Description of a new deep-sea Lantern Shark *Etmopterus viator* sp. nov. (Squaliformes: Etmopteridae) from the Southern Hemisphere

by

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ABSTRACT. - Lantern sharks (*Etmopterus* spp.) constitute a regular by-catch in longline fisheries conducted along the north-eastern Kerguelen Plateau shelf in depths of 600 to 1700 m. Kerguelen lantern sharks are morphologically close to *E. granulosus*, *E.* sp. B, South African *E.* cf. *granulosus*, and *E. litvinovi*. However, molecular phylogenetic analyses support the hypothesis that they represent a distinct cryptic species, which is in line with morphological characters separating the species from its Southern Hemisphere congeners. The new species is described as *Etmopterus viator* sp. nov. and differs significantly from *E. granulosus*, *E.* sp. B, and South African *E.* cf. *granulosus* in body shape characters as well as shape and density of dermal denticles. The poorly known *E. litvinovi* differs from Kerguelen specimens of *E. viator* sp. nov. by lacking flank and tail markings. Flank marking shape and molecular phylogenetic analyses of the new species support its assignation to the recently defined *E. spinax* clade. The species is widespread in the Southern Hemisphere.

RÉSUMÉ. - Description d'un nouveau requin lanterne de profondeur *Etmopterus viator* sp. nov. (Squaliformes : Etmopteridae) de l'hémisphère sud.

Les requins-lanternes (*Etmopterus* spp.) représentent des captures accessoires fréquentes lors des pêches à la palangre de fond menées le long de la partie nord-est du Plateau de Kerguelen entre 600 et 1700 m. Les requins-lanternes de Kerguelen sont morphologiquement proches d'*E. granulosus*, d'*E.* sp. B, d'*E.* cf. *granulosus* d'Afrique du sud, et d'*E. litvinovi*. Cependant les analyses phylogénétiques moléculaires soutiennent l'hypothèse qu'ils représentent une espèce cryptique distincte, ce qui est en accord avec les caractères morphologiques séparant l'espèce de ses congénères de l'hémisphère sud. La nouvelle espèce est décrite sous le nom d'*Etmopterus viator* sp. nov. et diffère significativement d' *E. granulosus*, d'*E.* sp. B, et d'*E.* cf. *granulosus* d'Afrique du sud par ses caractères de forme du corps aussi bien que par l'aspect de la forme et la densité des denticules dermiques. Le peu connu *E. litvinovi* diffère des spécimens d'*E. viator* sp. nov. de Kerguelen par l'absence de marques sur le flanc et la queue. La forme des marques du flanc et les analyses phylogénétiques moléculaires de la nouvelle espèce soulignent son appartenance au clade récemment défini d'*E. spinax*. L'espèce possède une vaste distribution dans l'hémisphère sud.

Key words. - New species - Deep-sea shark - Barcoding - Morphometrics - Dermal denticles.

Lantern sharks (Etmopteridae) are deep-water sharks inhabiting continental slope and seamount regions occurring almost globally in an average depth range of 200 to more than 2500 meters (Compagno *et al*., 2005; Last and Stevens, 2009). With an estimated 42 species, lantern sharks constitute the largest family of Squaliformes or dogfish sharks (Compagno *et al*., 2005). With 33 described species, the genus *Etmopterus* exceeds the remaining three genera within the family, *Trigonognathus*, *Aculeola*, and *Centroscyllium*, in species number (Compagno *et al*., 2005; Schaaf da Silva and Ebert, 2006). The common name lantern shark refers to the hormone-induced light emission ability of photophores in the sharks skin, which is probably used in the social (schooling) and camouflage context (counter shading against residual sunlight) (Claes and Mallefet, 2008, 2009a, 2009b,

2010a, 2010b, 2010c). Their phylogeny, life-history, and ecology has recently become of increased interest in shark research (e.g., Coelho and Erzini, 2008a, 2008b; Neiva *et al*., 2006; Klimpel *et al*., 2003; Straube *et al*., 2010, 2011). Many etmopterids are regular by-catch of commercial deep-sea fisheries (Clarke *et al*., 2005; Jakobsdottir, 2001; Wetherbee, 1996; Kyne and Simpfendorfer, 2007).

Lantern shark species are diagnosed based on classical characters used in shark systematics, i.e., body shape characters, morphology, density and arrangement of dermal denticles as well as tooth shape, and number of vertebrae (e.g., Garrick, 1957, 1960; Springer and Burgess, 1985; Yano, 1997; Yamakawa *et al*., 1986). In addition, the shape and position of flank and tail markings forming fields of photophores is in many cases species or species-group specific

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(Yamakawa *et al*., 1986; Last *et al*., 2002). Recent molecular phylogenetic analyses revealed four major clades within *Etmopterus*, which are distinguishable based on their flank mark shapes, i.e., the *Etmopterus lucifer* Jordan and Snyder, 1902 clade, the *E. gracilispinis* Krefft, 1968 clade, the *E. pusillus* (Lowe, 1839) clade, and the *E. spinax* (Linnaeus, 1758) clade (Straube *et al*., 2010). The latter clade comprises at least three species, which are morphologically very similar, *Etmopterus granulosus* (Günther, 1880), *E. unicolor* (Engelhardt, 1912), and *E. princeps* (Collett, 1904), as well as a high number of cryptic species, especially from the Southern Hemisphere, i.e., *E. baxteri* (Garrick, 1957) from South Africa and New Zealand, *E.* cf. *granulosus* (Kerguelen Plateau), and *E. unicolor* (South East Pacific) (Straube *et al*., 2010, 2011). Morphologically similar Southern Hemisphere species within the *E. spinax* clade comprise *E. granulosus* (including *E. baxteri* as synonym of *E. granulosus* referring to Straube *et al*., (2011)), *E.* cf. *granulosus* (i.e., the nominal *E. baxteri* from South Africa in Straube *et al*. (2010, 2011), and throughout Compagno *et al*. (1991)), and finally *E.* sp. B, which is not synonymous to the North Pacific *E. unicolor* according to results from Straube *et al*. (2010, 2011). In this study, we focus on the separation of *E.* cf. *granulosus sensu* Duhamel *et al*. (2005) from its congeners in the Southern Hemisphere and provide a description of the species. We contend it is a new species of the *E. spinax* clade (Straube *et al*., 2010) based on distinct morphological and molecular characters.

MATERIAL AND METHODS

Taxon sampling

Most specimens and samples of the new species were collected at the Kerguelen Plateau in the years 2001, 2002, 2003, 2004 and 2007 during cruises of French commercial fishing vessels in the Southern Indian Ocean. A total number of 63 specimens from the Kerguelen Plateau were available, of which 24 were accompanied by tissue samples for DNA-barcoding (*sensu* Ward *et al*., 2005). Additional specimens and samples of the new species were obtained from off New Zealand (tissue samples only, n = 7, collected by McMillan P., NIWA, New Zealand, 2007) and off South Africa (measurements only, n = 2, collected by Anderson M.E., SAIAB, South Africa, 2001). For comparison with closely related species, 27 specimens of *E. granulosus* sampled off Chile, New

Zealand, and the Indian Ocean (NE of Kerguelen Plateau and off Amsterdam Island) including the holotype (BMNH-1879.5.14.460), 17 specimens of *E.* sp. B (*sensu* Last and Stevens, 1994) and 16 specimens of *E.* cf. *granulosus* from South Africa were inspected. *E. litvinovi* (Kotlyarand Parin,

Table I. - Measurements of *Etmopterus viator* sp. nov. holotype (MNHN 2008-1899) and ranges of Kerguelen paratypes.

