



Monograph

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Echinoderes (Kinorhyncha: Cyclorhagida) from the Hikurangi Margin, New Zealand

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Abstract. Limited data are available for the kinorhynch fauna from the Southern Hemisphere, with little or no data from New Zealand. Here, we provide a first comprehensive overview of the diversity of mud dragons, with an emphasis on species of *Echinoderes* from the continental slope of New Zealand, from a variety of habitats such as slopes, canyons and seamounts located in the Hikurangi Margin region. The study revealed fifteen species of *Echinoderes*. Of these, ten are described as new to science: *E. aragorni* sp. nov., *E. blazeji* sp. nov., *E. dalzottoi* sp. nov., *E. frodoi* sp. nov., *E. galadrietae* sp. nov., *E. gandalfi* sp. nov., *E. landersi* sp. nov., *E. leduci* sp. nov., *E. legolasi* sp. nov. and *E. samwisei* sp. nov. Moreover, *Echinoderes juliae* Sørensen et al., 2018, *Echinoderes* sp. aff. *E. balerioni*, *Echinoderes* sp. aff. *E. galadrietae/beringiensis*, *Echinoderes* sp. aff. *E. lupherorum* and *Echinoderes* sp. aff. *E. unispinosus* are reported in the investigated region. The most abundant among all was *E. gandalfi* sp. nov., but it was found only in canyons. Interestingly, the second most common species was *E. juliae* that was found at several stations in canyons, seamount and on the slope. This species is one of the deep-sea species originally found on the abyssal plain off Oregon and along the continental rise off California, Northeast Pacific, recorded in polymetallic nodules in the tropical eastern Pacific, and recently found on the abyssal plains off Chile, east of the Atacama Trench. These findings, together with records of *Echinoderes* sp. aff. *E. lupherorum* and *Echinoderes* sp. aff. *E. unispinosus* indicate that, despite their low dispersal abilities, kinorhynchs, similar to other meiofaunal species, may exhibit a wider distribution pattern than previously assumed. The number of recorded species and numerous new species show that New Zealand sediments not only are inhabited by a diverse kinorhynch fauna, but *Echinoderes*, the most speciose genus, still holds much to discover.

Keywords. Echinoderidae, deep-sea canyons, kinorhynchs, meiofauna, seamounts, taxonomy.

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Introduction

Over the past years, studies on the taxonomic composition and distribution of kinorhynchs have intensified considerably, and the number of reports of new kinorhynch species from the most remote locations

increases steadily (e.g., Cepeda *et al.* 2020; Grzelak *et al.* 2021; Adrianov & Maiorova 2022). However, most of our knowledge about this group is still concentrated in regions in the Northern Hemisphere where taxonomists happened to be located, i.e., southern Europe (e.g., Sánchez *et al.* 2012; Dal Zotto & Todaro 2016), East Asia (e.g., Sørensen *et al.* 2012, 2013; Yamasaki & Fujimoto 2014; Yamasaki 2016, 2017), and North and Central America (e.g., Higgins 1983; Pardos *et al.* 2016a, 2016b; Sørensen *et al.* 2016b, 2018; Landers *et al.* 2018, 2022). Therefore, many areas, especially in the Southern Hemisphere, remain virtually unexplored, although the presence of mud dragons is reported in ecological studies. We find one of the largest gaps in known kinorhynch biodiversity in the Oceanian Region, and in particular around New Zealand – nearly a terra incognita in terms of kinorhynch fauna.

From several studies of the meiofauna of this region, it is known that mud dragons occur in a variety of shallow waters and deeper continental margin habitats, such as slopes, canyons and seamounts (Coull & Wells 1981; Kamenev *et al.* 1993; Pilditch *et al.* 2015; Rosli *et al.* 2016), but to date only six species have been described from New Zealand territory. The first formally described kinorhynch species from this region were *Echinoderes malakhovi* Adrianov, 1999 in Adrianov & Malakhov (1999) and *Pycnophyes newzealandiensis* Adrianov, 1999 in Adrianov & Malakhov (1999) from sandy sediments at a depth of 60 m in the Bay of Plenty (Adrianov & Malakhov 1999). Some years later, Neuhaus & Blasche (2006) described the new echinoderid genus *Fissuroderes* Neuhaus & Blasche, 2006 from deep-sea localities east of New Zealand, including four new species of this genus (Neuhaus & Blasche 2006). A more recent report of kinorhynchs in the area is restricted to a single species, *Campyloderes* cf. *vanhoeffeni* Zelinka, 1913, found at the Hikurangi Plateau and Chatham Rise at depths of 420–1940 m by Neuhaus & Sørensen (2013). In addition, Neuhaus (2013) cited Coull & Wells (1981) for reporting *Echinoderes coulli* Higgins, 1977 from Pauatahanui Bay, Porirua, north of Wellington. The reported identity of this species is rather doubtful though, and it is more likely that Coull & Wells (1981) collected a yet undescribed species and representative of the *E. coulli* species complex (see Yamasaki & Fujimoto 2014). The most recent overview of New Zealand's kinorhynch fauna was published by Neuhaus *et al.* (2010) in the Biodiversity Inventory series of Gordon (2010). An updated version is expected to be published in 2023 (Grzelak & Sørensen in prep.)

The present contribution is the result of studies of kinorhynchs found in the samples collected during the cruise TAN1004, which took place in April 2010, in the Hikurangi Margin region, as part of an extensive meiofauna sampling campaign conducted by the National Institute of Water and Atmospheric Research (Bowden *et al.* 2016; Rosli *et al.* 2016). The main purpose of this study is to provide the first assessment of the species richness and distribution of Kinorhyncha Reinhard, 1881 in the deep waters on the continental slope of New Zealand. Here, we contribute with the description of ten new species of *Echinoderes*. Furthermore, we provide detailed data of five known species of *Echinoderes*. It is clear that the kinorhynch fauna from New Zealand has been largely neglected so far; therefore, these new descriptions will help to significantly expand the knowledge of this group in Southwest Pacific.

Material and methods

The study area is located along the Hikurangi Margin, southeast of the Cook Strait that separates North and South Island, New Zealand (Fig. 1). Sampling was conducted at slope, canyon and seamount sites from the *RV Tangaroa* during the National Institute of Water and Atmospheric Research (NIWA) voyage TAN1004 in April 2010. A multicorer (MUC) with tubes of an internal diameter of 9.52 cm was used to retrieve bottom sediment from 20 stations, with depths ranging from 670 m to 1561 m (Table 1). From each deployment, one to three cores were taken from the MUC and dedicated to meiofauna analysis. The samples were fixed with 10% buffered formalin. More information about sampling sites and sampling methodology can be found in Bowden *et al.* (2016) and Rosli *et al.* (2016).

In the laboratory, samples were washed in a 45 µm sieve and meiofauna organisms were extracted from the sieved sediment by LUDOX flotation (Somerfield & Warwick 1996). First, main meiofauna taxa were identified under a stereo microscope, then kinorhynchs were picked up and transferred to slides with glycerine, sealed with paraffin and stored for several years at NIWA. After this, the slides with kinorhynch specimens were shipped to the Natural History Museum of Denmark (NHMD) for further examination and description. A total of 356 kinorhynchs, including 204 adult individuals, were found.

For preparation of light microscopy (LM) slides, original glass slides were opened, specimens were transferred directly to Fluoromount-G (mounting medium preferred for Kinorhyncha) and remounted. The new preparations were either made on regular glass slides, or, preferably, by mounting the individual specimens between two cover slips and attaching them to an H-S plastic slide. The specimens were examined with an Olympus BX51 microscope with differential interference contrast, and photographed with an Olympus DP27 camera. Measurements were made with Cell[^]D software. Line art figures were made with Adobe Illustrator CS6. Examined specimens were deposited in the collections of NHMD and NIWA (see Table 1 for catalogue numbers).

Preparation of specimens for scanning electron microscopy (SEM) was more complex than usual because the kinorhynchs were originally stored in glycerine. Therefore, at first, the specimens were rehydrated in a 50% v/v water-glycerine solution. Then, the specimens were transferred to demineralized water, and a small amount of liquid soap was added to get rid of the residual glycerine and organic particles. The detergent was mixed with water, and numerous bubbles were created to help capture particles adhering to the specimens. The samples were left overnight, after which bubbles were again produced. After three rounds of washing, specimens were transferred to clean, deionized water to wash off any remaining

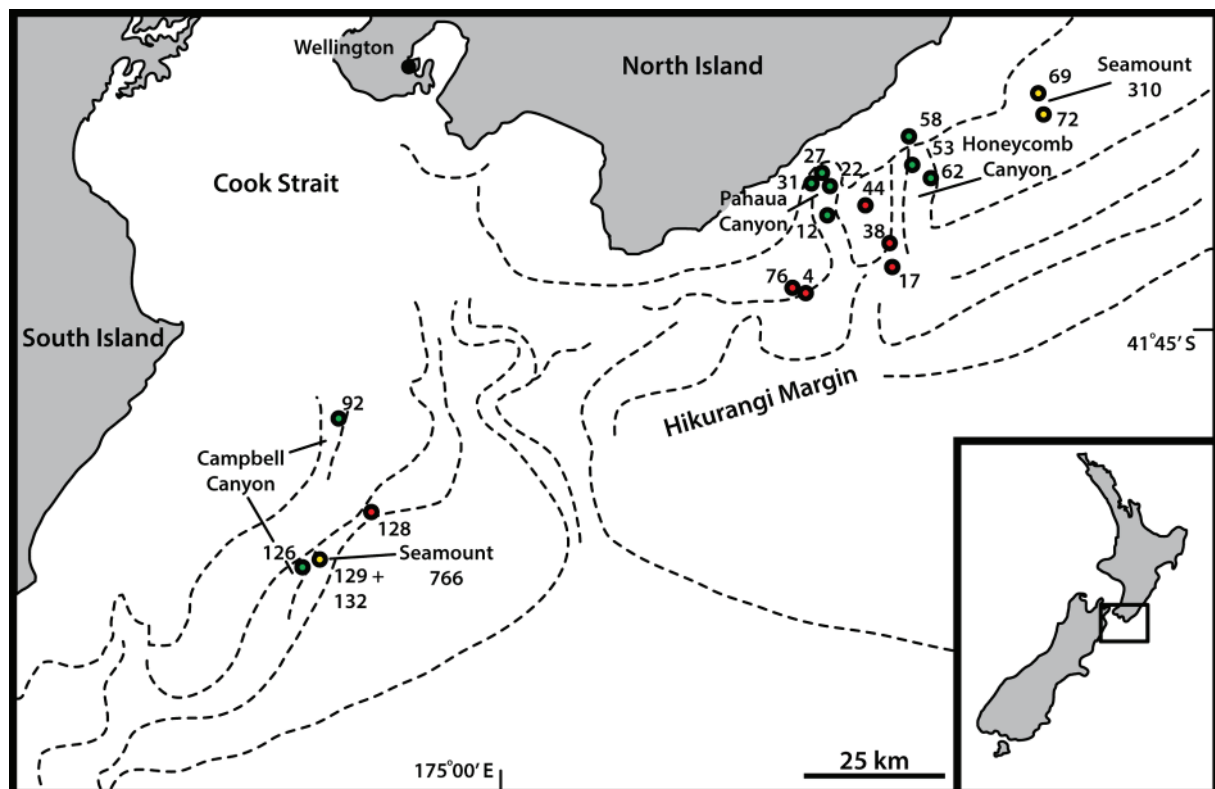


Fig. 1. Map showing the sampling stations. Colour codes indicate slopes (red), canyons (green), and seamounts (yellow). Inset shows New Zealand with a frame marking the sampling area.

Table 1 (continued on next four pages). Coordinates and basic data on sampling stations, and identities, type status and catalogue numbers of species of *Echinoderes* Claparède, 1863 from each station.

Location	Stn	Depth (m)	Latitude (°S)	Longitude (°E)	Species	Mounting	Type status and catalogue number			
Slope	4	1046	41.6837	175.6642	<i>E. aragorni</i> sp. nov.	LM	1 ♀, paratype (NIWA-159424)			
					<i>E. frodoii</i> sp. nov.	LM	1 ♂, paratype (NHMD-916331) 1 ♀, 1 ♂, paratypes (NIWA-159415–159416)			
	17	1514	41.6288	175.8682	<i>E. aff. galadriellae/beringensis</i>	LM	1 ♀, non-type (NIWA-159427)			
					<i>E. juliae</i>	LM	1 ♂, 1 ♀, non-types (NHMD-921715, NHMD-921717)			
					<i>E. aff. lupherorum</i>	LM	1 ♂, non-type (NIWA-159428)			
					<i>E. samwisei</i> sp. nov.	LM	1 ♀, 1 ♂, paratypes (NHMD-917299–917300) 2 ♂♂, paratypes (NIWA-159419–159420)			
					<i>E. juliae</i>	LM	1 ♀, 1 ♂, non-types (NHMD-921723–921724)			
					<i>E. aragorni</i> sp. nov.	LM	♀, holotype (NIWA-159423)			
					<i>E. frodoii</i> sp. nov.	LM	1 ♀, paratype (NHMD-916335)			
						SEM	1 ♀, 1 ♂, non-types			
					<i>E. aff. galadriellae/beringensis</i>	SEM	2 ♂♂, non-types			
					<i>E. juliae</i>	LM	1 ♂, non-type (NHMD-921729)			
<i>E. landersi</i> sp. nov.	LM	♀, holotype (NIWA-159402)								
38	1121	41.5937	175.8532	<i>E. aff. lupherorum</i>	LM	1 ♂, non-type (NHMD-921636)				
				<i>E. samwisei</i> sp. nov.	LM	♂, holotype (NIWA-159418) 1 ♂, paratype (NIWA-159421)				
					SEM	1 ♀, non-type				
				<i>E. aff. unispinosus</i>	LM	1 ♂, non-type (NHMD-921792)				
				<i>E. aragorni</i> sp. nov.	SEM	1 ♀, 1 ♂, non-types				
				<i>E. juliae</i>	SEM	1 ♀, non-type				
				44	728	41.5258	175.8003	<i>E. aragorni</i> sp. nov.	SEM	1 ♀, non-type
								<i>E. juliae</i>	SEM	1 ♀, non-type

Table 1 (continued). Coordinates and basic data on sampling stations, and identities, type status and catalogue numbers of species of *Echinoderes* Claparède, 1863 from each station.

Location	Stn	Depth (m)	Latitude (°S)	Longitude (°E)	Species	Mounting	Type status and catalogue number
Slope					<i>E. landersi</i> sp. nov.	SEM	1 ♀, non-type
					<i>E. legolasi</i> sp. nov.	SEM	1 ♂, non-type
					<i>E. aff. lupherorum</i>	SEM	1 ♀, non-type
					<i>E. samwisei</i> sp. nov.	SEM	1 ♀, non-type
	76	1282	41.6833	175.6500	<i>E. frodoi</i> sp. nov.	LM SEM	1 ♀, paratype (NHMD-916336) 1 ♀, non-type
					<i>E. galadriellae</i> sp. nov.	SEM	2 ♀♀, non-types
					<i>E. aff. galadriellae/beringensis</i>	LM	1 ♀, non-type (NHMD-921503)
						SEM	1 ♂, non-type
					<i>E. juliae</i>	SEM	1 ♀, non-type
					<i>E. aff. lupherorum</i>	SEM	2 ♂♂, non-types
Pahaua Canyon	128	1420	42.0485	174.7000	<i>E. frodoi</i> sp. nov.	LM	1 ♀, paratype (NHMD-916337)
					<i>E. aff. lupherorum</i>	LM	1 ♂, non-type (NHMD-921635)
	12	1350	41.5508	175.7250	<i>E. galadriellae</i> sp. nov.	LM	2 ♀♀, paratypes (NHMD-921496–921497)
					<i>E. aff. galadriellae/beringensis</i>	LM	1 ♀, 1 ♂, non-types (NHMD-921498–921499)
					<i>E. gandalfi</i> sp. nov.	LM	1 ♀, paratype (NIWA-159409)
					<i>E. juliae</i>	LM	2 ♀♀, 2 ♂♂, non-types (NHMD-921718–921721)
					<i>E. samwisei</i> sp. nov.	LM	1 ♂, paratype (NHMD-917301)
	22	1188	41.5100	175.7187	<i>E. frodoi</i> sp. nov.	LM	♂, holotype (NIWA-159414) 1 ♀, paratype (NIWA-159417)
					<i>E. gandalfi</i> sp. nov.	LM	1 ♀, paratype (NHMD-916362) 1 ♂, paratype (NIWA-159410)
					<i>E. juliae</i>	LM	1 ♀, non-type (NHMD-921728)

Table 1 (continued). Coordinates and basic data on sampling stations, and identities, type status and catalogue numbers of species of *Echinoderes* Claparède, 1863 from each station.

Location	Stn	Depth (m)	Latitude (°S)	Longitude (°E)	Species	Mounting	Type status and catalogue number
Pahaua Canyon	27	1013	41.4983	175.7043	<i>E. aff. lupherorum</i>	LM	1 ♂, non-type (NIWA-1592429)
					<i>E. blazeji</i> sp. nov.	LM	♂, holotype (NIWA-159400) 1 ♀, paratype (NHMD-917223) 1 ♂, paratype (NIWA-159401)
						SEM	1 ♂, non-type
					<i>E. dalzottoi</i> sp. nov.	LM	1 ♂, paratype (NHMD-917147)
						SEM	1 ♂, non-type
					<i>E. frodoi</i> sp. nov.	SEM	1 ♂, non-type
					<i>E. galadrietae</i> sp. nov.	SEM	3 ♀♀, 1 ♂, non-types
					<i>E. aff. galadrietae/beringensis</i>	SEM	2 ♂♂, non-types
					<i>E. gandalfi</i> sp. nov.	LM	1 ♂, paratype (NIWA-159411)
						SEM	5 ♀♀, 3 ♂♂, non-types
					<i>E. juliae</i>	SEM	1 ♂, non-type
					<i>E. landersi</i> sp. nov.	SEM	2 ♀♀, non-types
					<i>E. leduci</i> sp. nov.	SEM	1 ♂, non-type
	31	730		41.4962	175.6828	<i>E. aff. lupherorum</i>	LM
						SEM	3 ♀♀, 2 ♂, non-types
<i>E. dalzottoi</i> sp. nov.						LM	♀, holotype (NIWA-159403)
						SEM	1 ♂, non-type
<i>E. frodoi</i> sp. nov.						LM	1 ♂, paratype (NHMD-916332)
<i>E. gandalfi</i> sp. nov.						LM	♂ holotype (NIWA-159407) 1 ♀, paratype (NHMD-916356) 1 ♀, paratype (NIWA-159408)
				<i>E. juliae</i>	LM	1 ♂, non-type (NHMD-921725)	

Table 1 (continued). Coordinates and basic data on sampling stations, and identities, type status and catalogue numbers of species of *Echinoderes* Claparède, 1863 from each station.

Location	Stn	Depth (m)	Latitude (°S)	Longitude (°E)	Species	Mounting	Type status and catalogue number
Pahaua Canyon					<i>E. landersi</i> sp. nov.	LM	1 ♀, paratype (NHMD-916627)
					<i>E. leduci</i> sp. nov.	LM	♂, holotype (NIWA-159405)
Honeycomb Canyon	53	948	41.4563	175.8970	<i>E. aff. galadrietae/beringensis</i>	LM	1 ♂, non-type (NHMD-921500)
	58	670	41.4080	175.8977	<i>E. aragorni</i> sp. nov.	LM	1 ♀, paratype (NHMD-920115)
					<i>E. blazeji</i> sp. nov.	SEM	3 ♀♀, 1 ♂, non-types
					<i>E. dalzottoi</i> sp. nov.	LM	1 ♂, paratype (NIWA-159404)
						SEM	1 ♀, non-type
					<i>E. frodoi</i> sp. nov.	SEM	1 ♂, non-type
					<i>E. aff. galadrietae/beringensis</i>	LM	1 ♂, non-type (NHMD-921502)
					<i>E. gandalfi</i> sp. nov.	LM	2 ♂♂, paratypes (NHMD-916357–916358) 1 ♀, paratype (NIWA-159412)
					<i>E. juliae</i>	LM	2 ♀♀, non-types (NHMD-921726–921727)
						SEM	2 ♀♀, non-types
					<i>E. leduci</i> sp. nov.	LM	1 ♀, paratype (NIWA-159406)
						SEM	1 ♂, non-type
	62	1171	41.4760	175.9477	<i>E. aragorni</i> sp. nov.	SEM	1 ♂, non-type
					<i>E. blazeji</i> sp. nov.	SEM	1 ♂, non-type
					<i>E. galadrietae</i> sp. nov.	SEM	1 ♀, non-type
					<i>E. gandalfi</i> sp. nov.	SEM	1 ♀, 2 ♂♂, non-types
					<i>E. juliae</i>	SEM	1 ♀, non-type
					<i>E. aff. lupherorum</i>	SEM	1 ♀, non-type
					<i>E. samwisei</i> sp. nov.	SEM	1 ♀, non-type

Table 1 (continued). Coordinates and basic data on sampling stations, and identities, type status and catalogue numbers of species of *Echinoderes* Claparède, 1863.

Location	Stn	Depth (m)	Latitude (°S)	Longitude (°E)	Species	Mounting	Type status and catalogue number
Campbell Canyon	92	683	41.8922	174.6347	<i>E. frodoi</i> sp. nov.	SEM	1 ♂, non-type
	126	1495	42.1422	174.5492	<i>E. frodoi</i> sp. nov.	LM	1 ♀, paratype (NHMD-916333)
						SEM	1 ♀, non-type
Seamount 310	69	670	41.3353	176.1882	<i>E. galadrietae</i> sp. nov.	LM	♀, holotype (NIWA-159425)
						LM	2 ♂♂, 1 ♀, paratypes (NHMD-916359–916361)
							1 ♂, paratype (NIWA-159413)
						SEM	1 ♀, non-type
						LM	1 ♀, non-type (NHMD-921634)
						LM	1 ♂, non-type (NHMD-921971)
LM	1 ♀, non-type (NHMD-921501)						
Seamount 766	72	985	41.3657	176.1958	<i>E. aff. lupherorum</i>	LM	1 ♀, non-type (NHMD-921632)
						LM	♂, holotype (NIWA-159422)
						LM	1 ♂, non-type (NHMD-921633)
						SEM	1 ♀, non-type
Seamount 766	129	1456	42.1345	174.5860	<i>E. samwisei</i> sp. nov.	LM	1 ♀, paratype (NHMD-917302)
						SEM	1 ♂, non-type
						LM	1 ♂, paratype (NHMD-916334)
Seamount 766	132	1453	42.1345	174.5850	<i>E. galadrietae</i> sp. nov.	LM	1 ♀, paratype (NIWA-159426)
						LM	2 ♀♀, non-types (NHMD-921730, 9217032)
						LM	

detergent. Following this process, specimens were dehydrated through a graded water-alcohol and then alcohol-acetone series, and finally critical point dried. Dried specimens were mounted on aluminium stubs, sputter coated with a platinum/palladium mixture and examined with a JEOL JSM-6335F Field Emission scanning electron microscope.

All specimens of *Echinoderes* were identified to species level, except for the juveniles. Identification of kinorhynchs to species level was based on the relevant taxonomic literature (Sørensen *et al.* 2018; Yamasaki *et al.* 2018b; Grzelak & Sørensen 2019) and the interactive identification key to species of Echinoderidae (Yamasaki *et al.* 2020a).

Abbreviations

The following abbreviations are used for collections and museums:

INBRIV	=	National Institute of Biological Resources, Korea
NHMD	=	Natural History Museum of Denmark, Copenhagen, Denmark
NIWA	=	National Institute of Water and Atmospheric Research, Wellington

The following abbreviations are used in tables:

ac	=	acicular spine
fs	=	fringe-like structure
gco1/2	=	glandular cell outlet type 1/2
LA	=	lateral accessory
LD	=	laterodorsal
ltas	=	lateral terminal accessory spine
lts	=	lateral terminal spine
LV	=	lateroventral
MD	=	middorsal
ML	=	midlateral
MSW-X	=	maximum sternal width, with X indicating segment with greatest sternal width
n/a	=	data non-applicable
pa	=	female papillae
PD	=	paradorsal
pe	=	penile spines
pr	=	protuberance
S	=	segment length
SD	=	subdorsal
si	=	sieve plate
SL	=	sublateral
so	=	slit-like opening
ss	=	sensory spot
SW-10	=	standard width, always measured on segment 10
tbl	=	tubule
TL	=	trunk length
tu	=	tube
VL	=	ventrolateral
VM	=	ventromedial
*	=	character not present in all specimens
–	=	marks missing data
(♀)	=	female condition of sexually dimorphic character
(♂)	=	male condition of sexually dimorphic character
(♂/♀?)	=	character with uncertain gender affiliation

The following abbreviations are used in figures:

fpa	= female papillae
lagco2	= lateral accessory glandular cell outlet type 2
las	= lateral accessory spine, eventually followed by spine number
lat	= lateral accessory tube
ldgco2	= laterodorsal glandular cell outlet type 2
ldss	= laterodorsal sensory spot
ldt	= laterodorsal tube
ltas	= lateral terminal accessory spine
lts	= lateral terminal spine
lvgco2	= lateroventral glandular cell outlet type 2
lvs	= lateroventral spine, eventually followed by spine number
lvt	= lateroventral tube
mdgco1	= middorsal glandular cell outlet type 1
mds	= middorsal spine, eventually followed by spine number
mdss	= middorsal sensory spot
mlgco2	= midlateral glandular cell outlet type 2
mlso	= midlateral slit-like opening
mlss	= midlateral sensory spot
mlt	= midlateral tube
mtj	= midtergal junction
pdgco1/2	= paradorsal glandular cell outlet type 1/2
pdso	= paradorsal slit-like opening
pdss	= paradorsal sensory spot
pe	= penile spines
pr	= protuberance
pvgco1	= paraventral glandular cell outlet type 1
r-ldt	= reduced laterodorsal tube
sdgco1/2	= subdorsal glandular cell outlet type 1/2
sdso	= subdorsal slit-like opening
sdss	= subdorsal sensory spot
sdt	= subdorsal tube
si	= sieve plate
slgco2	= sublateral glandular cell outlet type 2
slss	= sublateral sensory spot
slt	= sublateral tube
spf	= secondary pectinate fringe
tbl	= tubule
te	= tergal extension
vlgco1/2	= ventrolateral glandular cell outlet type 1/2
vlss	= ventrolateral sensory spot
vlt	= ventrolateral tube
vmgco1	= ventromedial glandular cell outlet type 1
vmso	= ventromedial slit-like opening
vmss	= ventromedial sensory spot
*	= character not present in all specimens

Results

Species descriptions

Class Cyclorhagida Zelinka, 1896 sensu Herranz *et al.* 2022

Order Echinorhagata Sørensen *et al.*, 2015

Family Echinoderidae Carus, 1885

Genus *Echinoderes* Claparède, 1863

Echinoderes blazeji sp. nov.

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Figs 2–4; Tables 2–3

Diagnosis

Echinoderes with a very minute spine in middorsal position on segment 4 and in lateral accessory positions on segment 7. Tubes present in lateroventral positions on segment 5, sublateral positions on segment 8 and laterodorsal positions on segment 10; tubes on segment 10 well-developed in males, whereas much smaller in females. Glandular cell outlet type 2 present in midlateral positions on segment 8. Large, elongate sieve plates located midlaterally on segment 9. Lateral terminal spines twice as long in males as in females.

Etymology

The species is named after Blazej, the son of the first author – for his love of all dragons.

Material examined

Holotype

NEW ZEALAND • ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159400. Mounted for LM in Fluoromount G on HS slide.

Paratypes

NEW ZEALAND • 1 ♀; same collection data as for holotype; NHMD-917223 • 1 ♂; same collection data as for holotype; NIWA-159401. Mounted as holotype.

Additional material

NEW ZEALAND • 1 ♂; same collection data as for holotype; personal reference collection of MVS. Mounted for SEM • 3 ♀♀, 1 ♂; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8977° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Honeycomb Canyon, stn TAN1004/62; 41.4760° S, 175.9477° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 2–4). Overview of measurements and dimensions in Table 2. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 3. The head morphology could not be examined in detail in any of the available specimens.

NECK. Consists of 16 placids. Midventral placid broadest, 11 µm in width and 12 µm in length, whereas all others narrower, measuring 7 µm in width at bases (Fig. 2). Trichoscalid plates well developed (Fig. 3B).

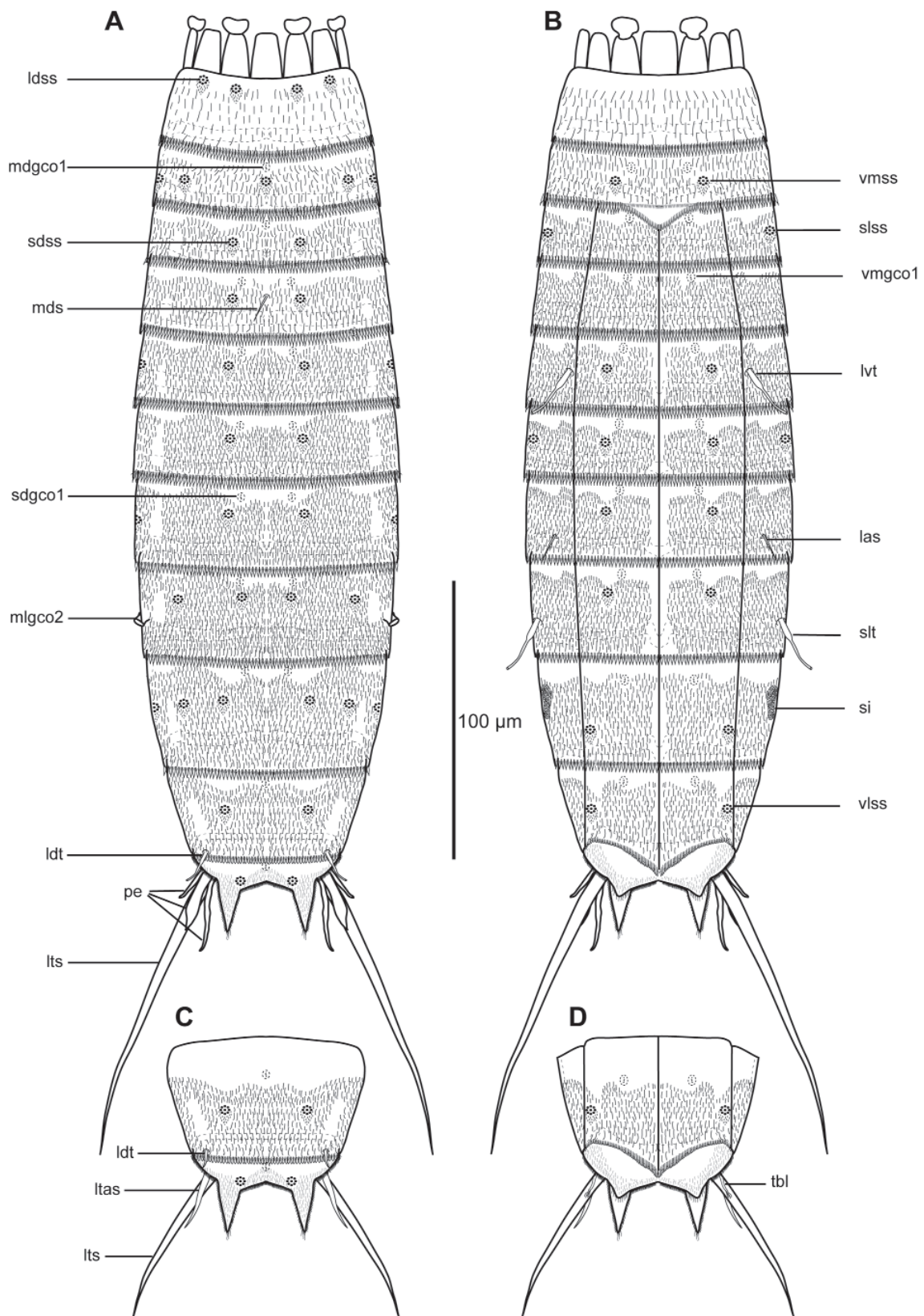


Fig. 2. Line art illustrations of *Echinoderes blazeji* sp. nov. **A.** ♂, dorsal view. **B.** ♂, ventral view. **C.** ♀, segments 10–11, dorsal view. **D.** ♀, segments 10–11, ventral view. Abbreviations: see Material and methods.

