic-fin flank marking base, a thinner posterior branch of pelvic-fin flank marking, a shorter posterior caudal-fin marking, relatively larger gill slits, fewer number of teeth, and relatively fewer vertebrae. The mean K2P distance between the two species based on NADH2 sequences is 11.0%. *Etmopterus sheikoi* is redescribed herein based on additional specimens collected from Taiwan. We provide the first morphological description of lower-jaw tooth of mature females, and reveal the first case of sexual dimorphism in tooth count within Squaliformes. The species-group status of *E. sheikoi* is discussed.

Key words. elasmobranch, deep sea, taxonomy, new species, redescription

INTRODUCTION

The lanternshark genus *Etmopterus* is one of the most diverse groups among all extant shark genera, comprising 41 valid species (Pollerspöck & Straube, 2023). They are widely distributed from tropical to subpolar oceans, at a depth range of 50–4,500 m (Ebert et al., 2021a). They are mostly small sharks, including the smallest known shark species, i.e., the dwarf lanternshark *E. perryi* Springer & Burgess, 1985 (21 cm TL, Ebert et al., 2021a), while some larger species grow up to about 100 cm TL [e.g., *E. granulosus* (Günther, 1880), 102 cm TL, Ebert et al., 2021a]. The vernacular name 'lanternshark' comes from their ability to produce blue-green light, known as bioluminescence, which has received increased attention in recent years (e.g., Claes et al., 2010; Claes & Mallefet, 2015; Duchatelet et al., 2020).

Straube et al. (2010) divided the genus into four clades based on multiple genetic markers: the *E. gracilispinis* clade, the *E. lucifer* clade, the *E. pusillus* clade, and the *E. spinax* clade. The *E. lucifer* clade contains 14 species, representing the most speciose group (Ebert et al., 2021b). Members of this group mainly share a characteristic flank marking shape, i.e., long, thin anterior branches and long thin, linear posterior branches (Straube et al., 2010). The linear arrangement of dermal denticles is also recognised as another characteristic of this group in some studies (e.g. White et al., 2017; Ebert et al., 2021b).

The rasptooth dogfish *Etmopterus sheikoi* (Dolganov, 1986), known only from the northwestern Pacific, was initially described as a member of the etmopterid genus *Centroscyllium* Müller & Henle, 1841. Later, Shirai & Nakaya (1990) erected the genus *Miroscyllium* for *C. sheikoi* based on its unique ontogenetic change of dentition from *Etmopterus*-like to *Centroscyllium*-like. Subsequently, Straube et al. (2010) synonymised *Miroscyllium* with *Etmopterus* based on both morphology and genetics: morphologically, *E. sheikoi* has *Etmopterus*-type lower-jaw dentition (unicuspid and blade-like) in its immature stage; and a short eye-stalk; genetically, *Miroscyllium* is deeply clustered within *Etmopterus*, which renders the latter paraphyletic. However, Straube et al. (2010) did not assign *E. sheikoi* to the *E. lucifer* clade, as they considered its flank-marking shape to closely resemble the shape of the species from the *E. pusillus* clade. To date, the intrageneric placement of this species is still uncertain (Ebert et al., 2013; Straube et al., 2013; Ebert et al., 2021a, 2021b). Despite many new etmopterid species descriptions

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in the 40 years since *E. sheikoi* was described, the species has rarely been discussed, pending a full redescription.

Recently, several *Etmopterus* specimens were collected in the bycatch of Taiwanese offshore bottom trawlers operating in the South China Sea. These specimens were similar to *E. sheikoi*, yet they differed in several aspects, leading us to suspect that these specimens may actually present a species new to science. In the present study, this new species is formally described. We also redescribe the poorly known *E. sheikoi* from Taiwanese waters, and comparisons between the two similar species are provided.

MATERIAL AND METHODS

The specimens were obtained as bycatch from the commercial bottom trawlers operating in various areas depending on the species: the South China Sea (proposed new species); northeastern and southwestern Taiwanese waters (*E. sheikoi*). The specimens of the proposed new species were frozen on board before being sampled. All specimens were tissue-sampled from below the second dorsal-fin base and preserved in 95% ethanol for subsequent DNA extraction and molecular analysis. Voucher specimens were then fixed in 10% formalin solution prior to preservation in 70% ethanol solution. The maturity of female specimens without umbilical scar were determined by observing the gonads through a small cut at the right lateral side of the abdomen. Methods for taking measurements generally followed Last et al. (2002), with measurements directly taken by either digital callipers or a tape ruler (precision=0.1 mm). Abbreviations in terminology mostly followed White et al. (2017). Proportional measurements are expressed as percentage of TL. X-rays of the specimens were taken in various institutions: National Taiwan Ocean University's (NTOU) Department of Aquaculture, National Museum of Marine Biology and Aquarium (NMMBA), Taiwan, and the Smithsonian Institution (USNM), USA. The specimens were either deposited in the Pisces collection of Academia Sinica (ASIZP), Taiwan, or in the Pisces collection of NMMBA (NMMB-P). Data of the holotype of *E. sheikoi* was obtained from Dolganov (1986). Comparative materials of *E. bigelowi* Shirai & Tachikawa, 1993, *E. lucifer* Jordan & Snyder, 1902, *E.* cf. *molleri* (Whitley, 1939) (sensu Ebert et al., 2013), and *E. pusillus* (Lowe, 1839) were examined from the USNM and the Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University (EBFS), respectively. The latter three species were also included in the molecular analysis.

We used the term 'group' instead of 'clade' in the subsequent parts of the study as the phylogenetic position of the proposed new species is uncertain.

Molecular analysis. DNA barcoding with the mitochondrial NADH dehydrogenase subunit 2 (NADH2) marker was conducted for identification of the proposed new species. DNA was extracted with the EasyPure genomic DNA mini-kit EP500 (Bioman, Taiwan) according to the manufacturer's recommendations. An approximately 1,200 bp fragment was PCR-amplified, using the primers ILEM-Mustelus (5′-AAG-GAC-CAC-TTT-GAT-AGA-GT-3′) and ASN-Mustelus (5′-AAC-GCT-TAG-CTG-TTA-ATT-AA-3′) (Naylor et al., 2005). Each 15 µl mixture contained 7.5 µl of PowerAmp 2X PCRmix-Green buffer (Bioman), 0.6 µl of each primer, 1 µl of template DNA, and 5.3 µl of ddH^2O. The mixture was denatured at 94°C for 3 minutes, then subjected to 35 cycles of denaturation at 94°C for 30 seconds, annealing at 48°C for 30 s, and finally extension at 72°C for 90 seconds, and finally a single extension at 72°C for 10 minutes. The PCR product was purified and sequenced by Genomics (Xizhi, Taiwan).

The resulting DNA sequences were processed using Bioedit v. 7.2.5 (USA). The sequences of *E. alphus* Ebert, Straube, Leslie & Weigmann, 2016 (GN11825, GN11826), *E. bigelowi* (GN3582, GN5026), *Centroscyllium fabricii* Reinhardt, 1825 (GN6558) and *Trigonongathus kabeyai* Mochizuki & Ohe, 1990 (GN12280) were downloaded from Genbank (www.ncbi.nlm.nih.gov/genbank/) for reconstruction of a phylogenetic tree. The subsequent analyses were all conducted in MEGA 11. The sequences were aligned using the algorithm 'MUSCLE'. The alignment was translated to amino acids to check for stop codons. A maximum likelihood phylogenetic tree based on the best-fitting General Time Reversible model (GTR) with Γ substitution (Tamura & Nei, 1993) determined by the best-fitting substitution model for phylogenetic inference (minimum bias corrected Akaike information criterion, AICc, Hurvich & Tsai, 1989) was reconstructed. To determine the statistical support on nodes, bootstrapping with 500 pseudoreplicates was performed and plotted on the tree. The average interspecific genetic distances were calculated using a K2P model. *Centroscyllium fabricii* and *T. kabeyai* were selected as outgroups.

RESULTS

Molecular analysis. The length of NADH2 sequences ranged from 1,043–1,044 bps, where 1,043 bps was used to reconstruct the phylogenetic tree and to calculate genetic distances. The maximum-likelihood tree shows monophyletic clades formed by the undescribed species and *E. sheikoi*, respectively (Fig. 1). The relationships in the tree are well-supported, with most of the bootstrap values reaching at least 90%. The intra- and interspecific K2P distance is shown in Table 1. The pairwise K2P distances between *Etmopterus* (3.5–17.4%) are lower than between *Etmopterus* and other genera (17.7–21.5%). The undescribed species is closest to *E. alphus*, with an average K2P distance of 3.5%, while *E. sheikoi* is closely related to *Etmopterus lucifer*, with an average K2P distance of 9.8%. Both the undescribed species and *E. sheikoi* clustered within the species of the *E. lucifer* group sensu Straube et al. (2010).

Table 1. Intra- (*Etmopterus lii*, new species and *E. sheikoi*) and interspecific K2P distance based on NADH2 sequences for selected *Etmopterus* species. Values in bold represent intraspecific distances.