Measurement (mm)	Holotype MNHN 2008-1899	Range in paratypes (minimum, maximum, mean, and sd)
Total length	524.7	350.0-577.2 (457.0; 106.2)
Pre-caudal fin length	415.0	280.0-440.5 (356.9; 77.2)
Pre-1st dorsal fin length	190.0	125.0-250.0 (173.0; 49.4)
Pre-2nd dorsal fin length	332.0	205.0-340.0 (270.4; 61.0)
Head length	108.0	80.74-140.0 (107.3; 25.2)
Pre-branchial length	89.2	62.0-110.0 (86.3; 22.7)
Pre-spiracle length	64.9	47.7-73.8 (60.3; 11.6)
Pre-orbital length	34.8	26.3-43.0 (34.5; 6.6)
Pre-narial length	14.9	10.7-20.0 (13.6; 3.6)
Pre-oral length	45.1	36.1-59.0 (44.9; 9.2)
Eye length	28.3	17.4-32.7 (24.3; 6.6)
Spiracle length	5.8	3.1-7.0 (5.4; 1.6)
Eye spiracle distance	14.8	8.0-17.2 (12.0; 3.7)
Mouth width	43.3	16.0-45.0 (34.4; 10.23)
Nostril width	12.4	10.9-16.5 (13.2; 2.3)
Snout width	39.9	27.5-51 (39.0; 9.2)
Interorbital distance	30.5	21.8-47.0 (34.2; 9.9)
Head width	55.5	36.5-75.0 (55.2; 15.7)
Head height	36.4	25.6-48.9 (36.9; 9.5)
Pre-pectoralis length	120.2	82.0-130.0 (99.6;23.3)
Pre-pelvic fin length	317	19.1-317.0 (208.2; 106.4)
Pectoralis pelvic fin distance	153.5	87.0-168 (125.1; 33.1)
Interdorsal distance	99.3	61.0-125.0 (87.6; 28.1)
2nd dorsal fin to caudal fin	46.7	32.0-57.8 (44.9; 11.0)
Pelvic fin to caudal fin	83.4	53.0-93.9 (76.5; 16.2)
Pectoralis – anterior margin	48.7	33.3-60.0 (45.6; 10.3)
Pectoralis inner margin	21.6	15.5-31.0 (22.7; 6.7)
Pectoralis posterior margin	33.7	21.1-32.0 (26.4;5.3)
Pectoralis base length	28.6	15.0-30.0 (21.5;6.3)
1st dorsal fin length	49.5	36.1-61.4 (48.0;10.5)
1st dorsal fin base length	20.1	10.6-30.0 (20.4;7.7)
1st dorsal inner margin	24.0	15.0-30.3 (19.8;5.4)
1st dorsal fin height	16.5	9.5-25.0 (16.3; 5.8)
2nd dorsal fin height	48.7	37.7-73.0 (54.5; 14.4)
2nd dorsal fin base length	16.0	12.0-24.0 (17.3; 4.6)
Pelvic fin length	57.1	38.5-70.0 (54.6; 15.2)
Pelvic fin anterior margin length	36.5	16.5-46.0 (33.3; 12.4)
Caudal fin dorsal caudal margin	104.3	80.5-127.9 (100.3; 17.7)
Caudal fin pre ventral margin	58.1	42.4-76.1 (57.0; 14.5)
Caudal fin subterminal margin	100.5	66.0-120.5 (91.6;21.2)

1990) is only known from a few specimens from the Nasca and Sala-y-Gómez Ridges off Chile and is considered to be an endemic species of this region (Kotlyar, 1990). It is likely that *E. litvinovi* is a member of the *E. spinax* clade based on morphological features describing sub clades of *Etmopterus* in Straube *et al.* (2010). Therefore, we included as much

Table II. - Measurements of comparative material used for morphometric analyses.

Measurement (mm)	*Etmopterus* sp. B *sensu* Last and Stevens, 1994				*Etmopterus* cf. *granulosus* (South Africa)				*Etmopterus granulosus*				*Etmopterus litvinovi*	
	min	max	mean	SD	min	max	mean	SD	min	max	mean	SD	ZMH 24994	ZMH 24993
Total length	325.3	672.0	476.2	127.5	270.0	665.0	524.1	103.0	212.3	742.0	493.3	128.6	440.4	404.1
Pre-caudal fin length	253.0	542.0	375.4	97.9	203.0	515.0	402.9	84.1	160.5	592.0	382.1	103.4	347.5	322.9
Pre-1st dorsal fin length	112.0	281.5	166.8	50.1	82.1	225.0	179.6	37.6	71.2	270.0	167.7	43.4	155.8	155.8
Pre-2nd-dorsal fin length	201.1	425.0	295.5	84.5	155.0	400.0	311.9	64.7	127.5	492.0	308.3	83.5	266.1	262.2
Head length	70.0	143.6	101.9	27.1	64.2	189.5	128.1	29.8	50.7	175.0	114.1	27.0	108.7	101.6
Pre-branchial fin length	49.0	109.8	77.5	19.6	53.3	129.3	101.9	21.7	42.9	126.4	94.1	21.3	88.6	87.8
Pre-spiracle length	34.1	76.8	55.2	14.1	37.1	86.7	71.9	13.7	29.6	100.0	67.4	15.2	58.7	61.6
Pre-orbital length	5.0	37.5	24.2	8.8	18.7	45.9	36.6	7.2	14.1	55.0	32.0	7.9	30.9	29.4
Pre-oral length	24.1	59.0	36.9	10.4	27.1	61.3	50.1	8.5	22.6	65.0	48.0	10.7	39.1	39.7
Eye length	9.1	31.0	19.3	7.6	17.3	35.1	29.8	4.9	11.1	38.1	28.1	6.2	27.0	26.6
Distance from eye to spiracle	3.1	20.4	9.2	6.11	7.4	36.7	18.2	6.3	5.9	30.0	17.2	4.3	16.1	14.4
Mouth width	18.3	65.4	38.7	14.4	23.7	72.1	51.1	12.5	19.0	85.0	48.4	15.8	47.4	37.7
Snout width	21.0	54.8	35.8	11.3	23.4	55.9	44.5	8.6	20.2	73.0	44.4	9.8	44.1	40.8
Interorbital distance	14.1	60.1	29.0	13.2	20.8	49.6	37.7	7.7	15.6	69.0	40.1	10.4	35.6	28.5
Head width	27.7	79.0	49.5	16.8	35.2	95.6	67.3	15.3	25.4	102.0	62.3	15.7	57.9	48.0
Head height	21.2	65.0	35.2	12.7	22.1	63.6	47.3	11.1	4.0	94.0	42.0	17.2	39.4	31.3
Pre-pectoral fin length	68.1	148.5	101.2	26.4	62.8	155.1	126.9	26.5	12.0	173.0	113.1	32.9	113.6	102.4
Pre-pelvic fin length	175.1	370.0	256.0	69.9	123.0	354.0	284.8	63.7	26.0	390.0	253.3	88.3	233.0	214.9
Pectoral fin to pelvic fin distance	83.1	183.0	129.1	36.4	64.7	200.7	142.3	34.2	46.6	220.0	140.6	40.4	128.8	119.8
Interdorsal distance	48.7	149.0	92.9	35.2	51.3	142.9	107.6	24.7	34.7	177.1	111.7	33.2	81.8	88.8
Distance from 2nd dorsal fin to caudal fin	25.8	63.8	40.3	12.8	26.3	62.7	46.4	10.2	19.2	73.5	52.2	13.1	43.5	36.4
Distance from pelvic fin to caudal fin	45.0	115.1	67.9	21.3	36.6	187.8	88.9	32.8	28.9	137.8	81.6	23.9	74.3	70.6
Pectoral fin-anterior margin length	23.9	58.0	38.7	12.7	27.4	64.9	47.9	10.7	13.2	72.2	45.1	13.4	48.9	48.0
1st dorsal fin maximum length	25.0	63.0	41.5	14.7	24.4	63.7	47.3	10.2	16.0	71.0	45.6	14.6	46.3	44.5
1st dorsal fin height	2.1	18.0	9.2	5.4	8.0	22.4	15.6	3.9	8.3	26.0	17.3	4.8	15.3	14.7
2nd dorsal fin maximum height	4.6	81.2	50.1	21.0	28.3	76.2	57.9	12.5	7.0	94.2	57.1	19.7	56.2	50.9
2nd dorsal fin-base length	5.4	27.0	14.7	7.3	10.0	27.5	19.9	4.5	2.0	32.0	20.6	7.1	20.2	19.2
Pelvic fin length	27.1	87.6	50.9	21.3	24.7	81.7	54.9	14.1	7.0	84.1	57.1	18.6	47.7	49.2
Caudal fin-dorsal caudal margin	64.7	133.1	97.5	24.1	62.1	138.9	108.5	19.9	52.6	195.4	106.4	26.2	96.6	88.0
Caudal fin-pre-ventral margin length	30.8	122.0	52.5	23.1	32.9	72.6	57.6	11.1	28.2	84.2	56.8	12.5	48.9	49.2
Caudal fin-subterminal margin length	55.0	128.1	92.1	26.5	55.9	129.7	103.5	19.9	12.0	140.0	95.1	28.8	84.5	72.9