SEGMENT 1. Consists of complete cuticular ring. Subdorsal and laterodorsal sensory spots present, situated on anterior half of segment. Sensory spots on this and following segments droplet-shaped, consisting of central pore surrounded by micropapillae (Fig. 4C, E, G). Glandular cell outlet type 1 not observed. Cuticular hairs arising from rounded perforation sites, distributed evenly around segment except in anterior part. Segment terminates in pectinate fringe with relatively long fringe tips (Fig. 4C).

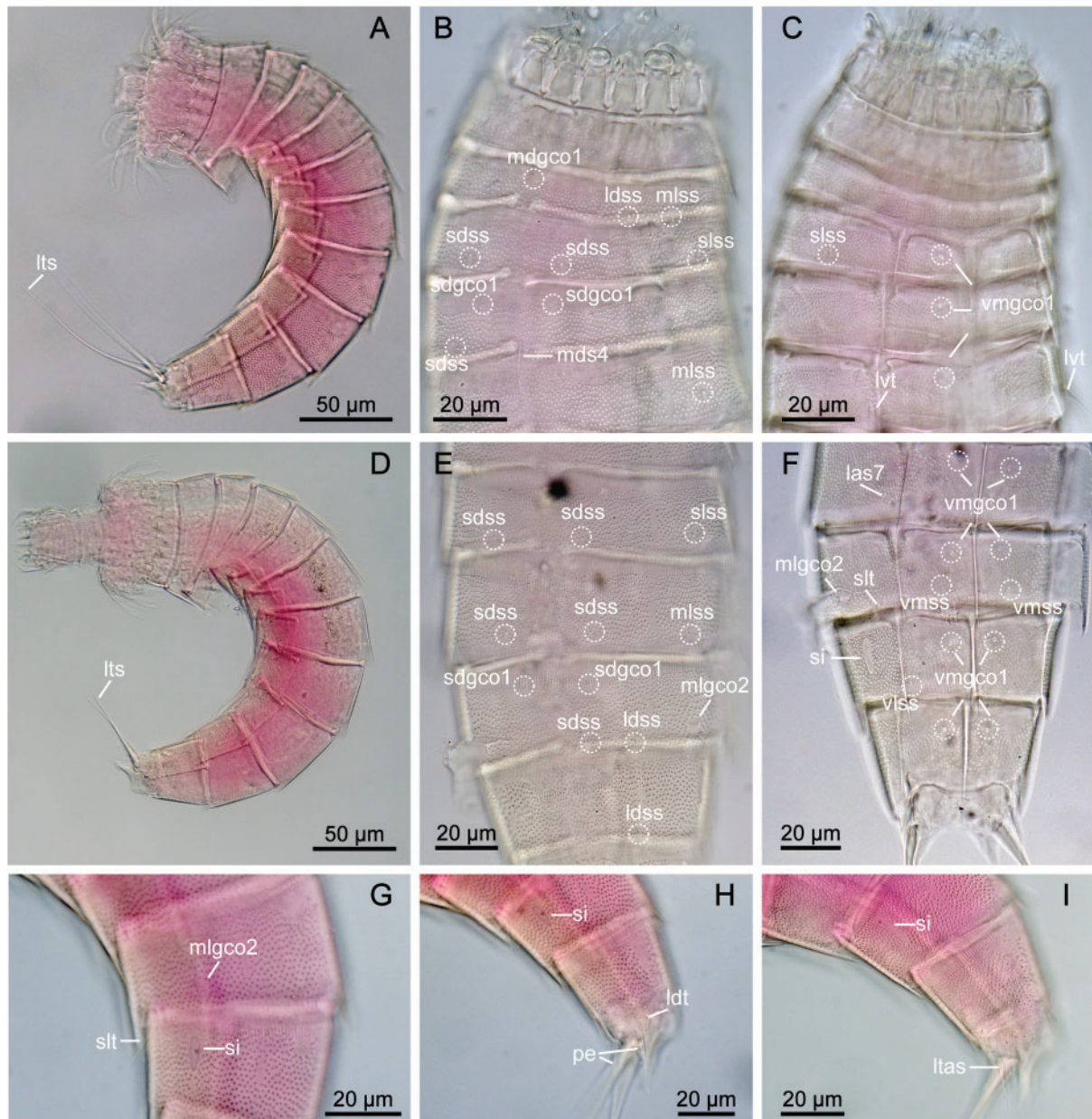


Fig. 3. Light micrographs showing overviews and details of *Echinoderes blazeji* sp. nov. **A, G–H.** ♂, paratype (NIWA-159401). **B–C, E–F.** ♂, holotype (NIWA-159400). **D, I.** ♀, paratype (NHMD-917223). **A.** Lateral overview of male. **B.** Segments 1 to 5, dorsal view. **C.** Segments 1 to 5, ventral view. **D.** Lateral overview of female. **E.** Segments 6 to 9, dorsal view. **F.** Segments 7 to 11, ventral view. **G.** Segments 8 to 9, lateroventral view. **H.** Segments 9 to 11 of male, lateral view. **I.** Segments 9 to 11 of female, lateral view. Abbreviations: see Material and methods.

Table 2. Measurements from light microscopy of *Echinoderes blazeji* sp. nov. (in μm) from the Hikurangi Margin.

Character	Holotype	Paratype	Paratype
	NIWA-159400 (♂)	NHMD-917223 (♀)	NIWA-159401 (♂)
TL	261	318	325
MSW-6	55	n/a	n/a
MSW-6/TL	21%	n/a	n/a
SW-10	46	n/a	n/a
SW-10/TL	18%	n/a	n/a
S1	26	27	27
S2	23	29	23
S3	28	32	30
S4	31	40	35
S5	31	42	34
S6	35	44	39
S7	33	47	43
S8	36	48	48
S9	40	38	46
S10	41	39	41
S11	27	25	28
MD4 (ac)	10	–	–
LA7 (ac)	6	–	–
LTS	105	54	104
LTS/TL	40%	17%	32%
LTAS	n/a	19	n/a

SEGMENT 2. Consists of complete cuticular ring with sensory spots present in middorsal, laterodorsal, midlateral and ventromedial positions (Figs 2A–B, 3B, 4B–C). Glandular cell outlet type 1 present in middorsal position and as a pair in ventromedial positions. Pachycyclus of anterior segment margin of regular thickness, interrupted in middorsal position on this and following segments. Cuticular hairs densely covering entire segment. Perforation sites on this and following eight segments appear as band around segment, easily visible in LM (Fig. 3B–C, E–I). Posterior segment margin straight along dorsal edge, but markedly extended posteriorly in midventral position (Fig. 4C). Primary pectinate fringe with tips similar to those of preceding segment in middorsal to ventrolateral position and smaller and thinner tips in ventromedial and paraventral positions (Figs 2A–B, 4B–C).

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 2A–B, 3A–D). Sensory spots present in subdorsal and sublateral positions (Fig. 3B–C). Glandular cell outlets type 1 located in middorsal and ventromedial positions. Cuticular hairs on this and following seven segments densely covering entire segment, except for narrow area in laterodorsal position (Fig. 2A). Posterior segment margin straight, terminating in pectinate fringe with relatively long and uniform fringe tips along entire segment margin.

SEGMENT 4. With minute ($\sim 10 \mu\text{m}$) middorsal spine (Figs 3B, 4E). Sensory spots located subdorsally (Figs 3B, 4B). Glandular cell outlet type 1 present in subdorsal and ventromedial positions (Fig. 3B–C). Segment otherwise as segment 3.

SEGMENT 5. With tubes in lateroventral positions (Figs 2B, 3C, 4F). Sensory spots present in subdorsal, midlateral and ventromedial positions (Figs 2A–B, 4E–F). Glandular cell outlets type 1 present in

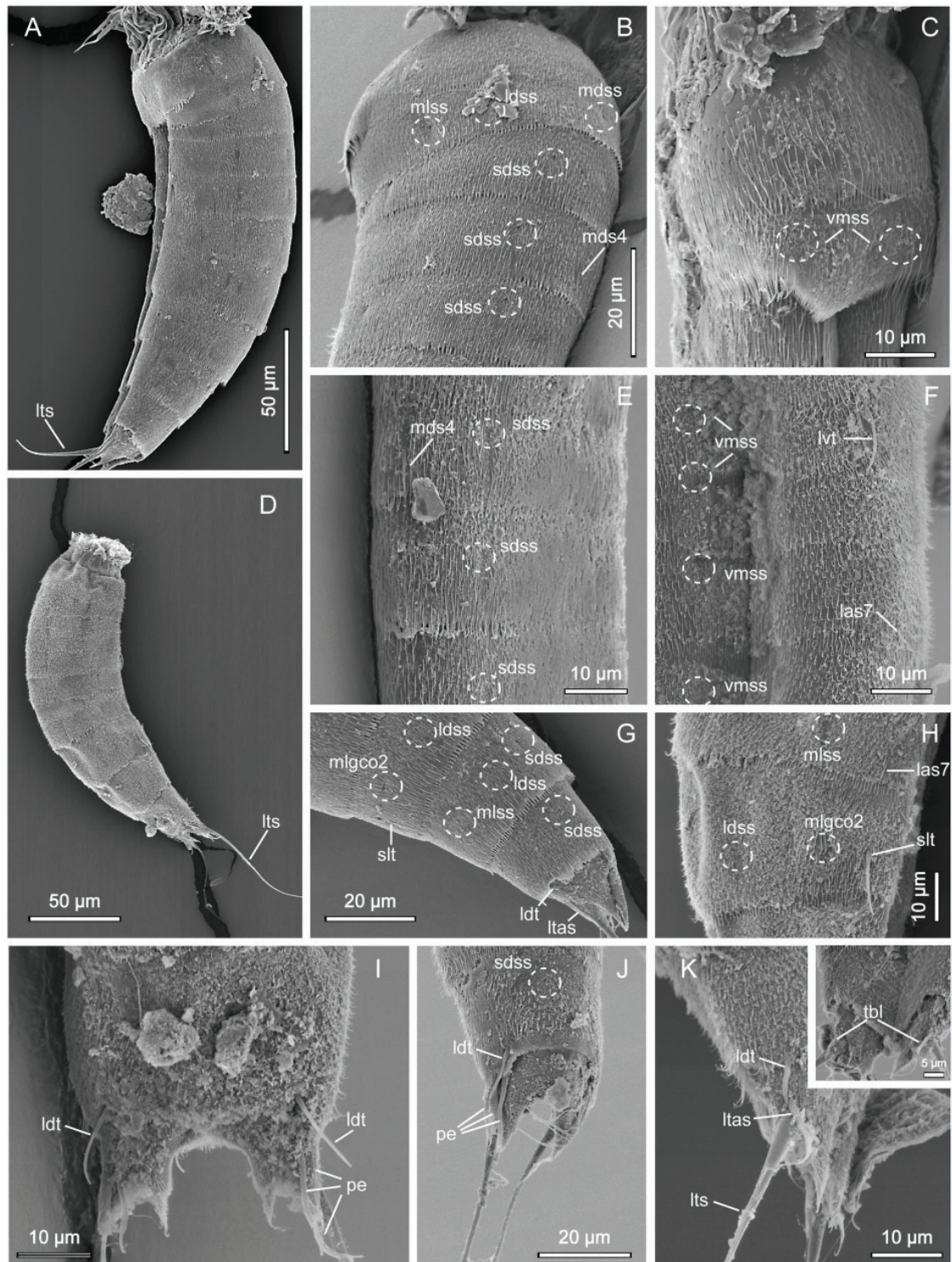


Fig. 4. Scanning electron micrographs showing overviews and details of *Echinoderes blazeji* sp. nov. **A.** Dorsolateral overview of female. **B.** Segments 1 to 4, dorsolateral view. **C.** Segments 1 to 3, ventral view. **D.** Lateral overview of male. **E.** Segments 4 to 6, dorsal view. **F.** Segments 5 to 7, ventral view. **G.** Segments 8 to 11 of female, laterodorsal view. **H.** Segments 7 to 8, lateral view. **I.** Segments 10 to 11 of male, dorsal view. **J.** Segments 10 to 11 of male, dorsolateral view. **K.** Segments 10 to 11 of female, lateral view, with close-up of segment 11 ventral side showing ventrolateral tubules. Abbreviations: see Material and methods.

Table 3. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes blazeji* sp. nov.

Position segment	MD	SD	LD	ML	SL	LA	LV	VL	VM
1		ss	ss						
2	gcol,ss		ss	ss					gcol,ss
3	gcol	ss			ss				gcol
4	ac	gcol,ss							gcol
5		gcol,ss		ss			tu		gcol,ss
6		gcol,ss			ss				gcol,ss
7		gcol,ss		ss		ac			gcol,ss
8		gcol,ss	ss	gco2	tu				gcol,ss
9		gcol,ss	ss	ss	si			ss	gcol
10	gcol	ss	tu					ss	gcol
11	gcol	ss		pe × 3 (♂)		ltas(♀)	lts	tbl(♂/♀?)	

subdorsal and ventromedial positions. Cuticular hair covering as on preceding segment except for hairless paraventral area. Secondary fringe and posterior segment margin as on preceding segment.

SEGMENT 6. With sensory spots present in subdorsal, sublateral and ventromedial positions (Figs 2A–B, 3E, 4E–F). Glandular cell outlets type 1 as on preceding segment. Cuticular hair covering and secondary pectinate fringe as on segment 5.

SEGMENT 7. With minute spines (<10 µm) in lateral accessory positions (Figs 2B, 3F, 4F); spines hardly visible in both LM and SEM due to dense cuticular hairs covering and their inconspicuous appearance. Sensory spots located in subdorsal, midlateral, and ventromedial positions. Glandular cell outlets type 1 present in subdorsal and ventromedial positions. Segment otherwise as segment 6.

SEGMENT 8. With tubes in sublateral positions and glandular cell outlets type 2 located in midlateral positions (Figs 2A–B, 3E–F, 4G–H). Sensory spots present in subdorsal, laterodorsal and ventromedial positions; subdorsal pair located closer to paradorsal line than on preceding segments. Glandular cell outlets type 1 present in subdorsal and ventromedial positions. Pectinate fringe tips slightly shorter than on preceding segments.

SEGMENT 9. Without spines or tubes. Sensory spots located in subdorsal, laterodorsal, midlateral and ventrolateral positions (Figs 2A–B, 4G). Pair of sieve plates, composed of large, elongated sieve area located anterior to rounded areas with central pore, located in sublateral positions (Figs 2A, 3F–I). Glandular cell outlets type 1, cuticular hair covering and posterior segment margin as on preceding segment.

SEGMENT 10. With laterodorsal tubes, located near posterior segment margin. In males, tubes long (~15 µm) (Figs 2A, 3H, 4I–J). In females, tubes much shorter (~6 µm) and more flexible (Figs 2C, 4K), without basal part characteristic for tubes in males as well as for tubes described on segments 5 and 8. Sensory spots present in subdorsal and ventrolateral positions. Glandular cell outlets type 1 present as middorsal one, and as pair in ventromedial positions. Posterior segment margin of tergal plate straight, while margins of sternal plates concave, reaching posterior margin of terminal segment. Pectinate fringe tips significantly shorter and narrower than on preceding segment.

SEGMENT 11. With lateral terminal spines; in males, lateral terminal spines twice long as in females (Figs 2, 3A, D, 4A, D; Table 2). Females with short and relatively thin lateral terminal accessory spines (Figs 2C–D, 3I, 4K); males with three penile spines, two of them flexible and elongated, one short and

stout (Figs 2A–B, 3H, 4I–J). Additionally, one female specimen shows pair of fringed tubes-like structures on ventral side (Fig. 4K); examination of ventral side of segment 11 not possible in other specimens; therefore, we cannot conclude whether it is a sexually dimorphic character or not. Sensory spots present in subdorsal positions. Unpaired glandular cell outlet type 1 present middorsally. Segment devoid of cuticular hairs, but very short cuticular hair-like structures covering tergal extensions and posterior parts of sternal plates. Very short fringes covering margins of tergal and sternal plates. Tergal extensions elongated and triangular (Figs 2A, C, 4J). Sternal extensions slightly extended posteriorly, not extending beyond tergal extensions (Fig. 2B, D).

Distribution

Canyons: Pahaua, Honeycomb, 670–1171 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes blazeji* sp. nov.

The arrangement of spines and tubes, with a minute middorsal spine on segment 4, minute lateral spines on segment 7 only and lateral tubes on segments 5 and 8, is not present in any other species of *Echinoderes*. These characters, combined with the large sieve plates and dense cuticular hairs, make *E. blazeji* sp. nov. even more distinctive and narrow the number of potential congeners down to species belonging to the so-called *Echinoderes coulli*-group (following the diagnosis of Yamasaki & Fujimoto 2014). Currently, this group accommodates 17 species (Randsø *et al.* 2019; Yamasaki *et al.* 2020a; Cepeda *et al.* 2022; Kennedy *et al.* 2022) that share a number of morphological characters and habitat preferences.

Echinoderes blazeji sp. nov. can easily be distinguished from all other *E. coulli*-group congeners by its presence of lateral spines only on segment 7. The group is suggested to share morphological features such as absence of middorsal spines or, if present, on segment 4 only; lateral spines absent or very minute and restricted to segments 6 and 7; presence of lateral tubes on segments 5 and 8; and female lateral terminal accessory spines being either poorly-developed or absent (Yamasaki & Fujimoto 2014). Therefore, the possession of only one pair of lateral spines makes *E. blazeji* unique among all other species of this group. Nevertheless, it should be stressed that these spines are extremely minute and might easily be overlooked due to the dense cuticular hair covering, especially during LM examination. But even if the presence of lateral spines on segment 7 had gone unnoticed among the nine species of the *E. coulli* group with a middorsal spine on segment 4 (i.e., *E. annae* Sørensen *et al.*, 2016, *E. cyaneafictus* Cepeda *et al.*, 2022, *E. maxwelli* (Omer-Cooper, 1957), *E. ohtsukai* Yamasaki & Kajihara, 2012, *E. parthenope* Cepeda *et al.*, 2022, *E. regina* Yamasaki, 2016, *E. rex* Lundbye *et al.*, 2011, *E. serratulus* Yamasaki, 2016 and *E. teretis* Brown, 1999 in Adrianov & Malakhov 1999), only *E. annae* shows the absence of lateral spines (Omer-Cooper 1957; Adrianov & Malakhov 1999; Lundbye *et al.* 2011; Yamasaki & Kajihara 2012; Sørensen *et al.* 2016a; Yamasaki 2016; Cepeda *et al.* 2022). However, other conditions in *E. annae* make this species easily distinguishable from *E. blazeji*. In contrast to the new species, which has only one pair of relatively big glandular cell outlets type 2 on segment 8, *E. annae* possesses numbers of minute glands distributed over several segments. Moreover, the latter species is characterized by the presence of midlateral tubes on segment 9, which are absent in *E. blazeji*, and by very short and stout lateral terminal spines, which cannot be confused with the longer and thinner lateral spines in *E. blazeji*.

Furthermore, the lateral terminal spines themselves seem to represent another characteristic feature for the new species, since they are twice as long in males as in females ($\sigma^{\text{LTS}}=104\ \mu\text{m}$ vs $\text{LTS}^{\text{f}}=50\ \mu\text{m}$, respectively). Echinoderid sexual dimorphism is usually displayed in the female presence of lateral terminal accessory spines, in the appearance of the laterodorsal tubes on segment 10 (i.e., Sørensen 2006; Pardos *et al.* 2016a; Grzelak & Sørensen 2018; present study) or presence of papillae/pores on the ventral side in females (Sørensen *et al.* 2020). Having sexual dimorphism expressed in lateral terminal

spine lengths is a rather unusual trait in *Echinoderes*. Differences in length of lateral terminal spines expressed as sexual dimorphism have been observed for *E. aquilonius* Higgins & Kristensen, 1988 and *E. lusitanicus* Neves *et al.*, 2016 (Higgins & Kristensen 1988; Neves *et al.* 2016), but more interestingly, also in *E. coulli* Higgins, 1977 – a species closely related with *E. blazeji* sp. nov. Higgins (1977) described two forms of females in *E. coulli*: one form with lateral terminal spines similar to those in males, and a second form with short lateral terminal spines being half the length of those of males. The latter short-spined form was, however, more abundant in the population and constituted about half of all examined specimens. In our case, all examined females (4 out of 9 specimens in total) had markedly shorter lateral terminal spines than males, which suggests that we might have the same kind of female dimorphism in *E. blazeji*. Sexual dimorphism expressed in spine lengths has also been reported for *E. levanderi* Karling, 1954 and the Arctic population of *E. pterus* Yamasaki *et al.*, 2018, but in these cases it was related to the length of lateroventral spines (Karling 1954; Sørensen 2018; Yamasaki *et al.* 2018a).

In addition, the pattern of glandular cell outlets type 1 on the dorsal side appears to be uncommon for the new species. The taxonomic significance of the glandular cell outlet type 1 pattern, in contrast to glandular cell outlets type 2, is not yet well explored or understood. In fact, it was only quite recently that Sørensen *et al.* (2020) drew attention to its potential taxonomic significance. They showed that a majority of species of *Echinoderes* (for which we have sufficient data) show outlets on segments 4 to 9 in paradorsal or paradorsal and middorsal (depends on the segment) positions (Sørensen *et al.* 2020). The presence of glandular cell outlets type 1 in subdorsal positions on segments 4 to 9, as observed for *E. blazeji* sp. nov., has so far only been reported from ten other, putatively closely related species, all belonging to the *E. dujardini* species group, and in *E. worthingi* Southern, 1914, a species also closely related to the *E. dujardini* group (Southern 1914; Sørensen *et al.* 2020). Since *E. blazeji* cannot be considered as closely related with the *E. dujardini*-group, our observation of glandular cell outlets type 1 in the new species thus indicates that this morphological trait may still hide some interesting aspects.

Finally, the new species has been found in a habitat that is quite unusual for species of the *E. coulli*-group. The majority of these species have been recorded in intertidal marine or brackish water, with the exception of four species that inhabit subtidal, but yet shallow, marine waters (Lundbye *et al.* 2011; Yamasaki 2016; Kennedy *et al.* 2022). In this context, *E. blazeji* sp. nov. is unique within the species group, since it is so far the only species inhabiting deep-sea waters.

***Echinoderes landersi* sp. nov.**

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Figs 5–7; Tables 4–5

Diagnosis

Echinoderes with spines in middorsal position on segments 4 and 6, and in lateroventral positions on segments 6 to 9. Tubes present in subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, lateroventral positions on segment 5, subdorsal, midlateral and lateral accessory positions on segment 8, and midlateral positions on segments 9 and 10.

Etymology

The species is named after Dr Stephen C. Landers in recognition of his contributions to kinorhynch taxonomy and ecology.

Material examined

Holotype

NEW ZEALAND • ♀; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159402. Mounted for LM in Fluoromount G on HS slide.

Paratype

NEW ZEALAND • 1 ♀; Pahaua Canyon, stn TAN1004/31; 41.4962° S, 175.6828° E; 730 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-916627. Mounted as holotype.

Additional material

NEW ZEALAND • 1 ♀; Hikurangi Slope, stn TAN1004/44; 41.5258° S, 175.8003° E; 728 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM
• 2 ♀♀; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 5–7). Overview of measurements and dimensions in Table 4. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 5. No details regarding scolid arrangement and morphology could be provided, because introverts of all specimens mounted for SEM fully retracted.

NECK. With 16 placids. Midventral placid broadest, 11 µm in width and 16 µm in length, whereas all others narrower, measuring 7 µm in width at their bases (Fig. 5). Trichoscolid plates well developed (Fig. 6B).

SEGMENT 1. Consists of complete cuticular ring. Sensory spots located on anterior half of segment, in subdorsal, laterodorsal and ventromedial positions; sensory spots on this and following segment with micropapillae surrounding central pore and long marginal hair (Figs 5A–B, 7C). Glandular cell outlet type 1 present in middorsal and ventrolateral positions. Cuticular hairs relatively long, distributed evenly around segment. Posterior segment margin almost straight, forming pectinate fringe with very short, sawtooth-like fringe tips along dorsal margin and with slightly longer tips along ventral margin.

SEGMENT 2. Consists of complete cuticular ring, with tubes located in subdorsal, laterodorsal, sublateral and ventrolateral positions (Figs 5A–B, 6A–B, 7C–D); in one specimen right subdorsal tube missing. Sensory spots present in middorsal, laterodorsal and ventromedial positions. Glandular cell outlets type 1 not observed. This structure better visible in LM than in SEM but none of LM specimens orientated in way that allowed detailed examination of segments, especially its ventral side; therefore, for this and following nine segments presence of glandular cell outlets type 1 in ventral positions can neither be confirmed nor rejected. Pachycyclus of anterior segment margin of regular thickness. Secondary pectinate fringe present near anterior segment margin of this and following segments, but usually covered by preceding segment. Cuticular hairs and pectinate fringe tips as on preceding segment.

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 5A–B, 7D). Segment with subdorsal and midlateral sensory spots. On this and following six segments, cuticular hairs arranged in three or four rows across tergal plate, except for hairless laterodorsal areas; paraventral areas devoid of hairs on this and following seven segments (Fig. 5). Posterior segment margin straight, terminating in pectinate fringe with longer and more slender fringe tips along dorsal margin than on preceding segments, otherwise as on preceding segment.

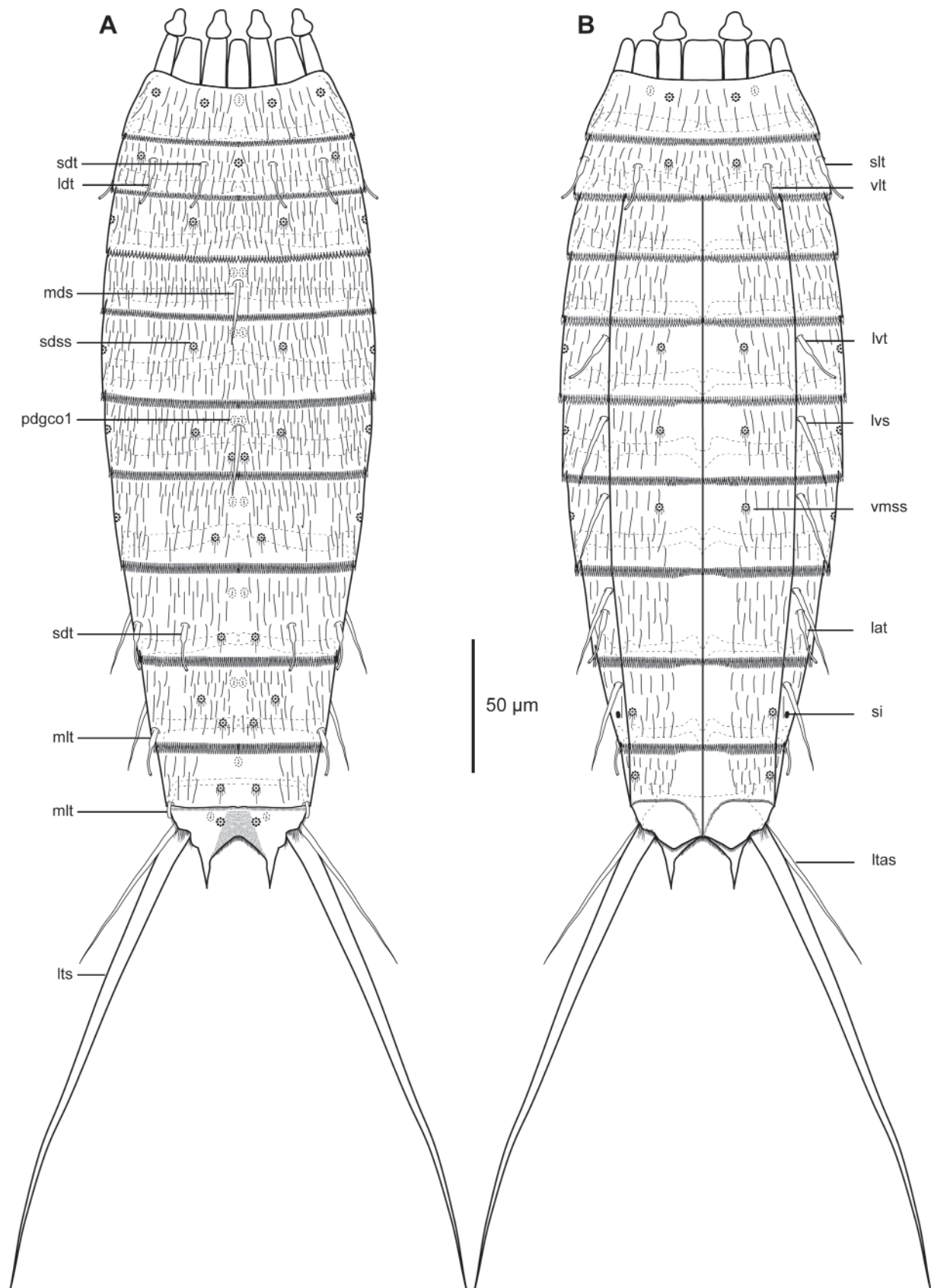


Fig. 5. Line art illustrations of *Echinoderes landersi* sp. nov. **A.** ♀, dorsal view. **B.** ♀, ventral view. Abbreviations: see Material and methods.

Table 4. Measurements from light microscopy of *Echinoderes landersi* sp. nov. (in μm) from the Hikurangi Margin.

Character	Holotype	Paratype
	NIWA-159402 (♀)	NHMD-916627 (♀)
TL	333	351
S1	27	24
S2	34	21
S3	40	37
S4	42	38
S5	47	42
S6	52	49
S7	54	50
S8	49	44
S9	44	40
S10	43	40
S11	42	39
MD4 (ac)	31	24
MD6 (ac)	33	30
LV6 (ac)	28	24
LV7 (ac)	29	25
LV8 (ac)	34	29
LV9 (ac)	38	33
LTS	198	173
LTS/TL	59.6%	49.3%
LTAS	70	60

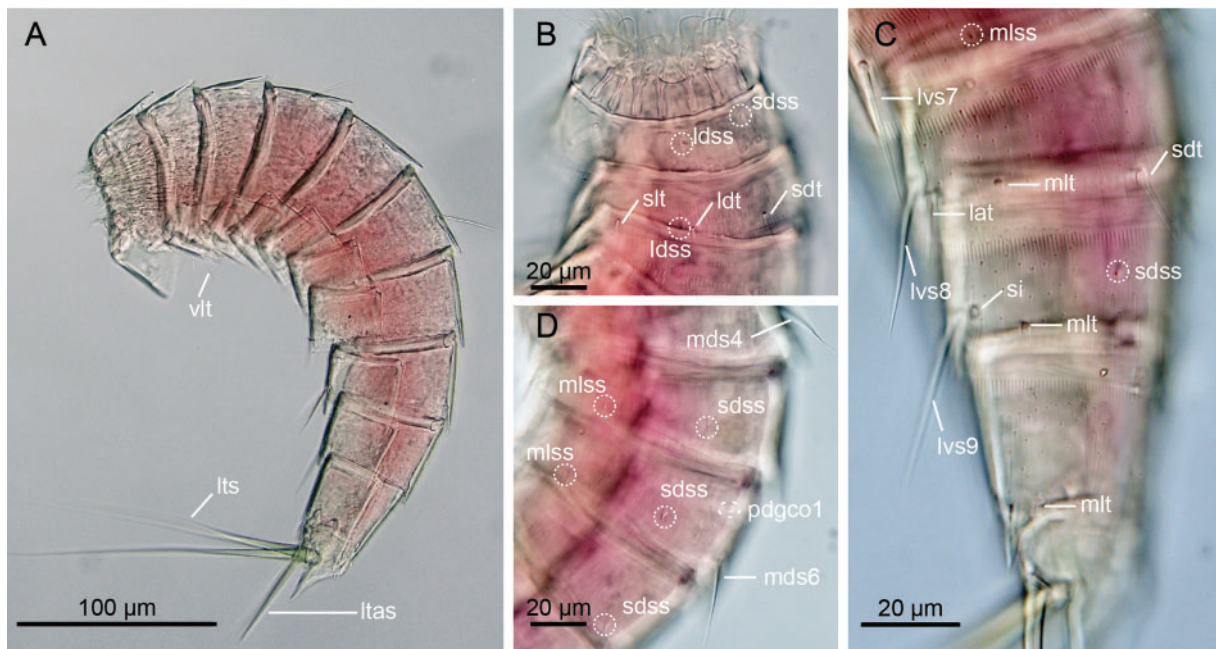
**Fig. 6.** Light micrographs showing overview and details of *Echinoderes landersi* sp. nov. **A.** ♀, paratype (NHMD-916627). **B–D.** ♀, holotype (NIWA-159402). **A.** Lateral overview. **B.** Segments 1 to 3, lateral view. **C.** Segments 7 to 11, lateral view. **D.** Segments 4 to 7, lateral view. Abbreviations: see Material and methods.

