



A group of species “*Psychropotes longicauda*” (Psychropotidae, Elasipodida, Holothuroidea) from the Kuril-Kamchatka Trench area (North-West Pacific)

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ABSTRACT

Collections of holothurians taken in 2012–2016 by three German-Russian deep-sea expeditions to the Kuril-Kamchatka Trench area (KuramBio, SokhoBio and KuramBio II) were examined. Here we present data on the genus *Psychropotes* (Psychropotidae, Elasipodida). Based on new material and some additional (mainly old) material from the North-West and East Pacific, we re-describe the species *Psychropotes longicauda* Théel, 1882, describe two varieties, *P. longicauda* var. *monstrosa* Théel, 1882 and *P. longicauda* var. *fuscopurpurea* Théel, 1882, as separate species, re-establish the species *P. raripe* Ludwig, 1893, *P. dubiosa* Ludwig, 1893 and *P. dyscrita* (Clark, 1920), and describe two new species: *P. moskalevi* sp. nov. and *P. pawsoni* sp. nov.

1. Introduction

The benthic fauna of the Kuril-Kamchatka Trench (KKT) and adjacent waters has been studied in a series of expeditions of the Soviet RV *Vityaz* between 1949 and 1966 (Belyaev, 1983; Vinogradova and Filatova, 1983). Data on deep-sea holothurians collected in these expeditions were presented in Belyaev (1970) on the genus *Myriotrochus*, Belyaev (1971) on *Elpidia*, Belyaev (1989) with a review of hadal fauna, Gebruk (1990) on Elpidiidae and Rogacheva (2012) on the genus *Kolga*. The KKT area was revisited in 2012–2016 by the series of German-Russian deep-sea expeditions: KuramBio (Kuril Kamchatka Biodiversity Studies) in 2012 on board of RV *Sonne* (Brandt and Malyutina, 2015), SokhoBio (Sea of Okhotsk Biodiversity Study) in 2015 on board of RV *Akademik M.A. Lavrentyev* (Malyutina et al., 2018) and KuramBio II in 2016 on board of RV *Sonne* (Brandt et al., 2016).

The KuramBio expedition sampled the abyssal seafloor in the Kuril Kamchatka Trench area in the depth range from 4830 m to 5780 m, with two stations west of the trench axis and 10 stations east of the trench. The SokhoBio expedition sampled the deep seafloor of the Sea of Okhotsk in the depth range from 1700 m to 4800 m. The target of KuramBio II was the hadal seafloor of the Kuril Kamchatka Trench.

Collections of holothurians taken by these three expeditions were examined. In the present study we focused on the genus *Psychropotes* in these collections. Data on other holothurian taxa will be published separately. We used additional samples from the North-West, East Pacific and Antarctic taken by expeditions of RV *Vityaz*, *Akademik Kurchatov*,

Dmitry Mendeleev and *Akademik M.A. Lavrentyev* and stored in the collection of the Shirshov Institute of Oceanology (Moscow). One sample from the tropical East Pacific was taken on the *Kilo Moana* Cruise 1808 in 2018.

Holothurians of the genus *Psychropotes* (Psychropotidae) are prominent representatives of deep-sea benthic fauna at lower bathyal – abyssal depths all over the world ocean (Hansen, 1975; Billett, 1991). These holothurians are notable for their large size, often reaching 300–400 mm (*in situ*) and long dorsal appendage, nicknamed “tail” or “sail”, in some species exceeding in length that of the body. The genus was established by Théel (1882) based on the collection of HMS *Challenger*. According to the World Register of Marine Species (WoRMS), the genus includes 12 valid species with an additional 10 species being synonymized (WoRMS, 2018. *Psychropotes* Théel, 1882. Accessed at: <http://marinespecies.org/aphia.php?p=taxdetails&id=123532> on 2019-04-22). The valid species include: *Psychropotes belyaevi* Hansen, 1975; *P. depressa* (Théel, 1882); *P. hyalinus* Pawson, 1985; *P. longicauda* Théel, 1882; *P. loveni* Théel, 1882; *P. pminuta* Koehler and Vaney, 1905; *P. mirabilis* Hansen, 1975; *P. raripe* Ludwig, 1893; *P. scotiae* (Vaney, 1908); *P. semperiana* Théel, 1882; *P. verrucosa* (Ludwig, 1893) and *P. xenochromata* Rogacheva & Billett in Rogacheva et al., 2009. Synonymized species include: *Psychropotes brucei* Vaney, 1908 (accepted as *Psychropotes longicauda* Théel, 1882); *P. buglossa* Perrier E., 1886 (accepted as *Psychropotes longicauda* Théel, 1882); *P. dubiosa* Ludwig, 1893 (accepted as *Psychropotes longicauda* Théel, 1882); *P. fucata* Perrier R., 1896 (accepted as *Psychropotes longicauda* Théel, 1882); *P. furcata* R.

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Perrier, 1896 (accepted as *Psychropotes longicauda* Théel, 1882); *P. grimaldii* Hérouard, 1896 (accepted as *Psychropotes longicauda* Théel, 1882); *P. kerhervei* Hérouard, 1902 (accepted as *Psychropotes semperiana* Théel, 1882); *P. laticauda* Vaney, 1908 (accepted as *Psychropotes longicauda* Théel, 1882); *P. longicauda* var. *antarctica* Vaney, 1908 (accepted as *Psychropotes longicauda* Théel, 1882); *P. longicauda* var. *fusco-purpurea* Théel, 1882 (accepted as *Psychropotes longicauda* Théel, 1882) and *P. longicauda* var. *monstrosa* Théel, 1882 (accepted as *Psychropotes longicauda* Théel, 1882).

In the present paper based on material of three German-Russian expeditions to the KKT area and additional material from the North-West, East Pacific and Antarctic we re-describe the species *Psychropotes longicauda* Théel, 1882, describe two varieties, *P. longicauda* var. *monstrosa* Théel, 1882 and *P. longicauda* var. *fusco-purpurea* Théel, 1882, as separate species, re-establish the species *P. raripes* Ludwig, 1894, *P. dubiosa* Ludwig, 1894 and *P. dyscrita* (Clark, 1920) and describe two new species: *P. moskalevi* sp. nov. and *P. pawsoni* sp. nov.

According to our unpublished data, there are more species of *Psychropotes* with long “tail” in other oceans (at least the Atlantic and Southern Oceans). We didn’t consider those species in the present work, this will be the subject of a separate publication.

2. Material and methods

In German-Russian expeditions to the KKT area holothurians were collected using the Agassiz trawl and the epibenthic sledge. Additional material used in the present study was taken in the North-West, East Pacific and Antarctic in expeditions of research vessels *Vityaz*, *Akademik Kurchatov* and *Dmitry Mendeleev* (Table 1). Sampling gear in these expeditions was the 2.5 m Sigsbee trawl. Specimens were preserved in 80% alcohol. On the 75th Cruise of *Akademik M.A. Lavrentyev* to the Bering Sea and the *Kilo Moana* Cruise 1808 to the Clarion-Clipperton fracture zone in Central East Pacific specimens of holothurians were taken using ROV.

Holothurians were identified based on standard characters used for psychropotid holothurians (Hansen, 1975). Features of external morphology were examined using stereo-microscope; slide preparations of calcareous elements (ossicles) of dorsal and ventral sides were examined using a compound microscope.

The type material was re-examined in the following species: *Psychropotes longicauda* Théel, 1882 (Natural History Museum, London); *P. longicauda* var. *monstrosa* Théel, 1882 (Natural History Museum, London); *P. longicauda* var. *fusco-purpurea* Théel, 1882 (Natural History Museum, London); *P. raripes* Ludwig, 1894 (National Museum of Natural History, Washington); *P. dubiosa* Ludwig, 1894 (National Museum of Natural History, Washington) and *P. dyscrita* (Clark, 1920) (National Museum of Natural History, Washington) (Table 1).

The holotypes of new species, *P. moskalevi* sp. nov., currently at the Shirshov Institute of Oceanology, Moscow (IORAS) will be deposited at the Senckenberg Research Institute and Natural History Museum, Frankfurt. Paratype of this species is stored at IORAS. Holotype of *P. pawsoni* is deposited at the IORAS.

Mitochondrial cytochrome *c* oxidase I (COI) and 16S rDNA sequences were generated for the new *Psychropotes* specimens (Table 2) using the primers and methods as outlined in Miller et al. (2017). The COI and 16S sequences and separately compared with the available on GenBank for Psychropotidae. Sequences were aligned using Muscle (Edgar, 2004) and maximum likelihood analyses were performed using RAxML v.8.2.10 (Stamatakis 2014) using the model GTR + G. Support was assessed via a minimum of 1000 thorough bootstrap replicates. The resulting trees were rooted using as shown in Xiao et al. (2019). GenBank accession numbers used are listed on the phylogenetic trees. Two of the specimens, which COI (GenBank Accession Number KU987474) and 16S rDNA sequences (KU987543 and KU987548) were obtained by Gubili et al. (2017), were examined morphologically and assigned to a new species, *Psychropotes pawsoni* (Table 2).

Abbreviations

KKT – Kuril-Kamchatka Trench
 CCZ – Clarion-Clipperton Fracture Zone area
 IORAS – P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences (Moscow)
 MNHN – Muséum National d’Histoire Naturelle (Paris)
 NHM – Natural History Museum (London)
 NMNH – National Museum of Natural History (Smithsonian Institution, Washington, DC)
 SGN – Senckenberg Research Institute and Natural History Museum, Frankfurt
 UHM – University of Hawaii at Manoa, USA
 ZMUC/NHMD – Zoological Museum of the Natural History Museum of Denmark (Copenhagen)
 DA – Dorsal appendage
 AGT – Agassiz trawl
 EBS – Epibenthic sledge

3. Systematic part

Order Elaspodida Théel, 1882
 Suborder Psychropotina Hansen, 1975
 Family Psychropotidae Théel, 1882
 Genus *Psychropotes* Théel, 1882
Psychropotes longicauda Théel, 1882

Fig. 1.

Psychropotes longicauda Théel, 1882: 96–98, Pls. XXVII: 1, XXVIII, XXXV: 13–17, XXXVII: 10; Hansen, 1975 (in part): 115–126, Fig. 49 (1–5); Rogacheva et al., 2009: 473–474, Fig. 7.

Non: *Psychropotes longicauda* var. *fusco-purpurea* Théel, 1882: 99, Pls. XXIX: 1, XXXV: 11.

Non: *Psychropotes longicauda* var. *monstrosa* Théel, 1882: 98–99, Pls. XXIX: 2, XXX, XXXIX: 1.

Non: *Psychropotes longicauda* var. *antarctica* Vaney, 1908: 419–420.

Type material. Holotype, NHM [1883.6.18.58], HMS *Challenger*, St. 157, 100 mm long (140–145 mm in the original description).

Type locality. Indian Ocean sector of the Antarctic, HMS *Challenger*, St. 157, 03.03.1874, 53°55’S, 108°35’E, depth ~ 3560 m.

Material examined. See Table 1.

Diagnosis [after Théel (1882)]. Colour in alcohol greyish violet, ventrum brownish. Body elongated, four to five times as long as broad (Fig. 1: A, B). Body height increasing gradually towards unpaired dorsal appendage (Fig. 1: C); body width slightly narrowing posteriorly. Tentacles 18. Ventrolateral tube feet minute, up to 25–26 pairs. Mid-ventral tube feet conspicuous, in alternating double row. Dorsal papillae minute, 5 pairs. Unpaired dorsal appendage large, placed close to posterior end of the body, the base almost as broad as the body (Fig. 1: A, C).

Dorsal deposits in outer layer with arms varying in length from short, 0.06 mm long, to long 0.24–0.4 mm long. Arm spines conspicuous, strong, 2–3 proximal largest, usually in single rows (Fig. 1: D–F). Deposits of inner body wall layer crosses, their arms slender, almost straight with thin, long irregularly placed spines. Deposits on ventrum crosses with arms 0.16–0.24 mm in length or smaller, with arms up to 0.08 mm, often of irregular shape, strongly spinose; rods and tripartite deposits also present (Fig. 1: H–J).

Remarks. In the original description of the genus *Psychropotes*, Théel distinguished the species *P. longicauda* and two varieties, *P. longicauda* var. *monstrosa* and *P. longicauda* var. *fusco-purpurea* (Théel, 1882). Differences between *P. longicauda* and the two varieties are summarized in Table 3. The variety *monstrosa* was distinguished based on differences in “size of the body, proportion between the length of the body and that of the dorsal appendage, the number of dorsal processes, and the presence or absence of deposits in the inner layer of the integument”. The variety *fusco-purpurea* was distinguished based on the dark violet colour, relatively shorter dorsal appendage, four pairs of minute

Table 1
Material used in the present study.