information as possible for *E. litvinovi* to compare this species to the new species. However, only two paratypes (ZMH-24994; ZMH-24993) were available for studying the full set of measurements and number of vertebrae; the holotype was inspected from images, but tissue samples were not available for any of the types used in this study.

Morphology: morphometrics, meristics, and dermal denticles

Morphometrics

Thirty-one body measurements of 50 specimens of the new species, 27 specimens of *E. granulosus*, 18 specimens of *E.* sp. B, and 16 specimens of *E.* cf. *granulosus sensu* Compagno *et al.* (1991) (sampled off South Africa), formed the comparative basis for the species description (see Tables I and II for measurements and their definitions). Out of these measurements, four ratios discussed in Kotlyar (1990) and Yano (1997) as potential species specific characters were used: head length vs. interdorsal distance (HL/ID), distance of the snout tip to the first dorsal-fin spine insertion vs. the interdorsal distance (PFDL/ID), head length vs. the interorbital distance (HL/IOD), and total length vs. the height of the first dorsal fin (TL/HFDF). Ratio value variation was tested for deviation from a Gaussian distribution by compiling normal probability plots. After testing for homogeneity of error variances (Levene Test, $p > 0.05$ for TL/HFDF, PFDL/ID, and HL/ID; $p < 0.05$ for HL/IOD), a multi-factorial analysis of variance (ANOVA) was performed for those three variables, which showed homogeneity of error variance. To test for significant differentiation of the new species with respect to these three ratios, a least significant difference (LSD) *post-hoc* test was conducted. For the fourth ratio (HL/IOD), homogeneity was rejected by the Levene Test ($p = 0.001$), so that Kruskal-Wallis and subsequent Dunnett *post-hoc* tests were performed as these do not require an assumption of homogeneity of error variance. Statistical analyses were conducted with the software Statistical Package for the Social Sciences (SPSS) v. 11.5.1 and visualization of resulting boxplots was accomplished using the software Palaeontological Statistics (PAST) v1.94b (Hammer *et al.*, 2001).

Meristics

A meristic character frequently used for species identification in sharks is the total number of vertebrae. X-rays of 38 specimens of the new species and of two paratypes of *E. litvinovi* were available. Data were compared with published vertebrae numbers for *E. granulosus* and *E.* sp. B (Yano, 1997). Since means of total vertebrae numbers of *E. granulosus* and *E.* sp. B were adopted from Yano (1997), potential differences were visualized by plotting means and standard deviations of species analysed. Data on the total number of vertebrae of *E.* cf. *granulosus* specimens sampled off South Africa were not available for this study.

Dermal denticles

Shape, density, and arrangement of dermal denticles of the new species and closest relatives *E. granulosus* and *E.* sp. B (n = 2 for each species) was investigated using a defined area below the 2nd dorsal fin with a dissecting microscope. For representative visualization, a LEO 1430 VP scanning electron microscope (SEM) was used after skin samples were mounted on SEM stubs and coated with gold in a POLARON SEM Coating System for 80 seconds. To obtain a quantitative correlate for differences in dermal denticle morphology, the length of the dorsal part of dermal denticles below the 2nd dorsal fin was measured by calibrating a calliper in TPSDig v2.15 (Rohlf, 2010) with the included size indication provided by the SEM. Levene's Test rejected homogeneity of error variance between values of the three species ($p = 0.001$). Therefore, the non-parametric Kruskal-Wallis test was performed to test for significant differences between species and a subsequent Dunnett *post-hoc* test was conducted to test for significant pairwise differentiation. Finally, the number of denticles in 3 mm^2 was counted by applying a 3 mm side-length frame to the SEM images of two specimens each.

DNA-barcoding

Muscle or fin tissue samples preserved in 96% ethanol p.a. were available for 31 specimens of the new species, 26 specimens of *E. granulosus*, 6 specimens of *E.* sp. B, and 8 specimens of *E.* cf. *granulosus* (South Africa). Total genomic DNA was extracted using the QIAmp tissue kit (Qiagen®, Valencia, CA). The Cytochrome Oxidase I (COI) locus is a well-established gene fragment for identification of shark species (Ward *et al.*, 2005, 2007, 2008). Hence, a part of the mitochondrial COI gene was amplified and sequenced from all available samples following the PCR protocol of Iglésias *et al.* (2005). PCR and sequencing primers are S0156 (5' TAGCTGATGAATCTGACCGTGAAAC 3') and R0084 (5' TGAACGCCAGATTTCATAGCGTTC 3'). PCR products were cleaned using the QIAquick PCR Purification Kit (Qiagen®, Valencia, CA) following the manufacturer's protocol. Cycle sequencing was performed at the sequencing service of the Department of Biology at the Ludwig-Maximilians-University (Munich), using ABI Big Dye 3.1 chemistry (PE Applied Biosystems®, Foster City, CA). Obtained back and forward sequences of COI were edited using BioEdit v7.0.9 (Hall, 1999) and aligned with MUSCLE v3.6 (Edgar, 2004). In addition, five COI sequences of *E.* cf. *unicolor* (Indonesia) and two COI sequences of *E. granulosus* (Tasman Sea) were included in the preliminary alignment from Genbank (accession numbers EU398778, EU398779, EU398780, EU398781, EU398782, DQ108216, DQ108226). Aliscore v.0.2 (Misof and Misof, 2009) was used to check the

alignment for ambiguous alignment positions to confirm the absence of nuclear inserts in the COI sequences, which were translated into amino acids. A most parsimonious phylogenetic network using default settings (weights = 10, epsilon = 0) was calculated using the median joining algorithm (allowing for multistate data) with the software NETWORK v4.5.1.6 (Bandelt *et al.*, 1999; fluxus-engineering.com). The dataset comprised the smallest sequenced fragments homologous to all taxa (overall size: 655 base pairs). COI sequences were submitted to Genbank.

RESULTS

Morphology: morphometrics, meristics, and dermal denticles

Morphometrics

Multifactorial ANOVA detected significant differences between the new species, *E.* sp. B, *E.* cf. *granulosus* (South Africa), and *E. granulosus* with regard to the four ratios (TL/FDFH; HL/IOD; PFDL/ID; HL/ID) analysed. Significant differences were found using multifactorial ANOVA comparing the new species with *E.* sp. B in TL/HFDF, PFDL/ID, and HL/ID. *E.* cf. *granulosus* (South Africa) differs significantly from the new species based on the same three ratios (Fig. 1). Further significant differences were detected between the new species and *E. granulosus* when comparing the ratio of distance from the snout tip to the first dorsal-fin spine insertion and the interdorsal distance (PFDL/ID) as well as the ratio of head length and the interdorsal distance (HL/ID), where *E. granulosus* displays significantly higher values (Fig. 1). No significant differences were found between the new species and *E. litvinoi*, which is most likely due to the small sample size of *E. litvinoi*. See tables III and IV for a summary of ANOVA results.