	***E. lii*, new species**	***E. alphus***	***E. lucifer***	***E.* cf. *molleri***	***E. sheikoi***	***E. bigelowi***	***E. pusillus***	***C. fabricii***
E. lii, new species	**0.001**							
E. alphus	0.035							
E. lucifer	0.051	0.056						
E. cf. *molleri*	0.114	0.118	0.106					
E. sheikoi	0.110	0.107	0.098	0.113	**0.001**			
E. bigelowi	0.151	0.153	0.152	0.161	0.163			
E. pusillus	0.154	0.155	0.153	0.170	0.174	0.080		
C. fabricii	0.180	0.180	0.181	0.188	0.177	0.188	0.207	
T. kabeyai	0.207	0.202	0.198	0.202	0.195	0.195	0.215	0.204

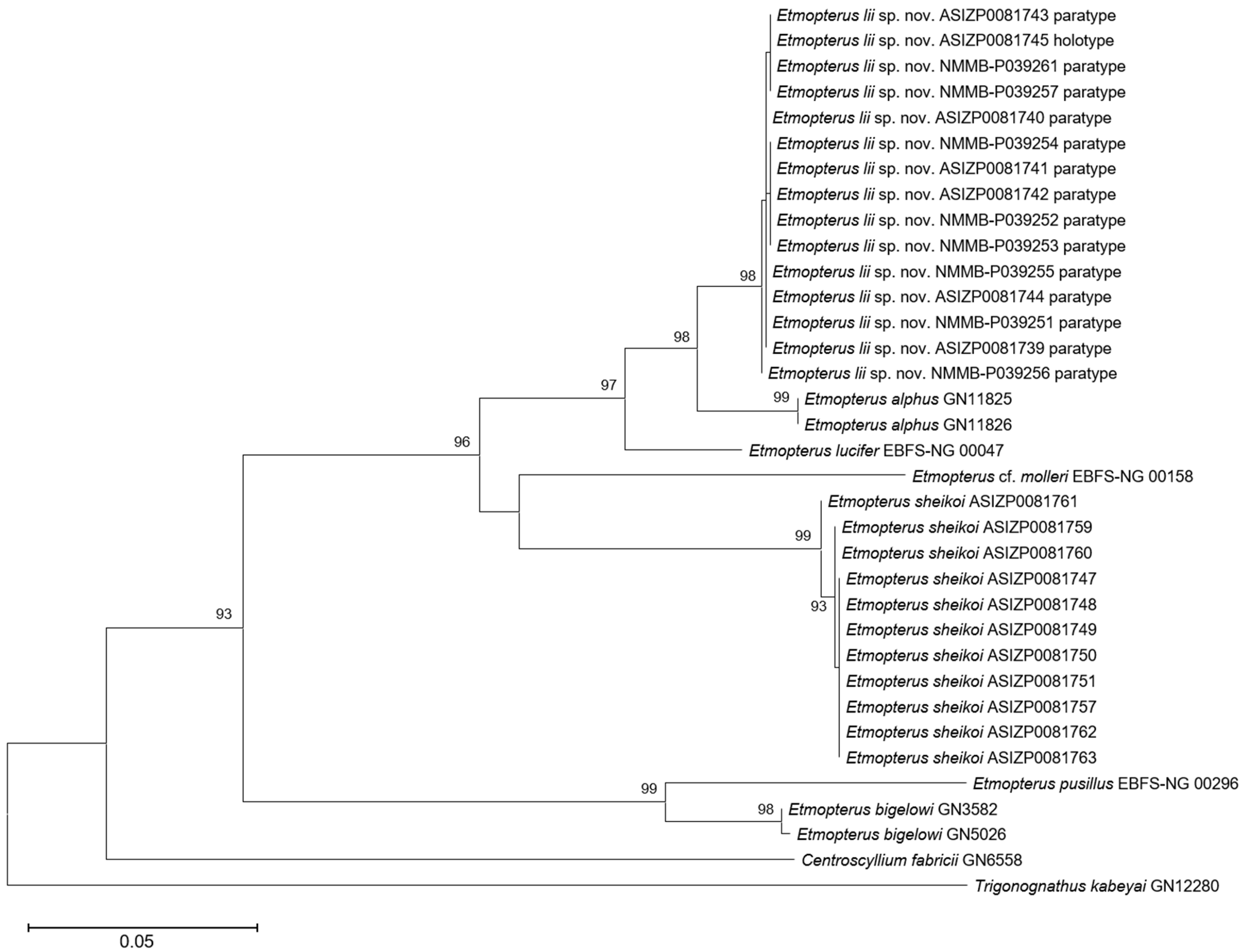

Fig. 1. The maximum likelihood phylogenetic tree reconstructed by the GTR+Γ model with 500 bootstraps pseudoreplicates based on NADH2 sequences of selected species of *Etmopterus*. Numbers at branches represent bootstrap support values. Bootstrap values below 70 are not shown.

Fig. 2. Lateral view of *Etmopterus lii*, new species, when fresh (after freezing). A, holotype, ASIZP0081745, mature male, 341 mm TL; B, paratype, ASIZP0081742, immature female, 381 mm TL. Scale bar=10 mm.

TAXONOMY

Family Etmopteridae

***Etmopterus lii*, new species**
Li's lanternshark
(Figs. 2, 3A, B, 4, 5A, 6A, C, 7–8; Tables 1–3)

Holotype. ASIZP0081745, 341 mm TL, mature male, South China Sea (ca. 19° N, 114° E), ca. 500 m depth, 12 March 2023.

Paratypes. 22 specimens: ASIZP0081739, 129 mm TL, immature male, ASIZP0081740, 252 mm TL, immature male, South China Sea (ca. 19° N, 114° E), ca. 500 m depth, 25 March 2022, C.-H. Lin; ASIZP0081741, 143 mm TL, immature female, South China Sea (ca. 19° N, 114° E), ca. 500 m depth, 31 May 2022; ASIZP0081742, 381 mm TL, immature female, ASIZP0081743, 301 mm TL, immature male, ASIZP0081744, 325 mm TL, mature male, collected with the holotype; NMMB-P039251, 127 mm TL, immature male, NMMB-P039252, 119 mm TL, immature female, NMMB-P039253, 228 mm TL, immature female, South China Sea (ca. 19° N, 114° E), ca. 500 m depth, 25 March 2022; NMMB-P039254, 176 mm TL, immature female, NMMB-P039255, 231 mm TL, immature male, South China Sea (ca. 19° N, 114° E), ca. 500 m depth, 25 April 2022; NMMB-P039256, 195 mm TL, immature male, NMMB-P039257, 126 mm TL, immature male, South China Sea (ca. 19° N, 114° E), ca. 500 m depth, 13 May 2022; NMMB-P039258, 353 mm TL, immature female, NMMB-P039259, 361 mm TL, immature female, NMMB-P039260, 335 mm TL, immature female, NMMB-P039261, 321 mm TL, mature male, NMMB-P039262, 288 mm TL, immature male, NMMB-P039263, 271 mm TL, immature male, NMMB-P039264, 315 mm TL, immature male, NMMB-P039265, 325 mm TL, mature male, NMMB-P039266, 332 mm TL, mature male, collected with the holotype.

Diagnosis. A medium-sized species of *Etmopterus* differing from all other congeners except *E. sheikoi*, by having a combination of flat and frustum-shaped denticles, elongated anterior and posterior lateral flank markings, and multicuspid lower jaw teeth in mature males. It differs from *E. sheikoi* by having a much narrower posterior flank marking, the shape and position of the caudal base marking, the length of posterior caudal marking, relatively larger gill slits, relatively more monospondylous, precaudal and total centra.

Description. Measurements are listed in Table 2. Values are expressed as a percentage of total length (TL) for the holotype, followed by the range of values for 22 paratypes in parentheses.

Body fusiform (Fig. 2), trunk sub-cylindrical, width 78.5 (36.9–88.3) % height; abdomen longer than lower caudal peduncle, pectoral-pelvic space 144.5 (102.5–193.5) % pelvic-caudal space; head subconical, length 24.3 (23.1–27.1) % TL, slightly depressed, height 80.6 (61.0–115.8) % width. Snout moderately long (very long in some paratypes), preorbital length 7.0 (6.1–8.7) % TL, 28.8 (25.0–33.8) % head length, 160.6 (128.5–215.9) % orbit length; snout bluntly rounded to slightly pointed in lateral view (Fig. 3A, B), narrowly rounded in dorsal view. Eyes oval, orbit width 57.8 (46.4–78.6) % height; orbits with both anterior and posterior notches; eyes narrowly spaced, interorbital width 73.8 (59.3–85.8) % head width, orbit length 60.2 (51.0–80.5) % interorbital width. Spiracles small, bean-shaped, length 34.2 (21.8–45.3) % orbit length, 6.1 (3.7–9.8) % head length. Nostrils oblique, length 71.3 (59.3–135.5) % internarial width, 45.2 (35.7–71.6) % orbit length; anterior nasal flap narrowly triangular, tip just reaching the nasal opening, length 40.7 (22.2–61.7) % nostril width. Gill openings large, nearly straight, intergill length 4.7 (2.4–7.8) % TL, gill-slits height 1.6–1.8 (1.3–3.0) % TL. Mouth broad, length 99.0 (73.0–173.4) % width, very slightly arched.

Table 2. Morphometric and meristic data for the holotype and ranges for the 22 paratypes of *Etmopterus lii*, new species, and the holotype (data obtained from Dolganov, 1986) and ranges for 17 non-types. * indicates values that are out of the range of non-types; ^ indicates values reproduced in the present study.