Vessel (cruise), station	Coordinates	Depth, m	Nr of specimens	L, mm	Storage
<i>Psychropotes longicauda</i> Théel, 1882					
Challenger, St. 156	62°26'S, 95°44'E	~3614	1	80	NHM
*Challenger, St. 157	53°55'S, 108°35'E	~3568	2	140–145	NHM
<i>Psychropotes monstrosa</i> Théel, 1882					
*Challenger, St. 157	53°55'S, 108°35'E	~3568	1	250	NHM
Dmitry Mendeleev (16), St. 1290	54°33'S, 159°24'E	5410–5450	1	120	IORAS
Vityaz (20), St. 3340	53° 53.2' N, 166° 55.6' E	6410–6757	1	144	IORAS
Vityaz (39), St. 5637	44°29'N, 149°6'E	3015–2665	1	150	IORAS
<i>Psychropotes fuscopurpurea</i> Théel, 1882					
*Challenger, St. 157	53°55'S, 108°35'E	~3568	2	200	NHM
<i>Psychropotes raripes</i> Ludwig, 1894					
*Albatross, St. 3398	1°7'N, 80°21'W	~2800	1	175	NMNH
Akademik M. A. Lavrentiev (75), St. 75–16	55.58°N, 167.33°E	4277–4278	1	330	IORAS
Akademik M. A. Lavrentiev (75), 75–16(1)	55.58°N, 167.33°E	4277–4278	1	100 young	IORAS
Akademik M. A. Lavrentiev (71 SokhoBio), St. 1–11	46° 09.0' N, 145° 59.5' E	3305	1	115	IORAS
Akademik M. A. Lavrentiev (71 SokhoBio), St. 4–3	47° 14.0' N, 149° 34.8' E	3366	1	115	IORAS
Akademik M. A. Lavrentiev (71 SokhoBio), St. 7–12	46° 54.6' N, 151° 03.7' E	3301	1	155	IORAS
Vityaz (39), St. 5621	45°18'N, 156°0'E	5035–5210	1	180	IORAS
Vityaz (39), St. 6088	53°58'N, 157°36'W	5740	1	fragm.	IORAS
Akademik Kurchatov (4), St. 271	17°42'S, 78°59'2W	3080–2710	1	155	IORAS
Akademik Kurchatov (4), St. 277	12°27'8S, 78°34'9W	4200	1	210	IORAS
Akademik Kurchatov (11), St. 916	56°29'8S, 50°51'W	5378–4664	1	170	IORAS
Galathea, St. 716	9°23'N, 89°32'W	3570	SP***		NHMD
Albatross, St. 4721	8.125°S, 104.167°W	2084	SP***		NHMD
<i>Psychropotes dubiosa</i> Ludwig, 1894					
*Albatross, St. 3374	02°25'N, 83°53' W	~3336	SP***	55	NMNH
<i>Psychropotes dyscrita</i> (Clark, 1920)					
*Albatross, St.4672	Peru, southwest of Palominos Lighthouse, 88 miles	~5206	1	75	NMNH
Kilo Moana, St. 1808–43	2.18°N, 149 56.37°W	5040	1	320	UHM
<i>Psychropotes moskalevi</i> sp.n.					
Sonne (223 KuramBio), St. 01–12 (ID *and ** 73)	43°58.19'N, 157°19.11'E	5422–5379	2	76–99	SGN/IORAS
Sonne (223 KuramBio), St. 01–12 (ID 94)	43°58.19'N, 157°19.11'E	5422–5379	6	75–131	SGN
Sonne (223 KuramBio), St.01–13 (ID 95)	43°58.36 N, 157°15.70'E	5427–5425	5	69–135	SGN
Sonne (223 KuramBio), St. 01–12 (ID 110, except 110A)	43°58.19'N, 157°19.11'E	5422–5379	8 + fragm.	81–122	SGN
Sonne (223 KuramBio), St. 07–11 (ID 1032)	43°02.66'N, 152°59.46'E	5218–5222	4 in fragm.	110–130	SGN
Sonne (223 KuramBio), St. 07–12 (ID 1132)	43°02.56'N, 152°59.48'E	5222–5222	1	144	SGN
Sonne (223 KuramBio), St. 09–10 (ID 1227)	40°36, 13'N, 151°0, 07'E	5406–5404	1	98	SGN
Sonne (223 KuramBio), St. 10–11 (ID 1413)	41°12.04'N, 150°05.87'E	5257–5236	1	fragm.	SGN
Sonne (223 KuramBio), St. 11–11 (ID 1486)	40°13.55'N, 148°06.77'E	5349–5352	1	132	SGN
Sonne (223 KuramBio), St. 06–9 (ID 2130)	42°29.25'N, 154°00.05'E	5293–5307	1	86	SGN
Sonne (223 KuramBio), St. 05–11 (ID 2137)	43°35.67'N, 153°57.93'E	5378–5379	3	75–138	SGN
Vityaz (19), St. 3162	43°15'3N, 157°48'2E	5502	1	85	IORAS
Vityaz (19), St. 3359	51°30.1' N, 172°4.5' E	5020	1	140	IORAS
Vityaz (20), St. 5625	45°28'N, 153°46'E	6205–6215	1	100	IORAS
<i>Psychropotes pawsoni</i> sp.n.					
Sonne (250 KuramBio II), St. 64 (ID 1556)	45°9.39'N, 153°44.97'E	5738–5726	1	185	SGN
Sonne (223 KuramBio), St. 01–12 (ID 110A)	43°58.19'N, 157°19.11'E	5422–5379	1	105	SGN
*Vityaz (19), St. 3156	39°57'N, 165°07.8'E	5535	1	150	IORAS
Vityaz (39), St. 5600	46°27'N, 152°0'E	2515	1	90	IORAS
Vityaz (39), St. 5622	45°14'N, 155°15'E	5090–5100	1 + fragm.	85	IORAS
Vityaz (39), St. 5623	45°26'N, 154°59'E	5045–4995	2 in fragm.		IORAS
Vityaz (39), St. 5633	44°17'N, 149°33'E	6090–6135	1 fragm.		IORAS

* Holotype.

** Paratype.

*** only slide preparation examined

dorsal papillae and more regular deposits with slightly curved arms about 0.1 mm in length and characteristic short process at the base of each arm.

Théel (1882) mentioned seven specimens of *P. longicauda* (including varieties) taken at three HMS *Challenger* stations: St. 156 (1 specimen), St. 157 (5 specimens) and St. 298 (1 spec.). Stations 156 and 157 were taken in the Antarctic part of the Indian Ocean, St. 298 off Valparaiso, Chile. No DNA sequence data was available for samples from this region or from the type specimens. The description of *P. longicauda* and two varieties is based on specimens from St. 157 (03.03.1874, 53°55, 108°35, depth 1950 fms). The syntype of *P. longicauda* is held at the British Museum of Natural History, London, Cat. Nr. 1883.6.18.58. The length of the type specimen indicated as 140–145 mm in the original description appeared to be 100 mm at re-examination by Hansen

(1975). The second syntype specimen, “slightly smaller individual obtained at the same station” according to Théel (1882), was 80 mm long at re-examination by Hansen (1975); this specimen is held at the Muséum National d'Histoire Naturelle in Paris. Specimens from stations 156 and 298 (one at each station) were referred to the species *P. longicauda* by Théel with some uncertainty.

The varieties *monstrosa* and *fuscopurpurea* were synonymized with the species *P. longicauda* by Agatep (1967) “because of extreme individual variation in *Psychropotes longicauda*” (p. 67). Hansen (1975) in the revision of the order Elaspodida agreed with this opinion. All the differences between the varieties Hansen has interpreted as the “variation” (geographic, local and age) (p. 126). Also, Hansen synonymized with *P. longicauda* the variety *P. longicauda* var. *antarctica* Vanev, 1908 and nine other species: *P. buglossa* E. Perrier, 1896; *P. raripes* Ludwig,

Table 2

Material used in the phylogenetic analysis. Collection localities and depth are given in the Table 1. Holotypes are in bold.

Species	Specimen voucher	GenBank accession number		Vessel/cruise/station	Voucher storage	Sequence source
		COI	16S			
<i>Psychropotes moskalevi</i>	SO223-10-11-H17	MN313650	MN310400	Sonne/223/10-11	SGN	This study
<i>Psychropotes moskalevi</i>	KB-73	MN313651		Sonne/223/1-12	SGN	This study
<i>Psychropotes moskalevi</i>	KB-1132	MN313652		Sonne/223/7-12	SGN	This study
<i>Psychropotes moskalevi</i>	SO223-5-11-H7	MN313653	MN310401	Sonne/223/5-11	SGN	This study
<i>Psychropotes moskalevi</i>	KB-1227	MN313654		Sonne/223/09-19	SGN	This study
<i>Psychropotes moskalevi</i>	KB-1486	MN313655		Sonne/223/11-11	SGN	This study
<i>Psychropotes raripes</i>	SB-4-3	MN313656	MN310403	Akademik M. A. Lavrentiev/71/4-3	IORAS	This study
<i>Psychropotes pawsoni</i>	ECH00036	KU987474*	KU987543	Vityaz/19/3156	IORAS	Gubili et al. (2017)
<i>Psychropotes pawsoni</i>	ECH00035	KU987474*	KU987548	Vityaz/39/5633	IORAS	Gubili et al. (2017)
<i>Benthothytes</i> sp.	SB-1-11	MN313657	MN310402	Akademik M. A. Lavrentiev/71/1-11	IORAS	This study

* Vouchers ECH00036 and ECH00035 have identical COI sequences.

1893; *P. dubiosa* Ludwig, 1893; *P. grimaldii* Hérouard, 1896; *P. fucata* R. Perrier, 1896; *P. laticauda* Vaney, 1908; *P. brucei* Vaney, 1908; *Euphronides dyscrita* Clark, 1920 and *Nectothuria translucida* Belyaev et Vinogradov, 1969. Thus, *P. longicauda* became a classical example of a “cosmopolitan” deep-sea species. It was believed to occur in all oceans except the Arctic in a wide depth range.

We re-examined the type material of *P. longicauda* and two varieties. The type specimen of *P. longicauda* in NHM was examined by AG in 1993 and found to be in a poor state. It was also re-examined by AK in 2009. The varieties *monstrosa* and *fusco-purpurea* were examined by AK in the NHM in 2009. Both authors (AG in 1993–1994 and AK in 2007–2008) also re-examined in the Zoological Museum, University of

Copenhagen numerous slide preparations of ossicles made by Bent Hansen and referred by him to *P. longicauda*. These preparations included ossicles of the type specimens of *P. longicauda*; they were prepared at re-examination of the type material by Bent Hansen.

Re-examinations of the type material revealed that dorsal ossicles in both varieties, *monstrosa* and *fusco-purpurea*, are different from those in *Psychropotes longicauda* Théel, 1882. Dorsal ossicles in each variety represent a unique type and thus justify the status of separate species.

There is also rather significant difference between ossicles in the two type specimens of *Psychropotes longicauda* Théel, 1882 from the *Challenger* St. 157. Ossicles corresponding to *P. longicauda* (*sensu stricto*) belong to the larger specimen: 140–145 mm in Théel (1882) [= 10 cm

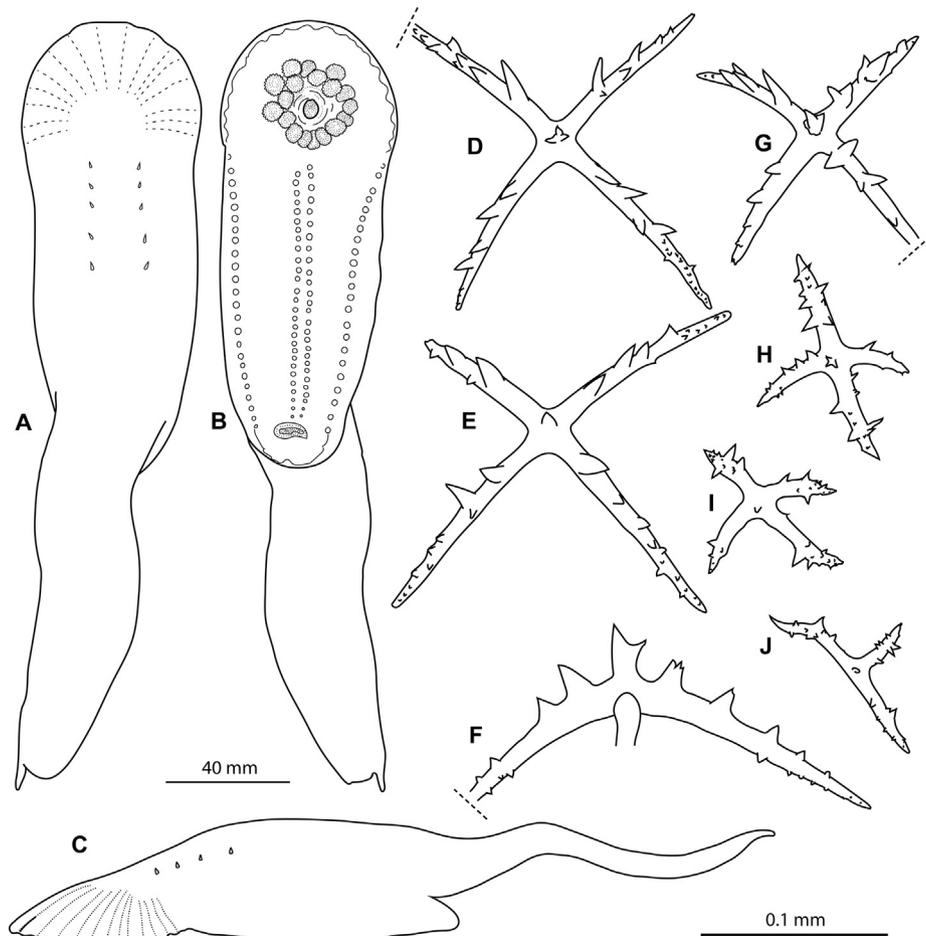


Fig. 1. *Psychropotes longicauda* Théel, 1882. A–C, dorsal, ventral and side view of the type specimen, scale 40 mm (from Théel, 1882); D–F, dorsal ossicles of the type specimen from HMS *Challenger*, St. 157; H–J, ventral ossicles of the type specimen from HMS *Challenger*, St. 157.