Multiple species comparisons of the ratio of head length and interorbital distance (HL/IOD) displayed further significant differences, i.e., the new species differs significantly from *E.* sp. B and *E.* cf. *granulosus* (South Africa) (Fig. 1B; Tab. V). Differences to *E. litvinoi* are visualized in figure 1, but could not be statistically verified due to low sample sizes.

Meristics

The total number of vertebrae of the new species ranges between 75 and 84 (n = 38). The data was compared with *E. granulosus*, *E.* sp. B and *E. litvinoi* using data from Yano (1997) and Kotlyar (1990). Figure 1F visualizes means and standard deviations of total counts. This result may read as an indicator of species-specific differences, especially with regard to *E. granulosus*, which appears to have on average a larger number of vertebrae; Krefft (1968) counted 89 vertebrae in the holotype of *E. granulosus*.

Dermal denticles

The morphology of dermal denticles of the new species is hook-like and they densely cover the body with approximately 23-40 denticles per 3 mm^2 counted below the 2nd dorsal fin (Fig. 2A, B) in adults. The shape of its dermal denticles differs strongly from the bristle-like denticles of its molecularly identified sister taxon *E.* sp. B (Fig. 2E, F). No significant differences in the length of dermal denticles below the second dorsal fin between the new species and *E.* sp. B were detected (Dunnett-test, mean difference = 0.258, p = 0.149).

E. granulosus has significantly shorter denticles compared to the new species (mean difference = 0.2303, p < 0.000) (Fig. 2C, D). However, the number of dermal denticles is significantly lower in the new species (23-40 per 3 mm^2) than in *E.* sp B (> 100 per 3 mm^2) (Fig. 2). The number of dermal denticles is also lower (23-40 3 mm^2 *vs* 34 to 58 3 mm^2) than *E. granulosus*. *Etmopterus granulosus* and the new species described herein additionally differ in the degree of coverage of the 2nd dorsal fin with denticles, i.e., it is densely covered in adults of the new species, but sparsely covered or even without any dermal denticles in *E. granulosus*. This was already described by Yano (1997) for New Zealand specimens of *E. granulosus*. The new species displays no shape differences between dermal denticles of males and females, adults, sub adults and pups (Fig. 3).

Etmopterus litvinoi is morphologically similar to the new species in showing hook-like dermal denticles. However, they are arranged in higher density in the two inspected paratypes (51 per mm^2 ZMH-24993 and 57 per 3 mm^2 in ZMH-24994). *Etmopterus litvinoi* further differs in having dermal denticles arranged in rows on the 2nd dorsal fin (holotype ZIN-49228) as compared to absence of denticle rows in the new species. Unfortunately, the 2nd dorsal fins of both inspected paratypes seemed to be abraded.

DNA barcoding

The mtDNA-alignment (COI) from all specimens has 541 constant, 17 variable but parsimony-uninformative and 101 parsimony-informative characters. Base frequencies are equally distributed in all positions (χ^2-test: χ^2 = 8.47, df = 267, p = 1.0). Empirical base frequencies are 0.25 for A, 0.25 for C, 0.18 for G, and 0.32 for T. The most-parsimonious network contains 55 haplotypes which are connected via an estimated 137 mutations along the shortest tree. Five major clades are recovered among the Southern Hemisphere species (Fig. 4). The new species unambiguously constitutes a distinct cluster, most closely connected to *E.* sp. B and *E.* cf. *unicolor*. *E. granulosus* and *E.* cf. *granulosus* form rather distant clusters with regard to the new species. Specimens sampled off New Zealand are included in the new species' cluster suggesting conspecificity of the Kerguelen and New Zealand populations.
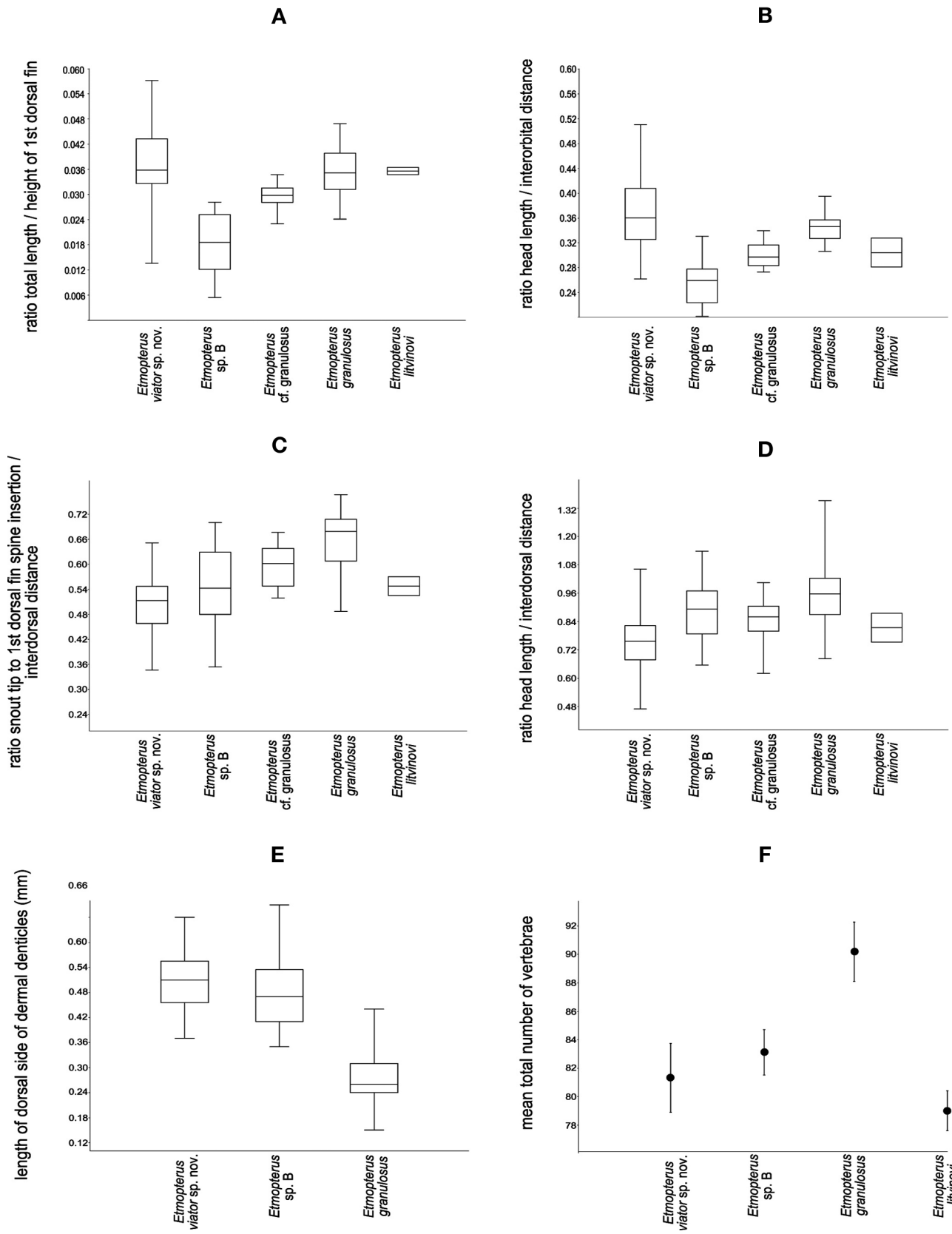
A

B

C

D

E

F

Figure 1. - Overview of box-plots visualizing results from morphometric and meristic analyses.