	***Etmopterus lii*, new species**			***Etmopterus sheikoi***		
	Holotype	Paratypes n=22		Holotype	Non-types n=17	
Total length (mm)	341.0	191.1	381.0	425.0	148.6	478.0
Measurements (%TL)						
Precaudal length	76.0	71.1	77.7	–	71.1	77.4
Prenarial length	2.9	2.0	4.5	–	2.5	4.0
Preoral length	9.7	4.4	12.5	12.0	9.8	14.2
Preorbital length	7.0	6.1	8.7	8.0	8.0	10.3
Prespiracle length	13.4	13.1	16.0	–	12.7	17.3
Prebranchial length	18.9	18.0	21.3	9.1*	18.2	22.5
Head length	24.3	23.1	27.1	–	22.6	27.2
Prepectoral length	23.3	22.3	26.4	22.8	22.2	26.4
Prepelvic length	51.7	18.3	55.9	49.6	46.5	50.5
Snout–anterior vent length	56.1	49.2	60.0	–	51.3	55.0
Pre D1 length	35.1	32.3	38.6	32.9	31.1	35.5
Pre D2 length	60.2	53.4	63.4	–	56.2	62.7
Interdorsal space	20.0	15.7	20.3	21.4	17.8	24.2
D2-caudal space	10.2	8.9	14.2	11.3	10.8	14.8
Pectoral-pelvic space	23.5	18.4	26.1	–	18.4	23.4
Pelvic-caudal space	16.3	13.5	19.8	17.2	16.9	21.1
Orbit length	4.4	3.8	5.7	4.2	3.9	6.7
Orbit height	2.5	2.0	3.4	–	2.1	4.1
Interorbital space	7.2	6.5	7.8	5.9	6.0	8.9
Nostril width	2.0	2.0	3.4	–	1.2	2.8
Internarial length	2.8	0.8	3.8	2.6	2.0	3.8
Anterior nasal flap length	0.8	0.7	1.9	–	0.5	1.2
Spiracle length	1.5	1.0	2.4	–	0.9	1.4
Eye-spiracle space	2.1	1.8	5.9	–	1.6	2.2
Mouth length	5.8	4.7	8.2	–	4.5	7.7
Mouth width	5.8	3.8	8.0	–	4.7	6.1
Upper labial furrow length	4.3	2.7	4.8	–	2.4	5.1
Lower labial furrow length	2.1	1.6	5.2	–	1.4	3.8
Intergill length	4.7	2.4	7.8	–	3.8	5.7
1st gill slit height	1.8	1.6	3.0	1.4	0.8	1.8
2nd gill slit height	1.6	1.5	3.0	–	0.7	1.9
3rd gill slit height	1.7	1.4	2.7	–	0.7	1.7
4th gill slit height	1.8	1.4	2.8	–	0.7	1.6
5th gill slit height	1.6	1.3	2.6	1.4	0.7	1.6
Head height	7.9	5.4	9.8	–	6.2	8.3
Head width	9.8	8.3	12.2	9.6	8.6	10.5
Abdomen width	5.5	3.2	8.4	–	5.1	7.1
Trunk height	8.9	7.3	10.2	–	5.5	9.4
Trunk width	7.0	3.0	8.6	–	5.7	8.6
Tail width	3.1	2.3	3.9	–	3.0	3.9
Caudal peduncle height	2.5	1.8	3.4	–	2.4	21.5
Caudal peduncle width	2.1	1.6	10.4	–	1.8	8.2
Pectoral fin length	10.1	8.1	12.3	9.4	7.0	11.2
Pectoral fin anterior margin length	10.1	7.7	11.2	–	5.3	11.3
Pectoral fin base length	5.6	4.2	6.5	–	4.0	6.1
Pectoral fin height	6.1	4.1	7.0	–	4.5	7.5
Pectoral fin inner margin length	3.3	3.7	7.2	–	3.9	6.5
Pectoral fin posterior margin length	5.4	3.2	6.5	–	3.8	7.2
Pelvic fin length	10.7	7.3	11.3	–	6.4	11.5

	***Etmopterus lii*, new species**			***Etmopterus sheikoi***		
	Holotype	Paratypes n=22		Holotype	Non-types n=17	
Pelvic fin anterior margin length	7.1	3.5	8.5	–	4.8	6.5
Pelvic fin base length	6.1	3.6	6.7	6.1	4.4	7.8
Pelvic fin height	3.5	1.6	4.5	–	2.5	4.4
Pelvic fin inner margin length	5.0	2.0	5.7	–	2.4	5.7
Pelvic fin posterior margin length	5.7	2.1	6.1	–	3.1	7.5
Clasper length outer	3.1	0.5	3.3	–	0.8	2.1
Clasper length inner	8.3	3.6	8.7	–	3.8	7.5
Clasper base width	6.3	1.0	3.3	–	0.8	1.6
D1 length	12.0	9.6	12.3	4.7*	7.7	11.0
D1 anterior margin length	6.5	4.8	8.1	–	3.6	6.4
D1 base length	2.6	2.0	3.8	–	2.0	3.4
D1 height	3.5	1.9	4.1	3.3	2.3	3.3
D1 inner margin length	5.4	3.4	6.5	–	3.4	5.0
D1 posterior margin length	3.0	1.9	4.6	–	2.0	3.5
D2 length	12.3	11.2	15.2	7.1*	11.0	13.0
D2 anterior margin length	6.7	4.2	8.5	–	5.0	9.3
D2 base length	4.6	3.7	4.9	–	2.9	4.6
D2 height	4.3	3.2	5.0	4.9	2.7	5.0
D2 inner margin length	5.7	3.4	7.1	–	3.6	5.7
D2 posterior margin length	5.5	3.6	5.7	–	2.8	6.4
Caudal dorsal margin	23.5	19.5	27.0	21.2	19.3	26.1
Caudal fork width	11.6	9.3	11.7	–	6.6	12.5
Caudal fork length	12.9	11.6	14.8	–	9.1	12.2
Caudal preventral margin length	12.9	10.1	14.1	–	8.4	11.4
Caudal lower postventral margin	2.7	1.3	7.6	–	1.2	3.3
Caudal upper postventral margin	7.7	4.2	11.5	–	7.4	9.9
Caudal fin subterminal margin	2.7	1.3	5.9	–	2.3	5.3
Caudal fin terminal margin length	3.7	2.1	4.8	–	1.7	5.2
Caudal fin terminal lobe length	6.3	3.3	6.2	–	3.4	5.6
D1 midpoint–pectoral fin insertion	13.4	9.7	14.6	–	8.6	18.1
D1 midpoint–pelvic-fin origin	15.6	10.6	17.7	–	11.6	17.6
Pelvic-fin midpoint–D1 insertion	18.8	11.3	18.4	–	13.9	17.9
Pelvic-fin midpoint–D2 origin	5.9	4.8	7.7	–	5.3	9.1
D1 spine length	Broken	3.8	6.6	–	3.5	6.5
D1 exposed spine length	Broken	2.0	4.8	–	2.1	4.6
D2 spine length	8.1	6.0	11.2	–	6.9	10.1
D2 exposed spine length	5.5	4.9	9.3	–	4.8	7.1
Anterior flank marking length	9.2	7.3	10.3	–	5.6	11.3
Posterior flank marking length	5.6	3.5	7.9	–	3.7	7.1
Posterior flank marking width	0.9	0.5	1.1	–	1.5	2.3
Flank marking base length	4.3	2.9	5.2	–	3.8	7.2
Caudal base marking length	5.7	5.3	8.9	–	7.0	9.1
Posterior caudal marking	3.4	2.3	5.7	–	7.8	11.3
Counts						
Monospondylous centra	41	38	43	41*	42	45
Diplospondylous trunk centra	14	12	17	21*	14	20
Caudal centra	26	22	28	25	23	31
Precaudal centra	55	50	59	62^	58	64
Total centra	81	72	84	87^	85	93
Tooth count	23/30	21/27	25/32	55/52*	24/26	48/44

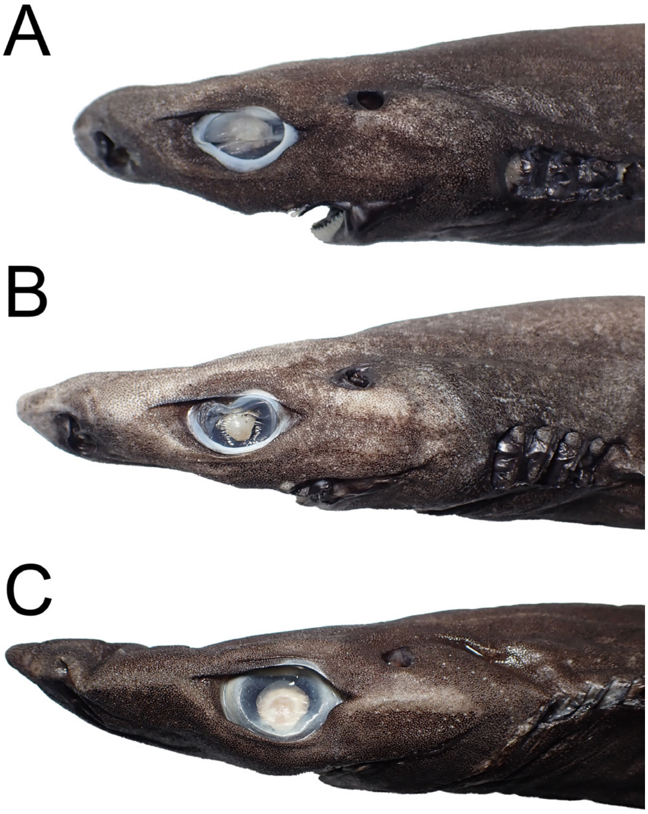

Fig. 3. Lateral view of snout of *Etmopterus lii*, new species (A, B) and *E. sheikoi* (C) after preservation. A, holotype, ASIZP0081745, mature male, 341 mm TL; B, paratype, ASIZP0081742, immature female, 381 mm TL; C, ASIZP0081761, mature female, 464 mm TL.