Table 3
Differences between *P. longicauda* and the two varieties, *monstrosa* and *fusco-purpurea*, after Théel (1882).

Character/variety	<i>Longicauda</i>	<i>Monstrosa</i>	<i>Fusco-purpurea</i>
Length (L)/width (W) (mm)	L 140–150; W 55	L 250, W 95	L 200; W 77 (in the largest of two specimens)
Colour	Dorsum greyish-violet, ventrum brownish	Dirty brown (with yellowish-brown pigment in the connective tissue of the integument)	Dark violet, almost black, with darker bands along dorsal ambulacra
Minute dorsal papillae (Nr of pairs)	5	5–7	4
Dorsal appendage (mm)	110–120 (in 10–15 mm from the posterior extremity of the body)	110	65 (in the largest ind.)
Deposits dorsal	“the largest” arms 0.24–0.4 mm, “the smallest” arms 0.04 mm; arms rather arcuated, with short strong spines directed outwards	“The calcareous bodies bear the strongest resemblance to those of the species” <i>P. longicauda</i>	Slightly curved and spinose arms, ~0.1 mm in length, with a couple of larger outwardly directed spines and the centre, where the arms are united, gives off an obtuse, short process
Deposits ventral	“the largest” arms 0.16–0.24 mm, “smaller ones” 0.08 mm, very irregular in shape		
Deposits in the inner layer of integument	Arms very slender, almost straight and giving off very long and narrow spines in all directions		

in Hansen (1975)]. These ossicles were illustrated by Théel in Pl. XXXV: 13–7 (Théel, 1882). In Bent Hansen’s collection of slide preparations ossicles from this specimen are marked 157 E2. Ossicles from the “second type specimen”, 80 mm long in Hansen (1975), were illustrated by Bent Hansen in Fig. 53 and are marked in his collection as 157 E1. Arms in ossicles of this type are longer (0.4–0.6 mm) and are characterised by distinct proximal arm spine much higher than other spines. As noted by Hansen (1975), ossicles of this type are typical for specimens of “*P. longicauda*” from the North Atlantic. It is very likely that this is a distinct type of ossicles corresponding to a separate species in the group “*P. longicauda*” (this type of ossicle was confirmed at examination of additional specimens from the North Atlantic by AG and AK).

Species described from the North Atlantic include *P. buglossa* E. Perrier, 1896; *P. fucata* R. Perrier, 1896 and *P. grimaldii* Hérouard, 1896. All these species were synonymized with *P. longicauda* by Bent Hansen (1975). However, it is obvious that further examination and revision of specimens of *Psychropotes* from the Atlantic Ocean is required. Here we shall not deal with Atlantic specimens in detail, but because of the reasons mentioned above, we decided to exclude *P. buglossa*, *P. fucata* and *P. grimaldii* from the synonymy of *P. longicauda* until a thorough re-examination of the material can be made.

The species *P. raripes* Ludwig, 1893, *P. dubiosa* Ludwig, 1893 and *P. dyscrita* (Clark, 1920) synonymized with *P. longicauda* by Bent Hansen (1975) are also re-established in the present paper as separate species. These three species are re-described in greater detail below.

Re-examination of Bent Hansen’s slide preparations revealed that specimens collected by the *Galathea* and identified by Bent Hansen as *P. longicauda* belong to a mixture of species. Ossicles resembling those in *P. xenochromata* Rogacheva and Billett, 2009 were found in specimens from the *Galathea* stations 234 and 235 from the Western Indian Ocean. Ossicles in specimens from St. 716 in the Central Eastern Pacific correspond to the species *P. raripes* Ludwig, 1894. A mixture of species appears at stations 663 and 664 from the Kermadec Trench. Ossicles in three “deviating” specimens from these stations resemble those in *P. longicauda* (s.s.). Ossicles of the 40 “typical” specimens from these two stations (uniformly yellow in colour) cannot be identified with certainty.

Ossicles in the juvenile specimen (32 mm long) from *Galathea* St. 663 referred to *P. longicauda* by Hansen (1975, Fig. 50) bear features typical of *P. raripes*: central apophysis and larger arm spines usually with secondary spines.

Ossicles in another juvenile specimen, also 32 mm long, described as *Nectothuria translucida* Belyaev et Vinogradov, 1969 and referred by different authors to *P. longicauda* correspond to ossicles of a new species *Psychropotes moskalevi* sp.nov. (details in the description of this species).

The description and illustrations of ossicles in Agatep (1967) (p. 67,

Pl. XI: 1–7) correspond to features in the species *P. raripes*, however details of external morphology, in particular, size and number of free tube feet, do not agree with characters of this species. For correct identification of Agatep’s specimens, re-examination of material is required.

Species described by Vanev (1908) from the Antarctic, *P. laticauda* (pp. 420–422, Pl. II: 14, 24) and *P. brucei* (pp. 422–423, Pls. I: 13, II: 21–22, III: 41–42), differ from *P. longicauda* (s.s.) by the type of ossicles and arrangement of ventrolateral free tube feet.

The description of *Psychropotes longicauda* var. *antarctica* Vanev, 1908 (pp. 419–420), based on a single specimen, lacks details of ossicles. Re-examination of this specimen is required for correct identification.

We did not include in the synonymy numerous historical “ecological” papers mentioning “*P. longicauda*”, because now it is obvious that different authors were dealing with different species of *Psychropotes* in different regions.

The description and illustrations of ossicles in Rogacheva et al. (2009) correspond to the amended diagnosis of *P. longicauda* (s.s.).

Distribution. Indian Ocean sector of the Antarctic, Kermadec Trench area, depths 3560–4540 m.

Psychropotes monstrosa Théel, 1882

Fig. 2.

Psychropotes longicauda var. *monstrosa* Théel, 1882: 98–99, Pls. XXIX: 2; XXX.

Type material. NHM [1883.6.18.60], HMS *Challenger*, St. 157, one specimen 190 mm long (250 mm in the original description).

Type locality. Indian Ocean sector of the Antarctic, HMS *Challenger*, St. 157, 03.03.1874, 53°55’S, 108°35’E, depth ~3560 m.

Material examined. See Table 1.

Diagnosis [after Théel (1882), modified]. Length (in alcohol) may reach 250 mm. Colour (in alcohol) dirty brown. Tentacles 18. Brim well developed especially at anterior and posterior ends of the body, with maximum width around anterior end (Fig. 2: J). Anterior brim consists of about 30 tube feet, and posterior brim of about 18 tube feet. Free lateral tube feet 18–20 pairs. Small dorsal papillae 5–7 pairs. Dorsal appendage in length almost ½ of the body length; developed at ~1/5 of the body length from the posterior body end (Fig. 2: I).

Dorsal deposits with strongly arcuate arms, 0.16–0.22 mm long. Two proximal spines very large, sometimes bifurcated; additional smaller irregular spines present, especially closer to arm tips. Central apophysis large, slightly longer or same length than proximal spines (Fig. 2: A–H). Deposits on ventrum irregular spinose crosses, with arms from 0.08 to 0.24 mm in length.

Description of material. Vityaz, St. 3340, one specimen 144 mm long, DA missing. Tentacles 18. Poor condition.

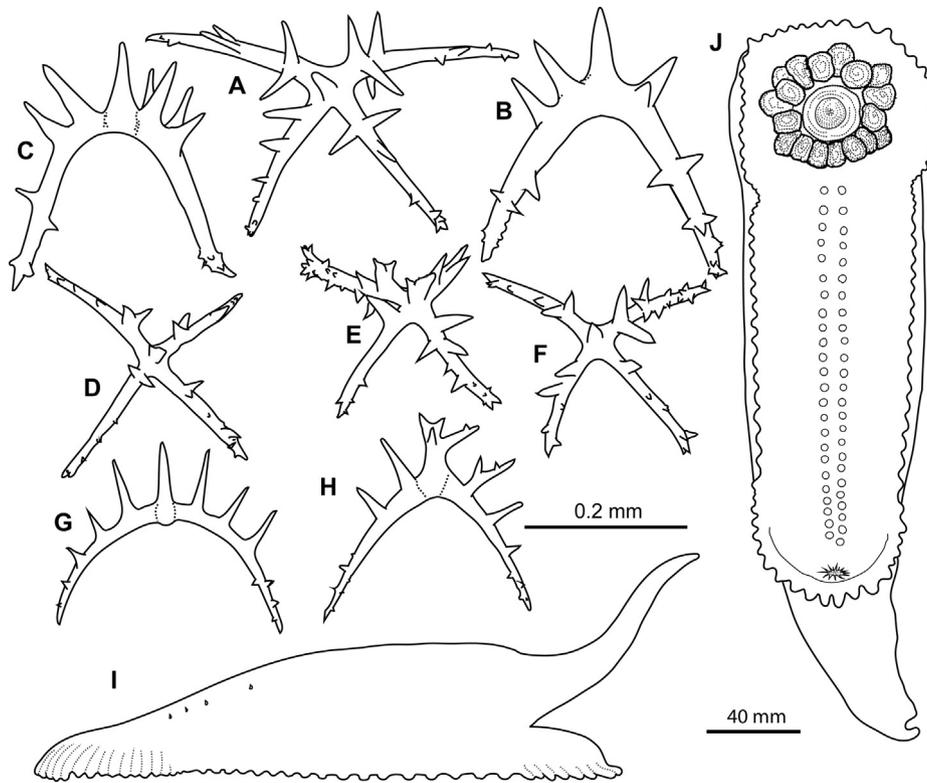


Fig. 2. *Psychropotes monstrosa* Théel, 1882. A–H, dorsal ossicles (scale 0.2 mm): A–F, ossicles of the type specimen from HMS *Challenger*, St. 157; G–H, RV *Vityaz*, St. 3340; I–J, side and dorsal view of the type specimen, scale 40 mm (from Théel, 1882).

Vityaz, St. 5637, one specimen 150 mm long, DA 120 mm. Tentacles 17. Colour violet.

Dmitry Mendeleev, St. 1290, one specimen 120 mm long, DA 35 mm. Tentacles 18. Colour dark violet.

Remarks. No DNA sequence data was available for this species. According to the original description, the specimen was 250 mm long, maximum width 95 mm, dorsal appendage 110 mm. Mid-ventral tube feet 24–25 pairs.

The holotype (Cat. No 83.6.18.60, NHM) was re-examined by AK in 2009. It was found in poor condition, though slide preparations of ossicles from the dorsum were made.

The size of the type specimen (250 mm) that gave the variety (and the species) name “*monstrosa*”, is not that unusual. Specimens of *Psychropotes* “with long tail” (unpaired dorsal appendage) commonly reach 300–400 mm in length (*in situ*) (original data, based on photo and video observations).

Relationships. *Psychropotes monstrosa* differs from *P. longicauda* (s.s.) and other species of *Psychropotes* by the unique type of ossicle on dorsum with strongly bent arms, bearing two large proximal spines, sometimes bifurcated, and large central apophysis, slightly longer or the same length than proximal spines

Distribution. Southern Indian Ocean, south-west of New Zealand, North-West Pacific, depths 3015–5450 m.

Psychropotes fuscopurpurea Théel, 1882

Fig. 3.

Psychropotes longicauda var. *fusco-purpurea* Théel, 1882: 99, Pls. XXIX: 1, XXXV: 11.

Type material. HMS *Challenger*, St. 157, two specimens: (1) 200 mm long [according to Théel (1882)], held at NHM (Cat. Nr 1883.6.18.61), and (2) 90 mm long, according to Hansen (1975), held at MNHN [not examined].

Type locality. Indian Ocean sector of the Antarctic, HMS *Challenger*, St. 157, 03.03.1874, 53°55'S, 108°35'E, depth ~ 3560 m.