Table III. - Results from ANOVA: tests of between subject effects. TL/HFDF = ratio of total length and height of first dorsal fin; PFDL/ ID = ratio of pre first dorsal fin length and interdorsal distance; HL/ ID = ratio of head length and interdorsal distance.

Source	Dependent variable	df	F	p
Species	TL / FDFH	4	4.313	0.003
	PFDL/ ID	4	22.026	0.000
	HL/ID	4	13.889	0.000
Error	TL / FDFH	116	n.a.	n.a.
	PFDL/ ID	116	n.a.	n.a.
	HL/ID	116	n.a.	n.a.

Table V. - Results from multiple comparisons (Dunnett-test) of *Etmopterus viator* sp. nov. with congeners under the assumption that homogeneity of variance is not given. HL/IOD = ratio of head length and interorbital distance. *: p ≤ 0.05.

	Comparison species	Mean difference HL/IOD
Etmopterus viator sp. nov.	*Etmopterus* sp. B	0.890*
	Etmopterus cf. *granulosus*	-0.674*
	Etmopterus granulosus	-0.0147
	Etmopterus litvinovi	-0.0606

Table IV. - Results from multiple comparisons of *Etmopterus viator* sp. nov. with congeners. TL/HFDF = ratio of total length and height of first dorsal fin; PFDL/ID = ratio of pre first dorsal fin length and interdorsal distance; HL/ID = ratio of head length and interdorsal distance. *: p ≤ 0.05.

	Comparison species	Mean difference TL/HFDF	Mean difference PFDL/ID	Mean difference HL/ID
Etmopterus viator sp. nov.	*Etmopterus* sp. B	0.544*	-0.0422*	-0.1318*
	Etmopterus cf. *granulosus*	-0.0452*	-0.0917*	-0.0838*
	Etmopterus granulosus	-0.0131	-0.1512*	-0.2073*
	Etmopterus litvinovi	-0.0019	-0.0409	-0.0549

In summary, morphological as well as molecular data support the diagnosable distinctiveness of the new species. Based on this diagnosability, we describe the new lantern shark species as *Etmopterus viator* sp. nov.

ETMOPTERUS VIATOR NEW SPECIES STRAUBE
Etmopterus cf. *granulosus* – Duhamel *et al*., 2005

Holotype

MNHN 2008-1899, pregnant female, 525 mm TL, Kerguelen Plateau, 49°39'29"S-72°45'0"E, Oct. 2006, longline fishing, depth 1111-1023 m, Genbank Accession number: HM998635

Paratypes

Specimens from the Kerguelen Plateau, Southern Indian Ocean:

MNHN 2007-1666, female, 517 mm TL, Kerguelen Plateau, 46°49'03"S-70°32'32"E, Jan. 2007, longline fishing, depth 1091-1288 m, Genbank Accession number: HM998638;

MNHN 2007-1667, female, 350 mm TL, Kerguelen Plateau, 50°1'42"S-74°0'33"E, Nov. 2006, longline fishing, depth 807-1038 m, Genbank Accession number: HM998635;

MNHN 2007-1668, pregnant female, 545 mm TL, Kerguelen Plateau, 50°5'13"S-73°55'59"E, Nov. 2006, longline fishing, depth 952-926 m, Genbank Accession number: GU130729;

MNHN 2008-1900, female, 577 mm TL, Kerguelen Plateau, 49°39'29"S-72°45'0"E, Oct. 2006, longline fishing, depth 1111-1023 m (Fig. 4A), Genbank Accession number: HM998646;

ZSM-38530 (ref. MNHN 2008-1898), male, 362 mm TL, Kerguelen Plateau, 47°15'36"S-71°49'26"E, Oct. 2006, longline fishing, depth 834-1052 m, Genbank Accession number: HM998645;

MNHN 2008-1896, male, 391 mm TL, Kerguelen Plateau, 47°51'S-73°30'E, Nov. 2006, longline fishing, depth 1600-1509 m, Genbank Accession number: HM998637.

Specimens from Chatham Rise, New Zealand, South West Pacific:

NMNZ P.42738, male, 357 mm TL, Genbank Accession number: HM998654;

NMNZ P.42739, female, 400 mm TL, Genbank Accession number: HM998653;

NMNZ P.42740, female, 340 mm TL, Genbank Accession number: GU130731;

NMNZ P.42741, female, 296 mm TL, Genbank Accession number: HM998642;

NMNZ P.42742, male, 378 mm TL, Genbank Accession number: GU130730;

all specimens caught during a research cruise of RV *Tangaroa*. Station TAN 0709/ 119, Central northern slope of Chatham Rise, New Zealand; 42°38.08'S-179°52.97'E to 42°37.90'S-179°55.10'E; bottom trawl, depth 1573-1610 m, Jul. 2007.