Teeth dissimilar in upper and lower jaw, with strong ontogenetic and sexual dimorphism (Fig. 4); upper teeth multicuspid, in three functional series, small, central cusp thick; immature males and females with two cusplets on each side of the cusp of upper teeth, while mature males have three cusplets; inner pair of cusplet longest, length about two-third of the central cusp; teeth in lower jaw unicuspid in immature individuals, in three series, one functional; lower teeth blade-like, with strongly oblique cusp; the cusps of lower teeth of mature males are flanked with two to three small cusplets on each side, the outer one minute. Tooth count of upper jaw 23 (21–25), lower jaw 30 (27–32), total count 53 (49–55).

First dorsal fin long and large, with a round apex, length of first dorsal fin 12.0 (9.6–12.3) % TL, origin posterior to pectoral-fin free rear tip; pre–first dorsal fin length 174.9 (181.3–235.5) % interdorsal space; first dorsal–fin spine (140.1–250.6) % first dorsal-fin height. Second dorsal fin larger than first dorsal fin, first dorsal-fin height 81.1 (51.9–91.4) % second dorsal-fin height; apex angular, posterior margin especially concave, free rear tip moderately elongated; second dorsal-fin length 12.3 (11.2–15.2) % TL, interdorsal space 196.9 (124.8–219.4) % dorsal-caudal space; second dorsal–fin spine long and curved; second dorsal-fin origin just posterior to insertion of pelvic fins. Interdorsal space 85.9 (61.9–86.7) % pre–pectoral length. Pectoral fins moderate, length 10.1 (8.1–12.3) % TL, with angular free rear tips, base narrow, 55.2 (42.4–66.8) % pectoral-fin length, posterior margin slightly concave. Pelvic fin narrowly triangular, height 33.0 (21.2–47.8) % length. Clasper of mature males rather long, inner length 77.2 (68.1–78.7) % pelvic-fin length. Caudal fin elongate, dorsal length 23.5 (19.5–27.0) % TL; caudal folk very poorly developed, lower postventral margin 34.3 (15.1–54.2) % upper postventral margin; terminal lobe broad.

Dermal denticles frustum-shaped, small, flat, very closely spaced, giving a smooth texture of the skin, not in defined rows (Fig. 5); denticles present on underside of snout, except for a narrow area around mouth; underside of gill slits with a V-shaped naked area, connecting gill slits between both lateral sides; inner margin of fins with very narrow naked area (inner margin of pectoral fin with a moderately large naked area in immature individuals); denticles present on fin bases, but absent on ceratotrichia.

Luminescent markings on head not distinct after frozen; head dorsal surface with a single line of dot-like markings, extending mid-dorsally from about the level of anterior fontanelle to the second dorsal-fin origin; ventral surface of pectoral fin with an arched marking, the tip not reaching the origin of pectoral-fin ceratotrichia; dash-like markings absent on lateral side. Pelvic-fin flank markings well defined in some specimens (sometimes difficult to inspect) (Fig. 6A, C), with elongated anterior and posterior branch; anterior branch rather short, length 9.2 (7.3–10.3) % TL, slender and straight, extending above pelvic–fin origin; posterior branch straight, thicker and shorter than anterior branch, length 60.8 (38.0–82.9) % length of anterior branch, width 0.9 (0.5–1.1) % TL, not extending beyond second dorsal-fin free rear tip; base of flank marking wide, base length 4.3 (2.9–5.2) % TL, origin slightly posterior to second dorsal-fin origin. Infracaudal marking barely visible, extending from the pelvic-fin flank marking base to about the same level of the posterior marking tip, not connecting to the caudal-fin base marking. Caudal-fin base marking thin, rod-like, oblique, moderately long, originate just before the lower caudal-fin origin, bifurcate after the origin, leaving a small black portion on the lower caudal-fin origin when viewed laterally. No central caudal-fin marking. Posterior caudal-fin marking short, its length 3.4 (2.3–5.7) % TL.

Vertebral counts: monospondylous 41 (38–43), diplospondylous precaudal 14 (12–17), caudal 26 (22–28), precaudal 55 (50–59), total 81 (72–84).

Colouration. After frozen, blackish grey to pale black, becoming dark black ventrally; transition between lateral and ventral sides not strongly demarcated. Dorsal midline without pale stripe; dash-like black markings absent on lateral side. Pectoral, pelvic and first dorsal fins generally dark grey to black, fin edges translucent, second dorsal fin black at fin base, becoming pale grey on ceratotrichia. Caudal fin dark grey, with black postventral margin. No dark blotch on caudal fin. No discernible blotch between infracaudal and caudal-fin base marking.

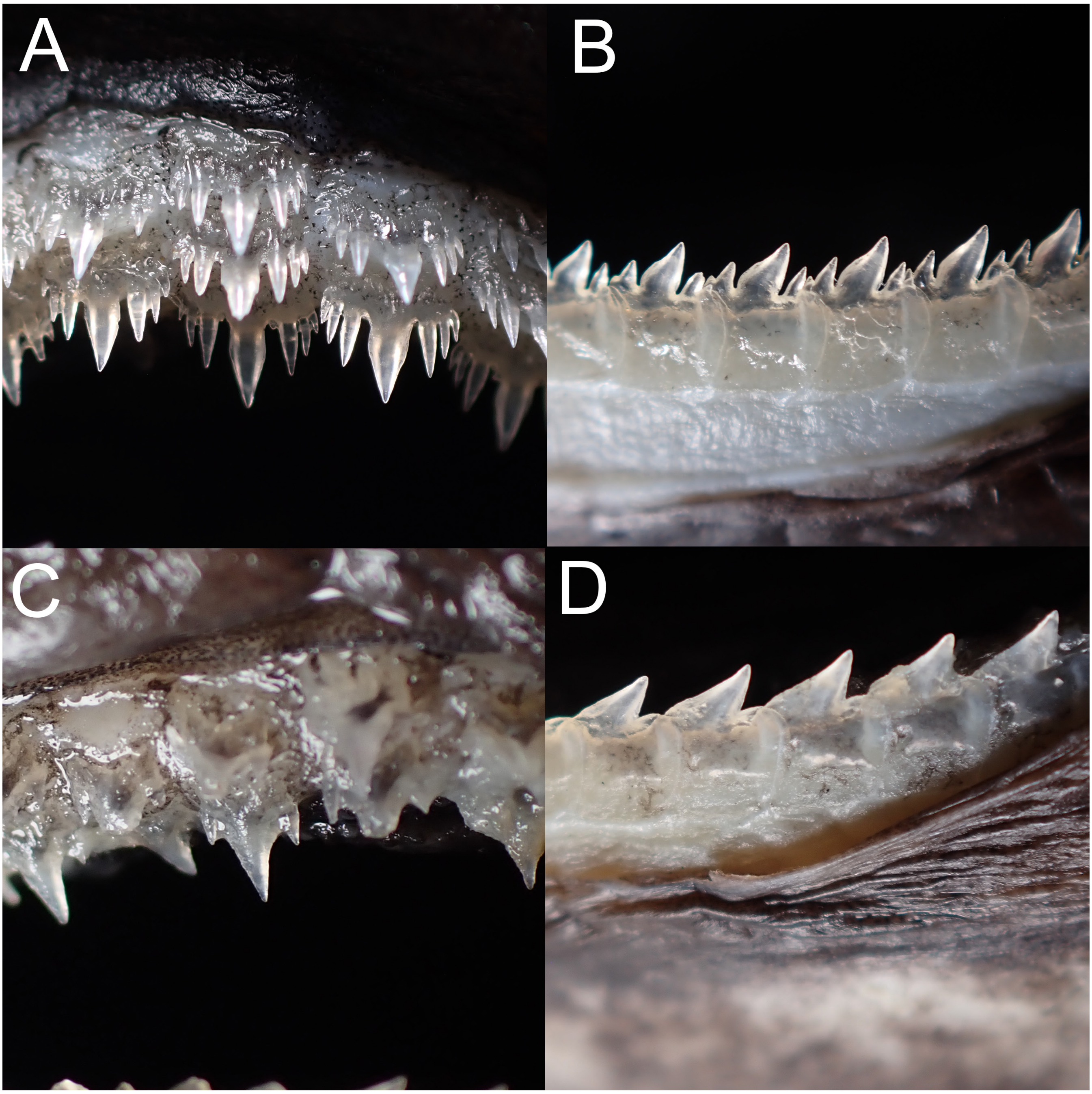

Fig. 4. Upper (A, C) and lower (B, D) teeth of *Etmopterus lii*, new species. A, B, holotype, ASIZP0081745, mature male, 341 mm TL; C, D, paratype, ASIZP0081742, immature female, 381 mm TL.

After preservation, body colouration becomes slightly paler; all the markings sometimes become less distinct (Fig. 7).

Size. Up to 381 mm TL and 341 mm TL for females and males, respectively. Specimens smaller than 143 mm TL have umbilical scars, representing the approximate birth size.

Distribution. Known so far only from the northern South China Sea, at a depth of approximately 500 m.