Table 5. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes landersi* sp. nov.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gcol		ss	ss					gcol	ss
2	ss		tu	tu,ss		tu			tu	ss
3			ss		ss					
4	ac	gcol								
5		gcol	ss		ss			tu		ss
6	ac	gcol,ss	ss		ss			ac		ss
7		gcol	ss		ss			ac		ss
8		gcol	ss,tu		tu		tu	ac		
9		gcol	ss,ss		tu		si	ac	ss	
10	gcol		ss		tu				ss	
11			ss,gcol				ltas(♀)	lts		

SEGMENT 4. With spine in middorsal position. Spine relatively short (27 µm), only slightly exceeding beyond posterior segment margin (Figs 5A, 6A, D, 7A, E). Glandular cell outlets type 1 present in paradorsal positions. No other traits observed. Cuticular hairs and secondary pectinate fringe as on preceding segment.

SEGMENT 5. With tubes in lateroventral positions (Figs 5B, 7D). Sensory spots present in subdorsal, midlateral and ventromedial positions (Figs 5A–B, 6D, 7D–E). Glandular cell outlets type 1 present in paradorsal positions. Tips of pectinate fringe of posterior segment margin slightly longer than on preceding segment. Cuticular hairs as on preceding segment.

SEGMENT 6. With spines in middorsal and lateroventral positions (Fig. 5A–B). Middorsal spine, as on segment 4, relatively short (31 µm), only slightly exceeding beyond posterior segment margin (Figs 6A, D, 7A, E). Sensory spots present in paradorsal, subdorsal, midlateral and ventromedial positions (Figs 5A–B, 6D, 7D–E). Glandular cell outlets type 1 present in paradorsal positions (Figs 5A, 6D). Pectinate fringe of posterior segment margin and cuticular hairs as on preceding segment.

SEGMENT 7. With spines in lateroventral positions, and sensory spots in subdorsal, midlateral and ventromedial positions (Figs 5A–B, 6C–D, 7E). Glandular cell outlets type 1 present in paradorsal positions. Tips of pectinate fringe of posterior segment margin slightly longer than on preceding segments. Segment otherwise as segment 6.

SEGMENT 8. With spines in lateroventral positions, and tubes in subdorsal, midlateral and lateral accessory positions (Figs 5A–B, 6C, 7G–H). Sensory spots present in subdorsal positions only. Glandular cell outlets type 1 present in paradorsal positions. Pectinate fringe of posterior segment margin and cuticular hairs as on preceding segment.

SEGMENT 9. With spines in lateroventral positions and tubes in midlateral positions (Figs 5A–B, 6C, 7G–H). In one specimen additional tube on right side of segment located in subdorsal position (Fig. 7I). Two pairs of sensory spots located in subdorsal positions and one ventrolateral pair (Figs 5A–B, 7H). Glandular cell outlets type 1 present in paradorsal positions. Small, rounded sieve plates located in lateral accessory positions (Fig. 6C). Cuticular hair covering and pectinate fringe of posterior segment margin as on preceding segment.

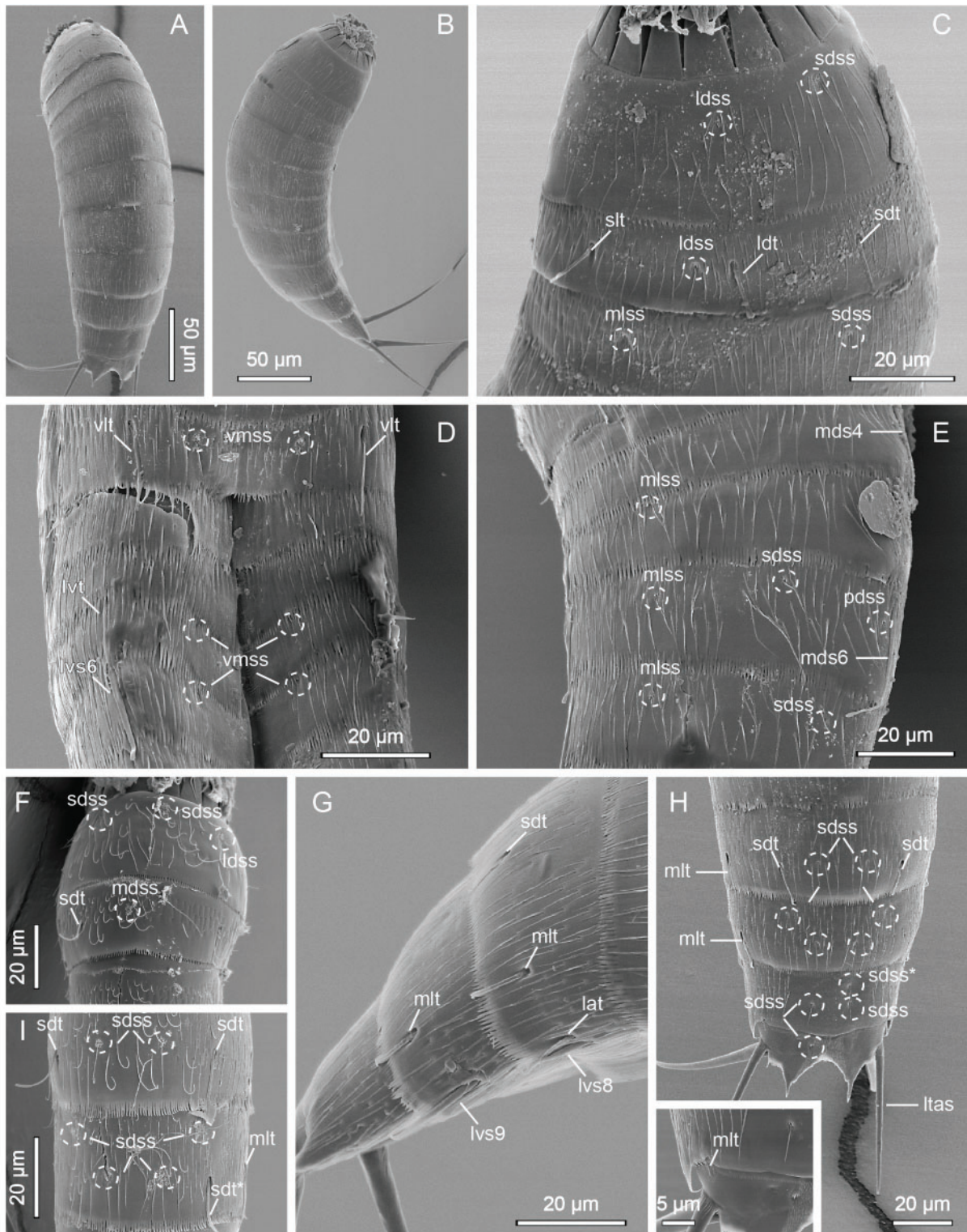


Fig. 7. Scanning electron micrographs showing overviews and details of *Echinoderes landersi* sp. nov. **A.** Dorsal overview. **B.** Lateral overview. **C.** Segments 1 to 3, lateral view. **D.** Segments 2 to 6, ventral view. **E.** Segments 4 to 7, dorsolateral view. **F.** Segments 1 to 3 of female with inconsistent tube pattern, dorsal view. **G.** Segments 8 to 10, lateral view. **H.** Segments 8 to 11, dorsal view, with inset showing close-up of midlateral tube on segment 10. **I.** Segments 8 to 9 of female with inconsistent tube pattern, dorsal view. Abbreviations: see Material and methods.

SEGMENT 10. With minute midlateral tubes located near posterior segment margin (Figs 5A, 6C, 7H). Sensory spots present in subdorsal and ventrolateral positions (Figs 5A–B, 7H); in one specimen extra subdorsal sensory spot present on left side of segment (Fig. 7H). Glandular cell outlet type 1 present in middorsal position. Cuticular hairs less dense on dorsal side than on preceding segment. Central part of tergal plate devoid of hairs. Hairs on sternal plates shorter than on preceding segments. Posterior segment margin of tergal plate straight, without fringe tips; margins of sternal plates concave, reaching posterior margin of terminal segment, with very short fringe tips.

SEGMENT 11. With lateral terminal spines (Figs 5A–B, 6A). Females with lateral terminal accessory spines (Figs 5A–B, 6A, 7H); male conditions unknown. Sensory spots and glandular cell outlets type 1 present in subdorsal positions; in one specimen sensory spot on right side of segment missing. Segment devoid of cuticular hairs, but with very short cuticular hair-like structures covering paradorsal area and very short fringes covering margins of tergal and sternal plates. Tergal extensions triangular, with elongate and pointed tips (Figs 5A, 7H). Sternal extensions do not extend beyond tergal extensions (Fig. 5B).

Distribution

Hikurangi slope and Pahaua Canyon, 728–1121 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes landersi* sp. nov.

Echinoderes landersi sp. nov. is easily distinguished from all other congeners by its combination of spines and tubes. The spine pattern on its dorsal side, with middorsal spines on segments 4 and 6, is already an uncommon feature within *Echinoderes*. This trait itself is shared only with *E. astridae* Sørensen, 2014, *E. bispinosus* Higgins, 1982, *E. uozumii* Yamasaki *et al.*, 2020 and *E. dalzottoi* sp. nov. described below in the present study (Higgins 1982; Sørensen 2014; Yamasaki *et al.* 2020b). This character in combination with its tubes on segment 2 makes *E. landersi* unique among its congeners. The abovementioned species possess either three pairs of tubes as in *E. dalzottoi* or only one pair as in *E. astridae*, *E. bispinosus* and *E. uozumii*. Therefore, having four pairs of tubes on segment 2, located in subdorsal, laterodorsal, sublateral and ventrolateral positions, is uncommon and found exclusively in *E. landersi*. The three latter species furthermore differ from *E. landersi* by being equipped with glandular cell outlets type 2; such outlets are absent in *E. landersi*. The regular hair covering found in *E. landersi* also distinguishes it from *E. dalzottoi*, which is characterized by having a trunk cuticle with perforation sites only but no cuticular hairs.

In addition, *E. landersi* sp. nov. can easily be distinguished from these species by other traits, among which the composition of segment 8 with tubes in subdorsal, midlateral and lateral accessory positions is the most important, as these are not present in any other species of *Echinoderes*. Numerous species have various combinations of tubes on this particular segment, but no other species has three pairs of tubes. There are several species with two pairs of tubes, in laterodorsal and lateral accessory positions as observed in, e.g., *E. abbreviatus* Higgins, 1983, *E. belenae* Pardos *et al.*, 2016 or *E. intermedius* Sørensen, 2006, or in subdorsal and lateral accessory positions as found in *E. capitatus* (Zelinka, 1928) and *E. isabelae* G^aOrdóñez *et al.*, 2008 (Zelinka 1928; Higgins 1983; G^aOrdóñez *et al.* 2008; Sørensen 2006; Pardos *et al.* 2016b); nevertheless, the most common tube pattern is the presence of only one pair of tubes on segment 8, typically in a sublateral or lateral accessory position. Furthermore, *E. landersi* possesses midlateral tubes on segment 9, which is another relatively rare trait, shared with only four species, i.e., *E. andamanensis* Higgins & Rao, 1979, *E. annae*, *E. newcaledoniensis* Higgins, 1967 and *E. serratulus* (Higgins 1967; Higgins & Rao 1979; Sørensen *et al.* 2016a; Yamasaki 2016). Nevertheless, none of these species can in any way be confused with *E. landersi* due to their significantly different middorsal spine patterns. Hence, besides its uncommon middorsal spine pattern with spines on segments 4 and 6 only, the new species is very easily recognized by the nature of its cuticular structures of segments 2, 8 and 9.

One noteworthy observation in *E. landersi* sp. nov. is the inconsistent tube pattern found in one specimen (Fig. 7F, I). However, in contrast to recent observations of intraspecific variation in species of *Echinoderes* where pairs of tubes may be present or absent, it was only one tube missing from the pair in *E. landersi*. Variation in tube patterns, regarding their presence or absence, has been documented, e.g., in *E. daenerysae* Grzelak & Sørensen, 2017 in Grzelak & Sørensen (2018) for ventrolateral tubes on segment 2, in *E. eximus* Higgins & Kristensen, 1988 for sublateral tubes on segment 9, in *E. levanderi* for subdorsal tubes on segment 2, and in *E. frodoi* sp. nov. (present study) for midlateral tubes on segment 1 (Grzelak & Sørensen 2018; Sørensen 2018). Among specimens of *E. landersi*, however, one specimen lacks the subdorsal tube on the right side on segment 2 (Fig. 7F), but has a subdorsal tube on the right side of segment 9 (Fig. 7I). Tubes in subdorsal positions on segment 9 were not observed in other specimens. A similar inconsistency was described by Yamasaki & Dal Zotto (2019) for specimens of *E. capitatus* that lack a ventrolateral tube on one side on segment 2 (Yamasaki & Dal Zotto 2019). Moreover, we observed that one specimen lacks a subdorsal sensory spot on the right side of segment 10, and that this lacking sensory spot seems to be relocated to segment 9 (Fig. 7H). For now, we cannot explain the reason for this observed variation, but it seems most likely that it is due to individual abnormalities, rather than intraspecific variation.

***Echinoderes dalzottoi* sp. nov.**

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Figs 8–10; Tables 6–7

Diagnosis

Echinoderes with spines in middorsal position on segments 4 and 6, and spines in lateroventral positions on segments 6 to 9. Tubes present in subdorsal, sublateral (might be missing in some specimens) and ventrolateral positions on segment 2, lateroventral positions on segment 5, sublateral positions on segment 8, and laterodorsal positions on segment 9. Sexually dimorphic tubes furthermore present in laterodorsal positions on segment 10 in males; females with fringe-like structure in midlateral positions. Minute scales present on segments 2 to 10, but regular cuticular hairs absent throughout trunk

Etymology

The species is named after Dr Matteo Dal Zotto in recognition of his contributions to kinorhynch taxonomy and ecology.

Material examined

Holotype

NEW ZEALAND • ♀; Pahaua Canyon, stn TAN1004/31; 41.4962° S, 175.6828° E; 730 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159403. Mounted for LM in Fluoromount G on HS slide.

Paratypes

NEW ZEALAND • 1 ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-917147. Mounted as holotype • 1 ♂; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8977° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159404. Mounted as holotype.

Additional material

NEW ZEALAND • 1 ♂; same collection data as for holotype; personal reference collection of MVS. Mounted for SEM • 1 ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for

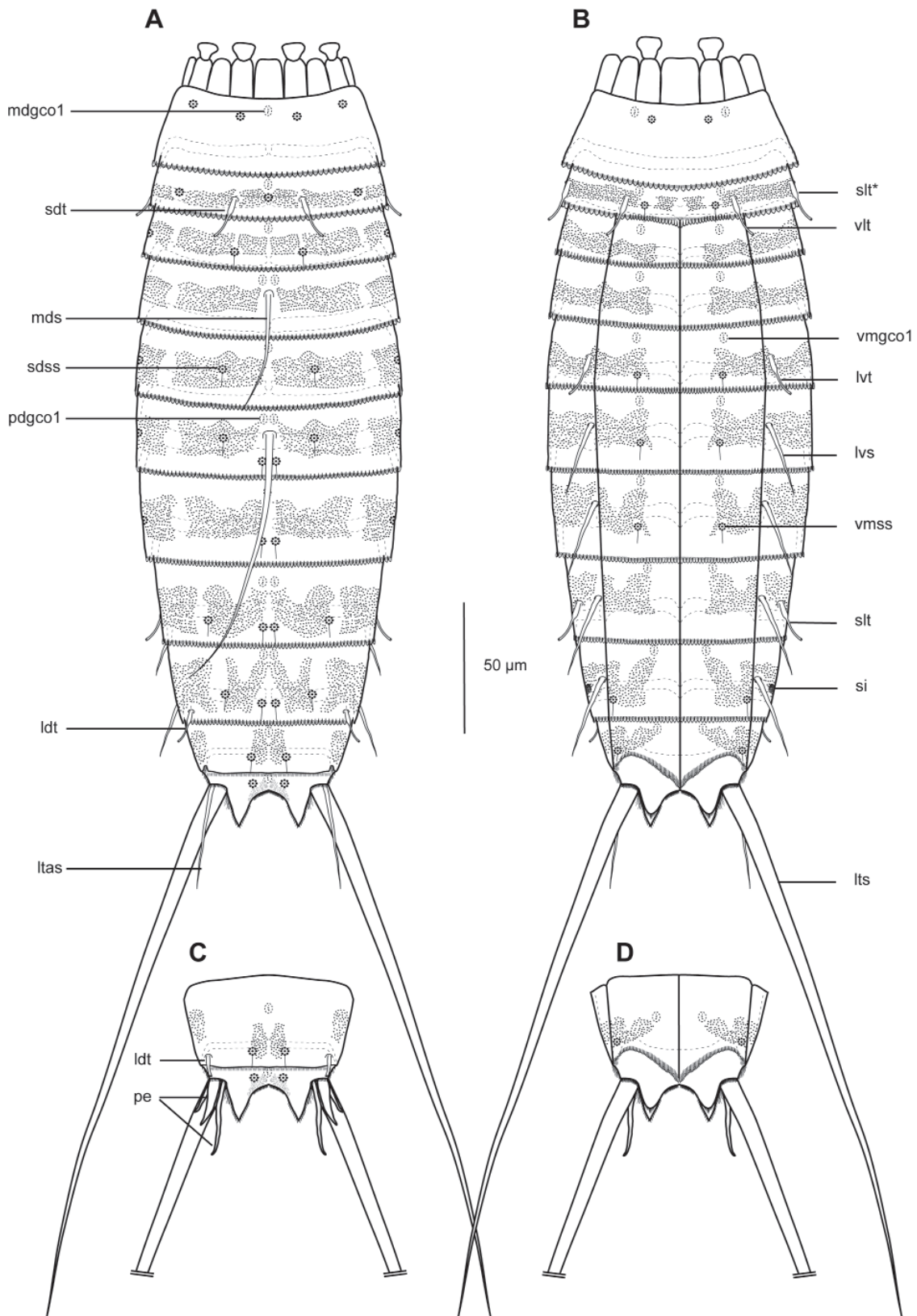


Fig. 8. Line art illustrations of *Echinoderes dalzottoi* sp. nov. **A.** ♀, dorsal view. **B.** ♀, ventral view. **C.** ♂, segments 10–11, dorsal view. **D.** ♂, segments 10–11, ventral view. Abbreviations: see Material and methods.

Table 6. Measurements from light microscopy of *Echinoderes dalzottoi* sp. nov. (in μm) from the Hikurangi Margin, including number of measured specimens (n) and standard deviation (SD).

Character	n	Range	Mean	SD
TL	3	209–310	267	52.0
MSW-6	3	54–66	60	8.8
MSW-6/TL	3	23–25%	25%	1.5%
SW-10	3	40–46	43	4.5
SW-10/TL	3	16–19%	18%	1.9%
S1	3	24–29	26	2.5
S2	3	22–29	26	3.5
S3	3	23–35	27	7.4
S4	3	26–42	32	8.9
S5	3	28–46	35	10.0
S6	3	27–47	36	10.7
S7	3	30–50	39	11.2
S8	3	34–50	40	9.7
S9	3	34–50	43	8.3
S10	3	36–46	43	6.2
S11	1	20	n/a	n/a
MD4 (ac)	3	43–62	51	10.1
MD6 (ac)	2	88–110	99	15.8
LV6 (ac)	3	24–29	27	2.4
LV7 (ac)	3	27–30	29	1.8
LV8 (ac)	3	28–34	31	2.7
LV9 (ac)	3	27–32	30	2.6
LTS	3	174–243	213	35.5
LTS/TL	3	78–83%	80%	2.6%
LTAS	1	40	n/a	n/a

SEM • 1 ♀; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8977° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 8–10). Overview of measurements and dimensions in Table 6. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 7. Head morphology could not be examined in detail in any of available specimens.

NECK. Consists of 16 placids. Midventral placid broadest, 13 μm in width and 15 μm in length, whereas all others narrower, measuring 7 μm in width at their bases (Fig. 8). The trichoscalid plates are well developed (Fig. 9D).

SEGMENT 1. Consists of complete cuticular ring. Sensory spots present in subdorsal, laterodorsal and ventromedial positions. Sensory spots relatively large and without marginal hairs, located on anterior half of segment (Figs 8A–B, 9C–D, 10B–C, E). Glandular cell outlet type 1 present in middorsal position and in ventrolateral positions. Cuticular hairs or perforation sites not present. Posterior segment margin almost straight, forming pectinate fringe with short, sawtooth-like fringe tips (Fig. 10B–C).

SEGMENT 2. Consists of complete cuticular ring, with tubes located in subdorsal, sublateral and ventrolateral positions (Figs 8A–B, 9C–D, 10B–C, E); sublateral tubes missing in one paratype and two SEM specimens; no sexual or developmental differences explain presence or absence of tubes. Sensory spots of similar sizes as on preceding segment, present in middorsal, laterodorsal and ventromedial positions; ventromedial ones with long marginal hair. Unpaired glandular cell outlet type 1 present in middorsal position and as pair in ventromedial positions. Pachycyclus of anterior segment margin of regular thickness, interrupted in middorsal position. Secondary pectinate fringe present near anterior segment margin of this and following segments, but usually covered by preceding segment. This and following nine segments completely hairless. Cuticular hairs reduced to minute scales distributed

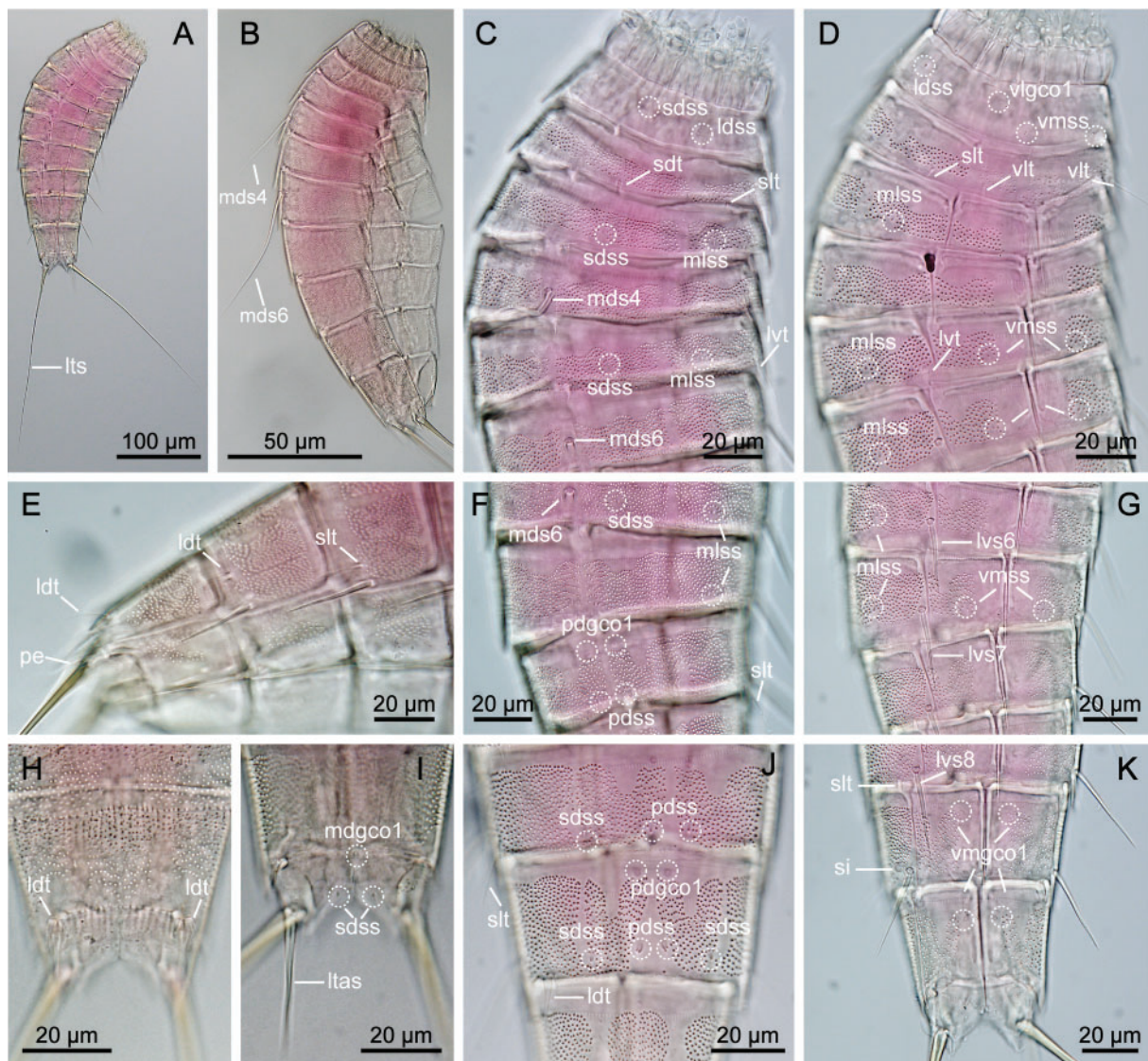


Fig. 9. Light micrographs showing overview and details of *Echinoderes dalzottoi* sp. nov. **A, C–D, F–G, J–K.** ♀, holotype (NIWA-159403). **B, E, H–I.** ♂, paratype (NHMD-917147). **A.** Ventral overview. **B.** Lateral overview. **C.** Segments 1 to 6, dorsolateral view. **D.** Segments 1 to 6, lateroventral view. **E.** Segments 8 to 11, lateral view. **F.** Segments 6 to 8, dorsolateral view. **G.** Segments 6 to 8, lateroventral view. **H.** Segments 10 to 11 of male, dorsal view. **I.** Segments 10 to 11 of female, dorsal view. **J.** Segments 8 to 10, dorsal view. **K.** Segments 8 to 11, ventral view. Abbreviations: see Material and methods.

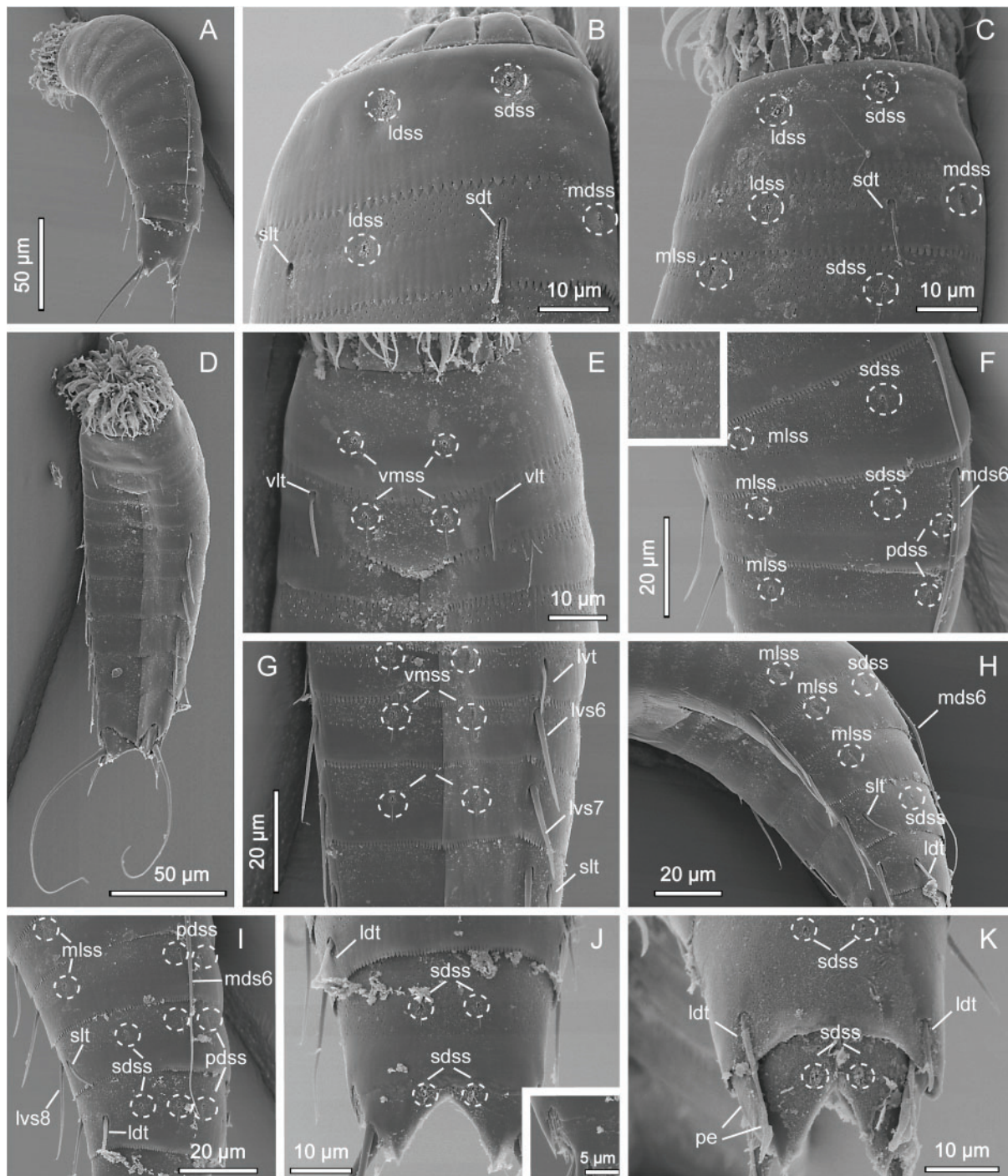


Fig. 10. Scanning electron micrographs showing overviews and details of *Echinoderes dalzottoi* sp. nov. **A.** Dorsolateral overview. **B.** Segments 1 to 2 of specimen with (broken) sublateral tube on segment 2, dorsolateral view. **C.** Segments 1 to 3 of specimen without sublateral tube on segment 2, dorsolateral view. **D.** Ventral overview. **E.** Segments 1 to 3, ventral view. **F.** Segments 4 to 7, dorsolateral view with inset showing close-up of cuticular hairs that are reduced to minute scales. **G.** Segments 5 to 8, ventral view. **H.** Segments 5 to 9, lateroventral view. **I.** Segments 6 to 9, dorsolateral view. **J.** Segments 10 to 11 of female, dorsal view with inset showing close-up of midlateral fringe-like structure on segment 10. **K.** Segments 10 to 11 of male, dorsal view. Abbreviations: see Material and methods.

Table 7. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes dalzottoi* sp. nov.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gcol		ss	ss					gcol	ss
2	gcol,ss		tu	ss		tu*			tu	gcol,ss
3	gcol		ss		ss					gcol
4	ac	gcol								gcol
5	gcol		ss		ss			tu		gcol,ss
6	ac	gcol,ss	ss		ss			ac		gcol,ss
7	gcol	ss			ss			ac		gcol,ss
8		gcol,ss	ss			tu		ac		gcol
9		gcol,ss	ss	tu		si		ac	ss	gcol
10	gcol		ss	tu(♂)	fs(♀)				ss	gcol
11	gcol		ss		pe × 3 (♂)		ltas(♀)	lts		

around segment (Fig. 10B–C, E–H), emerging through perforation sites; perforation sites easily visible in LM (Fig. 9C–K). Posterior segment margin almost straight, but with rounded midventral extension (Fig. 10D–E); pectinate fringe tips as on preceding segment, except midventral area with slightly narrower fringe tips.