Material examined. See Table 1.

Diagnosis [after Théel (1882), modified]. Length (in alcohol) may reach 200 mm. Colour dark violet, almost black, with darker bands along dorsal ambulacra. Dorsum convex. Tentacles 18. Free lateral tube feet 15–16 pairs (Fig. 3: A). Dorsal appendage with obtuse end, developed very close to posterior body end; in length ~1/3 of the body length. Small dorsal papillae in four pairs. Dorsal deposits (Fig. 3: B–I) with slightly curved or bent straight arms, 0.06–0.1 mm in length. Proximal spines large, often bifurcated; rarely additional smaller spines present. Central apophysis conical, short and smooth, shorter than proximal spines. Deposits on ventrum (Fig. 3: J–K) irregular spinose crosses, with arms from 0.08 to 0.24 mm in length.

Remarks. No DNA sequence data was available for this species. Two syntypes, the largest 200 mm long and 77 mm wide, with dorsal appendage 65 mm long according to Théel (1882). The second specimen 90 mm long, according to Hansen (1975). The specimen 200 mm long held at the NHM was re-examined by AK in 2009. The specimen was found in a poor condition. Details of external morphology could not be seen.

See remarks to *P. longicauda* for details of the original description of the variety *Psychropotes longicauda* var. *fusco-purpurea* Théel, 1882.

Relationships. *Psychropotes fuscopurpurea* differs from *P. longicauda* (s.s.) and other species of *Psychropotes* by the unique type of ossicle on dorsum with short and smooth central apophysis and relatively short arms (~0.1 mm in length) bearing usually one large proximal spine, often bifurcated.

Distribution. Known only from the type locality in the Southern Indian Ocean, depth ~ 3560 m.

Psychropotes raripes Ludwig, 1893 (re-established)

Figs. 4 and 5D.

Psychropotes raripes Ludwig, 1893: 107–108; 1894: 48–51, Pl. V: 1–16; Ohshima, 1915: 244; Clark 1920: 140–141, Pl. I: 1; Savelyeva, 1941: 79, Fig. 7; Hansen, 1975 (in part): 119, Fig. 50; 120, Fig. 51; Bluhm and Gebruk, 1999: 173–174, Fig. 3A; Mironov et al., 2018: 13, Fig. 8E.

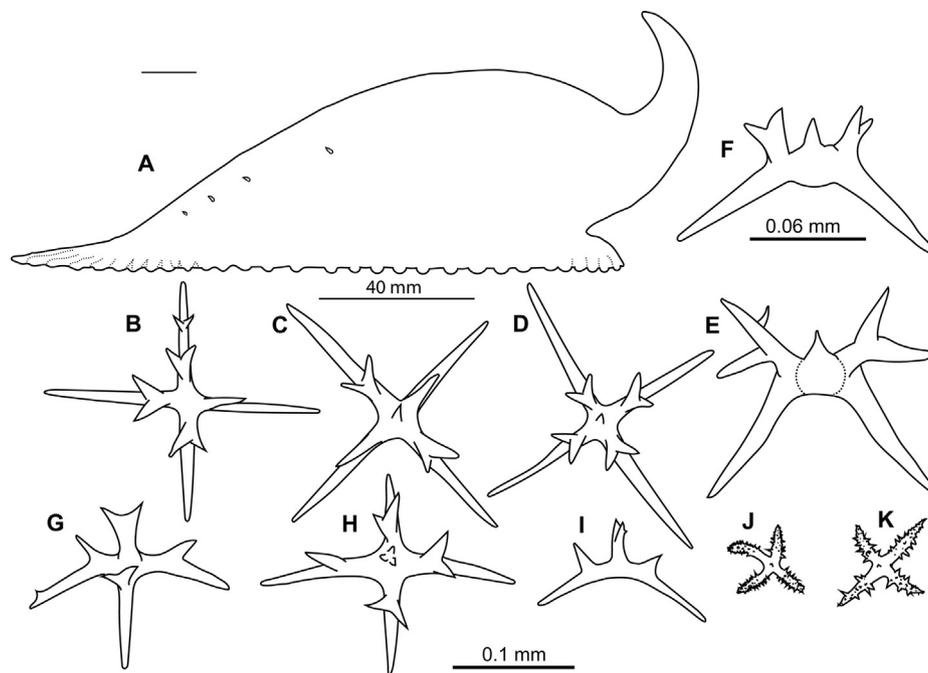


Fig. 3. *Psychropotes fuscopurpurea* Théel, 1882, type specimen. A, side view, scale 40 mm (from Théel, 1882); B–I, dorsal ossicles; J–K, ventral ossicles.

Type material. Holotype, *Albatross*, St. 3398, coll. 23.03.1891, NMNH [USNM 18173].

Type locality. East Pacific, off Ecuador, 1°7'N, 80°21'W, depth ~ 2800 m.

Material examined. See Table 1.

Diagnosis (amended). Body length up to 300 mm (preserved state). Colour in alcohol violet. Body elongated, 4–5 times as long as broad. Body height even. Tentacles 18. Brim well developed especially at anterior and posterior ends of the body, with maximum width around anterior end. Anterior brim consists of about 18–20 tube feet, and posterior brim of 13–14 tube feet. Ventrolateral tube feet large, 7–10 pairs. Mid-ventral tube feet conspicuous, in alternating double row. Dorsal papillae minute, 5–7 pairs. Unpaired dorsal appendage large, up to $\sim\frac{3}{4}$ of the body length; it is placed close to posterior end of the body, the base as broad as the body, terminal part rounded or tapering (Fig. 4: A–B).

Dorsal deposits with arms about 0.1 mm in length; arm form varies from almost straight, to sharply bent downwards from central apophysis or bent behind large proximal spines. Proximal spines are the largest, they are bipartite or tripartite or irregular; their length is equal to that of central apophysis, the latter often tripartite; small spines on arm ends (Fig. 4: C–M). Deposits on ventrum crosses with arms 0.05–0.09 mm in length, often of irregular shape, tripartite and star-shaped elements present; spines conspicuous, placed irregularly (Fig. 4: P–S).

Description of material. *Akademik Kurchatov*. St. 271, one specimen, 155 mm long, DA 25 mm (incomplete). Tentacles 18. Poor condition. St. 277, one specimen, 210 mm long, DA 50 mm (incomplete). Tentacles 18. Colour violet. St. 916, one specimen, 170 mm long, DA 30 mm (incomplete). Tentacles 18. Colour violet. Poor condition.

Vityaz St. 5621, one specimen, 180 mm long, DA 60 mm. Poor condition. St. 6088, one specimen in fragments, poor condition.

Akademik M.A. Lavrentyev (SokhoBio), St. 1–11, one specimen, 115 mm long, 25 mm wide, anterior lobe 32 mm in diameter, minute dorsal papillae 5 pairs. DA lost, it's traces 23 mm from the posterior end. Tentacles 19. Colour violet.

St. 4–3, one specimen, 115 mm long, 25 mm wide, anterior lobe 34 mm in diameter, posterior lobe built of 4 pairs of fused tube feet; minute dorsal papillae 5 pairs. DA 47 mm, 21 mm at the base, placed

11 mm from the posterior end. Free ventrolateral tube feet 8 pairs. Tentacles 18. Colour violet.

St. 7–12, one specimen, 155 mm long, 31 mm wide, anterior lobe 39 mm in diameter, posterior lobe built of 7 pairs of fused tube feet; minute dorsal papillae 3–4 (?) pairs. DA 75 mm, 30 mm at the base, placed 13 mm from the posterior end. Free ventrolateral tube feet 7 pairs. Mid-ventral tube feet \sim 29 pairs. Tentacles 18. Colour violet.

Akademik M.A. Lavrentyev St. 75–16, one specimen, 330 mm long, DA 110 mm. Tentacles 18. Free ventrolateral tube feet 8–9 pairs. St. 75–16 (1), one specimen, 85 mm long, 20 mm wide, DA 40 mm. Dorsal appendage developed at the very end of the body. Free ventrolateral tube feet 8 pairs. Colour *in situ* violet (observed using ROV before sampling), in preserved state whitish with traces of pink in dorsal appendage. Arms in dorsal ossicles in this specimen are longer and thinner (Fig. 4: N–O). This feature commonly is found in juvenile or young specimens. In *P. raripes* specimens can reach the size > 300 mm (*in vivo*), thus the specimen from St. 75–16 (1), 85 mm long, can be considered as “young”.

Remarks. This species was first briefly mentioned in Ludwig (1893) and described properly in Ludwig (1894). Hansen (1975) synonymized it with the species *P. longicauda* Théel, 1882. Based on the unique and characteristic type of dorsal ossicles, this species is re-established in the present paper. Unique ossicle features include arms about 0.1 mm in length, varying from straight to sharply bent, with large bipartite or tripartite proximal spines equal in length to that of the central apophysis. Additional characteristic feature of this species is a low number of free ventrolateral tube feet (7–10), large in size. This feature usually can be seen on *in situ* images (Fig. 5: D).

Ossicles illustrated in Savel'eva (1941) correspond to those of *P. raripes*. Specimens described by Ohshima (1915) and Clark (1920) agree with the description of Ludwig (1894). The specimen on the photograph in Fig. 3A in Bluhm and Gebruk (1999) corresponds to *P. raripes* based on a unique character of this species – eight (or seven) pairs of large tube feet.

Ossicles in specimens from the *Galathea* St. 716 (Hansen, 1975) in the Central Eastern Pacific correspond to the species *P. raripes*. Ossicles in the juvenile specimen (32 mm long) from the *Galathea* St. 663 referred to *P. longicauda* by Hansen (1975, Fig. 50) bear features typical of *P. raripes*: central apophysis and larger arm spines usually with

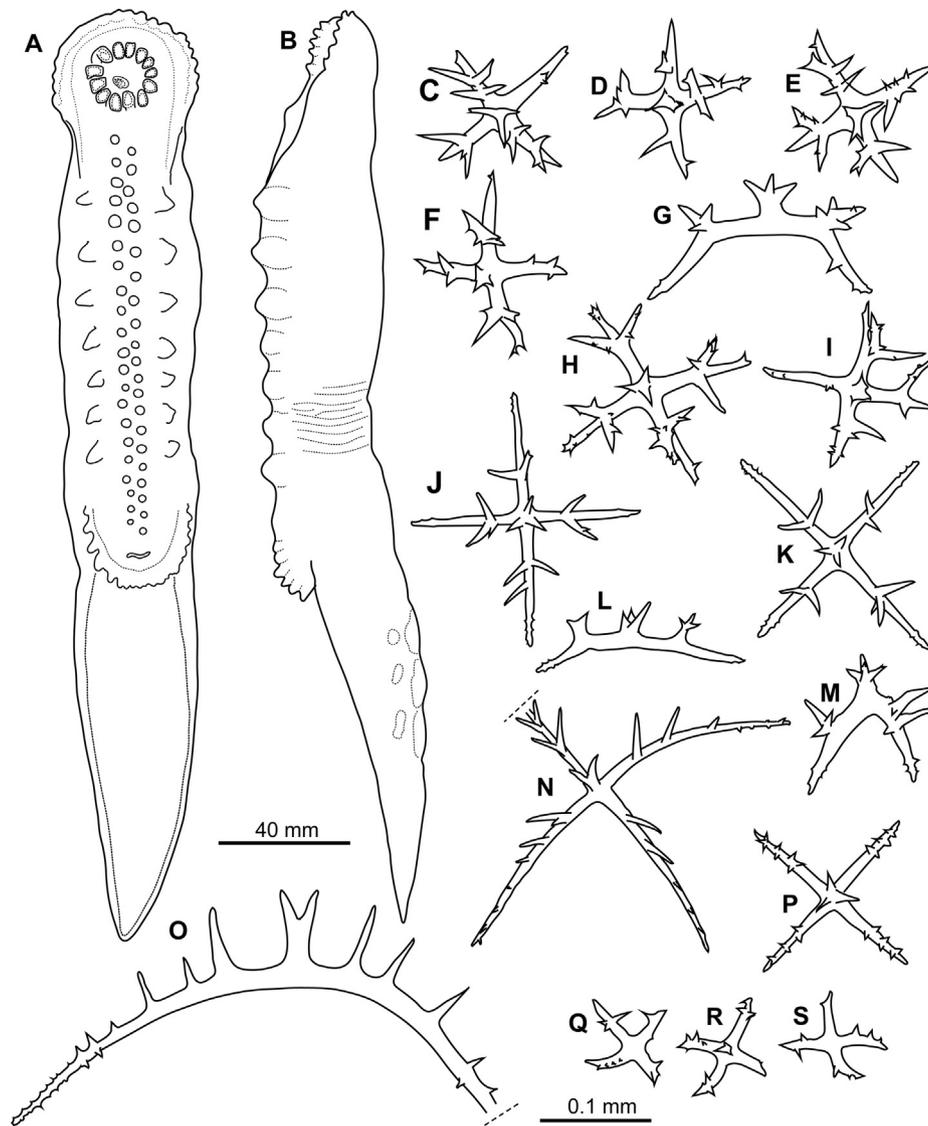


Fig. 4. *Psychropotes raripes* Ludwig, 1893. A–B, dorsal and side view, scale 40 mm (from Ludwig, 1894); C–O, dorsal ossicles; Q–S, ventral ossicles; C–F, P–R, RV Albatross St. 4721; G, J–M, P, RV Akademik Kurchatov, St. 277; H–I RV Galathea, St. 716; N–O, RV young specimen from RV Akademik M. A. Lavrentyev, St. 16.

secondary spines.