Biological notes. All the females are immature, while the smallest mature male examined is 325 mm TL. The largest female we examined (ASIZP0081742) has developing ovaries and uterus, representing a maturing stage, suggesting that mature females apparently attain sizes larger than 400 mm TL. Some specimens have whole lanternfishes (family Myctophidae) inside their stomachs, as observed under X-radiographs.

Etymology. The species is named after Mr. Yong-Tai Li, the captain of the fishing vessel *Xin Yong Tai*, for his assistance in not only obtaining the specimens in this study, but also many other deep-sea organisms from the South China Sea for other researchers, and thus making a great contribution to marine science research. Vernacular: Li's lanternshark.

Remarks. By having both anterior and posterior branches elongated and based on the phylogenetic tree based on the

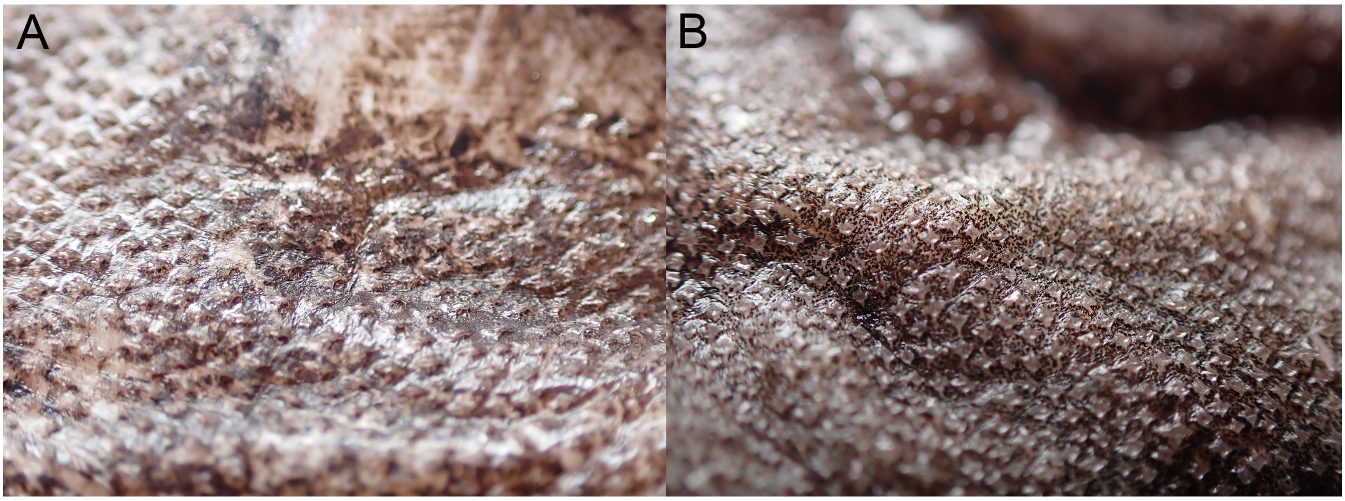

Fig. 5. Dermal denticles below second dorsal fin of *Etmopterus lii*, new species (A) and *E. sheikoi* (B). A, holotype, ASIZP0081745, mature male, 341 mm TL; B, ASIZP0081761, mature female, 464 mm TL.

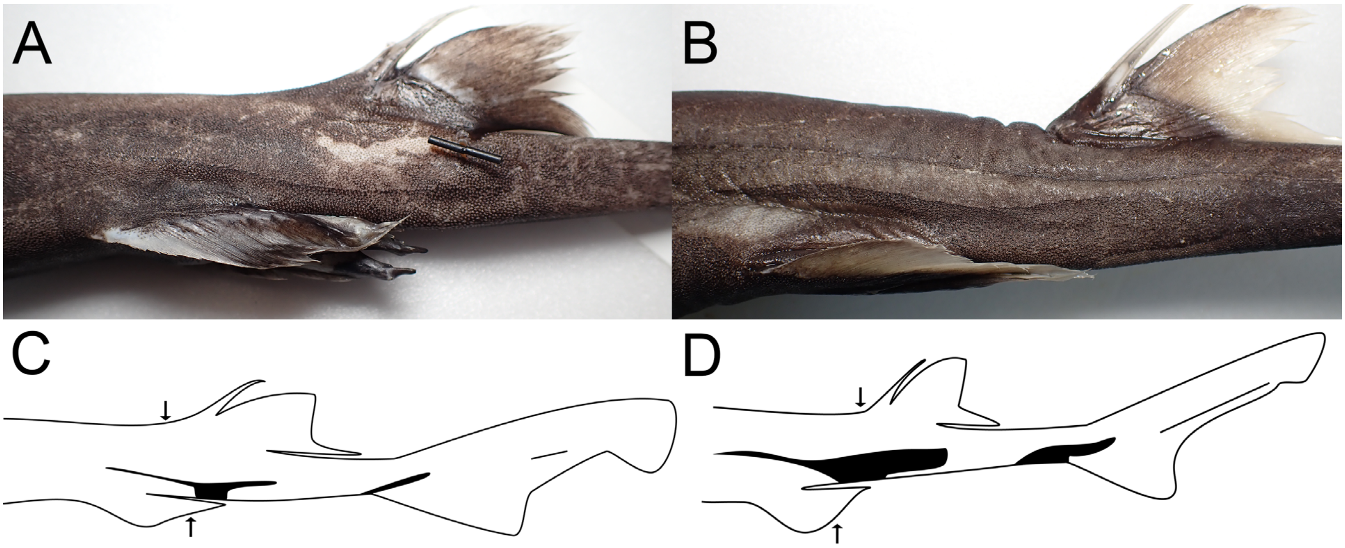

Fig. 6. Pelvic-fin flank markings (A, B) and illustrations of tail markings (C, D) of *Etmopterus lii*, new species (A,C) and *E. sheikoi* (B, D). A, holotype, ASIZP0081745, mature male, 341 mm TL; B, ASIZP0081761, mature female, 464 mm TL. Note the relative positions of second dorsal-fin origin and pelvic-fin flank-marking base origin indicated by arrows.

Fig. 7. Lateral view of *Etmopterus lii*, new species, after preservation. A, holotype, ASIZP0081745, mature male, 341 mm TL; B, paratype, ASIZP0081742, immature female, 381 mm TL. Scale bar=10 mm.

Table 3. Frequency distributions of precaudal and total centra of *Etmopterus lii*, new species and *E. sheikoi*.

Species	**Vertebral count**																	
	Precaudal centra																	
	52	53	54	55	56	57	58	59	60	61	62	63	64					
Etmopterus lii, new species	2		4	6	5	4	1	1										
Etmopterus sheikoi							2	2	4	5	2	2	2					
	Total centra																	
	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
Etmopterus lii, new species	1	3		4	4	5	2	2	2									
Etmopterus sheikoi										2	1	4	5	2	2		1	2

structure of NADH2 sequences, *Etmopterus lii* is assigned to the *E. lucifer* group (Straube et al., 2010). White et al. (2017) and Ebert et al. (2021) also considered the linear arrangement of dermal denticles a character of this group. However, this character is not only absent in *E. lii*, but also found in species of other groups (e.g. *E. granulosus* Compagno, 1984; *E. splendidus* Yano, 1988). Therefore, it should not be recognised as a shared character in the *E. lucifer* group.

The multicuspid lower teeth of the mature males of *Etmopterus lii* resembles the etmopterid genus *Centroscyllium*. However, all the immature males and females possess unicuspid lower teeth, which is not observed in *Centroscyllium*. Moreover, the molecular analysis shows that the new species clusters with other *Etmopterus* species instead of the *Centroscyllium* species, thus, our generic placement is supported by both morphology and genetics.

Ontogenetic and sexual dimorphism in tooth morphology has been documented in other lanternshark species (for example, *E. granulosus*, Straube et al., 2008; *E. spinax*, Straube & Pollerspöck, 2020; *E. sheikoi*, Adnet et al., 2006, present study). Mature males usually display more cusplets on upper-jaw teeth and have a more erect cusp on lower-jaw teeth compared to other ontogenetic stages and females. The mature males of the new species also have more cusplets on each side of the cusp (3) than females and immature individuals (1–2). Notably, mature males of *E. lii* have multicuspid lower teeth, which is the second known *Etmopterus* species showing this character. However, the dimorphism in lower teeth of mature females is uncertain, as all the female specimens obtained so far are immature. The absence of mature females in our sampling may be due to sexual or habitat segregation with the males.

Comparisons. Within the *E. lucifer* group, *Etmopterus lii* is especially unique by having frustum-shaped dermal denticles and having muticuspid lower-jaw teeth in mature males, thus is not likely to be misidentified or confused with other members. The new species is most similar to *E. sheikoi*, which is also assigned to the *E. lucifer* group based on our phylogenetic reconstruction (Fig. 1) (see remarks on *E. sheikoi* below), yet it can be readily distinguished from the latter by the following characters: a shorter snout, length 25.0–33.8% TL (vs. 34.5–40.9 % head length in *E. sheikoi*), the origin of second dorsal fin anterior to flank-marking base origin (vs. the origin of second dorsal fin well posterior to flank-marking base origin), a narrower posterior branch of flank marking, width 0.5–1.1% TL (vs. 1.5–2.3% TL), a thin, oblique, rod-like caudal-fin base marking originating just before the lower caudal-fin origin (vs. a thick, flat caudal-fin base marking, originating well before the lower caudal-fin origin), and shorter posterior caudal-fin marking, length 2.3–5.7% TL (vs. 7.8–11.3% TL). The new species also possesses relatively larger gill slits (Fig. 8) and has more monospondylous centra (38–43 vs. 42–45 in *E. sheikoi*), precaudal centra (52–59 vs. 58–64), and total centra (76–84 vs. 85–93), although the above characters share a little overlap (Table 3). In addition, *E. lii* has a smaller tooth count (21–25/27–32) than *E. sheikoi* specimens larger than 323 mm TL (32–48/34–44). That said, no ontogenetic changes in tooth count were observed in the former. When comparing the lower teeth of mature males, the inner pair of cusplets of *E. lii* is much shorter, with the length about half of the cusp, while in *E. sheikoi* the inner pair of cusplets (2nd pair) is about two-thirds to about the same height of the cusp.