Description

Diagnosis

A medium-sized *Etmopterus* species with the following combination of characters: body fusiform, caudal peduncle short 0.1 (0.09-0.1) % of total length (TL). Moderately long interdorsal distance 0.19 (0.17-0.24) % TL, very long dis-
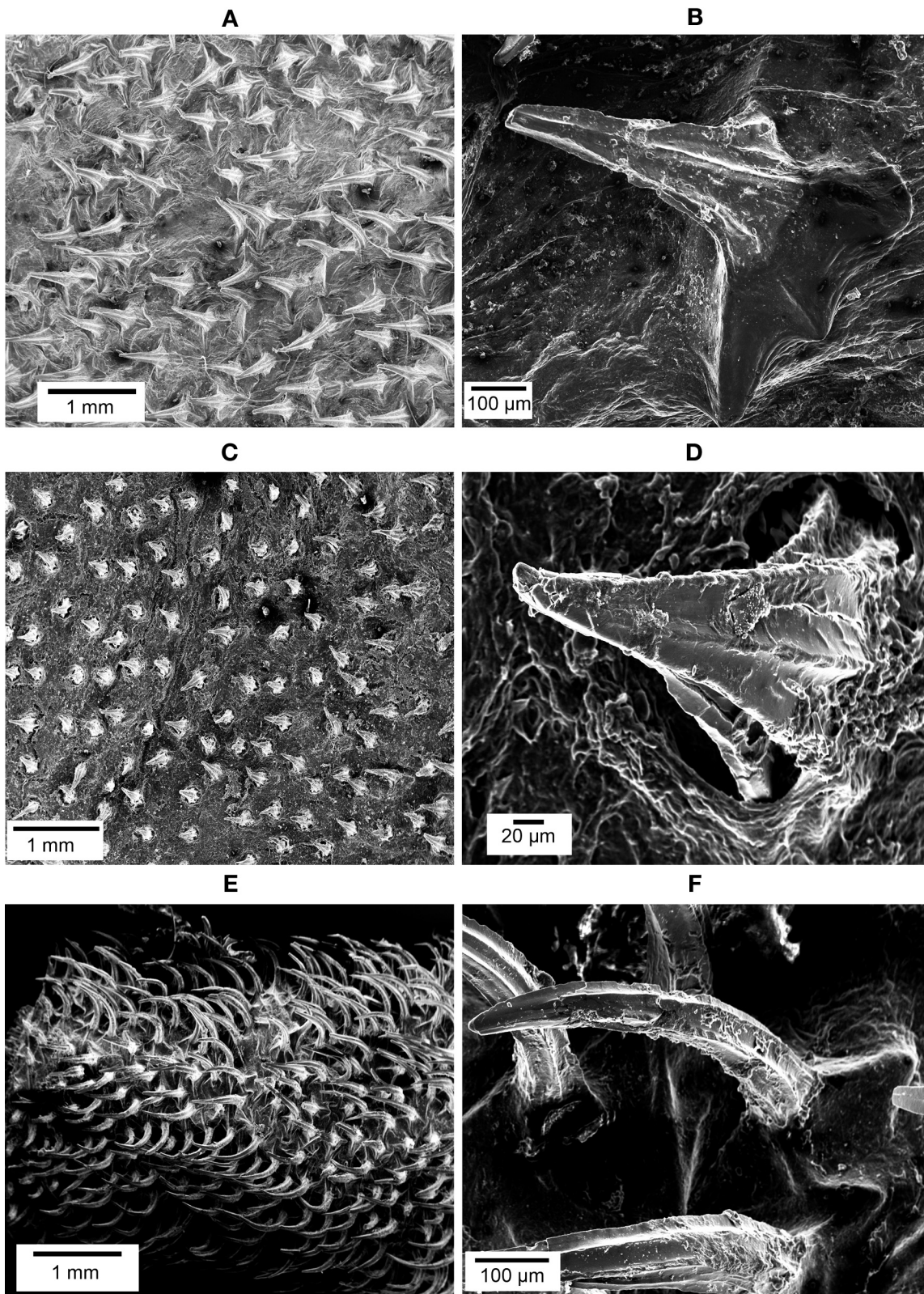
Figure 2. - SEM images of dermal denticles of *Etmopterus viator* sp. nov. (**A**, **B**; holotype MNHN 2008-1899), *Etmopterus granulosus* (**C**, **D**; ZSM-37667), and *Etmopterus* sp. B (**E**, **F**; MNHN 2005-2703). A, C, and E show the arrangement of dermal denticles below the 2nd dorsal fin on the right lateral side of specimens. B, D, and F display enlarged images of single dermal denticles.
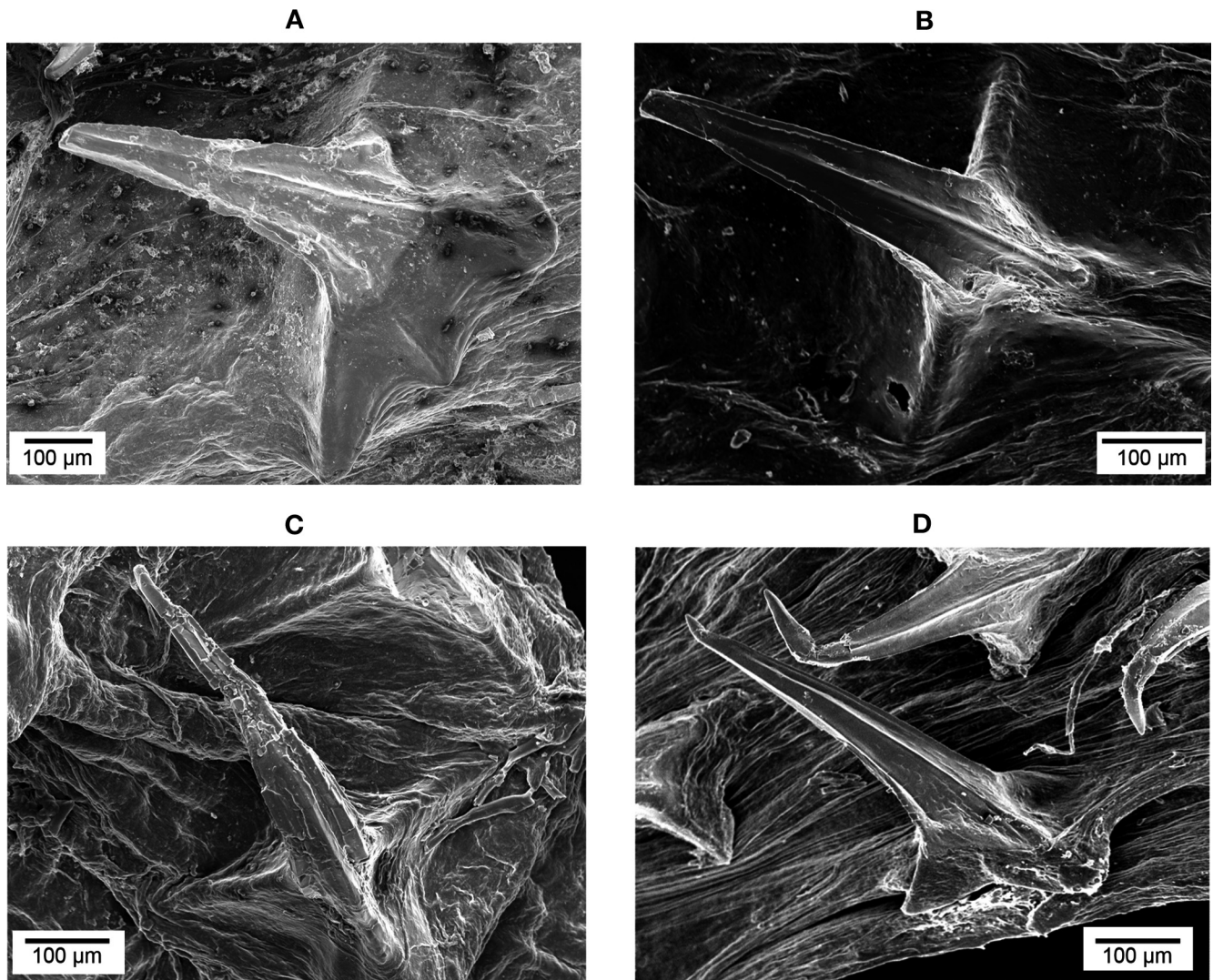
A

B

C

D

Figure 3. - SEM images of different ontogenetic stages in *Etmopterus viator* sp. nov. **A**: Adult female, holotype, MNHN 2008-1899; **B**: Adult male, paratype, MNHN 2008-1898; **C**: Subadult male, ZSM-37614; **D**: Almost ready to be born embryo extracted from holotype.

tance from first dorsal fin spine insertion to snout tip 0.36 (0.36-0.43) % TL. Head long 0.21 (0.21-0.26) % TL and broad 0.1 (0.1-0.15) % TL long, as long as caudal peduncle. Snout short 0.41 (0.40-0.46) % head length (HL) and broad 0.37 (0.34-0.38) % HL. Interorbital distance narrow 0.28 (0.26-0.36) % HL, shorter than snout width. Large oval eyes, eye length 0.26 (0.19-0.26) % HL. Eyes reflect greenish in fresh specimens. Large tear-drop shaped spiracles 0.05 (0.03-0.08) % HL. Mouth strongly arched and broad 0.4 (0.11-0.43) % HL with dignathic homodont dentition (see details below). Nostrils large and oblique 0.11 (0.11-0.15) % HL. Gill openings with distinct white margins. Pectoral fins rounded and white-edged with fringed ceratotrichia, moderate in size. Inner margin 0.04 (0.04-0.06) % TL, fin base short 0.05 (0.03-0.06) % TL. Dorsal fins densely covered with dermal denticles, 2nd dorsal fin significantly larger

than 1st dorsal fin, height 0.09 (0.10-0.15) % TL compared to 0.03 (0.03-0.05) % TL in 1st dorsal fin. 2nd dorsal fin deeply concave with drawn-out lower lobe. Both dorsal fins fringed, with strong fin spines. The 2nd dorsal fin spine is larger than 1st (broken in the holotype) pointing posteriorly. First dorsal fin originate distinctively behind the pectoral fin insertions, whereas origin of 2nd dorsal fin only slightly behind pelvic fin insertions (Fig. 5A, B). Large heterocercal caudal fin 0.2 (0.19-0.21) % TL with strong upper and weaker lower edged lobes, widely covered with dermal denticles. Morphometric data for the holotype and variations in Kerguelen paratypes are presented in table I.