Description and illustrations of ossicles in Agatep (1967) (p. 67, Pl. XI: 1–7) correspond to features in the species *P. raripes*, however details of external morphology such as the size of the body and the number of free tube feet, in particular, do not agree with characters of this species. For correct identification of Agatep's specimens, re-examination of material is required.

Geographic variation. There are some differences in dorsal ossicles in specimens from the East and the West Pacific: in the East Pacific specimens, ossicles on dorsum are more robust (Fig. 4: C–H). This feature was so stable in all the specimens we examined that we questioned whether specimens from the East and West Pacific belonged to the same species. All other main characters, including the low number of free ventrolateral tube feet (7–10), were the same. We suggest that there are not enough morphological features to resolve this problem. Genetic studies apparently could be a better instrument here.

Relationships. The species *Psychropotes raripes* differs from other species of *Psychropotes* by long dorsal appendage at the posterior end and ossicles on dorsum with arms about 0.1 mm in length, varying from straight to sharply bent, with large bipartite or tripartite proximal spines equal in length to that of the central apophysis. The number of free ventrolateral tube feet in this species is usually only 7–8 (up to 10),

in *P. longicauda* (s.s.) up to 25 (often 17–19). In other species of *Psychropotes* with long dorsal appendages the number of free ventrolateral tube feet is commonly 13–14.

The COI sequence obtained from specimen of *P. raripes* from the Sea of Okhotsk (Akademik Lavrentiev, St. 4–3) was identical with GenBank sequence KU987536 (Gubili et al 2017) from the Great Australian Bight (Fig. 10). These sequences are nested among sequences largely referred to as Lineage 2A by Gubili et al (2017), but our topology is different and referred to as Clade C. All of the other sequences in Clade C come from the NE Atlantic (Fig. 10). Further sequence data is needed to resolve the placement of *P. raripes* relative to other *Psychropotes* species.

Distribution. Antarctic (Scotia Sea), tropical Eastern Pacific, North and North-West Pacific, depths 2800–5378 m.

***Psychropotes dubiosa* Ludwig, 1893**

Fig. 6.

Psychropotes dubiosa Ludwig, 1893: 107–108; 1894: 52–53, Pl. II: 5–7.

Type material. Holotype, Albatross, St. 3374, coll. 03.03.1891, NHM [USNM 18172].

Type locality. East Pacific, 02°25'N, 83°53' W, depth ~ 3336 m

Material examined. See Table 1.

Diagnosis (after Ludwig, 1894, modified). Colour in preserved state

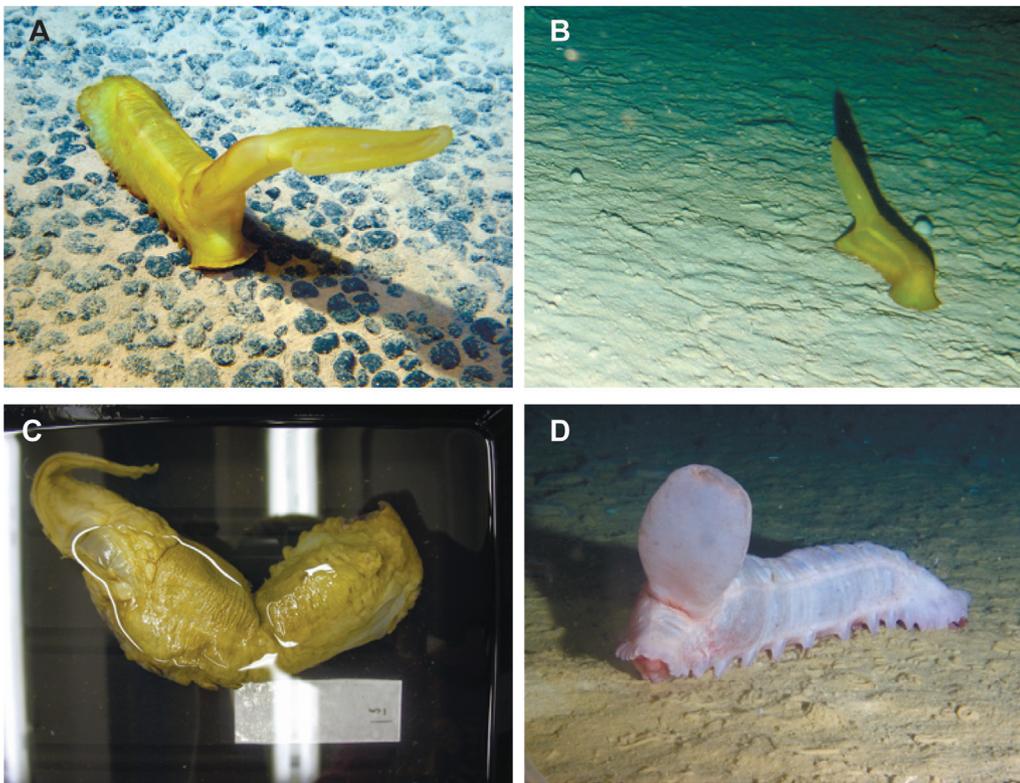


Fig. 5. A, *Psychropotes* sp. from Clarion-Clipperton Fracture Zone area (Copyright: Ifremer/Nautile, Nodinaut 2004); B–C, *Psychropotes moskalevi* from St. 01–10 and 07–11 (ID 1032) of *Sonne* respectively; D, *Psychropotes raripes* (*Akademik M.A. Lavrentyev* St. 75–16) (Copyright: Zhirmunsky National Scientific Centre of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia).

violet, darker on ventrum. Body elongated, 3–4 times as long as broad; body width slightly narrowing posteriorly. Tentacles 10. Brim well developed; posterior lobe consists of 10 tube feet. Ventrolateral tube feet 12 pairs. Length of unpaired dorsal appendage about 1/2 of the body length. Dorsal ossicles crosses, rarely with three arms; arms thin, about 0.15 mm in length; arm spines conspicuous, often bifurcated or three-radiate; largest spines often proximal. Deposits on ventrum crosses with arms up to 0.3 mm with smooth central apophysis ~ 0.2 mm long.

Remarks. No DNA sequence data was available for this species. The epithet name *dubiosa* was first briefly mentioned in Ludwig (1893) and described properly in Ludwig (1894). According to Ludwig (1894), the type specimen (Fig. 6: A) was 113 mm long *in vivo*, 31 mm in the preserved state and had only 10 tentacles, all of which suggest its juvenile stage. Although adult morphology of the ossicles cannot be predicted with certainty, the size of ossicles is known to decrease with

size (age) in some other species of *Psychropotes* such as *P. raripes* and *P. moskalevi* whereas spine shape and arrangement remain similar. At the same time, the original description of *P. dubiosa* is sufficient enough and includes some unique characters lacking in other species of the “*longicauda*” group. One of such characters is the type of ossicle on ventrum (Fig. 6: C) with long arms (up to 0.3 mm) and long central apophysis without spines described and illustrated by Ludwig (1894).

We attempted to examine the type specimen (and the only existing specimen) of this species held at the Smithsonian Institution. With a generous help of David Pawson, it was found that the type specimen is in bad condition and lacks ossicles.

Relationships. There are several species of *Psychropotes* with a long dorsal appendage developed very close to, or at a short distance from, the posterior body end. The species *P. dubiosa* (Ludwig, 1894) differs from other species in this group by occasionally present ventral crosses with long arms (up to 0.3 mm) and long central apophysis without

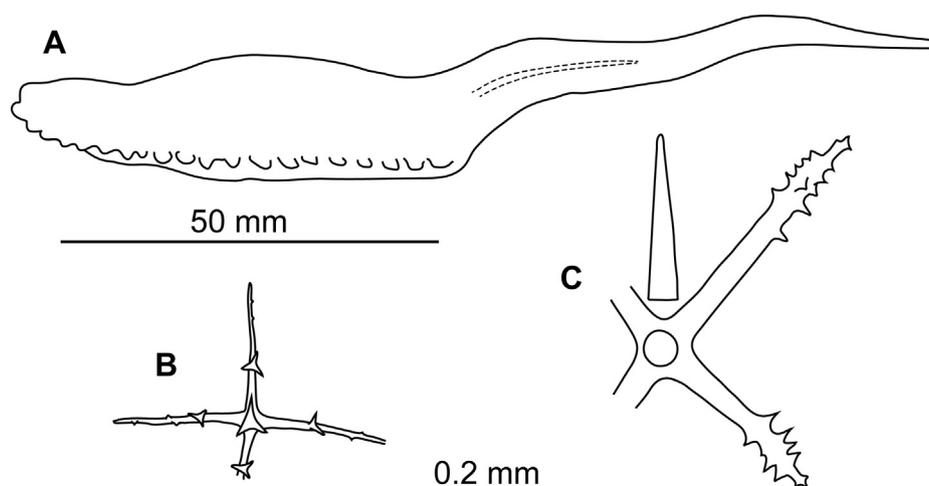


Fig. 6. *Psychropotes dubiosa* Ludwig, 1893 (from Ludwig, 1894). A, side view (from Ludwig, 1894); B, dorsal ossicle; C, ventral ossicle.

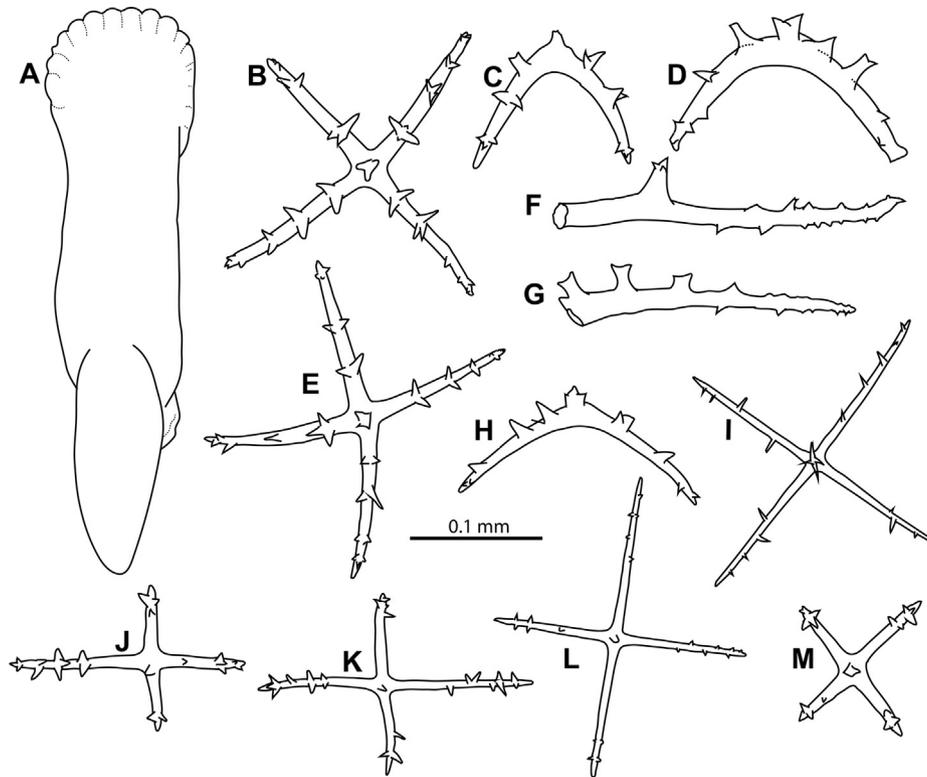


Fig. 7. *Psychropotes dyscrita* (Clark, 1920). A, dorsal view (from Ludwig, 1894); B–M from RV *Kilo Moana*, St. 1808-43: B–I, dorsal ossicles; J–M, ventral ossicles.

spines.

Distribution. Known only from its type locality.

Psychropotes dyscrita (Clark, 1920) (re-established)

Euphronides dyscrita Clark, 1920: 139, Pl. II: 3.

Figs. 5A and 7.

Type material. Albatross, St. 4672, “Peru, southwest of Palominos Lighthouse, 88 miles”, depth ~5206 m. Two specimens, NMNH. Holotype Cat. No USNM E 9899.

Material examined. See Table 1.