Etmopterus lii may also be confused with the only two other congeners possessing frustum-shaped dermal denticles, *E. bigelowi* and *E. pusillus*, yet it differs from the two species by having elongated posterior flank-marking branches (absent in both species), a much shorter caudal-fin base marking, length 5.3–8.9% TL (vs. 13.6–18.0% TL in *E. bigelowi*; 11.6% TL in *E. pusillus*), an arched pectoral-fin marking (vs. subrhombic-shaped in both species), much fewer monospondylous centra (38–43 vs. 53–55 in *E. bigelowi*, 52 in *E. pusillus*), and more diplospondylous trunk centra (12–17 vs. 7–12 in *E. bigelowi*, 9 in *E. pusillus*).

Although sharing a similar genetic structure with *E. alphus*, *E. lii* is easily distinguished from the former by having frustum-shaped denticles (vs. hook-like denticles in *E. alphus*), shorter

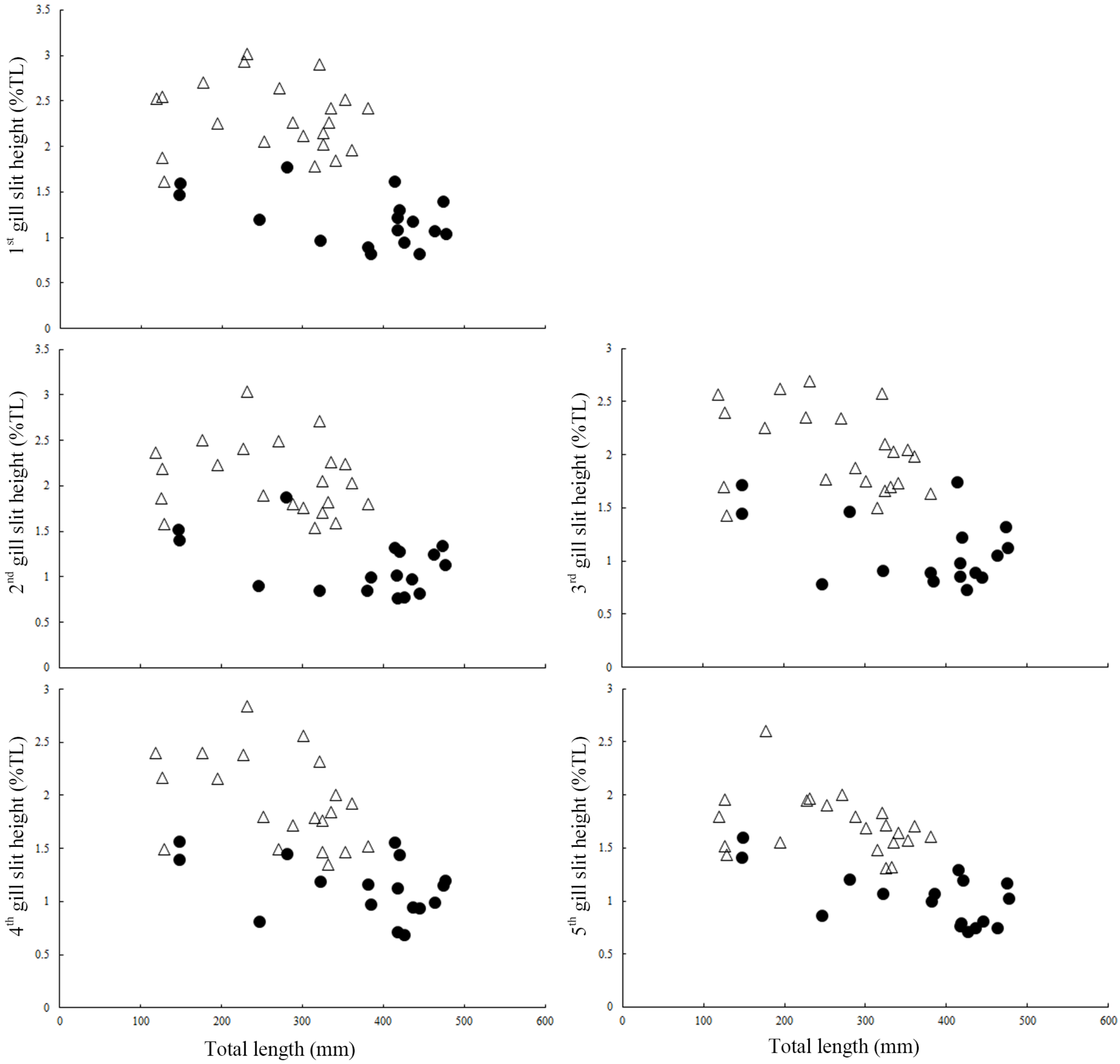

Fig. 8. Relationship between gill-slit length and total length (mm) in *Etmopterus lii*, new species (△) and *E. sheikoi* (●).

posterior caudal-fin marking (2.3–5.4 vs. 7.0–8.2% TL), pelvic-fin flank marking base origin posterior to second-dorsal fin origin (vs. just anterior to second dorsal-fin origin), and lateral and ventral side of body not demarcated (vs. strongly demarcated in both fresh and preserved condition).

Etmopterus sheikoi (Dolganov, 1986)

Rasptooth dogfish

(Figures 3C, 5B, 6B, D, 8–11; Tables 1–3)

Centroscyllium sheikoi Dolganov, 1986: 150–152 (holotype ZIN 46199, Kyushu-Palau Ridge, Southern Japan).

Miroscyllium sheikoi Shirai & Nakaya, 1990: 355 (new combination; description after Dolganov, 1986)

Centroscyllium sp. a. Nakaya in Okamura et al. (1982): 46, fig. 10

Etmopterus sp. Nakaya in Okamura et al. (1982): 52, fig. 15

Diagnosis. A moderately large species of *Etmopterus* differing from all other congeners, except *E. lii*, by having a combination of multicuspid lower jaw teeth in mature males, flat and frustum-shaped denticles, and elongated anterior and posterior lateral flank markings. It differs from *E. lii* by different aspects (see diagnosis in *E. lii*).

Description based on Taiwanese specimens. Measurements are listed in Table 1. Values are expressed as a percentage of total length (TL).

Body fusiform (Fig. 9), trunk sub-cylindrical, width 63.0–125.6 % height; abdomen usually longer than lower caudal peduncle, pectoral-pelvic space 102.1–135.6 % (89.3 % in one immature male ASIZP0081757) pelvic-caudal space; head conical, length 22.6–27.2 % TL, rather depressed, height 67.4–90.1 % width. Snout very long, preorbital length

Fig. 9. Lateral view of *Etmopterus sheikoi* after frozen (A), when fresh (B) and in preservative (C). A, ASIZP0081759, mature male, 386 mm TL; B–C, ASIZP0081761, mature female, 464 mm TL. Scale bar=10 mm.

8.0–10.3 % TL, 34.5–40.9 % head length, 151.6–247.1 % orbit length; snout narrowly pointed in both dorsal and lateral view. Eyes oval, orbit width 46.4–77.8 % height; orbits with both anterior and posterior notches; eyes narrowly spaced, interorbital width 62.0 % 85.5 % head width, orbit length 53.4–78.8 % interorbital width. Spiracles small, reversed 'D'-shaped, length 21.0–33.2 % orbit length, 3.8–5.6 % head length. Nostrils oblique, length 30.0–89.7 % internarial width, 29.1–57.6 % orbit length; anterior nasal flap narrowly triangular, tip reaching the nasal opening, length 22.9–61.0 % nostril width. Gill openings small, slightly oblique, intergill length 3.8–5.7 % TL, gill-slits height 0.7–1.9 % TL. Mouth broad, length 85.9–127.2 % width, nearly straight.