Dermal denticles

Stout, dense, single-cusped dermal denticles with a keel on the upper surface, the basis of denticles displays four
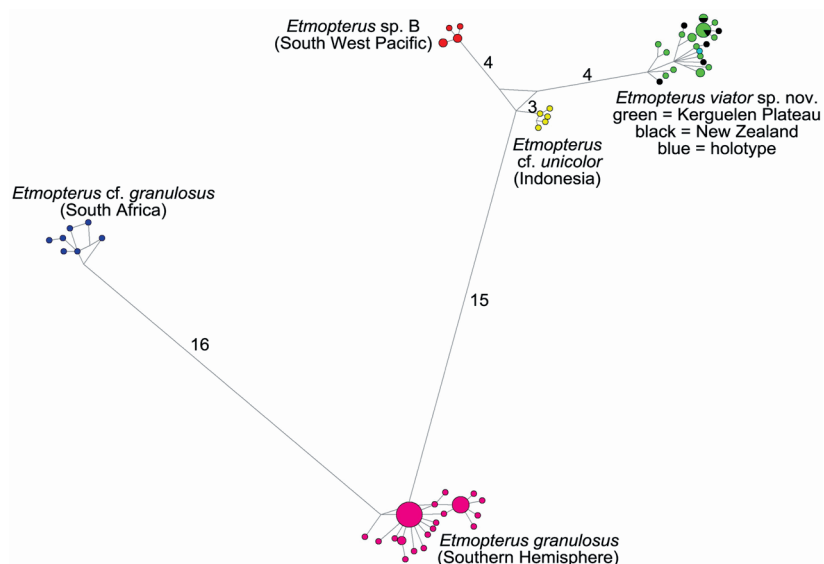
Figure 4. - Most parsimonious haplotype network structure attained from COI sequences (mtDNA). Numerals above branches indicate the number of mutated positions. Branches without numbers show 2 or less mutated positions.

branches. Skin appears rough-textured, the number of dermal denticles in a square of 3 mm^2 below the second dorsal fin ranges from 23-40 denticles in the Kerguelen paratypes, 39 in the holotype; arranged in short rows on the flanks and the caudal peduncle. Denticles appear less curved and thorn-like on head and ventral side, hook-like at flank and tail, on head less dense. Sub adults generally with a lower density of denticles compared to the high coverage of denticles in adults.

Markings

Photophores most densely clustered on ventral side of the body, flanks, caudal peduncle and caudal fin. Markings, especially flank markings, can differ substantially in their distinctiveness. Flank markings are distinct in sub adults but may be inconspicuous in adults. Indistinct triangular flank marking base below 2nd dorsal fin base. Posterior branch short, in contrast to the long, drawn-out anterior branch extending the 2nd dorsal fin spine insertion. Shape of the flank marking typical for the *E. spinax* clade (Straube *et al.*, 2010). Photophores are possibly present in a distinct white bar on the upper eye-lid.

Vertebrae

Total number of vertebrae 79 ranging from 75-84 (n = 38 including paratypes). 38 (38-68) precaudal vertebrae, 41 (34-51) caudal vertebrae.

Dentition

Upper teeth multicuspid with two lateral pairs of cusplets flanking a main cusp. Lateral cusplets smaller than the central cusp. Most males have, at least in the majority of upper teeth, only one pair of cusplets. Lower teeth single-cusped

and interlocking (Fig. 5C). Seven tooth rows in upper jaw with three functional rows and four replacement rows. Lower jaw with one functional tooth series and three replacement rows. Twenty-six teeth in upper and 37 in the lower jaw. There are no symphyseal teeth.

Distribution

The species is bentho-pelagic inhabitant of the sub photic zone: records range from 830 to 1400 meters depth on the northern part of the Kerguelen Plateau (Duhamel *et al.*, 2005) down to 1610 m from off New Zealand, suggesting it to be a rather deep-dwelling species of *Etmopterus*. The species has been collected at three geographically distant locations, i.e., South Africa, New Zealand, and the northern Kerguelen Plateau (Fig. 5D). It was further confirmed for the Macquarie Ridge (P. Last, pers. comm.). It hypothetically occurs in the whole Southern Hemisphere.

Biological notes

Etmopterus viator sp. nov. is ovoviviparous and gives birth to 2-10 pups per litter. Maturity is reached at approximately 50 cm TL in females and 46 cm TL in males (Duhamel *et al.*, 2005). Males are on average smaller than females, adult females reach at least 58 cm TL, adult males approximately 50 cm TL. Duhamel *et al.* (2005) report the species to feed on myctiphids, euphausiids, and squid.

Etymology

The species is named after the Latin word *viator* (the traveler), since the species is confirmed for geographically distant locations in the Southern Hemisphere.

Coloration

The body color is blackish to brown in adult females. Sub-adult specimens appear black. Preserved specimens mostly maintain original color. See figure 5 for general appearance.

Remarks

Within the genus *Etmopterus*, *E. viator* sp. nov. is identified in previous studies (nominal *E.* cf. *granulosus* in these studies) as member of the *E. spinax* clade (Straube *et al.*, 2010, 2011) based on flank mark shapes displaying long and thin anterior branches and weakly developed triangular posterior branches. It is hereby readily distinguished from all other remaining *Etmopterus* clades. Among species of the *E. spinax* clade, *E. viator* sp. nov. can be distinguished from *E. spinax*, *E. compagnoi* (Fricke and Koch, 1990) and
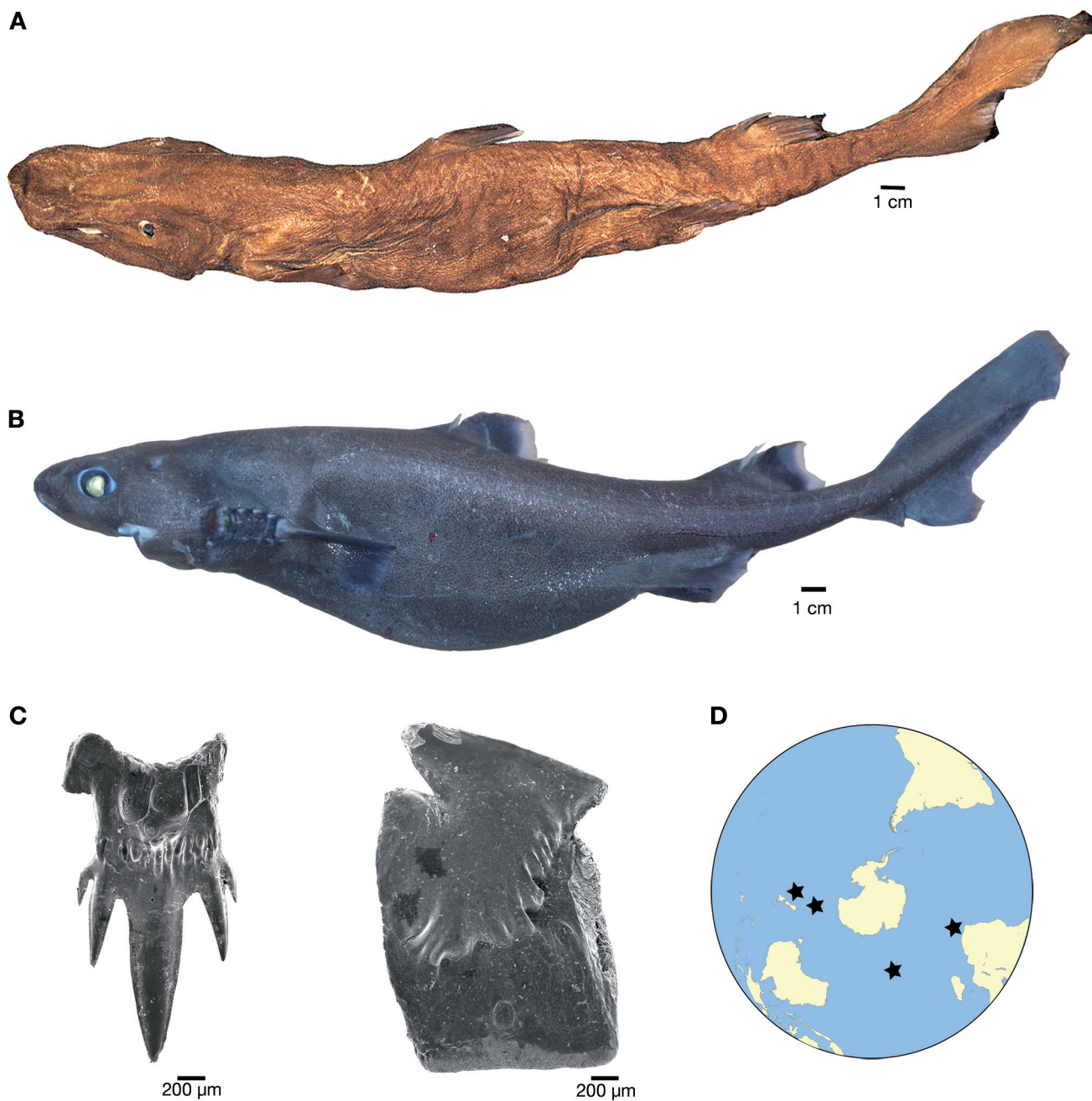
Figure 5. - Overview of morphological appearance and distribution of *Etmopterus viator* sp. nov. **A**: Preserved holotype MNHN 2008-1899; **B**: Freshly caught *E. viator* sp. nov. (Kerguelen Plateau, 06.2010); **C**: SEM images of upper and lower teeth extracted from holotype; **D**: Confirmed locations for *E. viator* sp. nov.