Diagnosis [strongly modified after Clark (1920)]. Length *in situ* reaches 300 + mm. Colour (*in situ*) yellow, ventral side (especially along ambulacra) and tentacles reddish-light purple. Tentacles 18. Free lateral tube feet 13–15 pairs. Dorsal appendage with round end, developed at some distance from the posterior body end; in length ~4/5 of the body length (Fig. 7: A).

Dorsal ossicles of two main types: (1) with arms 0.1–0.15 mm in length, from slightly to strongly arcuate; two–three conspicuous spines, often bifurcated, additional smaller spines at arm tips; central apophysis short and spinose (Fig. 7: B–E, H); (2) with bent arms, 0.2–0.4 mm in length, 1–3 large spines, often bifurcated and smaller irregular spines closer to arm tips (Fig. 7: F–G). Crosses with very thin spinose arms, 0.12–0.15 mm in length, typical of inner skin layers, also present (Fig. 7: I). Ventral ossicles smaller crosses with spiny arms 0.1 mm long or less.

Description of material. The specimen ~300 mm long, dorsal appendage 250 mm, placed in ~40 mm from the posterior body end. Free ventro-lateral tube feet 13 pairs. Mid-ventral tube feet ~21 pair. Body colour yellow; colour of tentacles and ventrum (especially along ambulacra) reddish.

Remarks. According to H.L. Clark (1920), “the holotype is in poor condition but the paratype is much worse” (p. 139). Continued from Clark (1920): “The species looks like a short-tailed *Psychropotes* but the appendage is so short and the calcareous particles are so strongly arcuate, it seems better placed in *Euphronides*” (p.139). The genera *Euphronides* and *Psychropotes* were established by Théel (1882) and

distinguished by the position of unpaired dorsal appendage placed at a “considerable distance” from the body end in the former. Hansen (1975) has demonstrated intermediate forms and synonymized *Euphronides* Théel, 1882 with *Psychropotes* Théel, 1882.

According to the original description, the holotype was 75 mm long, 17 mm wide, yellow-brown above, deep-purple below. Tentacles (“apparently 18”) very deep purple. Dorsal appendage 18 mm long and 10 mm wide at the base, 5 mm wide at tip, situated 8 mm from posterior body end (Clark, 1920). Ossicles on dorsum with “large” and “slender” arms indicated in the original description, were also present in our slide preparation, however they were rather occasional compared to other type of large dorsal ossicles.

The holotype (NMNH, Cat. No USNM E 9899) was accessed with the help of David Pawson. The specimen was found in a very poor condition, no external morphological features could be distinguished. Ossicles from the remaining dorsal tissue were re-examined. Most of the ossicles in our slide preparations appeared to be broken, however their main features could be figured out, including presence of two main types: (1) with arms 0.1–0.15 mm with two–three conspicuous spines, often bifurcated and (2) arms 0.2–0.4 mm in length, with more irregular pattern of spines. The same type of ossicle was found in the specimen from the Clarion-Clipperton fracture zone area (material examined).

Relationships. *Psychropotes dyscrita* differs from other species of *Psychropotes* by long unpaired dorsal appendage developed very close to or at a short distance from the posterior body end by ossicles on dorsum of two main types: (1) with arms 0.1–0.15 mm in length, with two–three conspicuous spines, often bifurcated and (2) arms 0.2–0.4 mm in length, with more irregular pattern of spines. Characteristic feature of this species also is a yellow colour of the body.

Distribution. Central East Pacific, depth 5040–5206 m.

Psychropotes moskalevi Gebruk et Kremenetskaia, sp. nov.

Figs. 5B–C and 8.

?*Nectothuria translucida* Belyaev et Vinogradov, 1969: pp.709–715, Figs. 1–4 (juvenile).

Holotype. KuramBio, Sonne, St. 223/01–12, ID 73, specimen 99 mm long, stored at SGN.

Paratype. KuramBio, Sonne, St. 223/01–12, ID 73, specimen 76 mm long. IORAS Cat. Nr ECH00881

Type locality. Northwest Pacific Ocean, 43°58.19'N, 157°19.11' E – 43°57.81' N, 157°21.58'E, depth 5422–5379 m.

Etymology. The species is named after the distinguished Soviet/Russian deep-sea zoologist, Dr. Lev Moskalev.

Material examined. See Table 1.

Diagnosis. Body length up to 350 + mm (preserved state). Colour in alcohol from grey to brownish on dorsum, brownish to dark violet on ventrum. Body elongated, 4–5 times as long as broad. Body height even or increasing gradually towards unpaired dorsal appendage; body width slightly narrowing posteriorly. Tentacles 18, occasionally 17 or 19–20. Brim well developed especially on anterior and posterior ends of the body, with maximum width around anterior end. Anterior brim consists of about 15 pairs of tube feet, and posterior brim of 7–9 tube feet. Ventrolateral tube feet up to 25 pairs, often 17–19. Mid-ventral tube feet conspicuous, in alternating double row. Dorsal papillae minute, up to 8 pairs between dorsal appendage and anterior brim. Unpaired dorsal appendage large, varying in length from 1/5 to almost the same length as the body; it is placed close to posterior end of the body (distance from posterior end is less than appendage width, often half the width), the base almost as broad as the body, terminal part rounded, bifurcated or irregular (Fig. 8: A–B).

Dorsal deposits with arms 0.15–0.30 mm in length, arms usually with a horizontal curvature; arm spines short, largest 1–3 proximal spines about the same length with central apophysis or shorter, the largest spines often bipartite or bearing secondary spines (Fig. 8: C–G). Deposits of inner body wall layer crosses, their arms slender, almost straight with thin irregularly placed spines. Deposits on ventrum crosses with arms 0.15–0.25 mm in length, often of irregular shape, strongly spinose; rods and tripartite deposits also present.

Description of the holotype. Specimen 99 mm long, 27 mm wide behind the anterior lobe, 26 mm wide posteriorly. Anterior lobe 32 mm in diameter. Free ventrolateral tube feet 14 pairs, there is gap ~15 mm behind the anterior lobe without tube feet. Dorsal appendage 48 mm, 18 mm at the base, placed in 9 mm from the posterior end. Tentacles 18. Colour grey on dorsum, violet on ventrum.

Description of the paratype. Specimen 76 mm long, 23 mm wide. Anterior lobe 32 mm in diameter. Free ventrolateral tube feet 14 pairs, there is gap ~15 mm behind the anterior lobe without tube feet. Dorsal appendage incomplete, 20 mm at the base, placed in 9 mm from the posterior end. Tentacles 18. Colour light grey on dorsum, violet on ventrum.

Description of material. KuramBio specimens:

ID 73. Two specimens, 76 and 99 mm long. (1) Specimen 99 mm long: 27 mm wide behind anterior lobe, 20 mm wide at the posterior end; anterior lobe 32 mm in diameter. Tube feet 14 pairs. DA 48 mm, 18 mm wide at the base, placed in 9 mm from the posterior body end. (2) Specimen 76 mm: 23 mm wide behind anterior lobe. Tube feet 14 pairs. DA 20 mm at the base, in 9 mm from posterior body end.

ID 94. Six specimens, 75–131 mm long. (1) Specimen 131 mm long, 28 mm wide, incomplete. (2) Specimen 121 mm long, 31 mm wide, DA incomplete, 24 mm at the base, placed in 15 mm from the posterior end. Dorsum light grey, ventrum violet. (3) Specimen 92 mm long, 31 mm wide, DA lacking. (4) Specimen 90 mm long, 29 mm wide, DA lacking. (5) Specimen 78 mm long, 22 mm wide, DA lacking. (6) Specimen 75 mm long, 19 mm wide, DA 42 mm, 14 mm at the base, placed in 12 mm from the posterior end, tentacles 18.

ID 95. Five specimens, from 69 mm to 135 mm long. In all dorsum light grey, anterior lobe violet at ventral side. (1) Specimen 128 mm long, 38 mm wide. DA 20 mm at the base, in 13 mm from the body end. Tentacles 18. (2) Specimen 110 mm long, 30 mm wide. DA 16 mm at the base, in 14 mm from the posterior end. Tentacles 19. (3) Specimen 135 mm long, 30 mm wide. DA 20 mm at the base, in 14 mm from the posterior end. Tentacles 18. (4) Specimen 95 mm long, 25 mm wide. Tentacles 18. DA 21 mm at the base, in 13 mm from the posterior end. (5) Specimen 69 mm long, 25 mm wide. Tentacles 17. Posterior end incomplete.

ID 110. Seven specimens, 81–122 mm long. In all dorsum brownish, ventrum violet. (1) Specimen 122 mm long, 30 mm wide, DA 64 mm. 18 mm at the base, placed in 14 mm from the posterior end. (2) Specimen 115 mm long, incomplete. (3) Specimen 110 mm long, incomplete. (4) Specimen 81 mm long, 20 mm wide. (5) Specimen 90 mm long, incomplete. (6) Specimen 90 mm long, incomplete. (7) Specimen 98 mm long, incomplete. In addition, fragments of two specimens.

ID 1032. Fragments of 4 specimens, from 110 to 130 mm long,

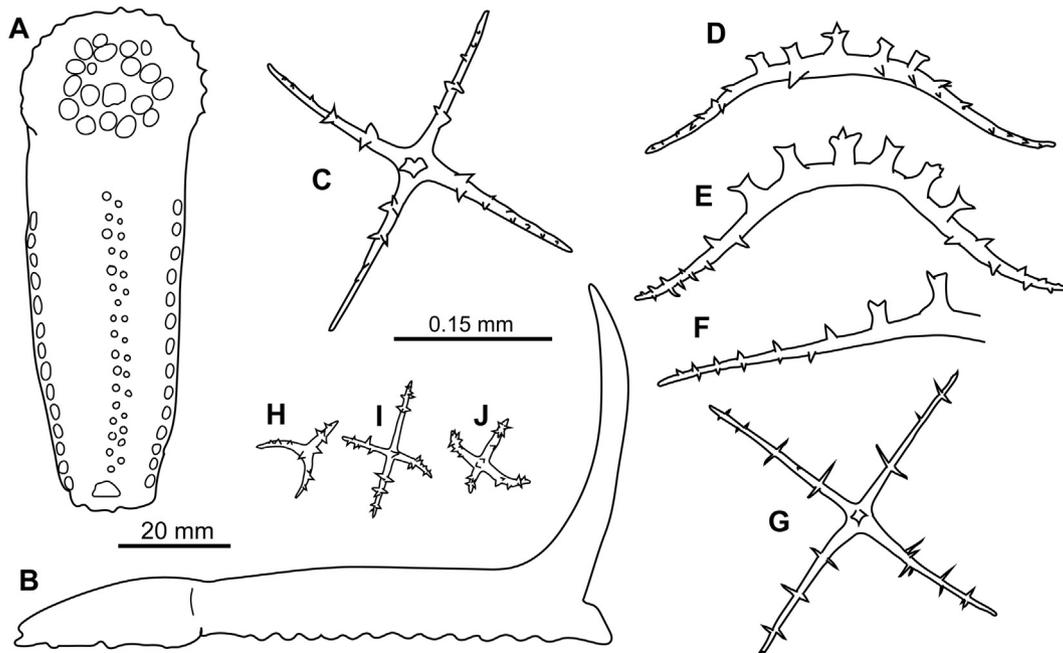


Fig. 8. *Psychropotes moskalevi* n. sp. A, B, ventral and side view of the holotype (scale 20 mm); C–G, dorsal ossicles (scale 0.15 mm), RV Sonne, St. 9–11; H–J, ventral ossicles of the holotype (scale 0.15 mm).

dorsum light or dark.

ID 1132. One specimen, 144 mm long, 39 mm wide (max), anterior lobe 48 mm in diameter. Tentacles 20. DA only distal part present, 24 mm at the base in 14 mm from the posterior end. Dorsum light grey, ventrum violet.

ID 1227. One specimen, 98 mm long, 30 mm wide, anterior lobe 35 mm in diameter. Tentacles 17. DA 50 mm long, 22 mm at the base, placed in 18 mm from the posterior end. Dorsum light grey, ventrum violet.

ID 1413. One specimen in fragments.

ID 1486. One specimen, 132 mm long, 35 mm wide, anterior lobe 40 mm in diameter. DA 90 mm, 27 mm at the base, placed in 20 mm from the posterior end. Dorsum light grey, ventrum violet.

ID 2130. One incomplete specimen, 86 mm long.

ID 2137. Three specimens, 75–138 mm long. (1) Specimen 138 mm long, 39 mm (max) wide, DA 24 mm, placed in 17 mm from the posterior end. Dorsum light grey, ventrum violet. (2) Specimen 85 mm long, 27 mm wide, DA lacking. (3) Specimen 75 mm long, incomplete.

Additional specimens:

Vityaz St. 3162. One specimen, in poor condition, 85 mm long, DA 40 mm.

Vityaz St. 3359. One specimen, 140 mm long, DA 40 mm.

Vityaz St. 5625. One specimen, 100 mm long, DA 35 mm long. Light grey, tentacles 18, violet. Poor condition.