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 8A–B, 9A, D). Sensory spots present in subdorsal and midlateral positions. Sensory spots on this and following segments smaller than on preceding segments, all with one long marginal hair. Glandular cell outlets type 1 as on preceding segment. Perforation sites appear as band around segment, interrupted in middorsal and laterodorsal areas and in central part of sternal plate on this and following five segments (Figs 8A–B, 9C–D, F–G, 10F–G). Posterior segment margin straight, terminating in pectinate fringe with slightly more slender fringe tips along ventral margin than on preceding segments, otherwise as on preceding segment.

SEGMENT 4. With spine in middorsal position; spine relatively long (51 µm), reaching posterior margin of segment 5 (Figs 8A, 10A, F). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. No other traits observed. Segment otherwise as segment 3.

SEGMENT 5. With tubes in lateroventral positions (Figs 8B, 9D, 10G). Sensory spots present in subdorsal, midlateral and ventromedial positions (Figs 8A–B, 9C, 10F). Glandular cell outlets type 1 present in middorsal and ventromedial positions. Perforation sites, secondary fringe and posterior segment margin as on preceding segment.

SEGMENT 6. With spines in middorsal and lateroventral positions (Fig. 8A–B). Middorsal spine, as on segment 4, relatively long (99 µm), reaching well beyond posterior segment margin of segment 8 (Fig. 10A, I). Sensory spots present in paradorsal, subdorsal, midlateral and ventromedial positions (Figs 8A–B, 10F–G). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Segment otherwise as segment 5.

SEGMENT 7. With spines in lateroventral positions, and sensory spots in paradorsal, midlateral and ventromedial positions (Figs 8A–B, 9G, 10F–G). Glandular cell outlets type 1 present in middorsal position and as pair in ventromedial positions. Tips of pectinate fringe of posterior segment margin slightly shorter and more slender than on preceding segments. Segment otherwise as segment 6.

SEGMENT 8. With spines in lateroventral positions, and tubes in sublateral positions (Figs 8A–B, 9E, 10H). Sensory spots present in paradorsal and subdorsal positions. Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Band of perforation site patches interrupted in subdorsal area instead of laterodorsally as on preceding segments. Segment otherwise as segment 7.

SEGMENT 9. With spines in lateroventral positions. Tubes present in laterodorsal positions, but very close to midlateral line (Figs 8A, 9E, 10H–I). Sensory spots located in paradorsal, subdorsal and ventrolateral positions (Figs 8A–B, 9J, 10I). Glandular cell outlets type 1 present paradorsally and ventromedially. Small, rounded sieve plates located in sublateral positions (Fig. 9K). Perforation sites, secondary fringe and posterior segment margin as on preceding segment.

SEGMENT 10. With well-developed laterodorsal tubes, present in males only, located near posterior segment margin and close to midlateral line (Figs 8C, 9H, 10K). Females without tubes, but with fringe-like structures present in midlateral positions (Figs 8A, 10J). Sensory spots present in subdorsal and ventrolateral positions (Figs 8A–B, 10J–K); subdorsal pair located rather close to paradorsal area. Glandular cell outlets type 1 present as middorsal one, and in ventromedial positions. Perforation sites restricted to paradorsal area, lateral sides of tergal plate, and lateral halves of sternal plates. Posterior segment margin of tergal plate straight, without fringe tips (Fig. 10J–K); margins of sternal plates concave, reaching posterior margin of terminal segment, with short and narrow fringe tips.

SEGMENT 11. With lateral terminal spines (Figs 8A–B, 9A, 10D). Females with lateral terminal accessory spines (Figs 8A–B, 9I, 10A, D); males with three penile spines (Fig. 10K). Dorsal and ventral penile spines slender and tubular, with dorsal ones much longer than ventral; median spines very stout, cone-shaped (Figs 8C, 10K). Sensory spots present in subdorsal positions. Glandular cell outlet type 1 present middorsally. Segment devoid of characteristic perforation site patches, but very short cuticular hair-like structures covering paradorsal area. Very short fringes covering margins of tergal and sternal plates. Tergal extensions triangular (Figs 8A, C, 10J). Sternal extensions rounded, not extending beyond tergal extensions (Figs 8B, D, 9K).

Distribution

Canyons: Pahaua, Honeycomb, 670–1013 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes dalzottoi* sp. nov.

See taxonomic remarks for *E. dalzottoi* sp. nov. below, together with remarks for *E. leduci* sp. nov.

***Echinoderes leduci* sp. nov.**

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Figs 11–13; Tables 8–9

Diagnosis

Echinoderes with spines in middorsal position on segments 4, 6 and 8 and spines in lateroventral positions on segments 6 to 9. Tubes present in laterodorsal and ventrolateral positions on segment 2, lateroventral positions on segment 5, sublateral positions on segment 8, and laterodorsal positions on segment 9. Sexually dimorphic tubes furthermore present in laterodorsal positions on segment 10 in males. Minute scales present on segments 2 to 10, but regular cuticular hairs absent throughout trunk.

Etymology

The species is named after Dr Daniel Leduc in recognition of his contribution in collecting Hikurangi Margin kinorhynchs and making them available for description to the authors of the present study.

Material examined

Holotype

NEW ZEALAND • ♂; Pahaua Canyon, stn TAN1004/31; 41.4962° S, 175.6828° E; 730 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159405. Mounted for LM in Fluoromount G on HS slide.

Paratype

NEW ZEALAND • 1 ♀; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8977° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159406. Mounted as holotype.

Additional material

NEW ZEALAND • 1 ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; same collection data as for paratype; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 11–13). Overview of measurements and dimensions in Table 8. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 9. Head morphology could not be examined in detail in any of available specimens.

NECK. Consists of 16 placids. Midventral placid broadest, 12 µm in width and 14 µm in length, whereas all others narrower, measuring 7 µm in width at their bases (Fig. 11). Trichoscalid plates well developed.

SEGMENT 1. Consists of complete cuticular ring. Sensory spots present in subdorsal, laterodorsal and ventromedial positions. Sensory spots relatively large with marginal hairs, located on anterior half of segment (Figs 11A–B, 12B–C, 13B–C). Glandular cell outlet type 1 present in middorsal position and in ventrolateral positions. Cuticular hairs or perforation sites not present. Posterior segment margin almost straight, forming pectinate fringe with short, sawtooth-like fringe tips (Fig. 13B–C).

SEGMENT 2. Consists of complete cuticular ring, with tubes located in laterodorsal and ventrolateral positions (Figs 11A–B, 12B–C, 13B–C). Sensory spots of similar sizes as on preceding segment with long marginal hair, present in middorsal, laterodorsal and ventromedial positions. Glandular cell outlet type 1 present in middorsal position and in ventromedial positions. Pachycyclus of anterior segment margin of regular thickness, interrupted in middorsal position. Secondary pectinate fringe present near anterior segment margin of this and following segments, but mostly covered by preceding segment. This and following nine segments completely hairless. Cuticular hairs reduced to minute scales distributed around segment (Fig. 13D–G), emerging through perforation sites; perforation sites easily visible in LM (Fig. 12A–H). Posterior segment margin almost straight (Fig. 13C); pectinate fringe tips as on preceding segment, except midventral area with slightly narrower fringe tips.

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 11A–B, 12C, E). Sensory spots present in subdorsal and midlateral positions. Sensory spots on this and following segments slightly smaller than on preceding segments, but still with one long marginal hair. Glandular cell outlets type 1 present in middorsal and in ventromedial positions. Perforation sites

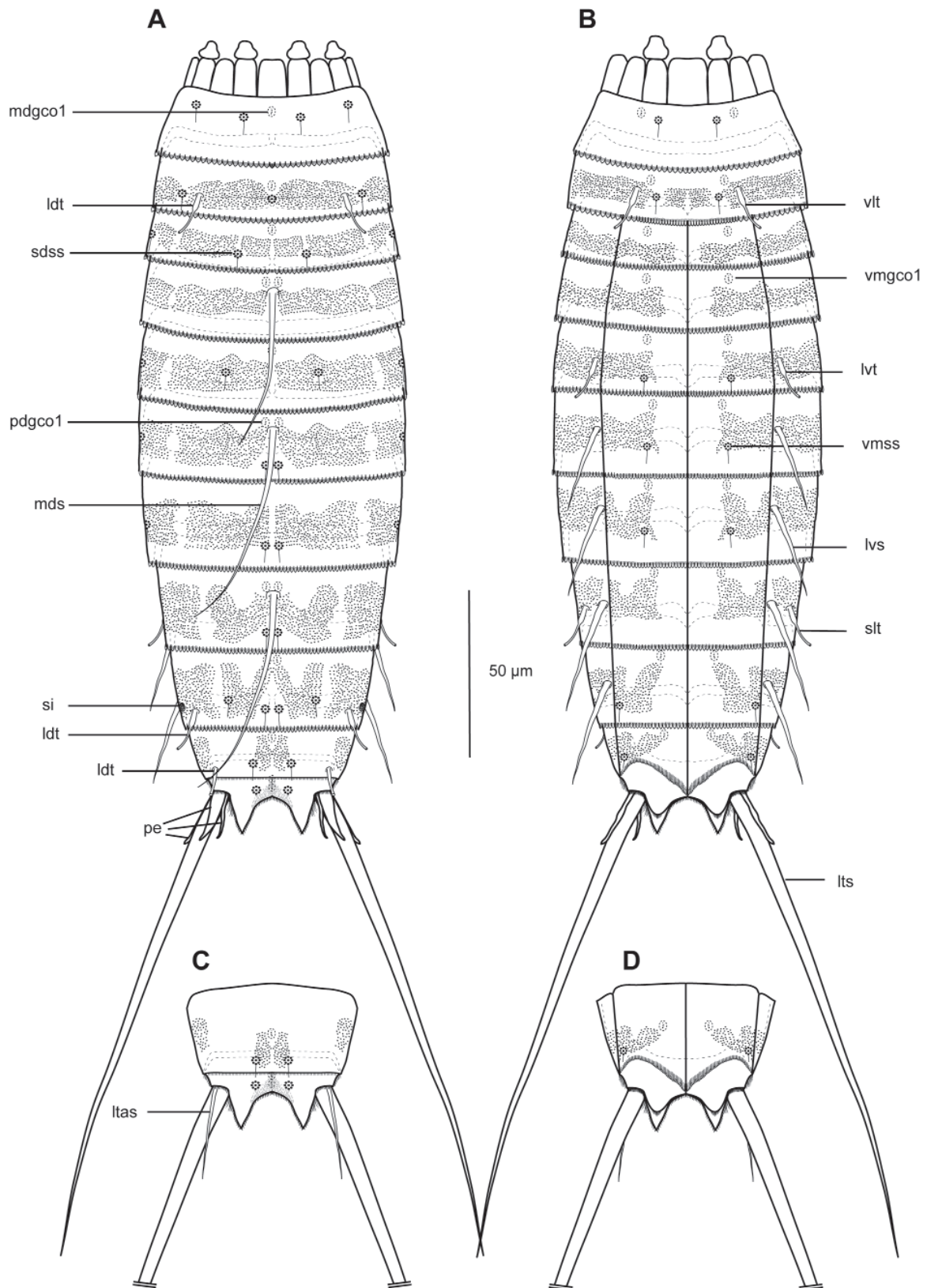


Fig. 11. Line art illustrations of *Echinoderes leduci* sp. nov. **A.** ♂, dorsal view. **B.** ♂, ventral view. **C.** ♀, segments 10–11, dorsal view. **D.** ♀, segments 10–11, ventral view. Abbreviations: see Material and methods.

Table 8. Measurements from light microscopy of *Echinoderes leduci* sp. nov. (in μm) from the Hikurangi Margin.

Character	Holotype	Paratype
	NIWA-159405 (♂)	NIWA-159406 (♀)
TL	212	234
MSW-6	60	62
MSW-6/TL	28%	27%
SW-10	45	47
SW-10/TL	21%	20%
S1	25	26
S2	23	25
S3	28	28
S4	28	29
S5	28	31
S6	32	33
S7	32	36
S8	35	37
S9	40	39
S10	40	38
S11	23	24
MD4 (ac)	47	52
MD6 (ac)	78	78
MD8 (ac)	82	86
LV6 (ac)	27	28
LV7 (ac)	30	29
LV8 (ac)	37	35
LV9 (ac)	32	35
LTS	172	163
LTS/TL	81%	70%
LTAS	n/a	27

appear as band around segment, interrupted in middorsal and laterodorsal areas and in central part of sternal plate on this and following five segments (Figs 11A–B, 12B–E). Secondary fringe and posterior segment margin as on preceding segment.

SEGMENT 4. With spine in middorsal position (Figs 11A, 12B, 13D). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. No other traits observed. Posterior segment margin straight, terminating in pectinate fringe with slightly slenderer fringe tips along ventral margin than on preceding segments, otherwise as on preceding segment.

SEGMENT 5. With tubes in lateroventral positions (Figs 11B, 12C, 13F). Sensory spots present in subdorsal, midlateral and ventromedial positions (Figs 11A–B, 12B–C, 13D, F). Glandular cell outlets type 1 present in middorsal and ventromedial positions. Perforation sites, secondary fringe and posterior segment margin as on preceding segment.

SEGMENT 6. With spines in middorsal and lateroventral positions (Fig. 11A–B). Sensory spots present in paradorsal, midlateral and ventromedial positions (Figs 11A–B, 13D, F). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Segment otherwise as segment 5.

SEGMENT 7. With spines in lateroventral positions, and sensory spots in paradorsal, midlateral and ventromedial positions (Figs 11A–B, 13F). Glandular cell outlets type 1 present in ventromedial positions only; no glands observed on dorsal side. Tips of pectinate fringe of posterior segment margin more slender than on preceding segments. Segment otherwise as segment 6.

SEGMENT 8. With spines in middorsal and lateroventral positions, and relatively long tubes (21 µm) in sublateral positions (Figs 11A–B, 12D–E, 13E, G). Sensory spots present in paradorsal positions only.

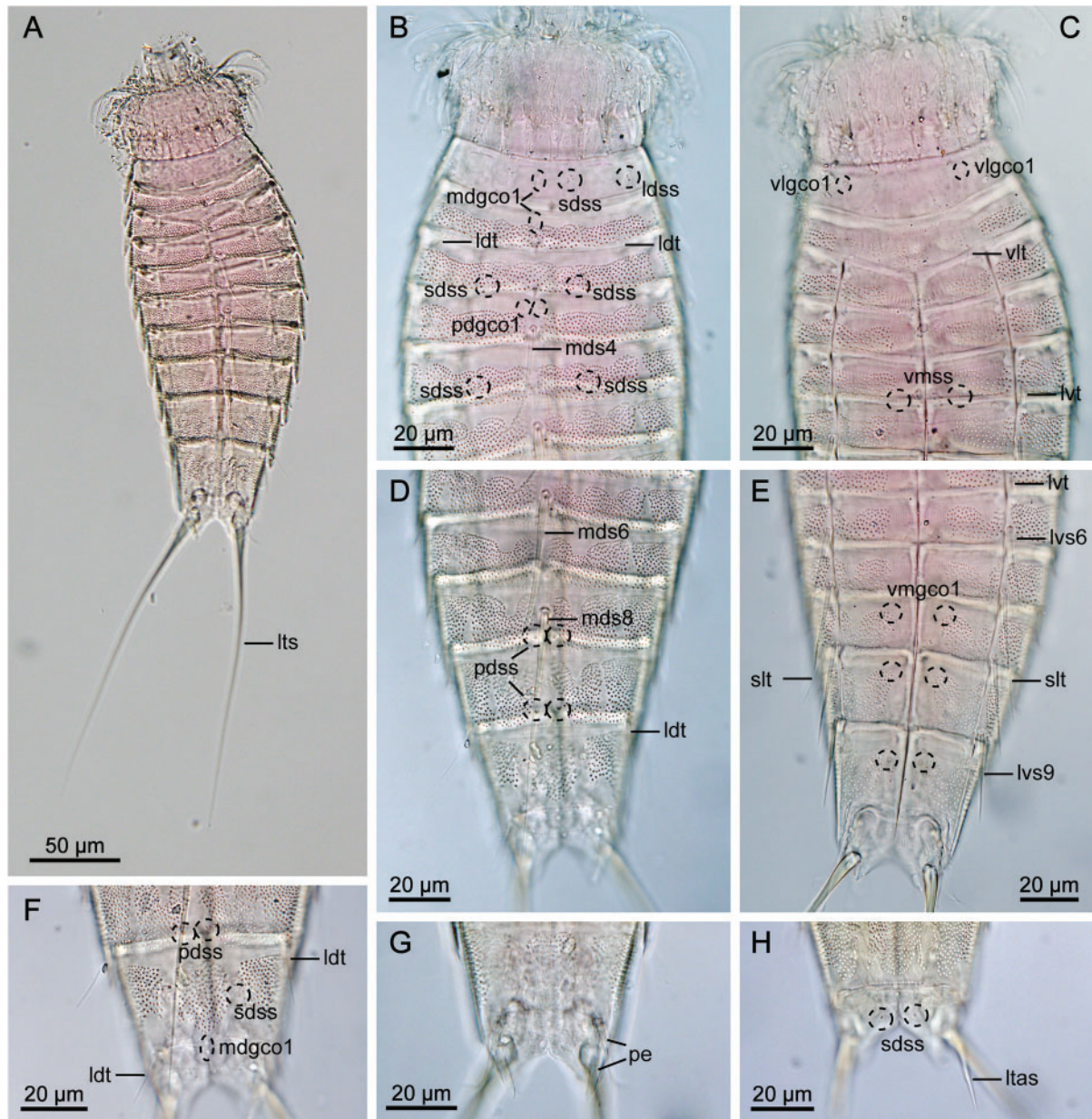


Fig. 12. Light micrographs showing overview and details of *Echinoderes leduci* sp. nov. **A–G.** ♂, holotype (NIWA-159405). **H.** ♀, paratype (NIWA-159406). **A.** Dorsal overview. **B.** Segments 1 to 6, dorsal view. **C.** Segments 1 to 6, ventral view. **D.** Segments 6 to 11, dorsal view. **E.** Segments 6 to 11, ventral view. **F.** Segments 9 to 11 of male, dorsal view. **G.** Segments 10 to 11 of male, dorsal view. **H.** Segments 10 to 11 of female, dorsal view. Abbreviations: see Material and methods.

Table 9. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes leduci* sp. nov.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gcol		ss	ss					gcol	ss
2	gcol,ss			tu,ss					tu	gcol,ss
3	gcol		ss		ss					gcol
4	ac	gcol								gcol
5	gcol		ss		ss			tu		gcol,ss
6	ac	gcol,ss			ss			ac		gcol,ss
7		ss			ss			ac		gcol,ss
8	ac	gcol,ss				tu		ac		gcol
9		gcol,ss	ss	tu	si			ac	ss	gcol
10	gcol		ss	tu(♂)					ss	gcol
11	gcol × 2		ss		pe × 3 (♂)		ltas(♀)	lts		

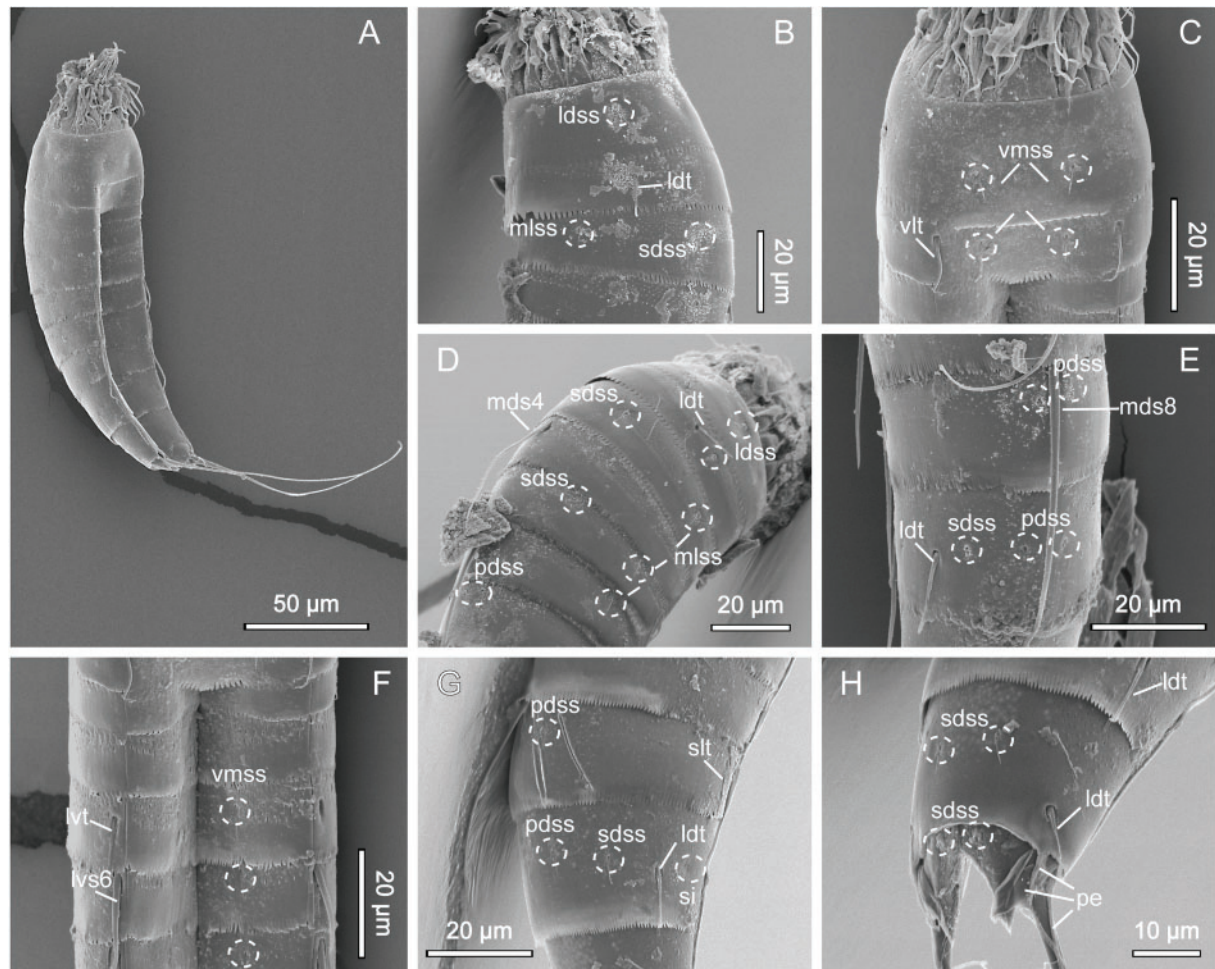


Fig. 13. Scanning electron micrographs showing overviews and details of *Echinoderes leduci* sp. nov. A. Lateroventral overview. B. Segments 1 to 3, lateral view. C. Segments 1 to 3, ventral view. D. Segments 1 to 6, laterodorsal view. E. Segments 8 to 9, dorsal view. F. Segments 3 to 7, ventral view. G. Segments 7 to 9, laterodorsal view. H. Segments 10 to 11 of male, dorsal view. Abbreviations: see Material and methods.

Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Segment otherwise as segment 7.

SEGMENT 9. With spines in lateroventral positions. Long tubes (20 µm) present in laterodorsal positions (Figs 11A, 12D, F, 13E, G). Sensory spots located in paradorsal, subdorsal and ventrolateral positions (Figs 11A–B, 12E–F, 13E, G). Glandular cell outlets type 1 present paradorsally and ventromedially. Small sieve plates located in midlateral positions (Fig. 13G). Band of perforation site patches interrupted in subdorsal area instead of laterodorsally as on preceding segments. Secondary fringe and posterior segment margin as on preceding segment.

SEGMENT 10. With well-developed laterodorsal tubes, present in males only, located near posterior segment margin (Figs 11A, 12F, 13H). Females without tubes (Figs 11C, 12H). Sensory spots present in subdorsal and ventrolateral positions (Figs 11A–B, 12E–F, 13H); subdorsal pair located rather close to paradorsal area. Glandular cell outlets type 1 present in middorsal and in ventromedial positions. Band of perforation site patches as on preceding segment but with additional patch present in paradorsal area. Posterior segment margin of tergal plate straight, without fringe tips (Fig. 13H); margins of sternal plates concave, reaching the posterior margin of the terminal segment, with short and narrow fringe tips.

SEGMENT 11. With lateral terminal spines (Figs 11A–B, 12A, 13A). Females with lateral terminal accessory spines (Figs 11C–D, 12H); males with three penile spines (Figs 12G, 13H). Dorsal and ventral spines slender and tubular, with ventral ones longer than dorsal ones; median spines very stout, cone-shaped (Figs 11A, 12G, 13H). Sensory spots present in subdorsal positions. Two unpaired glandular cell outlets type 1 present middorsally. Segment devoid of characteristic perforation sites patches, but with very short cuticular hair-like structures covering paradorsal area. Short fringes covering margins of tergal and sternal plates. Tergal extensions triangular (Figs 11A, C, 13H). Sternal extensions rounded, not extending beyond tergal extensions (Fig. 11B, D).

Distribution

Canyons: Pahaua, Honeycomb, 670–1013 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes dalzottoi* sp. nov. and *E. leduci* sp. nov.

Echinoderes dalzottoi sp. nov. and *E. leduci* sp. nov. can easily be recognized by the nature of their trunk appearance with cuticular hairs that are reduced to minute scales, and characteristic strong perforation sites present on segments 2 to 10. The complete lack of cuticular hairs is an uncommon feature among species of *Echinoderes*. Within Echinoderidae, the species' peculiar lack of cuticular hairs is shared only with *Meristoderes glaber* Sørensen *et al.*, 2013 (Sørensen *et al.* 2013). Resemblance with *M. glaber* is only superficial though, and the lack of lateral spines on segment 6, together with the presence of glandular cell outlets type 2 instead of tubes on segment 8 in *M. glaber* easily distinguish it from *E. dalzottoi* and *E. leduci*. The new species can also be distinguished from each other without any difficulty. Despite the number of similarities suggesting a close relationship, such as presence of lateroventral spines on segments 6–9, lateroventral tubes on segment 5, sublateral tubes on segment 8 and laterodorsal tubes on segment 9, it is possible to distinguish the two species based on several characters. The main difference is the number of middorsal spines, present on segments 4, 6 and 8 in *E. leduci* in contrast to spines on segments 4 and 6 only in *E. dalzottoi*. Furthermore, *E. leduci* lacks subdorsal tubes on segment 2 (present in *E. dalzottoi*), but has laterodorsal tubes on this segment instead.

Having tubes on segment 2 in only laterodorsal and ventrolateral positions as in *E. leduci* sp. nov. is quite a rare character, and only shared with two other species of *Echinoderes*, i.e., *E. daenerysae* and *E. higginsi* Huys & Coomans, 1989 (although a laterodorsal pair was not mentioned in the original

description of the latter species) (Huys & Coomans 1989; Grzelak & Sørensen 2018). Neither of them can be confused with *E. leduci*, however. Except for the dense cuticular hair covering observed in both species, *E. daenerysae* possesses only two middorsal spines on segments 6 and 8, while *E. higginsi*, although having the same number and arrangement of middorsal spines as *E. leduci*, is characterized by long, conspicuous spinous tergal extensions of segment 11 and the lack of tubes on segment 9.

Echinoderes dalzottoi sp. nov. is also easily distinguished from all other congeners by its combination of spines and tubes. Middorsal spines being restricted to segments 4 and 6 only is rare and shared only with four other species, i.e., *E. astridae*, *E. bispinosus*, *E. uozumii*, and *E. landersi* sp. nov. (Higgins 1982; Sørensen 2014; Yamasaki *et al.* 2020). However, *E. astridae*, *E. bispinosus* and *E. uozumii* lack dorsal and lateral tubes on segment 2, and have instead two pairs of glandular cell outlet type 2 – a gland type that is absent in *E. dalzottoi*. *Echinoderes landersi*, in turn, is characterized by four pairs of tubes on segment 2 and three pairs of tubes on segment 8 – a so far unique tube combination (see ‘Remarks’ in the description of *E. landersi* above for more details).

The combination of tubes in subdorsal, sublateral and ventrolateral positions on segment 2 is also quite rare. Numerous species present combinations of two or four pairs of tubes on this segment, but only four species have three pairs, among which only *E. hispanicus* Pardos *et al.*, 1998 and *E. peterseni* Higgins & Kristensen, 1988 have tube arrangements as in *E. dalzottoi* sp. nov. (Higgins & Kristensen 1988; Pardos *et al.* 1998; Grzelak & Sørensen 2018). However, both species also have three middorsal spines and lack laterodorsal tubes on segment 9, which easily distinguish them from *E. dalzottoi*. Even considering that sublateral tubes might be absent in some specimens of *E. dalzottoi* (a variation in the occurrence of tubes has recently been reported for a number of echinoderid species; see, e.g., Grzelak & Sørensen (2018) and Yamasaki & Dal Zotto (2019) for further details), none of the species having only subdorsal and ventrolateral tubes on segment 2 can be confused with *E. dalzottoi* due to their significantly different middorsal spine patterns and trunk cuticle appearance.

***Echinoderes gandalfi* sp. nov.**

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Figs 14–16; Tables 10–11

Diagnosis

Echinoderes with spines in middorsal position on segments 6 and 8, and spines in lateroventral positions on segments 6 to 9. Tubes present in ventrolateral positions on segment 2, lateroventral positions on segment 5, lateral accessory positions on segment 8, and laterodorsal positions on segments 9 and 10. A protuberance-like structure emerges between segments 10 and 11 in middorsal position. Lateral terminal spines long, always exceeding trunk length.

Etymology

The species name refers to Gandalf the Grey, one of the main characters in the novel “*The Fellowship of the Ring*”, the first volume of J.R.R. Tolkien’s “*The Lord of the Rings*”. He helped form the Fellowship of the Ring to destroy the One Ring.

Material examined

Holotype

NEW ZEALAND • ♂; Pahaua Canyon, stn TAN1004/31; 41.4962° S, 175.6828° E; 730 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159407. Mounted for LM in Fluoromount G on HS slide.

Paratypes

NEW ZEALAND • 2 ♀♀; same collection data as for holotype; ♀ NHMD-916356, ♀ NIWA-159408. Mounted as holotype • 1 ♀; Pahaua Canyon, stn TAN1004/12; 41.5508° S, 175.7250° E; 1350 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159409. Mounted as holotype • 1 ♀, 1 ♂; Pahaua Canyon, stn TAN1004/22; 41.5100° S, 175.7187° E; 1188 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; ♀ NHMD-916362, ♂ NIWA-159410. Mounted as holotype • 1 ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; ♂ NIWA-159411. Mounted as holotype • 1 ♀, 2 ♂♂; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8987° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; ♀ NIWA-159412, ♂♂ NHMD-916357–916358. Mounted as holotype • 1 ♀, 3 ♂♂; Campbell Canyon, stn TAN1004/126; 42.1422° S, 174.5492° E; 1495 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; ♀ NHMD-916360, 1 ♂ NIWA-159413, 2 ♂♂ NHMD-916359 and 916361. Mounted as holotype.

Additional material

NEW ZEALAND • 5 ♀♀, 3 ♂♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀, 2 ♂♂; Honeycomb Canyon, stn TAN1004/62; 41.4760° S, 175.9477° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀; Campbell Canyon, stn TAN1004/126; 42.1422° S, 174.5492° E; 1495 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 14–16). Overview of measurements and dimensions in Table 10. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 11. No details regarding scaldid arrangement and morphology could be provided, because introverts of all specimens mounted for SEM fully or partially retracted.

NECK. With 16 placids. Midventral placid broadest, 8 µm in width and 15 µm in length, whereas all others narrower, measuring 6 µm in width at their bases and 13 µm in length, similar in size (Fig. 15B–C). The trichoscalid plates are well-developed (Fig. 15B–C).