Teeth dissimilar in upper and lower jaw, with prominent ontogenetic and sexual dimorphism (Fig. 9); upper teeth multicuspid, in three functional series, very small, central cusp rather slender; immature males and females with two cusplets on each side of the cusp of upper teeth, while mature males have three to four cusplets; the third pair of cusplet (counted from mesial to distal side) longest, length about half to two-third of the central cusp; teeth in lower jaw unicuspid in immature individuals, in three series, one functional; lower teeth blade-like, with strongly oblique cusp; the cusps of lower teeth of mature males are flanked with two to three straight, erect cusplets on each side, the outer one minute; the cusps of lower teeth in one mature female (ASIZP0081763) are flanked with one minute cusplet on each side, while other mature females are unicuspid. Tooth count of upper jaw 24–48, lower jaw 26–44, total count 50–92. First dorsal fin moderate, with a broadly angular apex, length of first dorsal fin 7.7–11.0 % TL, origin within to just posterior to pectoral-fin free rear tip; pre–first dorsal fin length 130.6–194.1 % interdorsal space; first dorsal–fin spine 125.1–194.5 % first dorsal-fin height. Second dorsal fin much larger than first dorsal fin, first dorsal-fin height 46.9–75.0 % second dorsal-fin height; apex narrowly angular, posterior margin especially concave, free rear tip moderately elongated; second dorsal-fin length 11.0–13.0 % TL, interdorsal space 130.5–206.5 % dorsal-caudal space; second dorsal–fin spine long and curved; second dorsal-fin origin well posterior to insertion of pelvic fins. Interdorsal space 67.2–107.3 % pre–pectoral length. Pectoral fins moderate, length 7.0–11.2 % TL, with sharply pointed free rear tips, base narrow, 44.3–58.7 % pectoral-fin length, posterior margin slightly concave to slightly convex. Pelvic fin triangular, height 27.0–42.0 % length. Clasper of mature males rather long, inner length 61.6–74.3 % pelvic-fin length. Caudal fin elongated, dorsal length 19.3–26.1 % TL; caudal fork moderately developed, lower postventral margin 13.4–38.4 % upper postventral margin; terminal lobe somewhat broad.

Dermal denticles frustum-shaped, small, flat, extremely closely spaced, giving a smooth texture of the skin, not in defined rows; denticles present on underside of snout, except for a narrow area around mouth; underside of gill slits with a V-shaped naked area, connecting gill slits between both lateral sides; inner margin of fins with very narrow naked area, except for pectoral fin with a large naked area; denticles present on fin bases, scarcely present on ceratotrichia.

Luminescent markings on head distinct when fresh, a line originates from above nostril extend across a horizontal mid-orbit towards lower gill slits; head dorsal surface with a single line of dot-like markings, extending mid-dorsally from about the level of anterior fontanelle to the second dorsal-

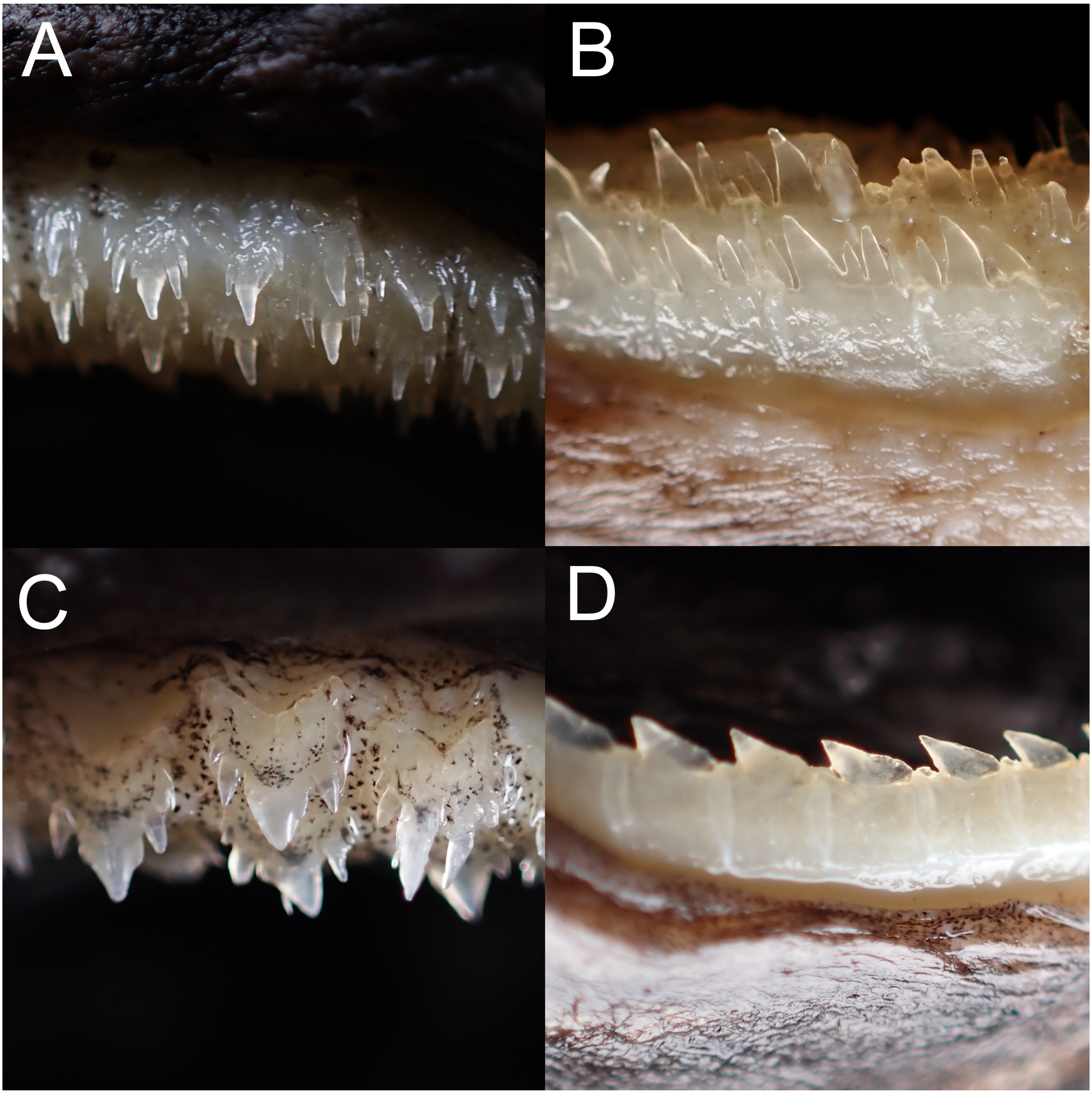

Fig. 10. Upper (A, C) and lower (B, D) teeth of *Etmopterus sheikoi*. A, B, ASIZP0081754, mature male, 421 mm TL; C, D, ASIZP0081761, mature female, 464 mm TL.

fin origin; ventral surface of pectoral fin with a triangular marking, sometimes arched, the tip not reaching the origin of pectoral-fin ceratotrichia; dash-like markings present on lateral side. Pelvic-fin flank markings well defined, with elongated anterior and posterior branch; anterior branch rather long and thick, length 5.6–11.3 % TL, slightly curved, extending above pelvic–fin origin; posterior branch straight, very thick and shorter than anterior branch, with a square-like tip, length 35.5–91.1% length of anterior branch, width 1.5–2.3 % TL, not extending beyond second dorsal-fin free rear tip; base of flank marking broad, base length 3.8–7.2 % TL, origin well anterior to second dorsal-fin origin. Infracaudal marking extending from the pelvic-fin flank marking base to about the same level of the posterior marking tip, not connecting to the caudal-fin base marking. Caudal-fin base marking thick and flat, rather long, originate well before lower caudal-fin origin, bifurcate after the origin, leaving a small black portion on the lower caudal-fin origin when viewed laterally. No central caudal-fin marking. Posterior caudal-fin marking very long, its length 7.8–11.3 % TL.

Vertebral counts: monospondylous 42–45, diplospondylous precaudal 14–20, caudal 23–31, precaudal 58–64, total 85–93.

Colouration. When fresh, body generally shiny purplish to dark grey, black ventrally; transition between lateral and ventral sides strongly demarcated. Dorsal midline without pale stripe; Markings on lateral side dot-like, prominent when fresh. Pectoral and pelvic fins generally translucent, with darker bases; dorsal fins mostly pale grey in two-third portions of ceratotrichia. Caudal-fin dorsal and postventral margins translucent, with a dark blotch covering from dorsal margin to mid-caudal fin, not extending to the upper postventral margin. A black blotch present between infracaudal and caudal-fin base marking. Caudal fin with a distinct black tip (terminal margin).

After preservation, body colouration slightly darker, yet most of the markings remain distinct (Fig. 10). Transition between lateral and ventral sides becomes less demarcated. Blotches between infracaudal and caudal-fin base marking, and on mid-caudal fin usually become less discernable (usually fade). A white spot on cheek area emerges, which is not as prominent as in fresh condition.

Size. Up to 478 mm TL and 446 mm TL for females and males, respectively. Possibly attains 500 mm TL. The two specimens with length 149 mm TL have an umbilical scar, which should represent the approximate birth size.

Distribution. Known from the northwestern Pacific, off southern Japan (Dolganov, 1986), northeastern and southwestern Taiwan, at depths of approximately 300–500 m.

Biological note. The smallest mature female and male measured 464 mm TL and 386 mm TL, respectively. Length of full-term embryos range from 98 to 139 mm TL. Maximum size probably exceeds 500 mm TL. This species feeds mainly on myctophids and small macrourids, based on observations from some specimens (not retained, Ng, unpublished data).

Remarks. Compagno (1984) recognised a 'slender, *Etmopterus*-like, long-nosed' *Centroscyllium* from Japan based on Nakaya in Okamura et al. (1982). This specimen is now reidentified as *E. sheikoi*.

Although deeply clustered within the *E. lucifer* group, Straube et al. (2010) did not clearly assign *E. sheikoi* to any groups, as they considered the shape of pelvic-fin flank markings to resemble the typical shape found in species in the *E. pusillus* group. However, after examining additional material of this species, this marking actually comprises both elongated anterior and posterior branches (absent in species of *E. pusillus* group) (Fig. 6B, D), which is a typical character in the species of *E. lucifer* group. Therefore, we formally assign *E. sheikoi* into a member of the *E. lucifer* group based on morphological and genetic evidence. Similarly, *E. sheikoi* does not show a linear arrangement of dermal denticles, which further supports that the character 'arrangement of denticles in linear rows' cannot be considered a shared character in this group.