Remarks. The specimen ID 1032 (SO223/St. 7-11) was photographed in the laboratory soon after sorting and fixation. The colour of this specimen (on a series of images) was dirty yellow (Fig. 5: C). One image of *Psychropotes* was taken *in situ* at SO223/St. 1–10 (Fig. 5: B). The colour of the specimen on this image is yellow-greenish. It seems likely that the natural colour of the upper side of *P. moskalevi* is yellowish/yellow-greenish, this colour changes in alcohol to grey/brownish.

Dorsal ossicles in the juvenile specimen, 32 mm long, described as *Nectothuria translucida* Belyaev et Vinogradov, 1969 and referred by different authors to *P. longicauda* correspond to ossicles in *P. moskalevi* sp.nov. based on the following characters: arms with a horizontal curvature; arm spines short, largest 1–3 proximal spines about the same length with central apophysis or shorter, the largest spines often bipartite or bearing secondary spines. The arm length in the juvenile reaches 0.5–0.6 mm, whereas in adults the maximum length is 0.3 mm.

The holotype of *N. translucida* (IORAS Cat. Nr ECH01300) was originally preserved in formalin, therefore ossicles are not suitable for morphological studies. We included this species in the synonymy with a question mark.

Relationships. Dorsal ossicles in this species are of a unique type. Unique features include arms up to 0.30 mm in length, with short spines, largest 1–3 proximal spines about the same length with the central apophysis or shorter; the largest spines often bipartite or bearing secondary spines.

The COI sequences from six specimens of *P. moskalevi* sp. nov. formed a clade (Clade B, Fig. 10) that was distinct from any other *Psychropotes* lineages. The intraspecific variation in COI was much less than 1% and the closest other sequences such as KU987487 were over 2% divergent (Fig. 10).

Distribution. North-West Pacific, depths 5020–6215 m.

Psychropotes pawsoni Gebruk et Kremenetskaia, sp. nov.

Fig. 9.

Holotype. Vityaz, cruise 19, St. 3156, specimen 140 mm long, IORAS Cat. Nr ECH00036.

Type locality. Northwest Pacific, 39°57'N, 165°07.8'E, depth 5535 m.

Material examined. See Table 1.

Etymology. The species is named after the prominent expert on deep-sea holothurians, Dr. David Pawson.

Diagnosis. Colour in alcohol grey/brown on dorsum, tentacle disks, ventrolateral and mid-ventral tube feet and middle part of ventrum violet. Body elongated, 3–4 times as long as broad. Body height even.

Tentacles 18. Brim narrow. Ventrolateral tube feet 20–21 pairs. Mid-ventral tube feet conspicuous, in alternating double row. Unpaired dorsal appendage ~1/2 of the body length, placed at some distance from posterior body end. Dorsal papillae minute, 4 pairs (Fig. 9: A–C).

Dorsal deposits with arms 0.1–0.18 mm in length; arms curved or bent to various degree. Spines numerous and conspicuous, diminishing in size towards arm ends, often in groups of three, often irregular or with secondary spines; spines can be developed on upper and under sides of arms (Fig. 9: E–F, H–J). Sometimes present is long central apophysis developed on under side of the cross (the “fifth arm”); this apophysis also spinous (Fig. 9: D, G). Deposits on ventrum crosses with arms 0.05–0.1 mm in length, often of irregular shape, spinose (Fig. 9: K–N).

Description of the holotype. The specimen 140 mm long, 27 mm wide. Dorsal appendage 60 mm long, incomplete, 30 mm at the base, placed in 30 mm from the posterior end. Minute dorsal papillae not seen.

Description of material. KuramBio, ID1556. One specimen, 185 cm long; DA 60 mm long, incomplete; minute papillae 4 pairs.

KuramBio, ID110A. One specimen 105 mm long; DA 23 mm, incomplete; minute papillae not seen.

Vityaz, St. 3156. One specimen, 150 mm long, DA 45 mm.

Vityaz, St. 5600. One specimen, 90 mm long, DA 45 mm, in very poor condition.

Vityaz, St. 5622. One specimen, 85 mm long, DA 45 mm. Second specimen fragmented.

Vityaz, St. 5623. Fragments of two specimens.

Vityaz, St. 5633. Fragment of one specimen.

Relationships. The species *Psychropotes pawsoni* sp. nov. differs from other species of *Psychropotes* by large, sometimes irregular, arm spines, often arranged in groups of three and commonly present crosses with long central apophysis developed on under side of the cross.

The single COI sequence of *P. pawsoni* sp. nov., KU987474, formed part of Clade A (Fig. 10) that was the sister group to the remainder of Clade A and was minimally 1% divergent from them (to KU987476). The single 16S sequence available for *P. pawsoni* sp. nov. was identical to a range of other *Psychropotes* (Fig. 11), suggesting this marker has low phylogenetic information.

Distribution. North-West Pacific, depths 2515–6135 m.

Molecular data

Based on the resulting maximum likelihood COI tree, the two new and one reinstated species for which data was available; *Psychropotes raripes*, *P. moskalevi* and *P. pawsoni*, were placed in separate clades. The Pacific species *Psychropotes moskalevi* sp. nov. formed a clade, with branch support of 62 (Fig. 10, Clade B) that was sistergroup to a clade largely comprised of Atlantic specimens, with a few Pacific examples (Fig. 10). The resurrected *Psychropotes raripes* was part of Clade C, which otherwise had northeast Atlantic representatives (Fig. 10). *Psychropotes pawsoni* was placed within clade A. Besides the northwest Pacific representative this clade includes specimens from the Eastern Pacific, northeast Atlantic, Southern Indian Ocean and the Antarctic. The analysis of the 16S rDNA dataset, which is much sparser than the COI data, showed much less structure and variation among the samples and appears to be a less informative marker. It placed all examined representatives of the *Psychropotes 'longicauda'* species complex in a largely unresolved single clade with branch support of 70 (Fig. 11).

4. Concluding remarks

Psychropotid holothurians with a long dorsal appendage developed very close to or at a short distance from the posterior body end until recently were all attributed to the species *P. longicauda* (s.l.). This species was recorded throughout the World Ocean except the Arctic, in a wide depth range. Morphological evidence that there are several species under this name appeared first in the late 1990s of the last century after re-examination of slide preparations of Bent Hansen [A. Gebruk, personal data, mentioned in Rogacheva et al. (2009)].

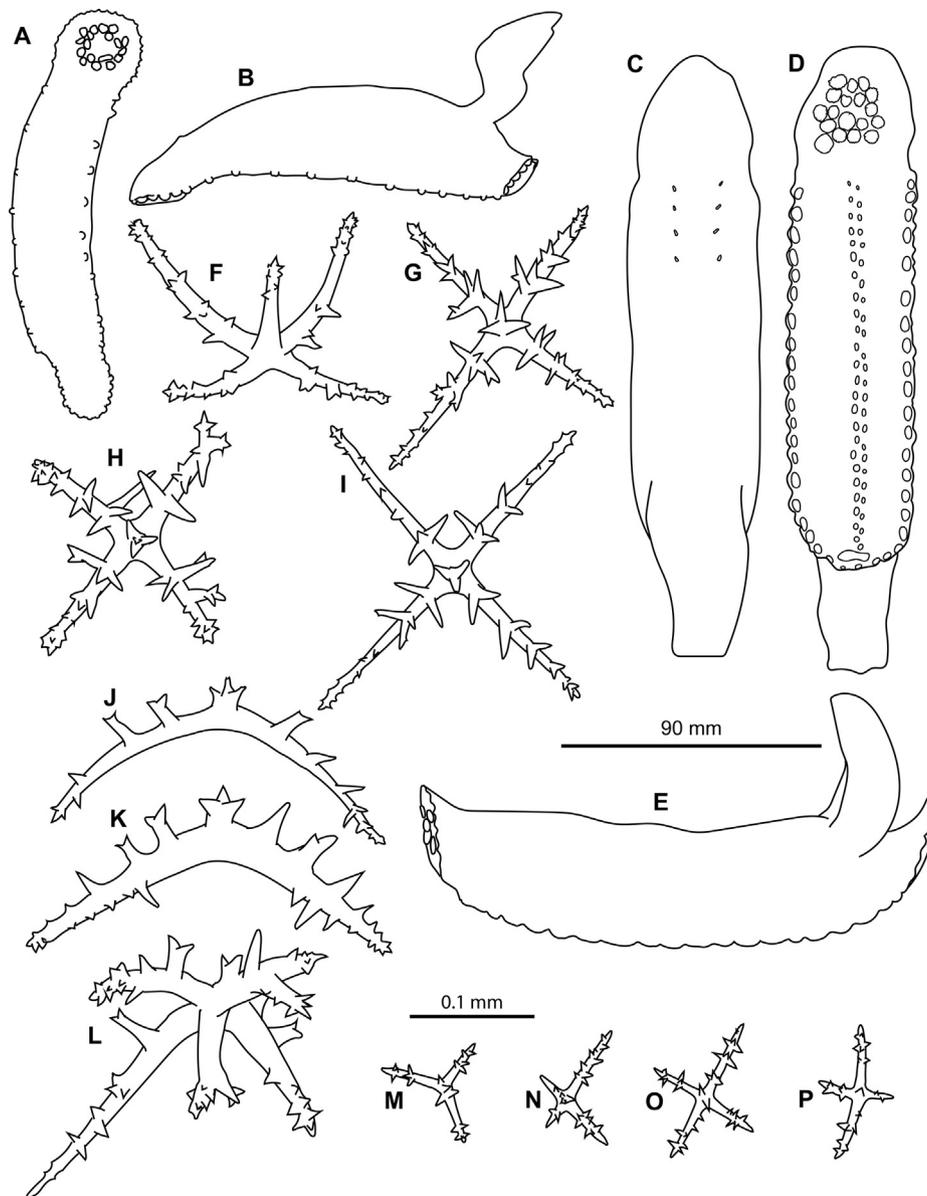


Fig. 9. *Psychropotes pawsoni* n. sp. A–B, ventral and side view of a holotype (scale 90 mm); C–E, dorsal, ventral and side view of a specimen from RV *Sonne* St. 64 (scale 90 mm); F–L, dorsal ossicles (scale 0.1 mm); F–J, RV *Vityaz*, St. 5622; K–L, RV *Vityaz*, St. 5633; M–P, ventral ossicles, RV *Sonne* St. 64 (scale 0.1 mm).

The species *P. xenochromata* Rogacheva and Billett, 2009 (Rogacheva et al., 2009) became the first example of the “long-tail” *Psychropotes* that was not *P. longicauda* in the interpretation of Bent Hansen who revised this genus in Hansen (1975). *P. xenochromata*, apart from characteristic dorsal ossicles is characterized by yellowish-green colour, considered to be unusual for this genus. Our new data showed that colouration in species of *Psychropotes* with long “tail” is diverse, varying in live specimens from purple/violet to yellow/green/brown. Thus, the yellow colour occurs in the species *P. dyscrita* (Clark, 1920), and also in *P. moskalevi* sp. nov. “Yellow” specimens also were described by Hansen (1975) from the *Galathea* station 663 in the Kermadec Trench (p.116). At present we were not able to identify these specimens with certainty. The yellow morphotype of “*P. longicauda*” was photographed and collected in the Clarion-Clipperton fracture zone area in the tropical east Pacific (Fifis and Scolan, 2005 and Fig. 5A). By colour and external morphology this specimen resembles *P. dyscrita* collected in the same area by *Kilo Moana* (St. 1808–43). Although Fifis and Scolan (2005) provided photographs of ossicles, species identification is complicated as it is not clear where these ossicles were taken

from.

Thus, the group of species of the “*P. longicauda*” morphotype (with long dorsal appendage developed very close to or at a short distance from the posterior body end) currently includes eight species: *Psychropotes longicauda* Théel, 1882, *P. monstrosa* (Théel, 1882), *P. fuscopurpurea* (Théel, 1882), *P. raripe* Ludwig, 1893, *P. dubiosa* Ludwig, 1893, *P. dyscrita* (Clark, 1920), *P. moskalevi* sp. nov. and *P. pawsoni* sp. nov.

Remarks on geographical distribution

In the present work we considered the group of species of *Psychropotes* with a “long tail” from the North-West Pacific (some of them were formerly referred to *P. longicauda* (s.L.). Type localities of some of these species and our additional material extended the geographical range to the East Pacific and Antarctic (Fig. 12). There is evidence (original data) that other species of *Psychropotes* with long dorsal appendages occur in the Antarctic and the North Atlantic. We did not deal with those species in the present study.