SEGMENT 1. Consists of complete cuticular ring. Sensory spots located on anterior half of segment, in subdorsal positions. Glandular cell outlet type 1 present in middorsal and ventrolateral positions (Figs 14A–B, 15B–C). Cuticular hairs relatively long, distributed around segment. Posterior segment margin almost straight, forming pectinate fringe with very short, sawtooth-like fringe tips.

SEGMENT 2. Consists of complete cuticular ring, with tubes located in ventrolateral positions (Figs 14A–B, 15C, 16C). Sensory spots present in middorsal, laterodorsal and ventromedial positions; sensory spots on this and following eight segments relatively large, with numerous micropapillae surrounding central pore and long marginal hair, giving them droplet-shaped appearance (Fig. 16B). Glandular cell outlets type 1 present in middorsal and ventromedial positions (Figs 14A–B, 15B). Pachycyclus of anterior segment margin of regular thickness, without interruption. Secondary pectinate fringe present near anterior segment margin of this and following segments, but usually covered by preceding segment. Fairly long cuticular hairs evenly distributed across tergal plate; paraventral areas on this and following three segments with thinner and much shorter, non-bracteate hairs, emerging through perforation sites visible in SEM only. Posterior segment margin almost straight, but with rounded midventral extension; pectinate fringe tips as on preceding segment.

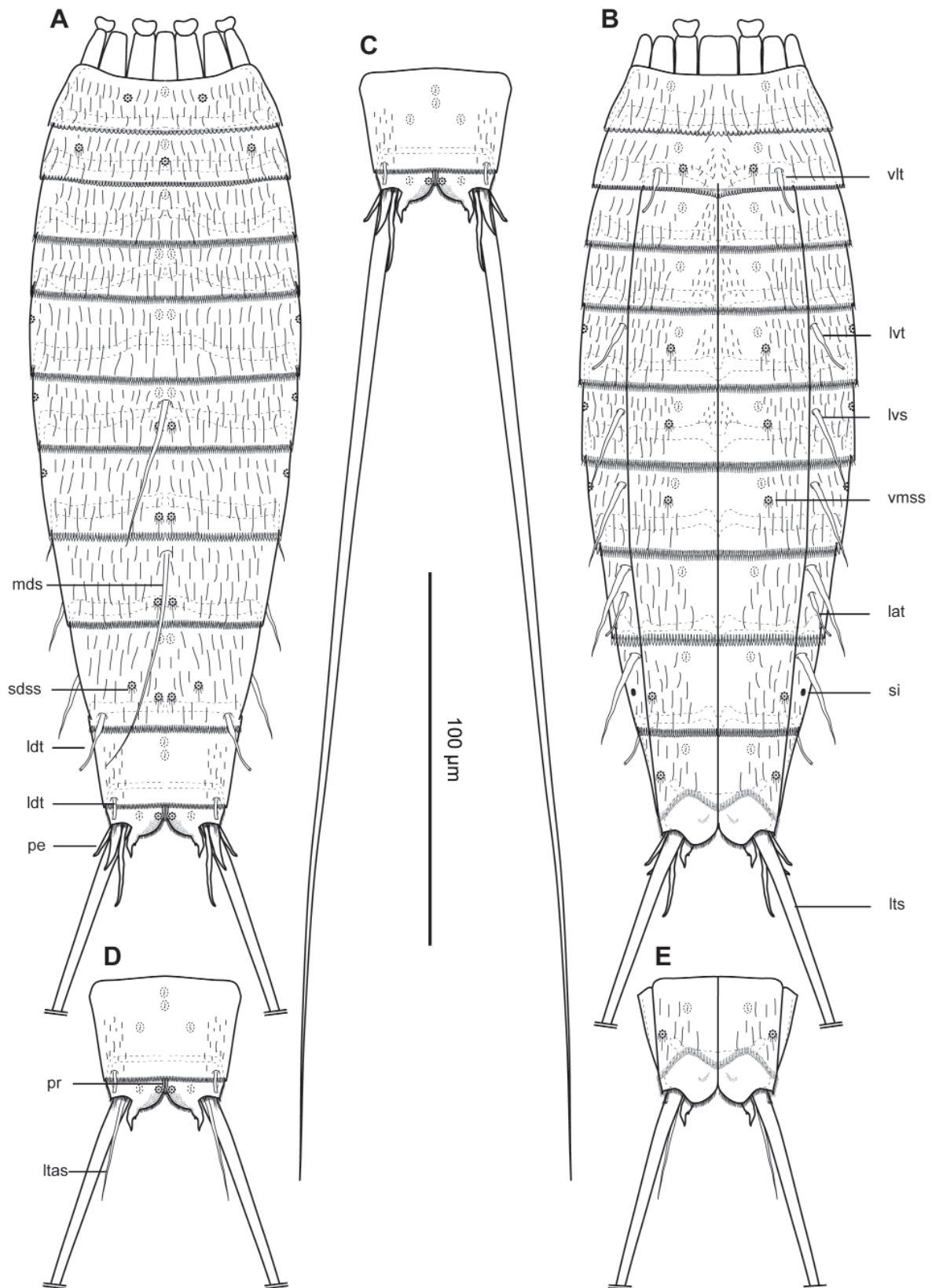


Fig. 14. Line art illustrations of *Echinoderes gandalfi* sp. nov. **A.** ♂, dorsal view. **B.** ♂, ventral view. **C.** ♂, segments 10 to 11, with lateral terminal spines drawn in full length, dorsal view. **D.** ♀, segments 10 to 11, dorsal view. **E.** ♀, segments 10 to 11, ventral view. Abbreviations: see Material and methods.

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 14A–B, 15A–C, 16B–C). Pachycyclus of anterior segment margin of medium thickness, interrupted at tergo-sternal and midsternal junctions and middorsally, on this and following seven segments. Segment with middorsal and ventromedial glandular cell outlets type 1; no sensory spots or other traits observed. Cuticular hairs interrupted by hairless midlateral area, otherwise as on preceding segment. Posterior segment margin straight, terminating in pectinate fringe with longer and more slender fringe tips than on preceding segments.

SEGMENT 4. With glandular cell outlets type 1 present in paradorsal and ventromedial positions. Segment otherwise as segment 3.

SEGMENT 5. With tubes in lateroventral positions (Figs 14B, 15C, 16A–B). Sensory spots present in midlateral and ventromedial positions; the latter, however, missing in some specimens examined under

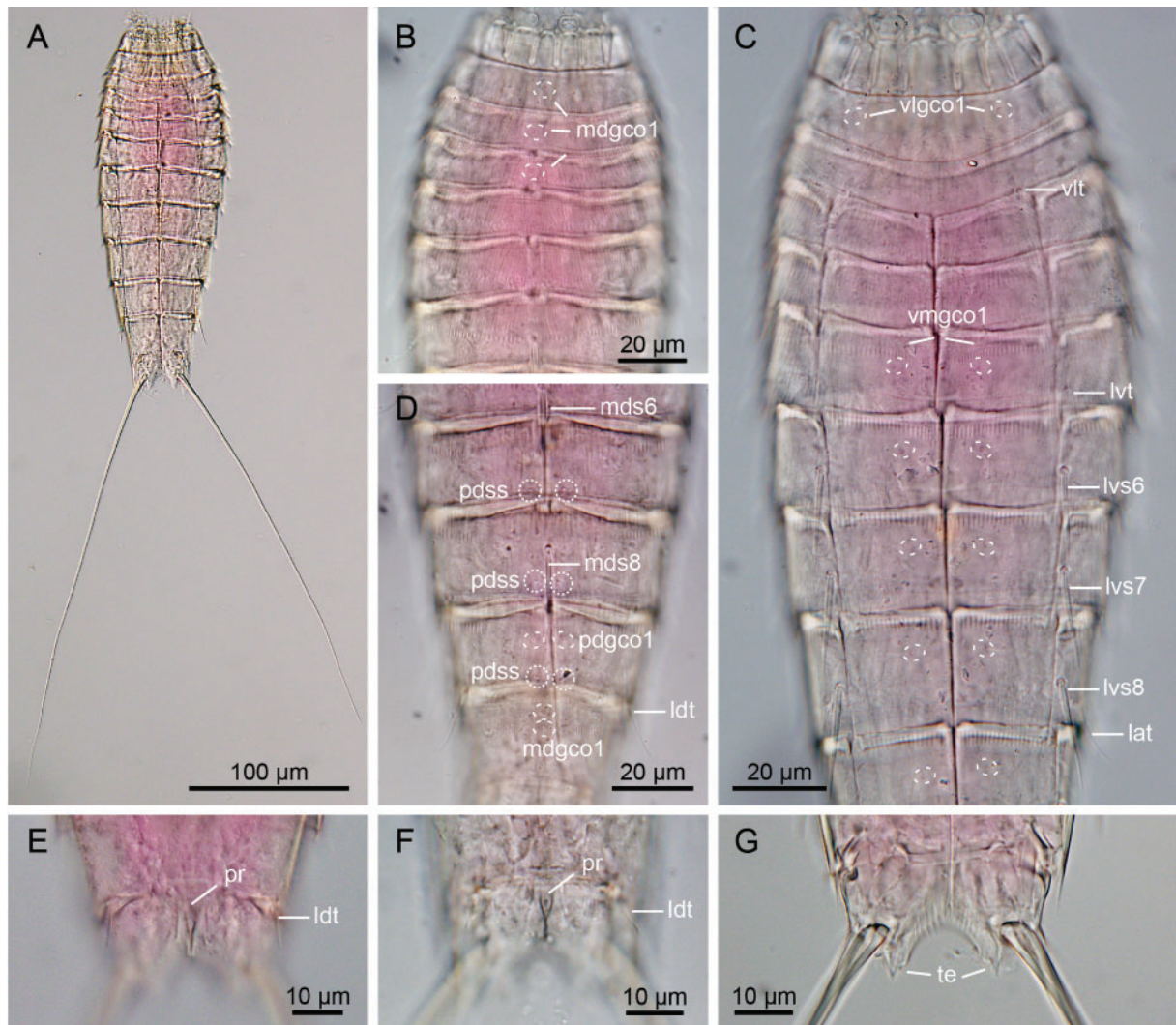


Fig. 15. Light micrographs showing overview and details of *Echinoderes gandalfi* sp. nov. **A–D, F.** ♂, holotype (NIWA-159407). **E, G.** ♀, paratype (NHMD-916362). **A.** Ventral overview. **B.** Segments 1 to 6, dorsal view. **C.** Segments 1 to 9, ventral view. **D.** Segments 6 to 10, dorsal view. **E.** Segments 10 to 11 of female, dorsal view. **F.** Segments 10 to 11 of male, dorsal view. **G.** Segment 11 of female, ventral view. Abbreviations: see Material and methods.

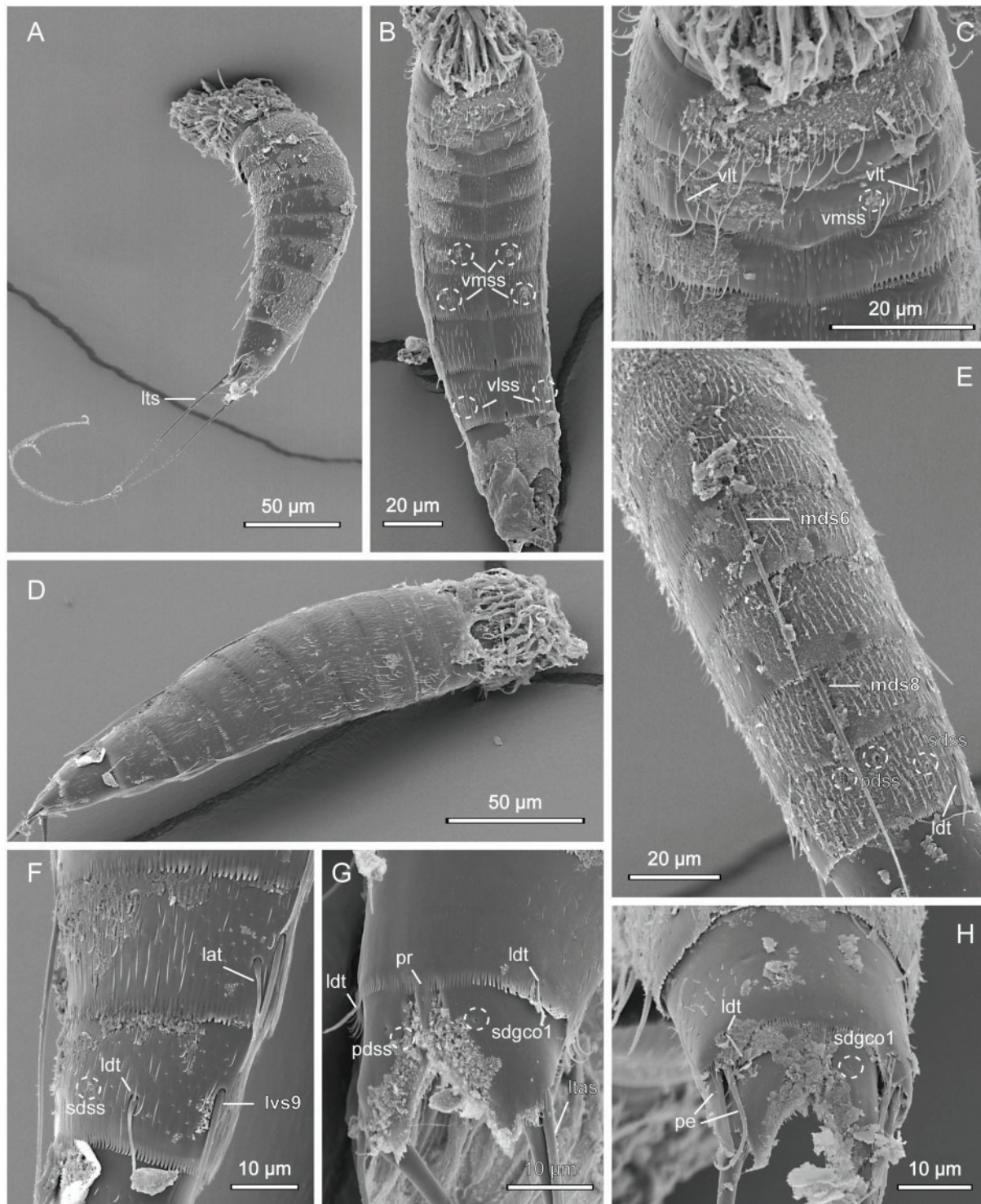


Fig. 16. Scanning electron micrographs showing overviews and details of *Echinoderes gandalfi* sp. nov. **A.** Lateral overview. **B.** Ventral overview. **C.** Segments 1 to 4, ventral view. **D.** Lateral overview. **E.** Segments 4 to 10, dorsal view. **F.** Segments 8 to 9, lateral view. **G.** Segments 10 to 11 of female, dorsal view. **H.** Segments 10 to 11 of male, dorsal view. Abbreviations: see Material and methods.

Table 10. Measurements from light microscopy of *Echinoderes gandalfi* sp. nov. (in μm) from the Hikurangi Margin, including number of measured specimens (n) and standard deviation (SD).

Character	n	Range	Mean	SD
TL	10	140–222	186	24.5
MSW-6	7	42–55	50	4.8
MSW-6/TL	7	21.6–32.0%	27.6%	4.3%
SW-10	7	37–42	39	1.9
SW-10/TL	7	18.3–26.4%	21.6%	3.2%
S1	9	18–21	19	1.8
S2	9	17–23	19	1.7
S3	9	15–25	21	3.4
S4	9	17–29	23	4.1
S5	9	22–31	26	2.9
S6	9	24–31	27	2.1
S7	9	24–33	30	2.2
S8	9	29–37	32	2.3
S9	9	29–36	33	2.3
S10	9	26–33	30	2.2
S11	9	19–28	23	5.1
MD6 (ac)	10	34–42	39	2.9
MD8 (ac)	8	49–56	52	2.1
LV6 (ac)	10	17–23	20	2.3
LV7 (ac)	10	19–25	22	2.7
LV8 (ac)	10	23–28	25	2.5
LV9 (ac)	10	24–31	26	2.4
LTS	10	191–275	241	26.2
LTS/TL	10	103–169.3%	132.0%	24.1%
LTAS	3	28–34	30	3.2

SEM (Fig. 16B) and for some specimens (including holotype) examined under LM presence/absence of ventromedial sensory spots could not be confirmed. Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Pectinate fringe of posterior segment margin and cuticular hairs as on preceding segment.

SEGMENT 6. With spines in middorsal and lateroventral positions (Figs 14A–B, 15C–D, 16A–B, D–F). Sensory spots present in paradorsal, midlateral and ventromedial positions (Fig. 14A–B). Glandular cell outlets type 1 present in paradorsal and ventromedial positions (Figs 14A–B, 15C). Tips of pectinate fringe of posterior segment margin slightly longer than on preceding segments. Segment otherwise as segment 5.

SEGMENT 7. With spines in lateroventral positions, and sensory spots in paradorsal, midlateral and ventromedial positions (Figs 14A–B, 15C–D, 16B). Glandular cell outlets type 1 present in ventromedial positions, not observed on the dorsal side. Cuticular hairs covering as on preceding segment except for hairless paraventral and ventromedial areas, on this and following four segments.

SEGMENT 8. With spines in middorsal and lateroventral positions, and tubes in lateral accessory positions (Figs 14A–B, 15C–D, 16D, F). Sensory spots present in paradorsal positions only. Glandular cell outlets

Table 11. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes gandalfi* sp. nov.

Position segment	MD	PD	SD	LD	ML	LA	LV	VL	VM
1	gcol		ss					gcol	
2	gcol,ss			ss				tu	gcol,ss
3	gcol								gcol
4		gcol							gcol
5		gcol			ss		tu		ss*,gcol
6	ac	gcol,ss			ss		ac		ss, gcol
7		ss			ss		ac		ss,gcol
8	ac	ss				tu	ac		gcol
9		gcol,ss	ss	tu		si	ac	ss	gcol
10	gcol,gcol			tu				ss	gcol
11	pr	ss	gcol		pe 3(♂)	ltas(♀)	lts		

type 1 as on preceding segment. Pectinate fringe of posterior segment margin and cuticular hairs as on preceding segment.

SEGMENT 9. With spines in lateroventral positions and long (~18 µm) tubes in laterodorsal positions (Figs 14A–B, 15D, 16D–F). Sensory spots located in paradorsal, subdorsal and ventrolateral positions (Figs 14A–B, 15B–C, 16F). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Small, rounded sieve plates located in lateral accessory positions. Cuticular hairs covering as on preceding segment, but less dense on dorsal side around sensory spots and tubes. Pectinate fringe of posterior segment margin with tips slightly shorter than on preceding segments.

SEGMENT 10. With laterodorsal tubes located near posterior segment margin; tubes well developed in both sexes (Figs 15E–F, 16G–H). Sensory spots present in ventrolateral positions. Glandular cell outlets type 1 present as two middorsal ones, and in ventromedial positions. Cuticular hairs significantly scarcer than on preceding segment. Central part of tergal palate devoid of hairs; short cuticular hairs lightly scattered on lateral halves only. Hairs on sternal plates short and present mostly on lateral halves and near posterior segment margin. Posterior segment margin of tergal plate straight, with shorter fringe tips than those on preceding segment; margins of sternal plates with longer fringe tips than those on tergal plate and extend midventrally, almost reaching posterior margin of terminal segment.

SEGMENT 11. With very long lateral terminal spines, always exceeding trunk length (Fig. 14C; Table 10). Males with three pairs of penile spines; dorsal and ventral ones are long, relatively thin tubes, whereas median ones markedly thicker, conical and stout (Figs 14A–B, 16H). Females with lateral terminal accessory spines (Fig. 14D–E). Sensory spots present in paradorsal positions (Figs 14A, D, 16D); sensory spots smaller than on preceding segments, without long marginal hairs. Glandular cell outlets type 1 present in subdorsal positions. Middorsal protuberance-like structure extends from intersegmentary joint (Figs 14A,D, 15E–F, 16G). Segment devoid of cuticular hairs, but with short cuticular hair-like structures covering paradorsal area and short fringes covering margins of tergal and sternal plates. Tergal extensions short and pointed, with small tooth at inner margin (Fig. 15G). Sternal extensions broadly rounded, not extending beyond tergal extensions.

Distribution

Canyons: Pahaua, Campbell, Honeycomb, 730–1495 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes gandalfi* sp. nov.

The spine pattern with middorsal spines on segments 6 and 8 is rare among species of *Echinoderes*, and is shared with only three species, i.e., *E. daenerysae*, *E. hviidarum* Sørensen *et al.*, 2018 and *E. ultraabyssalis* Adrianov & Maiorova, 2019, and an undescribed species, *Echinoderes* sp. 1, from the Atacama Trench (Grzelak & Sørensen 2018; Sørensen *et al.* 2018; Adrianov & Maiorova 2019; Grzelak *et al.* 2021). Furthermore, *E. gandalfi* sp. nov. possesses laterodorsal tubes on segment 9, which is another relatively rare trait, shared with all the abovementioned species, which suggests that these species might represent a group of closely related species. The only other species with tubes in this position on the dorsal side of segment 9 is *E. belenae* (see Pardos *et al.* 2016b) and *E. frodoi* sp. nov., *E. dalzottoi* sp. nov. and *E. leduci* sp. nov., all described in the present study. Nevertheless, none of these species can in any way be confused with *E. gandalfi* due to their significantly different spine patterns.

Echinoderes gandalfi sp. nov. probably shows most resemblance to *E. ultraabyssalis*, the deepest kinorhynch species described so far (> 9000 m water depth) from the Kuril-Kamchatka Trench, and *Echinoderes* sp. 1, found in the Atacama Trench at a water depth of 7700 m (Adrianov & Maiorova 2019; Grzelak *et al.* 2021). *Echinoderes gandalfi* shares several features with these hadal/deep-sea trench species, including the presence of tubes in ventrolateral positions on segment 2, lateroventral positions on segment 5, and in lateral accessory positions on segment 8, the presence of a middorsal protuberance between segments 10 and 11, as well as very long lateral terminal spines, the shape of the tergal extensions and the lack of glandular cell outlets type 2. Nevertheless, despite the overall similarity, *E. gandalfi* can be distinguished from both congeners by its morphometrics. *Echinoderes gandalfi* is markedly smaller in trunk length than both species (TL: 186 µm vs 267 µm and 257 µm, respectively) but has proportionally longer lateral terminal spines, which always exceed the trunk length, resulting in a markedly higher LTS/TL ratio in *E. gandalfi* in comparison with *E. ultraabyssalis* and *Echinoderes* sp. 1 (LTS/TL: 132% vs 59% and 91%, respectively) (Adrianov & Maiorova 2019; Grzelak *et al.* 2021). It appears that also the arrangement and number of sensory spots show some differences. Unique for *E. gandalfi* is the presence of laterodorsal sensory spots on segment 2 but the lack of these structures in ventrolateral positions on segment 1, and in middorsal position on segment 10 as found in the other two species. In addition, *E. ultraabyssalis* lacks well-developed laterodorsal tubes on segment 10, which are present in both sexes and easy to visualize even with LM in *E. gandalfi*.

***Echinoderes frodoi* sp. nov.**

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Figs 17–19; Tables 12–13

Diagnosis

Echinoderes with spines in middorsal position on segments 4, 6 and 8, and in lateroventral positions on segments 6 to 9. Tubes present in midlateral positions on segment 1 (might be missing in some specimens), subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, lateroventral positions on segment 5, lateral accessory positions on segment 8, and laterodorsal positions on segment 9. Sexually dimorphic tubes furthermore present in laterodorsal positions on segment 10: male tubes well-developed; female tubes minute.

Etymology

The species name refers to Frodo Baggins, the main character in the novel “*The Fellowship of the Ring*”, the first volume of J.R.R. Tolkien’s “*The Lord of the Rings*”.

Material examined

Holotype

NEW ZEALAND • ♂; Pahaua Canyon, stn TAN1004/22; 41.5100° S, 175.7187° E; 1188 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159414. Mounted for LM in Fluoromount G on HS slide.

Paratypes

NEW ZEALAND • 1 ♀, 2 ♂♂; Hikurangi Slope, stn TAN1004/4; 41.6837° S, 175.6642° E; 1046 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; ♀ NIWA-159415, 1 ♂ NHMD-916331, 1 ♂ NIWA-159416. Mounted for LM in Fluoromount G on glass slides • 1 ♀; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-916335. Mounted as holotype • 1 ♀; Hikurangi Slope, stn TAN1004/76; 41.6833° S, 175.6500° E; 1282 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-916336. Mounted as holotype • 1 ♀; Hikurangi Slope, stn TAN1004/128; 42.0485° S, 174.7000° E; 1420 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-916337. Mounted for LM in Fluoromount G on glass slide • 1 ♀; same collection data as for holotype; NIWA-159417. Mounted as holotype • 1 ♂; Hikurangi Slope, stn TAN1004/31; 41.4962° S, 175.6828° E; 730 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-916332. Mounted for LM in Fluoromount G on glass slide • 1 ♀; Campbell Canyon, stn TAN1004/126; 42.1422° S, 174.5492° E; 1495 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-916333. Mounted for LM in Fluoromount G on glass slide • 1 ♂; Seamount 766, stn TAN1004/129; 42.1345° S, 174.5860° E; 1456 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-916334. Mounted as holotype.

Additional material

NEW ZEALAND • 1 ♀, 1 ♂; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀; Hikurangi Slope, stn TAN1004/76; 41.6833° S, 175.6500° E; 1282 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8977° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Campbell Canyon, stn TAN1004/92; 41.8922° S, 174.6347° E; 683 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀; Campbell Canyon, stn TAN1004/126; 42.1422° S, 174.5492° E; 1495 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 17–19). Overview of measurements and dimensions in Table 12. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 13. No details regarding scolid arrangement and morphology could be provided, because introverts of all specimens mounted for SEM fully or partially retracted.

NECK. With 16 placids. Midventral placid broadest, 9 µm in width and 16 µm in length. Remaining placids narrower, 7 µm in width and 15 µm in length, similar in size (Fig. 19B). The trichoscolid plates well developed.

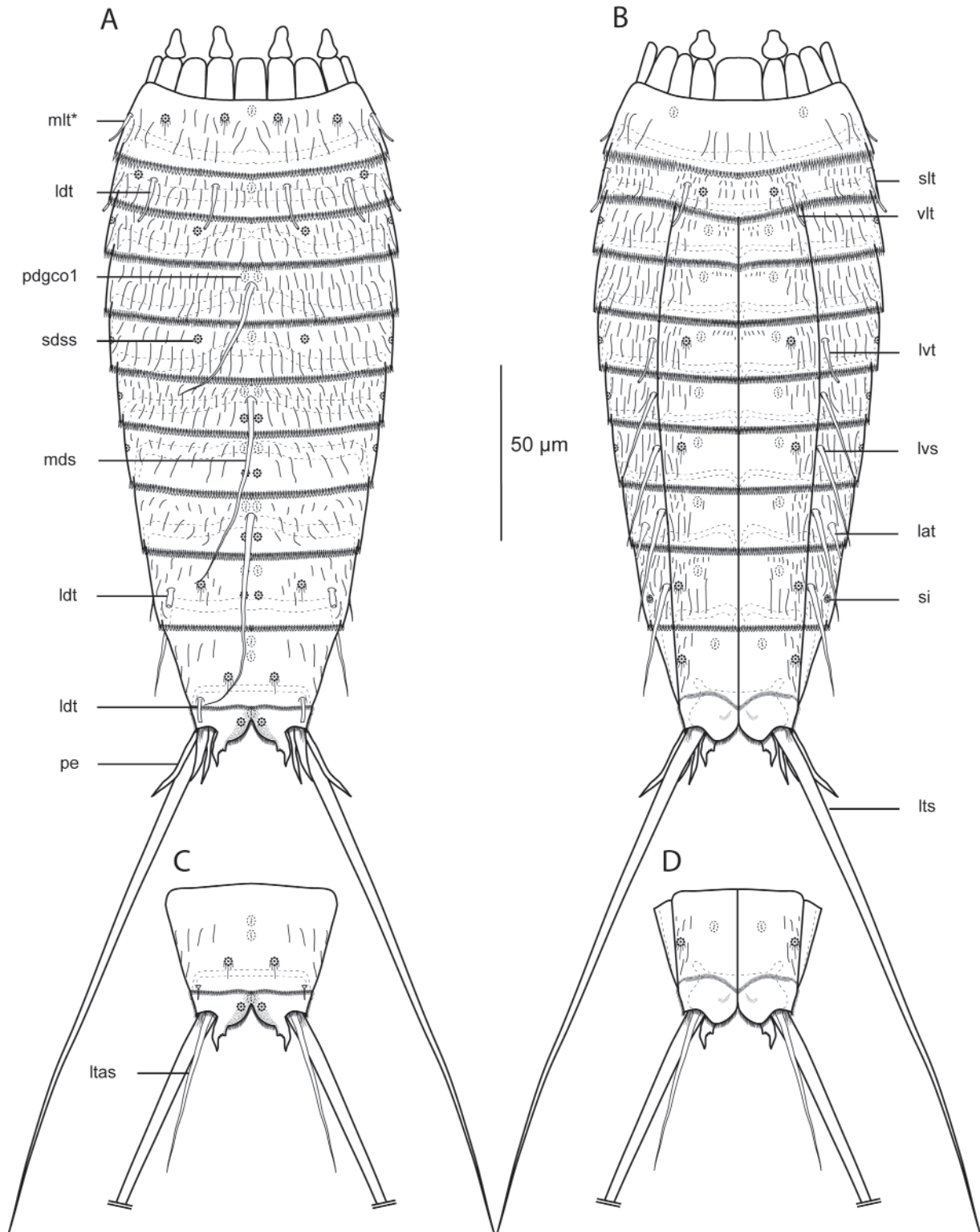


Fig. 17. Line art illustrations of *Echinoderes frodoi* sp. nov. **A.** ♂, dorsal view. **B.** ♂, ventral view. **C.** ♀, segments 10–11, dorsal view. **D.** ♀, segments 10–11, ventral view. Abbreviations: see Material and methods.



Fig. 18. Light micrographs showing overview and details of *Echinoderes frodoi* sp. nov. **A, C** (close-up). ♂, holotype (NIWA-159414). **B–D, F.** ♀, paratype (NHMD-916336). **E.** ♀, paratype (NHMD-916335). **G–H.** ♂, paratype (NIWA-159416). **A.** Ventral overview. **B.** Segments 1 to 8, dorsal view. **C.** Segments 1 to 8, ventral view with close-up showing midlateral tube on segment 1. **D.** Segments 9 to 10, dorsal view. **E.** Segments 8 to 10, ventral view. **F.** Segments 10 to 11, ventral view. **G.** Segments 9 to 10, lateral view. **H.** Segments 10 to 11, lateral view. Abbreviations: see Material and methods.