The specimens examined in this study are generally consistent with the original description of the holotype (Dolganov, 1986), except for some morphometrics, which are substantially lower than the range of our specimens. For example, the prebranchial length is 9.1 % TL in the holotype (vs. 18.2–22.5 % TL in other specimens), which is obviously an error because it is even shorter than its preoral length (12.1 % TL), which is always shorter than prebranchial length in all elasmobranchs. The dorsal-fin length is also shorter than our specimens (D1 length 4.7 % TL in the holotype vs. 7.7–11.0 % TL; D2 length 7.1 % TL vs. 11.0–13.0 % TL). In the present study, the length of the dorsal fin was measured from the origin of the fin spine to the free rear tip end. However, Dolganov (1986) did not state the methods of measurement in detail, so we cannot exclude the possibility that only the fin portion was measured in the latter. Thus, the difference in dorsal-fin length may be attributed to different methodologies.

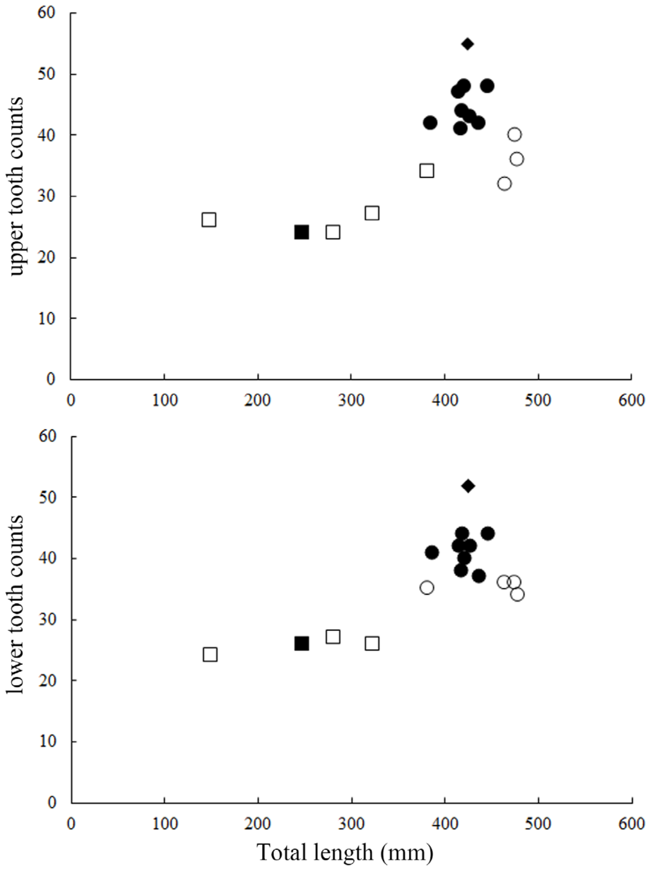

Fig. 11. Relationship between upper and lower tooth counts and total length (mm) in *Etmopterus sheikoi*, including the holotype (♦), mature male (●), mature female (○), immature male (■) and immature female (□).

The holotype also has slightly fewer monospondylous vertebrae and slightly more diplospondylous trunk vertebrae than our specimens (Table 1). Such subtle differences (1 vertebra each) can be reasonably considered as individual variations, which can be assessed when examining more specimens. In addition, the holotype has substantially more teeth (55/52 vs. 24–48/26–44). As the holotype was collected in Japan, the more numerous teeth may reflect geographical variations, as reported in other lanternshark species (e.g. *E. pusillus*, Shirai & Tachikawa, 1993).

Ontogenetic differences in tooth count were reported in some lanternshark species (e.g. *E. spinax*, Straube & Pollerspöck, 2020), where large individuals have more teeth than small individuals. In *E. sheikoi*, we also noted this phenomenon, with large individuals (>382 mm TL) having more teeth (32–55/34–52) than small individuals (<323 mm TL) (24–27/24–27). Notably, mature males have more teeth than mature females (41–55/37–52 vs. 32–40/34–36) reflecting sexual dimorphism in tooth count, which is possibly the first documented case within the order Squaliformes.

The ontogenetic changes in morphology of teeth have been well described in Adnet et al. (2006). While reporting the strong ontogenetic heterodonty, the comparative materials in Adnet et al. (2006) were mature and immature males, therefore, the dentition and possible changes in dentition throughout the ontogeny of females are still unknown to date. Here, we document the first heterodonty in the lower teeth of mature females of *E. sheikoi*, observing mature females with a pair of cusplets on each side of the main cusp. The size of the cusplets is minute when comparing to the slender, erect ones in males. The ecological function of sexual and ontogenetic heterodonty in counts and morphologies maybe explained by intraspecific niche partitioning, in other words, that mature males and females may inhabit different depths encountering different prey taxa. In fact, mature females of *E. sheikoi* are much rarer than mature males in Taiwanese fishing ports based on intensive sampling efforts (Ng, unpublished data), which possibly suggests that mature females live in deeper waters where fishing activities rarely occur.

Comparisons. *Etmopterus sheikoi* is a unique species within the genus by having a remarkable long, narrowly pointed snout, which makes it readily distinguishable from most of its congeners. The combination of frustum-shaped denticles, thick posterior branch of the pelvic-fin and caudal-base markings, and multicuspid lower teeth in mature males, also make it distinctive among the *E. lucifer* group. It is most similar to *Etmopterus lii* but can be readily separated from it (see comparisons of *E. lii* above).

Etmopterus bigelowi also possesses a relatively long snout and frustum-shaped denticles, which looks quite similar to *E. sheikoi* at first glance. Nevertheless, *E. sheikoi* differs from the former by possessing a longer snout (34.5–40.9 vs. 23.6–32.8 % head length), a much shorter caudal-fin base marking, length 7.0–9.1% TL (vs. 13.6–18.0 % TL), a much longer posterior caudal-fin marking, length 7.8–11.3 % TL (vs. 2.3–3.7 % TL) an elongated posterior flank marking branches (vs. absent), multicuspid lower teeth in mature males (vs. unicuspid), a triangular pectoral-fin marking (vs. subrhombic-shaped), much fewer monospondylous centra (41–45 vs. 53–55), and much more diplospondylous trunk centra (14–21 vs. 7–12).

Materials examined. ***Etmopterus alphus* (n=2):** USNM 43291, paratype, 282 mm TL, immature male, USNM 432492, paratype, 315 mm TL, mature male, off Mozambique (18°14′ S, 37°31′ E), 472 m, 17 July 1994, R.W. Leslie; ***Etmopterus bigelowi* (n=11):** USNM 157835, paratype, 422 mm TL, mature male, off Pensacola (29°13′ N, 87°54′ W), 458 m, R/V Oregon,13 March 1955; USNM 220331, 8 paratypes, 157–222 mm TL, Gulf of Mexico, western Central Atlantic (29°01′ N, 88°59′ W), 403 m, R/V Oregon, 24 August 1962; USNM 220332, 2, paratypes, 250–347 mm TL, off Panama, Caribbean Sea (09°22′ N, 80°72′ W), 274 m, R/V Oregon, 30 May 1962; ***Etmopterus lucifer* (n=1):** EBFS-NG 00047, 317 mm TL, mature male, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 19 November 2021; ***Etmopterus* cf. *molleri* (n=1):** EBFS-NG 00158, 349 mm TL, mature female, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 21 June 2022; ***Etmopterus pusillus* (n=1):** EBFS-NG 00296, 419 mm TL, mature male, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 12 June 2022; ***Etmopterus sheikoi* (n=23):** ASIZP0081746, 6, 98–139 mm TL, full-term embryos, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 20 October 2018; ASIZP0081747, 418 mm TL, mature male, ASIZP0081748, 419 mm TL, mature male, ASIZP0081749, 437 mm TL, mature male, ASIZP0081750, 427 mm TL, mature male, ASIZP0081751, 446 mm TL, mature male, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 1 March 2022, J.-H. Hong; ASIZP0081752, 282 mm TL, immature female, ASIZP0081753, 323 mm TL, immature female, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 27 August 2021; ASIZP0081754, 421 mm TL, mature male, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 11 October 2021; ASIZP0081755, 415 mm TL, mature male, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 17 April 2021; ASIZP0081756, 382 mm TL, immature female, off Donggang, southwestern Taiwan (ca. 22° N, 120° E), ca. 400 m, 10 December 2021; ASIZP0081757, 149 mm TL, immature male, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 26 March 2021; ASIZP0081758, 149 mm TL, immature female, off Donggang, southwestern Taiwan (ca. 22° N, 120° E), ca. 400 m, 10 December 2021; ASIZP0081759, 386 mm TL, mature male, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 18 May 2022; ASIZP0081760, 248 mm TL, immature male, off Donggang, southwestern Taiwan (ca. 22° N, 120° E), ca. 400 m, 9 November 2022; ASIZP0081761, 464 mm TL, mature female, off Donggang, southwestern Taiwan (ca. 22° N, 120° E), ca. 400 m, 16 September 2022; ASIZP0081762, mature female 478 mm TL, ASIZP0081763, mature female 478 mm TL, off Daxi, northeastern Taiwan (ca. 24°90′ N, 122°00′ E), ca. 400 m, 12 June 2022.

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