Cryptic diversity in the cosmopolitan species “*P. longicauda*” (s.L.) was recently studied by Gubili et al. (2017) based on molecular genetic

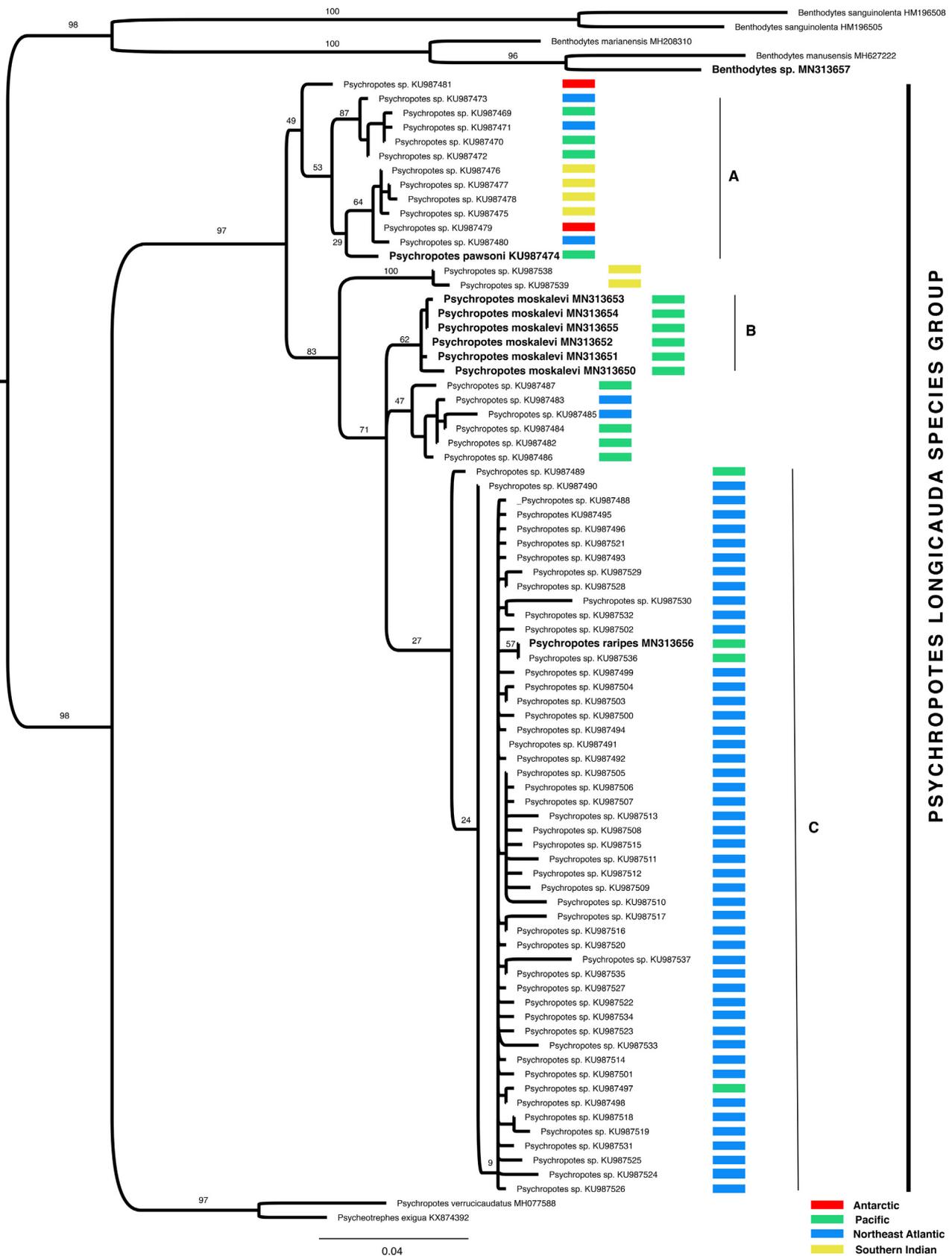


Fig. 10. Maximum likelihood tree based on mtDNA COI analysis. Numbers on nodes indicate bootstrap support. Specimens examined in this study are in bold.

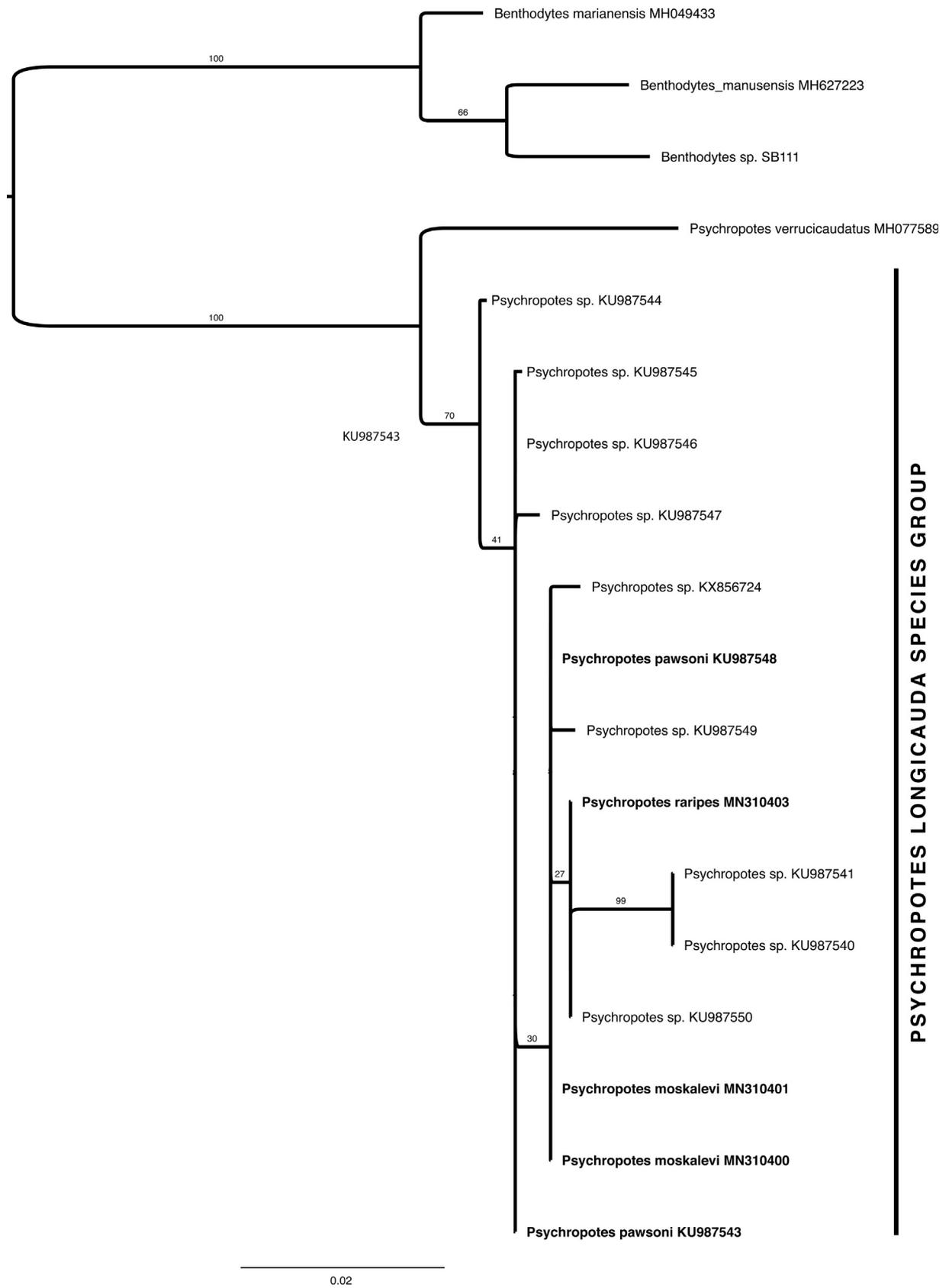


Fig. 11. Maximum likelihood tree based on 16S rDNA analysis. Numbers on nodes indicate bootstrap support. Specimens examined in this study are in bold.

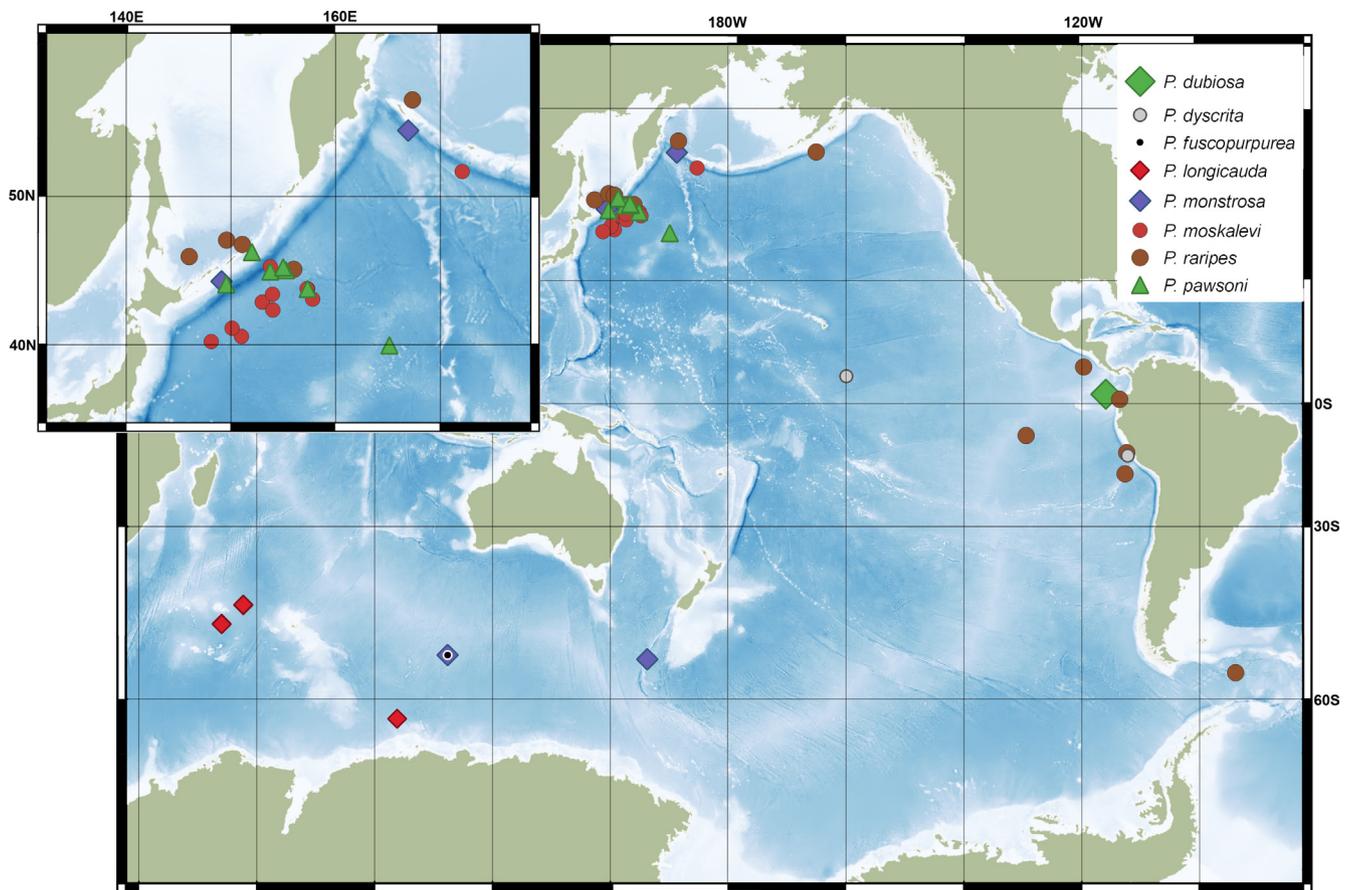


Fig. 12. Distribution of examined species of *P. longicauda* species complex.

data (the mitochondrial COI and 16S genes). The authors identified two distinct lineages within the global distribution of this species and suggested that the sister clades could be classified as separate species based on the observed genetic divergence. Both lineages were cosmopolitically distributed in the ocean. Our data partly support this idea. In particular, *pawsoni* clade (Fig. 10, clade A) is distributed in all four oceans. However, *moskalevi* clade has very narrow distribution range occurring only in the northwest Pacific. A significant population differentiation also was emphasized between the North Atlantic localities and localities in both the Pacific and Indian Oceans.

There are a number of other records of *Psychropotes* “*longicauda*” in the Pacific, including central regions and the North-East Pacific, shown for example in Gubili et al. (2017). However, many of these historical records were mentioned in ecological papers (not taxonomical) with unreliable species identification, especially in a view of species diversity in this group according to our new data. Re-examination of these old materials is required to clarify biogeographical questions.

According to our new data and records summarised by Gubili et al. (2017), species of the “*P. longicauda*” group are nearly absent in the central West Pacific. If this not the problem of undersampling, it can be suggested that this group of species dispersed from the Antarctic to the North Pacific via the East Pacific, one of the routes demonstrated by Mironov et al. (2018) for other abyssal echinoderms.

Declaration of Competing Interest

No conflict of interest.

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