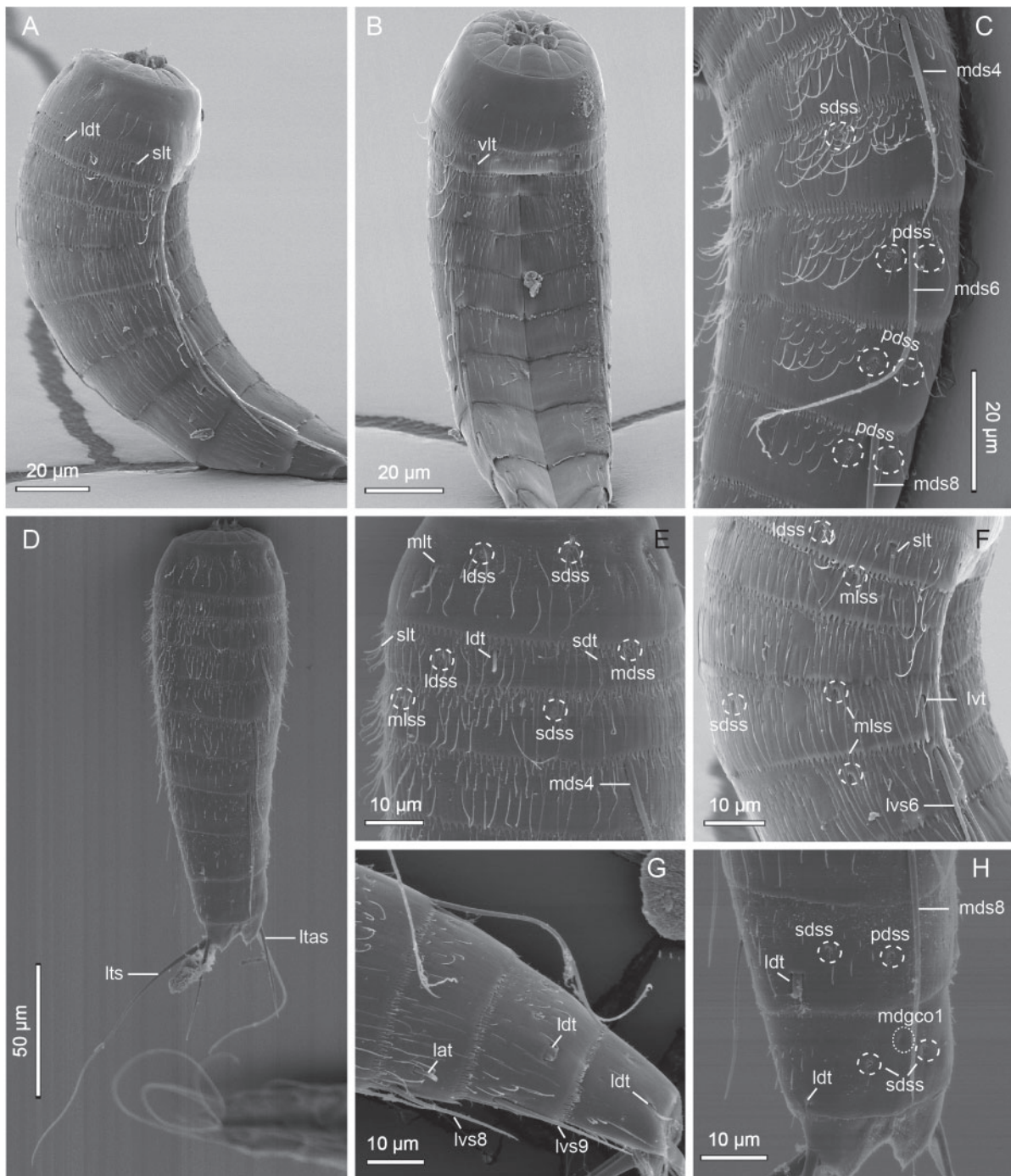


Fig. 19. Scanning electron micrographs showing overviews and details of *Echinoderes frodoi* sp. nov. **A.** Lateral overview. **B.** Ventral overview. **C.** Segments 4 to 8, laterodorsal view. **D.** Dorsal overview. **E.** Segments 1 to 4, laterodorsal view. **F.** Segments 2 to 6, lateral view. **G.** Segments 8 to 10 of male, lateral view. **H.** Segments 9 to 11 of female, laterodorsal view. Abbreviations: see Material and methods.

Table 12. Measurements from light microscopy of *Echinoderes frodoi* sp. nov. (in μm) from the Hikurangi Margin, including number of measured specimens (n) and standard deviation (SD).

Character	n	Range	Mean	SD
TL	8	161–202	185	16.2
MSW-7	6	42–47	45	1.4
MSW-7/TL	6	22.2–27.3%	24.7%	1.9%
SW-10	6	32–38	36	2.3
SW-10/TL	6	18.8–22.2%	20.1%	1.4%
S1	9	18–23	21	1.7
S2	9	17–21	19	1.2
S3	9	19–24	22	1.4
S4	9	22–28	24	2.0
S5	9	22–31	26	2.8
S6	9	24–32	27	2.4
S7	9	23–34	29	3.3
S8	9	26–35	30	3.0
S9	9	28–35	30	2.2
S10	9	25–30	28	1.9
S11	9	17–24	21	2.1
MD4 (ac)	9	33–40	37	2.7
MD6 (ac)	9	55–60	58	1.9
MD8 (ac)	9	61–66	64	1.6
LV6 (ac)	9	24–27	25	0.9
LV7 (ac)	9	25–30	28	1.8
LV8 (ac)	9	28–33	31	2.0
LV9 (ac)	9	27–32	30	1.5
LTS	8	144–155	148	3.5
LTS/TL	7	70.3–88.2%	79.0%	6.3%
LTAS	5	34–48	43	5.4

SEGMENT 1. Consists of complete cuticular ring (Figs 17A–B, 18A–C, 19B). Tubes present in midlateral positions in holotype and some paratypes; however, this character missing in other specimens and thus shows variation at population level (Figs 17A, 18C, 19A, E); no morphological or developmental differences explain presence or absence of tubes. Sensory spots located anteriorly on segment, but not at anterior margin, in subdorsal and laterodorsal positions. Sensory spots on this and following segments rounded, with numerous micropapillae surrounding central pore and several longer hairs along posterior margin. Glandular cell outlet type 1 present in middorsal position, and in lateroventral positions (Fig. 17A–B). Cuticular hairs lightly scattered on dorsal and lateral sides, and in small cluster ventromedially. Posterior segment margin almost straight, forming pectinate fringe with short and pointed fringe tips.

SEGMENT 2. Consists of complete cuticular ring, with tubes located in subdorsal, laterodorsal, sublateral and ventrolateral positions (Figs 17A–B, 18A–C, 19A–B, E). Sensory spots present in laterodorsal and ventromedial positions. Glandular cell outlet type 1 located middorsally. Pachycyclus of anterior segment margin interrupted in middorsal position. Secondary pectinate fringe present near anterior segment margin of this and following segments, but usually covered by preceding segment. Cuticular hairs lightly scattered on ventral side and more densely in dorsal and lateral areas. Pectinate fringe of posterior margin slightly longer in ventromedial areas, otherwise as on preceding segment.

Table 13. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes frodoi* sp. nov.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gcol		ss	ss	tu*			gcol		
2	gcol		tu	tu,ss		tu			tu	ss
3			ss		ss					gcol
4	ac	gcol								gcol
5	gcol		ss		ss			tu		ss,gcol
6	ac	gcol,ss			ss			ac		gcol
7		gcol,ss			ss			ac		ss,gcol
8	ac	gcol,ss					tu	ac		gcol
9		gcol,ss	ss	tu			si	ac	ss	gcol
10	gcol,gcol		ss	tu					ss	gcol
11	gcol	ss			pe×3(♂)		ltas(♀)	lts		

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 17A–B, 18A, C, 19B). Pachycyclus of anterior segment margin of regular thickness, with middorsal interruption in addition to interruptions around tergo-sternal and midsternal junctions, on this and following segments. Segment with sensory spots in subdorsal and midlateral positions, and glandular cell outlets type 1 located ventromedially. On this and following four segments, cuticular hairs arranged in two or three rows across tergal plate, except for hairless midlateral areas and on lateral halves of sternal plates; paraventral and ventromedial areas devoid of hairs. Pectinate fringe as on preceding segment.

SEGMENT 4. With flexible spine in middorsal position and glandular cell outlets type 1 in paradorsal and ventromedial positions (Figs 17A, 18B, 19C). Sensory spots not present. Cuticular hairs and posterior segment margin as on preceding segment.

SEGMENT 5. With tubes in lateroventral positions, and sensory spots present in subdorsal, midlateral and ventromedial positions (Figs 17A–B, 18B–C, 19F). Glandular cell outlet type 1 present in middorsal position and in ventromedial positions. Pectinate fringe of posterior segment margin slightly longer; cuticular hairs as on preceding segment.

SEGMENT 6. With spines in middorsal and lateroventral positions (Figs 17A, 18B, 19C, F). Sensory spots present in paradorsal and midlateral positions. Glandular cell outlets type 1 present in pairs in paradorsal and ventromedial positions. Pectinate fringe on this and following two segments as on preceding one.

SEGMENT 7. With acicular spines in lateroventral positions, and sensory spots in paradorsal, midlateral and ventromedial positions (Figs 17A–B, 18C, 19C). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Cuticular hairs on dorsal side less dense than on preceding segment, with hairless middorsal and paradorsal patches. Pectinate fringe as on preceding segment.

SEGMENT 8. With acicular spines in middorsal and lateroventral positions, and tubes in lateral accessory positions (Figs 17A–B, 18B, E, 19G). Sensory spots present in paradorsal positions only. Glandular cell outlets type 1 and other structures as on preceding segment.

SEGMENT 9. With spines in lateroventral positions, and tubes in laterodorsal positions (Figs 17A–B, 18D–E, G, 19G–H). Tubes rather short with truncated tips, not differentiated into thicker proximal and thinner distal part. Sensory spots present in paradorsal, subdorsal and ventrolateral positions. Glandular

cell outlets type 1 present in paradorsal and ventromedial positions. Small, rounded sieve plates located in lateral accessory positions. Cuticular hairs lightly scattered on dorsal side; central part of tergal plate devoid of hairs. Pectinate fringe of posterior segment margin with tips shorter than on preceding segments.

SEGMENT 10. With well-developed laterodorsal tubes in males, and minute, very slender tubes in females, located near posterior segment margin (Figs 17A, C, 18H, 19G–H). Sensory spots present in subdorsal and ventrolateral positions. Glandular cell outlets type 1 present as two middorsal ones and in ventromedial positions. Cuticular hairs scarcer than on preceding segment. Central part of tergal plate devoid of hairs; hairs on sternal plates present only on lateral halves. Pectinate fringe with very short tips.

SEGMENT 11. With pair of long lateral terminal spines (Figs 17A–B, 19D). Males with three pairs of penile spines; dorsal and ventral spines relatively long, slender and tubular, while median ones much stouter (Figs 17A–B, 18A, H). Females with lateral accessory spines (Figs 17C–D, 18F, 19D). Sensory spots present in paradorsal positions. One middorsal glandular cell outlet type 1 present. Segment devoid of cuticular hairs in both sexes, but with short cuticular hair-like structures covering paradorsal area and short fringes covering margins of tergal and sternal plates. Tergal extensions short and pointed, with two small denticles at inner margin (Figs 17A–D, 18F). Sternal extensions rounded, not extending beyond tergal extensions (Figs 17B, D, 18F).

Distribution

Hikurangi Margin, from slope, through canyon, and seamount habitats, 670–1495 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes frodoi* sp. nov.

The spine and tube distribution in the middorsal and lateroventral series of *E. frodoi* sp. nov., with middorsal spines on segments 4, 6 and 8, and tubes/spines in lateroventral positions on segments 5 to 9, is a common pattern observed among the species of *Echinoderes* and shared by 24 congeners (Yamasaki *et al.* 2020a). However, when we combine these characters with the presence of four pairs of tubes on segment 2, we shorten the list to only one described species, i.e., *E. hakaensis* Herranz *et al.*, 2018 from British Columbia and an undescribed species, *Echinoderes* sp. 3, from the Atacama Trench (Herranz *et al.* 2018; Grzelak *et al.* 2021). However, *E. frodoi* is easily distinguished from both species by the presence of short laterodorsal tubes on segment 9, and the (occasional) presence of midlateral tubes on segment 1. All three share the presence of tubes on segment 8, the positions of several sensory spots and glandular cell outlets type 1, as well as the shape of the tergal extensions. However, *E. frodoi* has tubes in lateral accessory positions on segment 8, which distinguishes it from *E. hakaensis* and *Echinoderes* sp. 3, which have their tubes in sublateral positions, making the space between lateroventral spines and the tubes conspicuously larger. Another significant difference between *E. frodoi*, *E. hakaensis* and *Echinoderes* sp. 3 is evident in morphometric details. *Echinoderes frodoi* is markedly smaller in trunk length than both species (TL: 185 μm vs 324 μm and 211 μm , respectively), but has proportionally longer lateral terminal spines, resulting in a markedly higher LTS/TL ratio in *E. frodoi* in comparison with *E. hakaensis* and *Echinoderes* sp. 3 (LTS/TL: 79% vs 40% and 69%, respectively) (Herranz *et al.* 2018; Grzelak *et al.* 2021).

The occurrence of cuticular structures on segment 1 is very rare in echinoderid species, and the midlateral tubes on segment 1 as in *E. frodoi* sp. nov. is a trait shared exclusively with *E. cantabricus* Pardos *et al.*, 1998 (see Pardos *et al.* 1998). However, *E. cantabricus* cannot in any way be confused with *E. frodoi*. The species has only a single middorsal spine on segment 4 and can also be distinguished by the absence of lateroventral spines on segment 9 (Pardos *et al.* 1998). What might make the picture a bit unclear is the fact that these tubes apparently are not consistently present in all specimens of *E. frodoi*. We did not find

any clear explanation for this intraspecific dimorphism, since the variation in tube pattern was not related to the sexual or developmental stage, neither to intraspecific variation between populations: the presence or absence of tubes were noted for specimens from the same locality. Nevertheless, a variation in spine/tube pattern in Echinoderidae has recently been documented for several species (e.g., *E. arlis* Higgins, 1966, *E. eximus*, *E. levanderi* and *E. rhaegali* Grzelak & Sørensen, 2017 in Grzelak & Sørensen 2018) and it seems that such morphological variation might be more frequent among *Echinoderes* species than previously thought (Grzelak & Sørensen 2018, 2019; Sørensen, 2018).

Furthermore, the presence of laterodorsal tubes on segment 9 is also a rather rare feature among echinoderids. This trait has previously been described for only four species, i.e., *E. belenae*, *E. daenerysae*, *E. hviidarum*, *E. ultraabyssalis* and in the yet undescribed *Echinoderes* sp. 1 from the Atacama Trench (Pardos *et al.* 2016b; Grzelak & Sørensen 2018; Sørensen *et al.* 2018; Adrianov & Maiorova 2019; Grzelak *et al.* 2021). The latter four cannot in any way be confused with *E. frodoi* sp. nov. due to the presence of only 2 middorsal spines, on segments 6 and 8. The only other species with middorsal spines on segments 4, 6 and 8 and tubes in laterodorsal position on segment 9 is *E. belenae*, but this species is generally very rich in tubes, and carries no less than thirteen pairs on its eleven trunk segments. The species furthermore has conspicuously short lateral terminal spines (Pardos *et al.* 2016b). Laterodorsal tubes on segment 9 were also found during the present study in *E. gandalfi* sp. nov., *E. dalzottoi* sp. nov. and *E. leduci* sp. nov. However, the former two species can easily be distinguished from *E. frodoi* by the presence of only two middorsal spines. The latter, *E. leduci*, similarly to *E. frodoi*, is characterized by having middorsal spines on segments 4, 6 and 8, but can nevertheless be distinguished from *E. frodoi* by the lack of subdorsal and sublateral tubes on segment 2.

Echinoderes samwisei sp. nov.

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Figs 20–22; Tables 14–15

Diagnosis

Echinoderes with spines in middorsal position on segments 4, 6 and 8, and spines in lateroventral positions on segments 6 to 9. Tubes present in lateroventral positions on segment 5, lateral accessory positions on segment 8, and laterodorsal positions on segment 10. A protuberance-like structure emerges between segments 10 and 11 in middorsal position.

Etymology

The species name refers to Samwise Gamgee, one of the main characters in the novel “*The Fellowship of the Ring*”, the first volume of J.R.R. Tolkien’s “*The Lord of the Rings*”. Samwise was a hobbit from the Shire, Frodo Baggins’ best friend and one of the most loyal members of the Fellowship of the Ring.

Material examined

Holotype

NEW ZEALAND • ♂; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159418. Mounted for LM in Fluoromount G on HS slide.

Paratypes

NEW ZEALAND • 1 ♀, 3 ♂♂; Hikurangi Slope, stn TAN1004/4; 41.6837° S, 175.6642° E; 1046 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; 1 ♀ NHMD-917299, 1 ♂ NHMD-917300, 2 ♂♂ NIWA-159419 to 159420. 1 ♀ and 2 ♂♂ mounted for LM in Fluoromount G on glass slides, 1 ♂ mounted as holotype • 1 ♂; Pahaua Canyon, stn TAN1004/12; 41.5508° S, 175.7250° E; 1350 m b.s.l.;

Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-917301. Mounted for LM in Fluoromount G on glass slide • 1 ♂; same collection data as for holotype; NIWA-159421. Mounted as holotype • 1 ♀; Seamount 310, stn TAN1004/72; 41.3657° S, 176.1958° E; 985 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-917302. Mounted for LM in Fluoromount G on glass slide.

Additional material

NEW ZEALAND • 1 ♀; same collection data as for holotype; personal reference collection of MVS. Mounted for SEM • 1 ♀; Hikurangi Slope, stn TAN1004/44; 41.5258° S, 175.8003° E; 728 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀; Honeycomb Canyon, stn TAN1004/62; 41.4760° S, 175.9477° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Seamount 310, stn TAN1004/72; 41.3657° S, 176.1958° E; 985 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 20–22). Overview of measurements and dimensions in Table 14. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 15. No details regarding scolid arrangement and morphology could be provided, because introverts of all specimens mounted for SEM fully or partially retracted.

NECK. With 16 placids. Midventral placid broadest, 10 µm in width and 13 µm in length, whereas all others narrower, measuring 5 µm in width at bases and 12 µm in length, similar in size (Figs 21C, 22D). Trichoscolid plates well developed.

SEGMENT 1. Consists of complete cuticular ring. Sensory spots located on anterior half of segment, in subdorsal positions. Glandular cell outlet type 1 present in middorsal, subdorsal and ventrolateral positions (Figs 20A–B, 21C). Segment almost completely hairless (Fig. 22B–E). Posterior segment margin almost straight, forming pectinate fringe. Fringe with well-developed, relatively long tips, homogenous along segment margin (Fig. 22C, E).

SEGMENT 2. Consists of complete cuticular ring, without tubes. Sensory spots present in middorsal, midlateral and ventromedial positions (Figs 20A–B, 22B, E). Glandular cell outlets type 1 present in middorsal position (Figs 20A–B, 21B). Other structures not observed. Pachycyclus of anterior segment margin of regular thickness, without interruption. Secondary pectinate fringe present near anterior segment margin of this and following segments, but covered by preceding segment. Fairly long, single cuticular hairs sparsely scattered around segment. Posterior segment margin almost straight; pectinate fringe tips as on preceding segment.

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 20A–B, 21C, E–F, 22D). Pachycyclus of anterior segment margin of regular thickness, interrupted at tergosternal and midsternal junctions and middorsally, on this and following seven segments. Segment with middorsal glandular cell outlet type 1 and subdorsal sensory spots only; no other traits observed. Cuticular hairs more densely distributed across tergal plate than on preceding segment, except for narrow hairless line in laterodorsal area; sternal plates with very few cuticular hairs; on this and following segments paraventral areas completely devoid of hairs. Posterior segment margin straight, terminating in pectinate fringe with fringe tips as on preceding segments.

SEGMENT 4. With spine in middorsal position; spine relatively short (23 µm), only slightly exceeding posterior segment margin (Figs 20A, 22A). Pair of glandular cell outlets type 1 present in paradorsal positions. No other traits observed. Segment otherwise as segment 3.

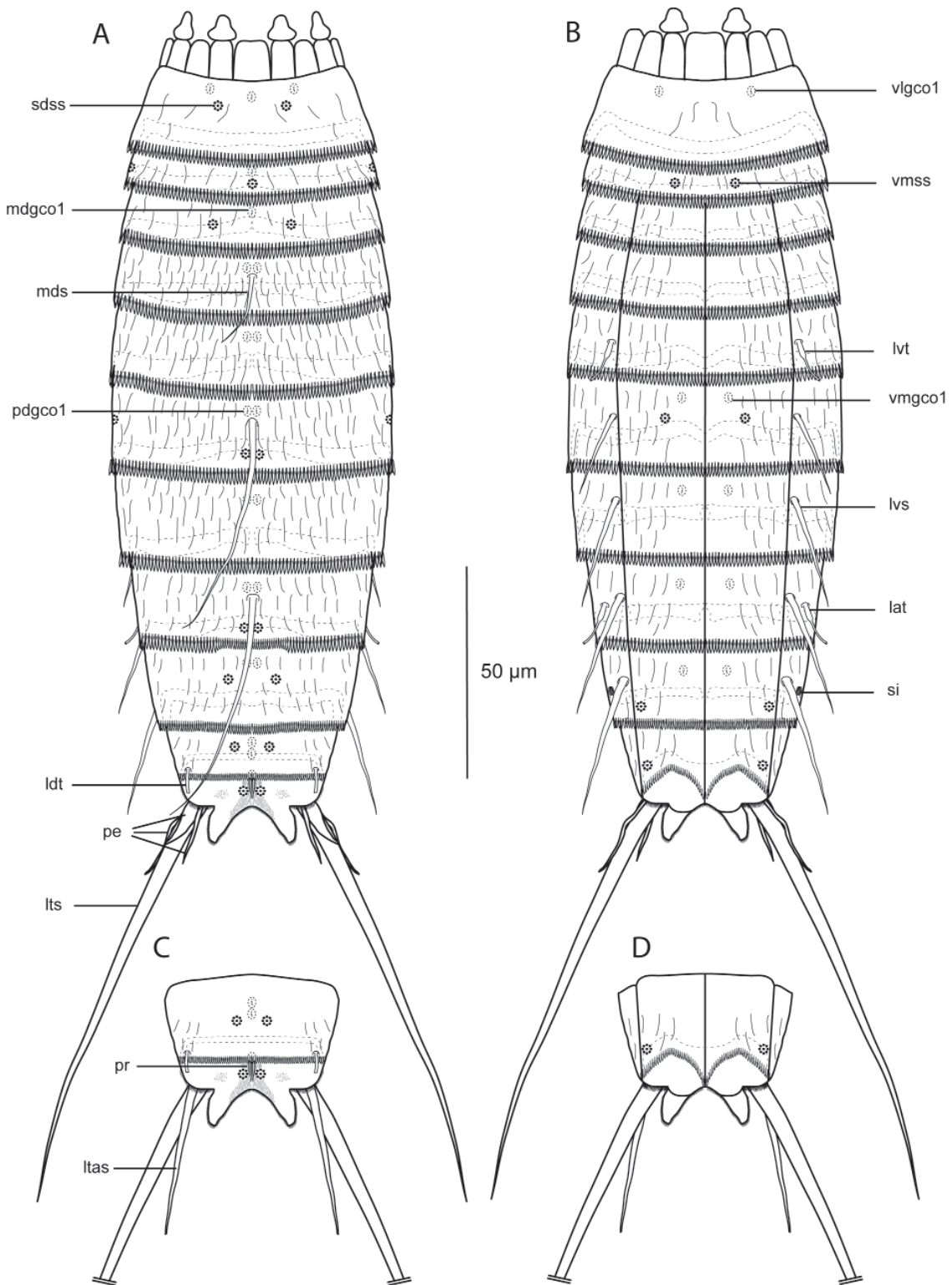


Fig. 20. Line art illustrations of *Echinoderes samwisei* sp. nov. **A.** ♂, dorsal view. **B.** ♂, ventral view. **C.** ♀, segments 10–11, dorsal view. **D.** ♀, segments 10–11, ventral view. Abbreviations: see Material and methods.

SEGMENT 5. With tubes in lateroventral positions (Figs 20B, 21C, E–F, 22C, F). Glandular cell outlets type 1 present in paradorsal positions only. No sensory spots or other structures present. Pectinate fringe of posterior segment margin and cuticular hairs as on preceding segment.

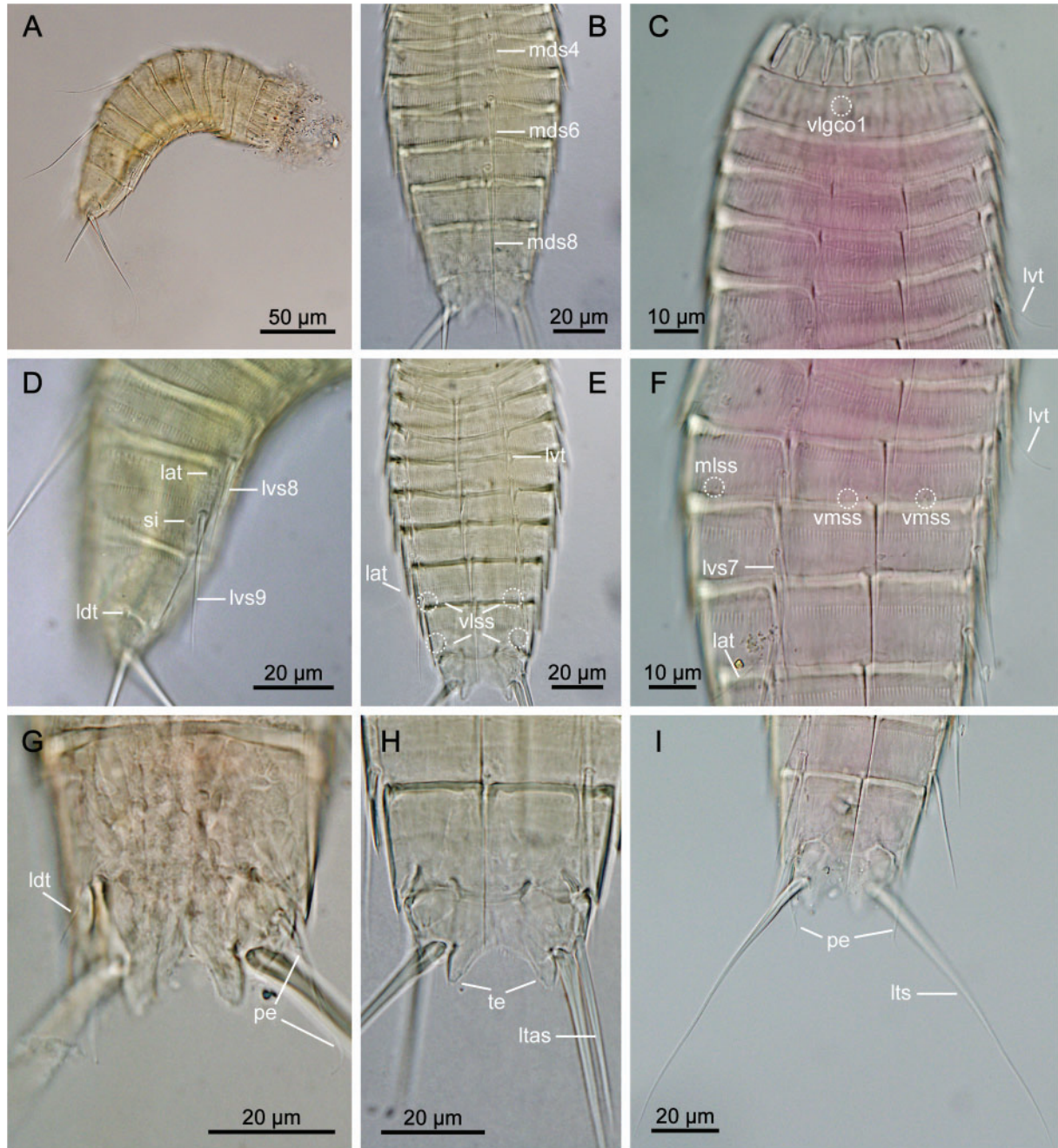


Fig. 21. Light micrographs showing overview and details of *Echinoderes samwisei* sp. nov. **A, D.** ♀, paratype (NHMD-917299). **B, E, H.** ♀, paratype (NHMD-917302). **C, F, I.** ♂, holotype (NIWA-159418). **G.** ♂, paratype (NHMD-917300). **A.** Lateral overview. **B.** Segments 3 to 11, dorsal view. **C.** Segments 1 to 5, ventral view. **D.** Segments 7 to 11, lateral view. **E.** Segments 2 to 11, ventral view. **F.** Segments 5 to 8, ventral view. **G.** Segments 10 to 11 of male, dorsal view. **H.** Segments 9 to 11 of female, ventral view. **I.** Segments 9 to 11 of male, ventral view. Abbreviations: see Material and methods.

SEGMENT 6. With spines in middorsal and lateroventral positions (Figs 20A–B, 21A, 22B). Sensory spots present in paradorsal, midlateral and ventromedial positions (Figs 20A–B, 21F, 22C, F). Glandular cell outlets type 1 present in paradorsal and ventromedial positions (Figs 20A–B, 21F). Tips of pectinate fringe of posterior segment margin as on preceding segments. Segment otherwise as segment 5.

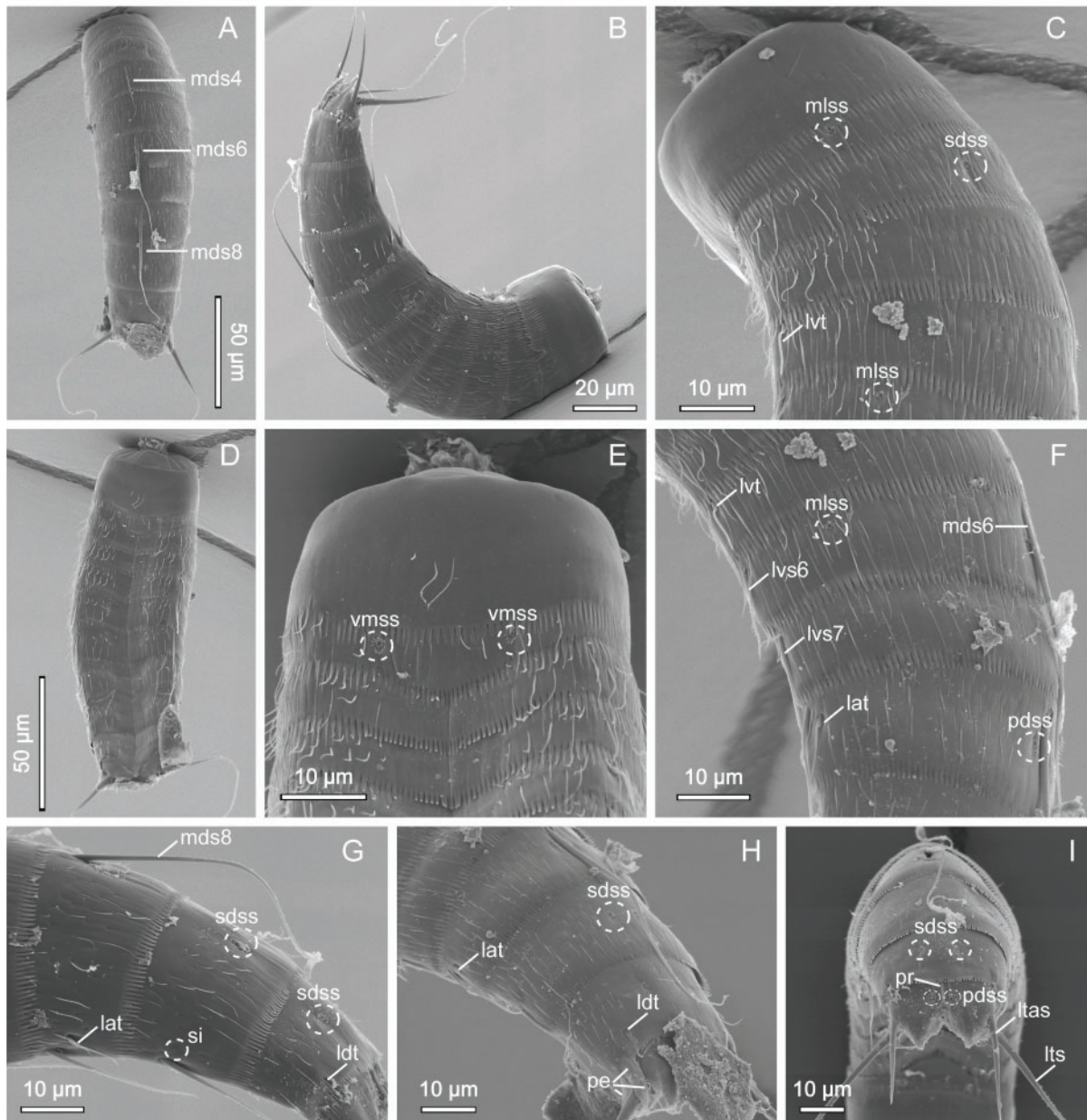


Fig. 22. Scanning electron micrographs showing overviews and details of *Echinoderes samwisei* sp. nov. **A.** Dorsal overview of male. **B.** Lateral overview of female. **C.** Segments 1 to 5, lateral view. **D.** Ventral overview of male. **E.** Segments 1 to 5, ventral view. **F.** Segments 5 to 8, lateral view. **G.** Segments 8 to 10 of female, lateral view. **H.** Segments 8 to 11 of male, lateral view. **I.** Segments 9 to 11 of female, dorsal view. Abbreviations: see Material and methods.