E. dianthus (Last *et al.*, 2002) by a uniform coloration without an abrupt transition of a light dorsal to a black ventral side. It differs from *E. princeps* in geographical occurrence (Southern Hemisphere *vs* North Atlantic), depth distribution range (600-1600 m *vs* 350-4500 m), and maximum total length (57 cm *vs* 75 cm). It differs from North Pacific *E. unicolor* in its dermal denticle shape. *E. unicolor* displays dense and bristle-like denticles as in *E.* sp. B. Further, *E. unicolor*

matures at larger body sizes, i.e., 53 cm for male specimens (Compagno *et al.* 2005), which implies even larger sizes at maturity for females.

Within the *E. spinax* clade, *E. viator* sp. nov. is a member of a group of morphologically similar species from the Southern Hemisphere. This group includes several cryptic species, which have been preliminarily assigned to formally described species (Straube *et al.*, 2011). Southern

Hemisphere congeners are *E.* sp. B (*sensu* Last and Stevens, 1994), *E. granulosus*, *E.* cf. *granulosus* (South Africa), and *E. litvinovi*. *E. viator* sp. nov. differs from *E.* sp. B in having fewer dermal denticles in a 3 mm^2 area below the 2nd dorsal fin (23-40 *vs* > 100) and in the combination of the following body measurement ratios: ratio of TL/HFDF (0.42-0.82 *vs* 0.44-0.98), PFDL/ID (0.01-0.03 *vs* 0.01-0.02), HL/ID (1.21-2.37 *vs* 1.02-2.25), and HL/IOD (0.01-0.07 *vs* 0.01-0.03). It differs from *E.* cf. *granulosus* (South Africa) in the ratios TL/HFDF (0.42-0.82 *vs* 0.52-0.62), PFDL/ID (0.01-0.03 *vs* 0.01-0.02), HL/ID (1.21-2.37 *vs* 1.61-1.94), and HL/IOD (0.01-0.07 *vs* 0.01-0.03). Further morphometric differences of *E. viator* sp. nov. to *E. granulosus* are found comparing ratios PFDL/ID (0.01-0.03 *vs* 0.01-0.08) and HL/ID (1.21-2.37 *vs* 0.17-2.17). *Etmopterus viator* sp. nov. has fewer dermal denticles in a 3 mm^2 area below the 2nd dorsal fin (23-40 *vs* 34-58) compared to *E. granulosus* and the two species also differ in the length of dermal denticles (0.37-0.66 μm *vs* 0.15-0.44 μm). Although the density and size of dermal denticles differs between *E. granulosus* and *E. viator* sp. nov., its shape is very similar. Sub adult specimens of *E. viator* sp. nov. strongly resemble sub adults of *E. granulosus*, as the density of dermal denticles in sub adult *E. viator* sp. nov. is much lower compared to adults. *Etmopterus granulosus* generally reaches a larger total length and matures at larger body sizes. Maturity is reached at 55-60 cm TL for male *E. granulosus*, and at 64-69 cm in females (Compagno *et al*., 2005), whereas male *E. viator* sp. nov mature at 46 cm TL and female specimens at 54 cm TL. The situation is similar comparing *E.* sp. B, where males mature around 50 cm TL and females at 60 cm TL (Last and Stevens, 2009), with *E. viator* sp. nov..

The most striking difference between *E. litvinovi* and *E. viator* sp. nov. is the lack of any markings in *E. litvinovi*, as described by Kotlyar (1990). Re-inspections of two paratypes of *E. litvinovi* support this observation (NS, pers. obs.). The conspicuousness of flank markings vary for ontogenetic stages in *E. viator* sp. nov., but markings at the caudal peduncle as well as the upper lobe of the tail fin are always clearly visible. The body colour of the preserved paratypes of two adult specimens of *E. litvinovi* is uniformly black. Preserved as well as fresh specimens of *E. viator* sp. nov. appear rather brownish in adult specimens. Although sub adult *E. viator* sp. nov are blackish in body color, specimens display clearly visible flank markings. Potential morphometric and meristic differences are the ratio of HL/IOD and the total number of vertebrae, but these results have to be verified analyzing a larger sample of *E. litvinovi*. The density of dermal denticles is higher in *E. litvinovi* (> 50 denticles below the 2nd dorsal fin in *E. litvinovi vs* < 50 in *E. viator* sp. nov.).

Kotlyar (1990) discusses the similarity of *E. litvinovi* with a South African species briefly described in Bass *et al*. (1986). We conclude that the *Etmopterus* sp. in Bass *et al*. (1986) may in fact be our newly described *E. viator* sp. nov., as its presence is confirmed off the coast of South Africa. Generally, the usage of flank markings of *E. viator* sp. nov. as species-specific character has to be treated with care, since *E. granulosus* displays flank markings of highly similar shape.

Results from mtDNA sequence analyses show a monophyletic lineage clearly separating *E. viator* sp. nov. from its congeners. The barcode approach readily allows identifying the new species. Interestingly, *E. viator* sp. nov. is distributed off New Zealand and morphometric analyses confirm its presence off South Africa as well, indicating *E. viator* sp. nov. to be a wide ranging species in the Southern Hemisphere (Fig. 5D), which is comparable to the distribution range of *E. granulosus* (Straube *et al*., 2011). The *E. spinax* clade is still likely to yield a number of cryptic species, which need to be analysed and described in the near future. *Etmopterus viator* sp. nov. is caught as common by-catch in longline and trawl fisheries, but these specimens were so far identified incorrectly as *E.* cf. *granulosus*. The description of the new species will have a direct effect on its monitoring, since fisheries observers are now able to distinguish between *E. viator* sp. nov. and congeners. Nevertheless, the *E. spinax* clade most likely contains additional cryptic species, which need to be analysed and described in the near future.

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