Table 14. Measurements from light microscopy of *Echinoderes samwisei* sp. nov. (in μm) from the Hikurangi Margin, including number of measured specimens (n) and standard deviation (SD).

Character	n	Range	Mean	SD
TL	7	140–191	174	17.2
MSW-6	4	40–41	41	0.5
MSW-6/TL	4	21–24%	32%	1.7%
SW-10	4	36–37	36	0.5
SW-10/TL	4	19–22%	21%	1.0%
S1	7	17–22	19	1.9
S2	7	15–18	16	1.2
S3	7	18–20	19	0.9
S4	7	21–25	22	1.5
S5	7	23–28	26	1.9
S6	7	24–28	26	1.8
S7	7	26–30	28	2.0
S8	7	27–32	29	1.8
S9	7	27–34	31	2.6
S10	7	24–32	28	3.0
S11	7	19–20	20	0.4
MD4 (ac)	7	21–25	23	1.4
MD6 (ac)	7	53–60	57	2.6
MD8 (ac)	7	64–68	66	1.6
LV6 (ac)	6	17–20	19	1.3
LV7 (ac)	6	24–27	26	1.2
LV8 (ac)	6	27–33	29	2.0
LV9 (ac)	7	27–37	33	3.4
LTS	6	78–109	94	15.2
LTS/TL	6	44–75%	55%	11.3%
LTAS	2	35–37	36	1.8

SEGMENT 7. With spines in lateroventral positions, and glandular cell outlets type 1 in paradorsal and ventromedial positions (Figs 20A–B, 21F). Sensory spots not observed. Cuticular hairs covering as on preceding segment.

SEGMENT 8. With spines in middorsal and lateroventral positions, and tubes in lateral accessory positions (Figs 20A–B, 21D–F, 22F–H). Middorsal spine long, reaching posterior part of segment 10 (Figs 21A–B, 22A). Sensory spots present in paradorsal positions only. Glandular cell outlets type 1 in paradorsal and ventromedial positions. Pectinate fringe of posterior segment margin as on preceding segment, except slightly shorter and narrower fringe tips along paradorsal and subdorsal areas of segment margin.

SEGMENT 9. With spines in lateroventral positions (Figs 20B, 21D). Sensory spots located in subdorsal and ventrolateral positions; subdorsal pair situated close to paradorsal area (Figs 20A–B, 21E, 22G–H). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Small, rounded sieve plates located in lateral accessory positions. Cuticular hair covering and pectinate fringe as on preceding segment.

SEGMENT 10. With laterodorsal tubes located near posterior segment margin; tubes well developed in both sexes, but slightly longer in males (Figs 21G, 22G–H). Sensory spots present in subdorsal and

Table 15. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes samwisei* sp. nov.

Position segment	MD	PD	SD	LD	ML	LA	LV	VL	VM
1	gcol		gcol,ss					gcol	
2	gcol,ss				ss				ss
3	gcol		ss						
4	ac	gcol							
5		gcol					tu		
6	ac	gcol,ss			ss		ac		gcol,ss
7		gcol					ac		gcol
8	ac	gcol,ss				tu	ac		gcol
9		gcol	ss			si	ac	ss	gcol
10	gcol ×2		ss	tu				ss	
11	gcol,pr	ss			pe ×3(♂)	ltas(♀)	lts		

ventrolateral positions (Fig. 22I). Glandular cell outlets type 1 present as two middorsal ones. Cuticular hairs scarcer than on preceding segment. Central part of tergal plate devoid of hairs; short cuticular hairs lightly scattered on lateral halves only. Posterior segment margin of tergal plate straight, with much shorter fringe and narrower tips than those on preceding segment; margins of sternal plates extend midventrally, reaching posterior margin of terminal segment (Fig. 22D).

SEGMENT 11. With pair of lateral terminal spines (Fig. 20C). Females with relatively strong, stout lateral terminal accessory spines (Figs 21H, 22I). Males with three pairs of penile spines; dorsal ones of medium length, ventral ones long and relatively thin, whereas median ones markedly thicker, conical and stout (Figs 20A–B, 21G, I 22H). Sensory spots present in paradorsal positions (Figs 20A, C, 22I). Glandular cell outlet type 1 present in middorsal position. Middorsal protuberance-like structure extends from intersegmentary joint (Figs 20A, C, 22I). Segment devoid of cuticular hairs, but with dense covering of relatively long hair-like extensions in paradorsal area, as well as small patches of shorter ones in subdorsal area. Short fringes covering margins of tergal and sternal plates. Tergal extensions short and triangular (Figs 21H, 22I). Sternal extensions do not extend beyond tergal extensions.

Distribution

Hikurangi Margin, from slope, through canyon, and seamount habitats, 728–1350 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes samwisei* sp. nov.

The spine pattern with middorsal spines on segments 4, 6 and 8 and lateroventral spines on segments 6 to 9 is very common within *Echinoderes*, and is shared with 33 species (Yamasaki *et al.* 2020). Nevertheless, among these only *E. anniae* Sørensen *et al.*, 2018, *E. meteorensis* Yamasaki *et al.*, 2018, and an undescribed species, *Echinoderes* sp. 3, from Senghor Seamount reported by Yamasaki *et al.* (2019) resemble *E. samwisei* sp. nov. by lacking tubes on segment 2 (Sørensen *et al.* 2018; Yamasaki *et al.* 2018c, 2019). Thus, none of these species can be confused with *E. samwisei*. *Echinoderes anniae* and *E. meteorensis* differ from *E. samwisei* in having several glandular cell outlets type 2 – structures not observed in *E. samwisei*. Moreover, both species are characterized by very long lateral terminal spines and a lack of tubes on segments 5 and 8. *Echinoderes samwisei* differs from *Echinoderes* sp. 3 in Yamasaki *et al.* (2019) as well, because the latter lacks tubes on segment 8 and possesses characteristic long and spinose tergal extensions, whereas the new species has lateral accessory tubes on segment 8 and relatively short tergal extensions.

Moreover, *E. samwisei* sp. nov. is generally characterized by a low number of cuticular structures. The new species not only lacks glandular cell outlets type 2, but also its number of sensory spots and glandular cell outlets type 1 is relatively low, as compared with other species. It is indeed possible to miss certain glandular cell outlets type 1, in particular in species with an extraordinary thin cuticle, but the availability of several specimens for SEM examination makes it less likely that any sensory spots have been overlooked. The available SEM specimens were generally in a good condition and relatively clean, which allowed for a thorough examination using SEM. In spite of this, we observed only 13 pairs of sensory spots on the trunk.

Therefore, the combination of spine and tube patterns, together with the lack of tubes or glandular cell outlets type 2 on segment 2 and the relatively ‘simple’ overall appearance of the trunk, makes *E. samwisei* sp. nov. unique among its congeners.

***Echinoderes legolasi* sp. nov.**

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Figs 23–25; Tables 16–17

Diagnosis

Echinoderes with spines in middorsal position on segments 4, 6 and 8, and spines in lateroventral positions on segments 6 to 9. Tubes present in lateroventral positions on segment 5 and laterodorsal positions on segment 10. Glandular cell outlets type 2 in sublateral positions on segment 1, subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2 and midlateral positions on segment 8. A protuberance-like structure emerges between segments 10 and 11 in middorsal position.

Etymology

The species name refers to Legolas – Elf of Mirkwood, one of the characters in J.R.R. Tolkien’s “*The Lord of the Rings*”. Legolas was an excellent archer, and another very valuable member of the Fellowship of the Ring.

Material examined

Holotype

NEW ZEALAND • ♂; Seamount 310, stn TAN1004/72; 41.3657° S, 176.1958° E; 985 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159422. Mounted for LM in Fluoromount G on HS slide.

Additional material

NEW ZEALAND • 1 ♂; Hikurangi Slope, stn TAN1004/44; 41.5258° S, 175.8003° E; 728 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 23–25). Overview of measurements and dimensions in Table 16. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 17. No details regarding scolid arrangement and morphology could be provided, because introvert of specimen mounted for SEM was partially retracted.

NECK. With 16 placids. Midventral placid broadest, 9 µm in width and 11 µm in length, whereas all others narrower, measuring 6 µm in width at bases and 11 µm in length, similar in size (Figs 24C, 25D). Trichoscolid plates well developed.

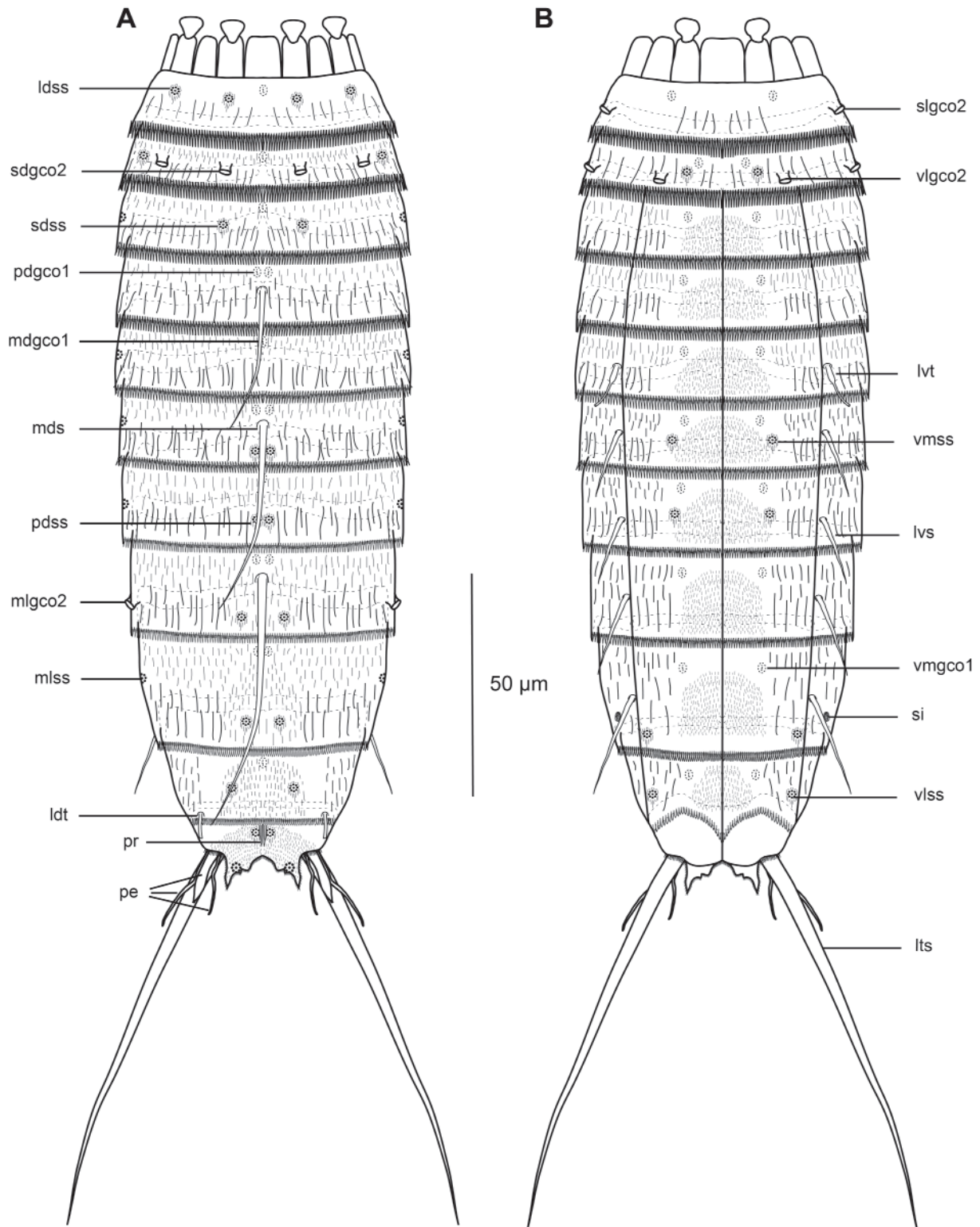


Fig. 23. Line art illustrations of *Echinoderes legolasi* sp. nov. **A.** ♂, dorsal view. **B.** ♂, ventral view. Abbreviations: see Material and methods.

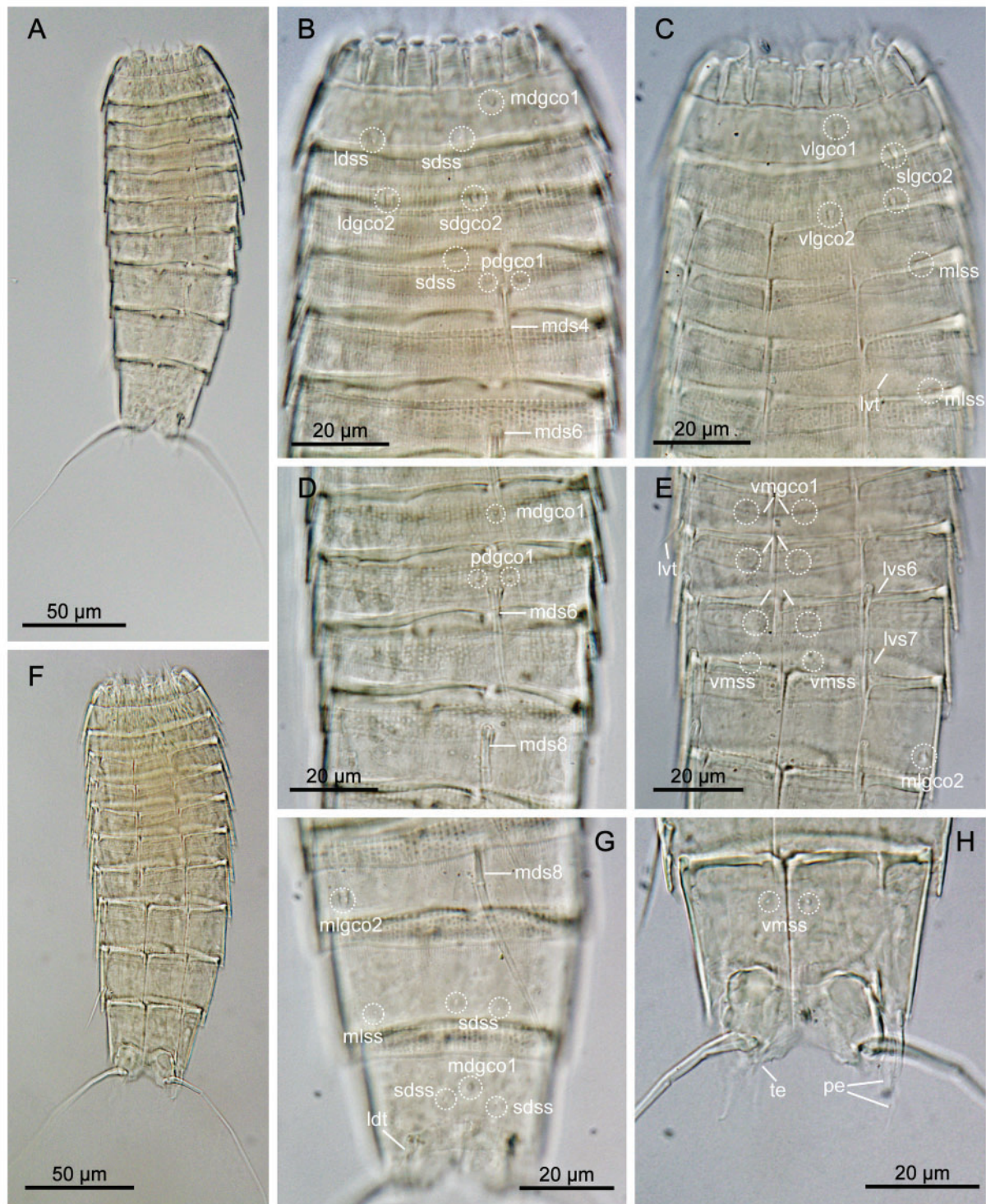


Fig. 24. Light micrographs showing overview and details of *Echinoderes legolasi* sp. nov., ♂, holotype (NIWA-159422). **A.** Dorsal overview. **B.** Segments 1 to 6, dorsal view. **C.** Segments 1 to 6, ventral view. **D.** Segments 5 to 8, dorsal view. **E.** Segments 5 to 8, ventral view. **F.** Ventral overview. **G.** Segments 8 to 11, dorsal view. **H.** Segments 10 to 11, ventral view. Abbreviations: see Material and methods.

SEGMENT 1. Consists of complete cuticular ring. Pair of glandular cell outlets type 2 present in sublateral positions (Figs 23B, 24C, 25B). Sensory spots located medially on segment, in subdorsal and laterodorsal positions (Figs 23A, 24B, 25B); sensory spots on this and following segments relatively large, with tuft of micropapillae surrounding central pore. Glandular cell outlet type 1 present in middorsal, and ventrolateral positions (Figs 23A–B, 24B–C). Cuticular hairs relatively long, arranged in single transverse row medially on segment. Posterior segment margin almost straight, forming pectinate fringe. Fringe with well-developed long and flexible tips, homogenous along segment margin (Fig. 25B).

SEGMENT 2. Consists of complete cuticular ring. Glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and ventrolateral positions (Figs 23A–B, 24B–C, 25B). Sensory spots located in laterodorsal and ventromedial positions (Figs 23A–B, 25B). Glandular cell outlets type 1 present in middorsal and ventromedial positions. Pachycyclus of anterior segment margin of regular thickness, without interruption. Secondary pectinate fringe present near anterior segment margin of this and following segments (Fig. 25E, G). Cuticular hairs evenly distributed over dorsal part of segment, ventral areas less hairy; cuticular hairs shorter and thinner on anterior part of segment. Posterior segment margin almost straight; pectinate fringe tips as on preceding segment.

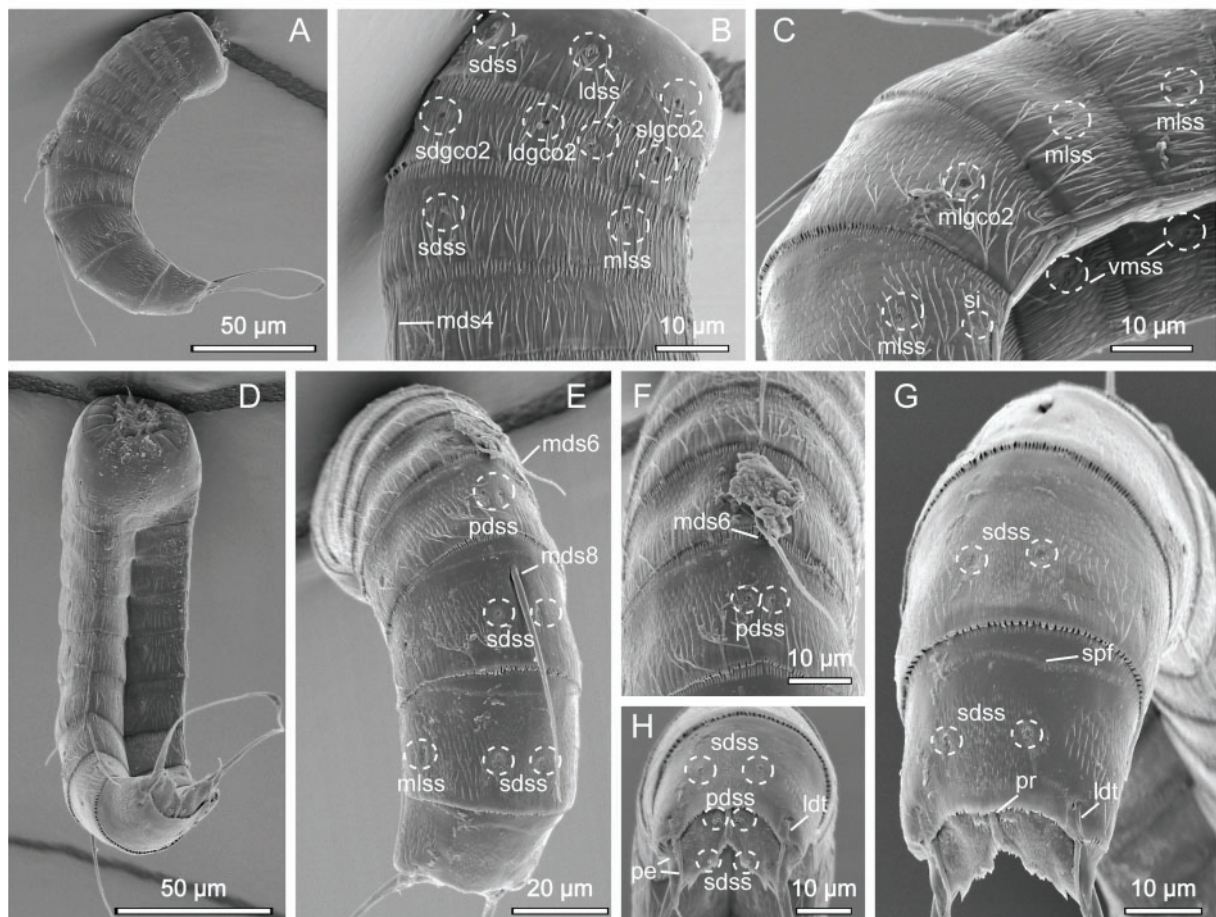


Fig. 25. Scanning electron micrographs showing overviews and details of *Echinoderes legolasi* sp. nov. **A.** Lateral overview. **B.** Segments 1 to 4, dorsolateral view. **C.** Segments 6 to 9, lateral view. **D.** Ventral overview. **E.** Segments 6 to 10, dorsal view. **F.** Segments 5 to 7, dorsal view. **G.** Segments 8 to 11, dorsal view. **H.** Segments 10 to 11, dorsal view. Abbreviations: see Material and methods.

Table 16. Measurements from light microscopy of *Echinoderes legolasi* sp. nov. (in μm) from the Hikurangi Margin.

Character	Holotype NIWA-159422 (♂)
TL	175
MSW-7	40
MSW-7/TL	23%
SW-10	33
SW-10/TL	19%
S1	19
S2	19
S3	17
S4	17
S5	18
S6	23
S7	27
S8	29
S9	31
S10	29
S11	19
MD4 (ac)	34
MD6 (ac)	51
MD8 (ac)	65
LVS6 (ac)	16
LVS7 (ac)	17
LVS8 (ac)	19
LVS9 (ac)	23
LTS	89
LTS/TL	51%

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 23A–B, 24C, E–F, 25D). Pachycyclus of anterior segment margin slightly thinner than on preceding segment, interrupted at tergo-sternal and midsternal junctions and middorsally, on this and following seven segments. Segment with sensory spots located in subdorsal and midlateral positions (Figs 24B–C, 25B), and glandular cell outlets type 1 in middorsal and ventromedial positions. Cuticular hairs distributed across tergal plate as on preceding segment; ventromedial and paraventral areas on this and following seven segments with thinner and much shorter, non-bracteate hairs. Posterior segment margin straight, terminating in pectinate fringe with fringe tips slightly shorter, as on preceding segments, but still long and flexible.

SEGMENT 4. With spine in middorsal position (Figs 23A, 24B). Sensory spots not present. Pair of glandular cell outlet type 1 present in paradorsal and ventromedial positions. Pachycycli, pectinate fringe and cuticular hairs as on preceding segment.

SEGMENT 5. With tubes in lateroventral positions (Figs 23B, 24C, E). Sensory spots located midlaterally. Glandular cell outlets type 1 present in middorsal and ventromedial positions. Segment otherwise as segment 4.

Table 17. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes legolasi* sp. nov.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1		ss	ss		gco2			gco1	
2	gco1		gco2	gco2,ss		gco2			gco2	gco1,ss
3	gco1		ss		ss					gco1
4	ac	gco1								gco1
5	gco1				ss			tu		gco1
6	ac	gco1,ss			ss			ac		gco1,ss
7	gco1	ss			ss			ac		gco1,ss
8	ac	gco1	ss		gco2			ac		gco1
9		gco1	ss		ss		si	ac	ss	gco1
10	gco1		ss	tu					ss	gco1
11	pr	ss	ss		pe×3(♂)			lts		

SEGMENT 6. With spines in middorsal and lateroventral positions (Figs 23A–B, 24D–E, 25D–F). Sensory spots present in paradorsal, midlateral and ventromedial positions (Figs 23A–B, 25C). Glandular cell outlets type 1 present in paradorsal and ventromedial positions (Figs 23A–B, 24D–E). Tips of pectinate fringe of posterior segment margin as on preceding segments. Segment otherwise as segment 5.

SEGMENT 7. With spines in lateroventral positions (Figs 23B, 24E). Sensory spots present in paradorsal, midlateral and ventromedial positions (Figs 23A–B, 25C, E–F), and glandular cell outlets type 1 in middorsal and ventromedial positions (Figs 23A–B, 24E). Cuticular hair covering as on preceding segment. Pectinate fringe of posterior segment margin with slightly narrower and shorter tips.

SEGMENT 8. With spines in middorsal and lateroventral positions (Figs 23A–B, 24G, 25E), and glandular cell outlets type 2 in midlateral positions (Figs 23A, 24E, G, 25C). Sensory spots present in subdorsal positions, but located close to paradorsal line (Fig. 25E). Glandular cell outlets type 1 in paradorsal and ventromedial positions. Pectinate fringe of posterior segment margin as on preceding segment.

SEGMENT 9. With spines in lateroventral positions (Figs 23B, 25D). Sensory spots located in subdorsal, midlateral and ventrolateral positions; subdorsal pair situated close to paradorsal area (Figs 23A–B, 24G, 25E, G). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Small, rounded sieve plates in lateral accessory positions (Fig. 25C). Pectinate fringe as on preceding segment. Cuticular hairs shorter, but cuticular hair covering similar to as on preceding segment, except middorsal and paradorsal areas covered with very short and thin non-bracteate hairs (Fig. 25G) similar to ones present on lateral halves of sternal plates, posteriorly expanding into subdorsal areas.

SEGMENT 10. With laterodorsal tubes located near posterior segment margin (Figs 23A, 24G, 25G–H). Sensory spots present in subdorsal and ventrolateral positions (Figs 24G, 25G–H). Glandular cell outlets type 1 present as one middorsal and pair of ventromedial ones. Cuticular hairs scarcer than on preceding segment. Central part of tergal plate covered with short and thin non-bracteate hairs as on preceding segment (Fig. 25G–H). Posterior segment margin of tergal plate straight, with much shorter fringe and narrower tips than those on preceding segment (Fig. 25G–H); margins of sternal plates extend midventrally (Fig. 23B).

SEGMENT 11. With pair of lateral terminal spines (Fig. 23C). Males with three pairs of penile spines; dorsal and ventral penile spines thin and flexible tubes, whereas median ones markedly thicker, conical and stout (Figs 23A, 24H, 25G–H). Female condition unknown. Sensory spots present in paradorsal

and subdorsal positions; subdorsal pair located near posterior margin of tergal extensions (Figs 23A, 25H). Middorsal protuberance-like structure extends from intersegmentary joint (Figs 23A, 25G). Segment devoid of cuticular hairs, but with dense covering of short hair-like extensions in dorsal areas of tergal plates. Short fringes covering margins of tergal and sternal plates. Tergal extensions short, sternal extensions do not extend beyond tergal extensions (Figs 23A–B, 24H, 25G).

Distribution

Hikurangi slope and Seamount 310, 728–985 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes legolasi* sp. nov.

Echinoderes legolasi sp. nov. is one of 34 species (including *E. frodoi* sp. nov., *E. samwisei* sp. nov., *E. leduci* sp. nov., and *E. aragorni* sp. nov.) having middorsal spines on segments 4, 6 and 8, but can easily be distinguished from all other congeners by its unique patterns of spines, tubes and glandular cell outlets type 2. The most exclusive feature of *E. legolasi* is the presence of four pairs of glandular cell outlets type 2 on segment 2. This character is shared only with one other species, i.e., *E. anniae* described by Sørensen *et al.* (2018) from the United States west coast. Except for the identical pattern of cuticular structures on segment 2, both species also share the presence of glandular cell outlets type 2 in midlateral/sublateral positions on segments 1 and 8. However, *E. anniae* can be discriminated from *E. legolasi* by its tube pattern, lacking the lateroventral tubes on segment 5. Instead, *E. anniae* has glandular cell outlets type 2 in this position (Sørensen *et al.* 2018). Furthermore, *E. legolasi* possesses short tergal extensions, which differ considerably from the relatively long and narrow tergal extensions present in *E. anniae*, and significantly shorter lateral terminal spines in relation to the trunk length (LTS/TL=51% in *E. legolasi* vs 99% in *E. anniae*).

The new species shows most resemblance to *Echinoderes hamiltonorum* Sørensen *et al.*, 2018. *Echinoderes hamiltonorum* is also described from deep waters (> 3000 m deep) off the United States west coast (Sørensen *et al.* 2018). The two species have almost identical arrangements of cuticular structures, a highly similar trunk appearance, and they share the shape of the tergal extensions, the presence of a protuberance protruding from the intersegmental joint between segments 10 and 11, and an even length and shape of the pectinate fringes. The main difference between the two species is the possession of either tubes or glandular cell outlets type 2 in ventrolateral positions on segment 2. Both species have subdorsal, laterodorsal and sublateral glands on segment 2, but in ventrolateral positions *E. hamiltonorum* has tubes instead of glandular cell outlets type 2 as in *E. legolasi* sp. nov. Both structures (glands vs tubes) are easily distinguishable in SEM, but the ventrolateral tubes in *E. hamiltonorum* are hard to visualize in LM (Sørensen *et al.* 2018). The attachment point of the tubes might resemble the margins of the outlets, which might potentially be a source of confusion during the identification process. Therefore, the easiest way to distinguish the species would be through SEM examination. However, even without access to SEM information, it should be possible to distinguish *E. legolasi* and *E. hamiltonorum* by the location of type 2 glands on segment 8 and some morphometric details. *Echinoderes legolasi* has glandular cell outlets type 2 in midlateral positions on segment 8, whereas these structures are displaced to sublateral positions in *E. hamiltonorum* (Sørensen *et al.* 2018). Furthermore, the new species has a shorter trunk (175 µm vs 233 µm) and has a proportionally longer middorsal spine on segment 8. In *E. hamiltonorum*, the middorsal spines on segments 6 and 8 are comparable in length (74 µm vs 75 µm, respectively), while the spine on segment 6 is noticeably shorter than the one on segment 8 in *E. legolasi* (51 µm vs 65 µm, respectively).

Hence, in summary, *E. legolasi* sp. nov. and *E. hamiltonorum* can be distinguished by the presence of ventrolateral glands type 2 on segment 2 and sublateral glands type 2 on segment 8 in *E. legolasi*, and in the general combination of spine and glandular cell outlet type 2 patterns.

Echinoderes aragorni sp. nov.

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Figs 26–28; Tables 18–19

Diagnosis

Echinoderes with spines in middorsal position on segments 4, 6 and 8, and spines in lateroventral positions on segments 8 and 9. Tubes present in lateroventral positions on segment 5. Glandular cell outlets type 2 present in paradorsal positions on segments 2 and 3, subdorsal and laterodorsal positions on segments 2 to 9, midlateral positions on segments 3 to 5 and 9, sublateral positions on segments 2 and 6 to 8, and in lateral accessory positions on segments 5, 8 and 9. Furthermore, lateroventral glandular cell outlets type 2 present on segments 3, 4, 6, 7, and ventrolateral ones on segment 2. Males with additional pair of glandular cell outlets type 2 in laterodorsal positions on segment 10. A protuberance-like structure emerges between segments 10 and 11 in middorsal position.

Etymology

The species name refers to Aragorn – King of Arnor and Gondor, one of the characters in J.R.R. Tolkien's “*The Lord of the Rings*”. Aragorn was a confidant of Gandalf, a great warrior and the true leader of the Fellowship of the Ring.

Material examined

Holotype

NEW ZEALAND • ♀; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159423. Mounted for LM in Fluoromount G on HS slide.

Paratypes

NEW ZEALAND • 1 ♀; Hikurangi Slope, stn TAN1004/4; 41.6837° S, 175.6642° E; 1046 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159424. Mounted for LM in Fluoromount G on glass slide • 1 ♀; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8977° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-920115. Mounted as holotype.

Additional material

NEW ZEALAND • 1 ♀; Hikurangi Slope, stn TAN1004/44; 41.5258° S, 175.8003° E; 728 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Honeycomb Canyon, stn TAN1004/62; 41.4760° S, 175.9477° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 26–28). Overview of measurements and dimensions in Table 18. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 19. No details regarding scalid arrangement and morphology could be provided.

NECK. With 16 placids. Midventral placid broadest, 9 µm in width and 10 µm in length, whereas all others narrower, measuring 6 µm in width at bases and 10 µm in length, similar in size (Figs 27B–C, 28F). Trichoscalid plates well developed.

SEGMENT 1. Consists of complete cuticular ring. Sensory spots located medially on segment, in subdorsal and laterodorsal positions (Figs 26A, 27B, 28B). Glandular cell outlets type 1 present in middorsal and ventrolateral positions (Figs 26A–B, 27B–C). Furthermore, row of unusual cuticular openings present

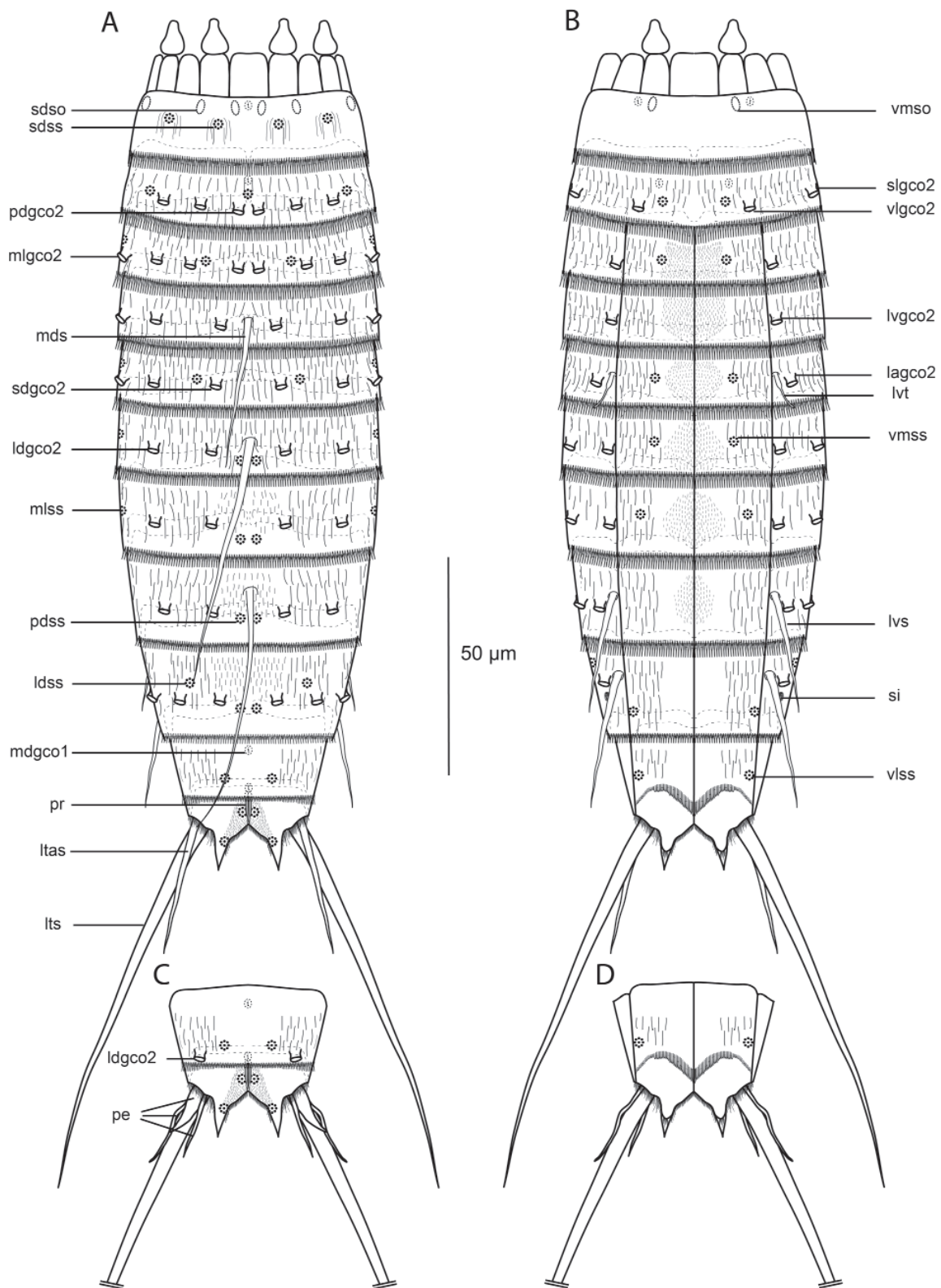


Fig. 26. Line art illustrations of *Echinoderes aragorni* sp. nov. **A.** ♀, dorsal view. **B.** ♀, ventral view. **C.** ♂, segments 10–11, dorsal view. **D.** ♂, segments 10–11, ventral view. Abbreviations: see Material and methods.

near anterior segment margin in paradorsal, subdorsal, midlateral and ventromedial positions. Openings elongate, or ‘slit-like’, and without any other cuticular characteristic, thus resembling neither sensory spots, flosculi, nor glandular cell outlets of any kind. Due to uncertain nature of these openings, they will simply be referred to as ‘slit-like openings’ (Figs 26A–B, 27B–C, 28B–C). Segment devoid of cuticular hairs, except for a few very long hairs arranged around sensory spots. Posterior segment margin almost straight, forming pectinate fringe. Fringe with well-developed long and flexible tips, homogenous along segment margin (Fig. 28B–C).

SEGMENT 2. Consists of complete cuticular ring. Glandular cell outlets type 2 present in paradorsal, subdorsal, laterodorsal, sublateral and ventrolateral positions (Figs 26A–B, 27B–C, 28B, D). Sensory

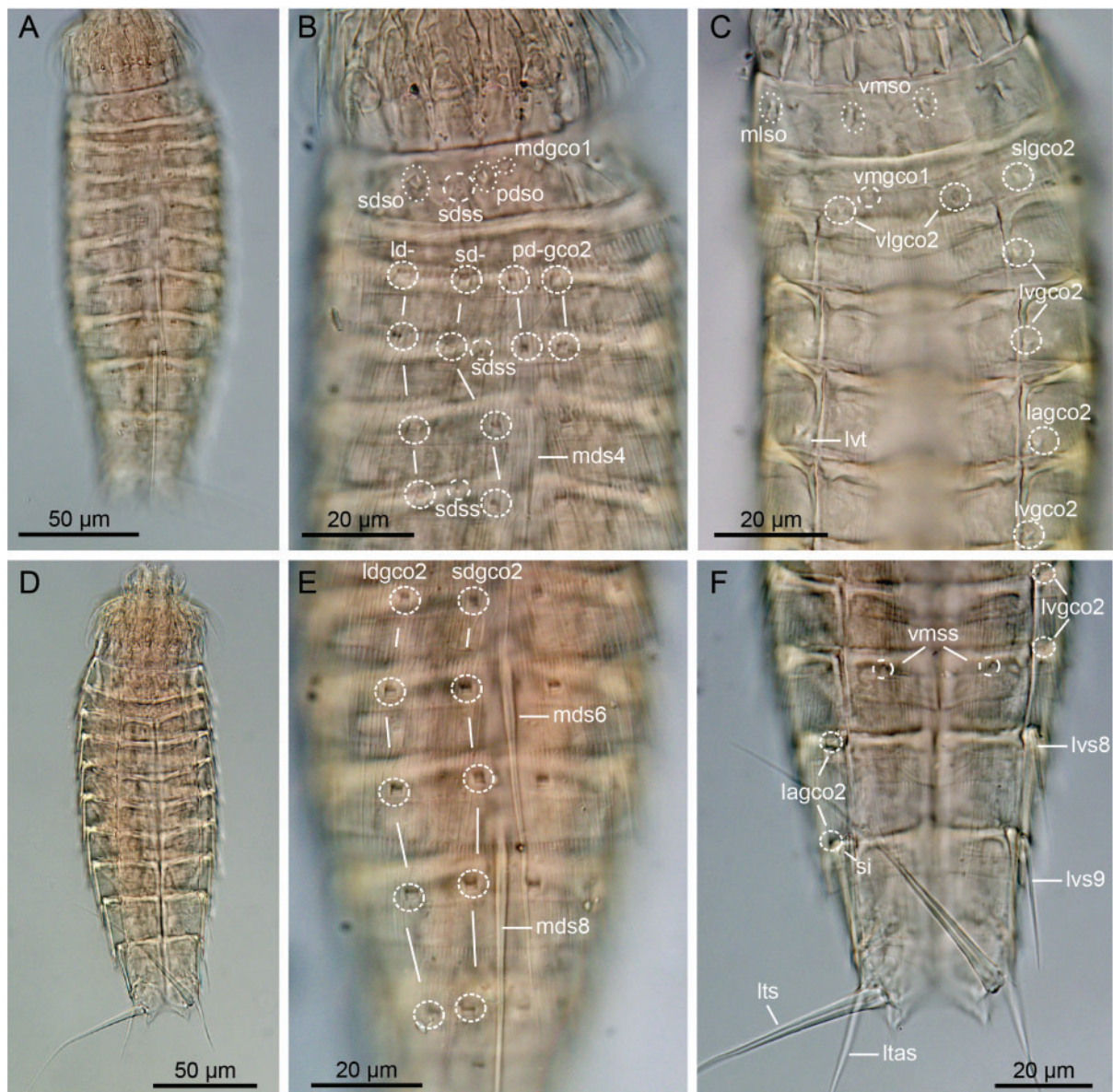


Fig. 27. Light micrographs showing overview and details of *Echinoderes aragorni* sp. nov. **A–B,** ♀, holotype (NIWA-159423). **C–F,** ♀, paratype (NIWA-159424). **A.** Dorsal overview. **B.** Segments 1 to 6, dorsal view. **C.** Segments 1 to 6, ventral view. **D.** Ventral overview. **E.** Segments 5 to 9, dorsal view. **F.** Segments 7 to 11, ventral view. Abbreviations: see Material and methods.

Table 18. Measurements from light microscopy of *Echinoderes aragorni* sp. nov. (in μm) from the Hikurangi Margin, including number of measured specimens (n) and standard deviation (SD).

Character	n	Range	Mean	SD
TL	3	171–232	196	32.0
MSW-7	2	37–40	38	1.8
MSW-7/TL	2	20–23%	22%	2.2%
SW-10	2	30–33	32	2.5
SW-10/TL	2	16–20%	18%	2.4%
S1	3	22–25	23	1.7
S2	3	19–22	20	1.6
S3	3	22–25	23	1.9
S4	3	22–28	25	3.5
S5	3	25–30	28	2.4
S6	3	27–34	29	3.9
S7	3	28–36	32	3.8
S8	3	32–36	33	1.9
S9	3	33–35	34	0.8
S10	3	26–30	27	2.3
S11	3	18–20	19	1.6
MD4 (ac)	3	34–43	38	4.6
MD6 (ac)	3	60–65	62	2.8
MD8 (ac)	3	67–72	70	2.6
LV8 (ac)	3	25–32	29	3.5
LV9 (ac)	3	29–39	34	5.1
LTS	3	78–98	89	9.8
LTS/TL	3	39–53%	46%	7.1%
LTAS	3	29–36	33	3.8

segment margin of this and following segments. Cuticular hairs evenly distributed across segment. Posterior segment margin almost straight; pectinate fringe tips as on preceding segment.

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 26A–B, 27C, E–F, 28D). Pachycyclus of anterior segment margin of regular thickness, interrupted at tergo-sternal and midsternal junctions and middorsally, on this and following seven segments. Segment with glandular cell outlets type 2 in paradorsal, subdorsal, laterodorsal, midlateral and lateroventral positions (Figs 26A–B, 27B–C, 28C–E). Sensory spots in subdorsal, midlateral and ventromedial positions (Figs 27B, 28D–E). Glandular cell outlets type 1 not observed. On this and following three segments cuticular hairs evenly distributed across tergal plate, except for hairless areas located close to midlateral line; ventromedial and paraventral areas on this and following five segments with thinner and much shorter, non-bracteate hairs. Posterior segment margin straight, terminating in pectinate fringe with fringe tips as on preceding segments.

SEGMENT 4. With spine in middorsal position (Figs 26A, 27B). Glandular cell outlets type 2 present in subdorsal, laterodorsal, midlateral and lateroventral positions (Figs 26A–B, 27B–C, 28D–E). Sensory spots or glandular cell outlets type 1 not present. Pachycycli, pectinate fringe and cuticular hairs as on preceding segment.

Table 19. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes aragorni* sp. nov.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1	so	ss,so	ss	so				gco1	so
2	gco1,ss	gco2	gco2	gco2,ss		gco2			gco2	gco1,ss
3		gco2	ss,gco2	gco2	gco2,ss			gco2		ss
4	ac		gco2	gco2	gco2			gco2		
5			gco2,ss	gco2	gco2,ss		gco2	tu		ss
6	ac	ss	gco2	gco2	ss	gco2		gco2		ss
7		ss	gco2	gco2	ss	gco2		gco2		ss
8	ac	ss	gco2	gco2		gco2	gco2	ac		
9		ss	gco2	ss,gco2	gco2	ss	gco2,si	ac	ss	
10	gco1		ss	gco2(♂)					ss	
11	gco1 ×2,pr	ss	ss		pe ×3(♂)		ltas(♀)	lts		

SEGMENT 5. With tubes in lateroventral positions (Figs 26B, 27C, 28C, H). Glandular cell outlets type 2 located in subdorsal, laterodorsal, midlateral and lateral accessory positions (Figs 26A–B, 27C, E, 28E,G–H). Sensory spots present in subdorsal, midlateral and ventromedial positions; in holotype and other female specimens midlateral sensory spots located closer to sublateral line, on outer/lateral side of midlateral glandular cell outlets type 2 (Fig. 28E), while in male specimen this pair of sensory spots on dorsal side of midlateral glands (Fig. 28I). Segment otherwise as segment 4.

SEGMENT 6. With spine in middorsal position only (Figs 26A–B, 27A, E, 28A, G). Glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and lateroventral positions (Figs 26A–B, 27C, E, 28G–H). Sensory spots located in paradorsal, midlateral and ventromedial positions (Figs 26A–B, 28G–H). Tips of pectinate fringe of posterior segment margin as on preceding segments. Segment otherwise as segment 5.

SEGMENT 7. Without spines or tubes (Figs 26B, 27E). Glandular cell outlets type 2 and sensory spots as on segment 6 (Figs 26A–B, 27E–F, 28G–H), but ventromedial pair of sensory spots located closer to ventrolateral line than on preceding segment (Fig. 28H). Cuticular hair covering as on segment 6, except for paraventral areas with much shorter and thinner hairs than on preceding segments.

SEGMENT 8. With spines in middorsal and lateroventral positions (Figs 26A–B, 27G, 28E). Glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and lateral accessory positions (Figs 26A–B, 27E–F, 28M–N). Sensory spots present in paradorsal positions only (Fig. 28M). Pectinate fringe of posterior segment margin with slightly narrower and shorter tips on the dorsal side. Segment otherwise as segment 7.

SEGMENT 9. With spines in lateroventral positions (Figs 26B, 27F, 28N). Glandular cell outlets type 2 present in subdorsal, laterodorsal, midlateral and lateral accessory positions (Figs 26A–B, 27E–F, 28J, N); subdorsal pair situated close to paradorsal area (Fig. 28J). Sensory spots present in paradorsal, laterodorsal, sublateral and ventrolateral positions; laterodorsal pair located more anteriorly on segment than other pairs (Figs 26A–B, 28J). Small, rounded sieve plates located in lateral accessory positions (Fig. 27F). Pectinate fringe with shorter tips than on preceding segment, homogenous along segment margin. Cuticular hair covering of tergal plate similar to that on preceding segment, but with broader area of short and thin non-bracteate hairs, covering paradorsal and subdorsal areas; sternal plates devoid of hairs in paraventral and ventromedial areas.

SEGMENT 10. With laterodorsal glandular cell outlets type 2 located near posterior segment margin in males; females without glandular cell outlets type 2 on this segment (Figs 26A,,C, 28K–L). Sensory spots present in subdorsal and ventrolateral positions (Fig. 28L). Glandular cell outlet type 1 present in middorsal position. Cuticular hairs sparser than on preceding segment. Central part of tergal plate almost completely hairless, sternal plate hair covering as on preceding segment. Posterior segment margin of tergal plate straight, with much shorter fringe and narrower tips than those on preceding segment (Fig. 28K–L); margins of sternal plates extend midventrally (Fig. 26B).

SEGMENT 11. With pair of lateral terminal spines (Fig. 27D, F). Males with three pairs of penile spines; dorsal and ventral penile spines thin and flexible tubes, whereas median ones markedly thicker, conical and stout (Figs 26C, 28L); females with lateral terminal accessory spines (Figs 26A, 27F, 28K). Sensory spots present in paradorsal and subdorsal positions; subdorsal pair located near posterior margin of tergal extensions (Figs 26A, 28K). Pair of glandular cell outlets type 1 present in middorsal position, covered by middorsal protuberance-like structure extending from intersegmentary joint (Figs 26A,C, 28K–L). Segment devoid of cuticular hairs, but with dense covering of short hair-like extensions on dorsal areas of tergal plates. Short fringes covering margins of tergal and sternal plates; fringe tips slightly longer near insertion of lateral terminal spines. Tergal extensions triangular, sternal extensions do not extend beyond tergal extensions.

Distribution

Hikurangi slope and Honeycomb Canyon, 670–1171 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes aragorni* sp. nov.

Echinoderes aragorni sp. nov. can very easily be distinguished from all other congeners by the number and arrangement of glandular cell outlets type 2. No less than 34 pairs of glandular cell outlets type 2 (35 in males) are present in *E. aragorni*, which is not present in any other kinorhynch species. The only other species displaying a somewhat similar trait is *E. orestauri* Pardos *et al.*, 2016 with 30 fringed tubules distributed on segments 2 to 9 (Pardos *et al.* 2016a). It seems likely that glandular cell outlets type 2 and fringed tubes are homologous, but they still differ morphologically since only the fringed tubes form actual external appendages. In contrast, the glands in *E. aragorni* are relatively large openings (although smaller in male specimens than in females: see Fig. 28I vs Fig. 28J), easily distinguishable in both SEM and LM and present on segments 2 to 10.

A second rare feature in *E. aragorni* sp. nov. is the presence of lateroventral tubes/spines on segments 5, 8 and 9 only. This feature is shared with three other species only: *E. caribiensis* Kirsteuer, 1964, *E. lusitanicus* and *E. skipperae* Sørensen & Landers, 2014 (Kirsteuer 1964; Neves *et al.* 2016; Sørensen & Landers 2014). However, none of these species can be confused with *E. aragorni*, as they do not possess even a single pair of glandular cell outlets type 2. Moreover, *E. caribiensis* belongs to the *E. coulli* species group and is characterized by the absence of middorsal spines, while in contrast *E. lusitanicus* has five middorsal spines. Only *E. skipperae* has, similar to the new species, a middorsal spine arrangement with spines present on segments 4, 6 and 8.

The presence of slit-like openings on segment 1 is also unique to *E. aragorni* sp. nov. Other species show an occurrence of cuticular structures on segment 1 like tubes or glandular cell outlets type 2 (e.g., *E. frodoi* sp. nov., *E. legolasi* sp. nov., *E. anniae*, and *E. hamiltonorum*) (Sørensen *et al.* 2018; present study), but the structures observed in *E. aragorni* have not been observed before. Although it may represent another type of glandular cell outlets – or a modified kind of glandular cell outlets type 2 – we are currently uncertain about their nature and function. Therefore, it is difficult to discuss this observation further, but it is obviously a structure that deserves more attention in future works.

Echinoderes galadrielae sp. nov.

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Figs 29–31; Tables 20–21

Diagnosis

Echinoderes with spines in middorsal position on segments 4 to 8, and spines in lateroventral positions on segments 6 to 9. Tubes present in lateral accessory positions on segment 5. Glandular cell outlets type 2 in subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, midlateral positions on segment 5 and sublateral positions on segment 8. Males with minute laterodorsal tubes on segment 10; females with nearly reduced tubes. Segment 11 composed of two tergal and two sternal plates.

Etymology

The species name refers to Galadriel – ‘Lady’ of Lothlórien, one of the greatest of the elves in Middle-Earth, and a character in J.R.R. Tolkien’s “*The Lord of the Rings*” and “*Silmarillion*”. Galadriel helped the Fellowship of the Ring significantly in achieving their goals, hosting them after their escape from the mines of Moria and giving each member a valuable gift for their onward journey.

Material examined

Holotype

NEW ZEALAND • ♀; Campbell Canyon, stn TAN1004/126; 42.1422° S, 174.5492° E; 1495 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159425. Mounted for LM in Fluoromount G on HS slide.

Paratypes

NEW ZEALAND • 2 ♀♀; Pahaua Canyon, stn TAN1004/12; 41.5508° S, 175.7250° E; 1350 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921496 to 921497. Mounted for LM in Fluoromount G on glass slide • 1 ♀; Seamount 766, stn TAN1004/132; 42.1345° S, 174.5850° E; 1453 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159426. Mounted as holotype.

Additional material

NEW ZEALAND • 2 ♀♀; Hikurangi Slope, stn TAN1004/76; 41.6833° S, 175.6500° E; 1282 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 3 ♀♀, 1 ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀; Honeycomb Canyon, stn TAN1004/62; 41.4760° S, 175.9477° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM.

Description

GENERAL. Adults with head, neck and eleven trunk segments (Figs 29–31). Overview of measurements and dimensions in Table 20. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 21. No details regarding scalid arrangement and morphology could be provided, because introvert of specimens mounted for SEM was fully or partially retracted.

NECK. With 16 placids. Midventral placid broadest, 9 µm in width and 11 µm in length, whereas all others narrower, measuring 6 µm in width at their bases and 11 µm in length, similar in size (Fig. 30C, 31D). Trichoscalid plates are well developed.

SEGMENT 1. Consists of complete cuticular ring. Sensory spots located anteriorly on segment, in subdorsal and laterodorsal positions (Figs 29A, 30B, 31B). Glandular cell outlets type 1 present in middorsal, and ventrolateral positions. Cuticular hairs lightly scattered on dorsal and lateral sides and absent on ventral

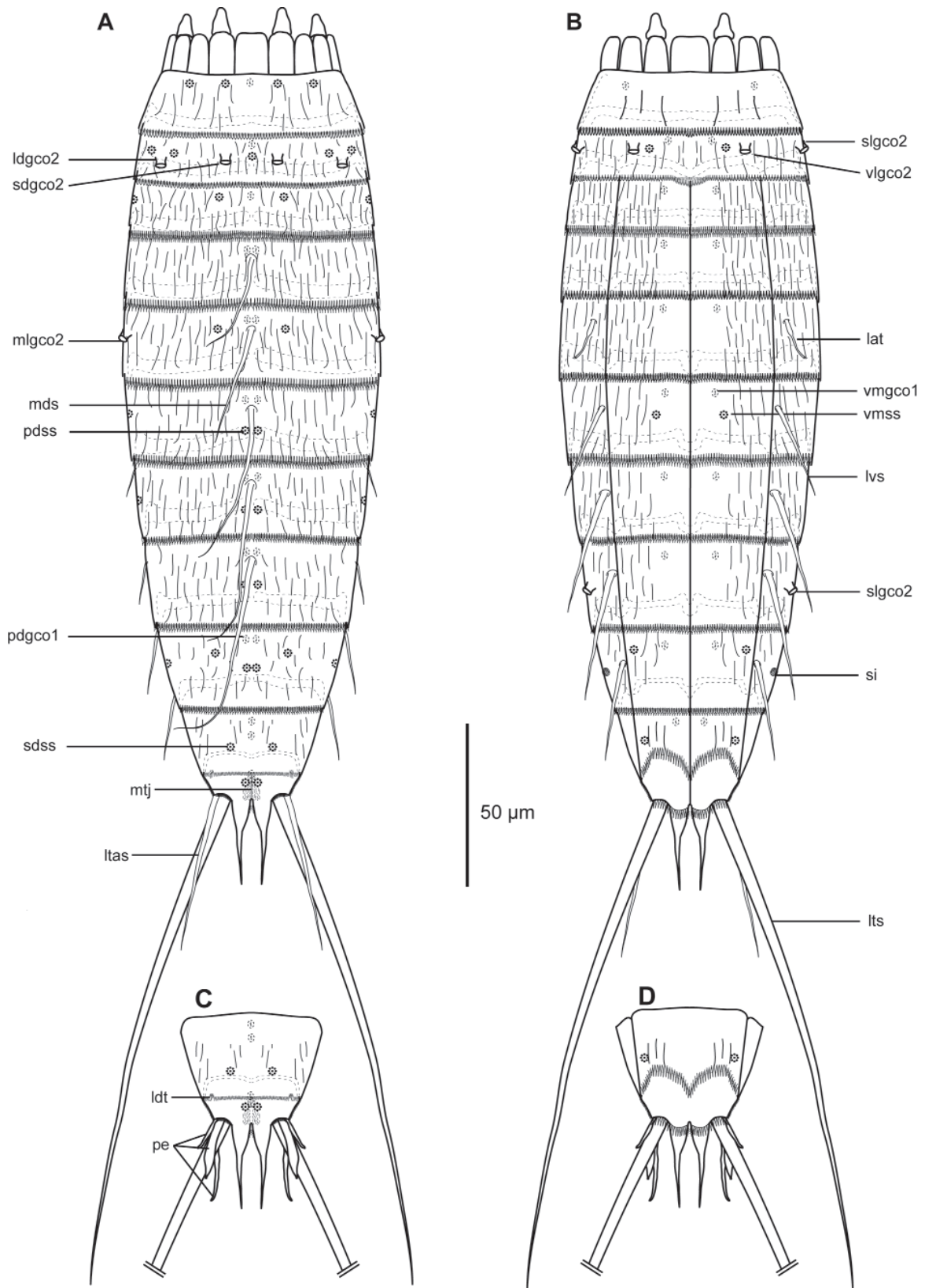


Fig. 29. Line art illustrations of *Echinoderes galadrietae* sp. nov. **A.** ♀, dorsal view. **B.** ♀, ventral view. **C.** ♂, segments 10–11, dorsal view. **D.** ♂, segments 10–11, ventral view. Abbreviations: see Material and methods.

side (Fig. 30B–C). Posterior segment margin almost straight along dorsal edge, but slightly extended posteriorly in midventral position (Fig. 31C). Pectinate fringe with well-developed fringe tips, slightly shorter and rounded along dorsal margin, and longer and more pointed along lateral and ventral margins (Fig. 31B–C).

SEGMENT 2. Consists of complete cuticular ring. Glandular cell outlets type 2 present in subdorsal, laterodorsal, sublateral and ventrolateral positions (Figs 29A–B, 30B–C, 31B–C); glands on ventral side located closer to anterior margin of segment (Fig. 31C). Sensory spots located in middorsal, laterodorsal (two pairs) and ventromedial positions (Fig. 29A–B); sensory spots on this and following segments very small. Glandular cell outlets type 1 present in middorsal and ventromedial positions. Pachycyclus of anterior segment margin of regular thickness, interrupted in middorsal position. Secondary pectinate fringe present near anterior segment margin of this and following segments. Long cuticular hairs lightly scattered on dorsal and lateral sides; ventral side with few hairs. Paraventral and midventral areas in this and following eight segments hairless. Posterior segment margin straight along dorsal side, while extended posteriorly in midventral position. Fringe tips shorter than on preceding segment.

SEGMENT 3. Present segment, and eight remaining ones, consist of one tergal and two sternal plates (Figs 29A–B, 30A, C, 31A). Segment with sensory spots located in subdorsal and midlateral positions (Figs 30B, 31B), and glandular cell outlets type 1 in middorsal and ventromedial positions. Pachycyclus of anterior segment margin of regular thickness, interrupted at tergo-sternal and midsternal junctions

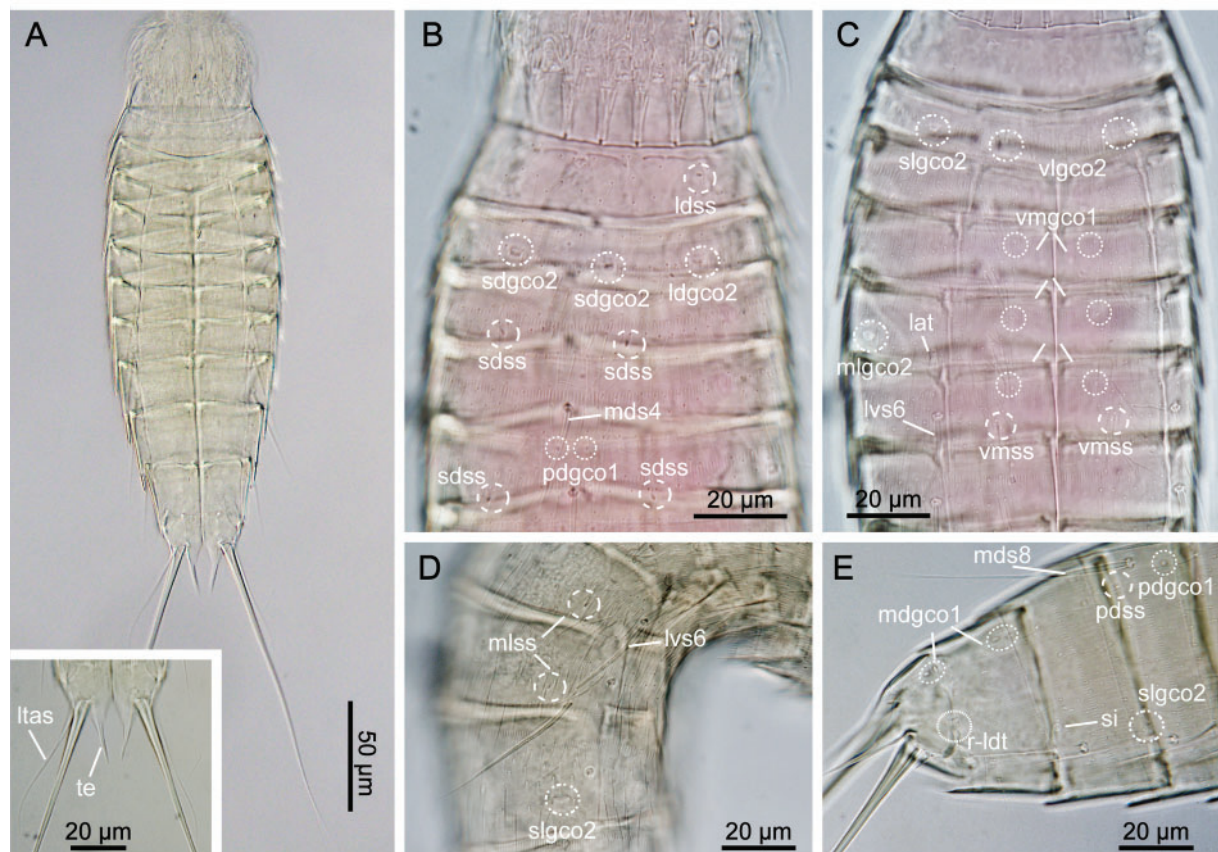


Fig. 30. Light micrographs showing overview and details of *Echinoderes galadrietae* sp. nov. **A.** ♀, paratype (NHMD-921497). **B–C.** ♀, holotype (NIWA-159425). **D.** ♀, paratype (NHMD-921496). **E.** ♀, paratype (NIWA-159426). **A.** Ventral overview, with inset showing close-up of segment 11. **B.** Segments 1 to 5, dorsal view. **C.** Segments 1 to 7, ventral view. **D.** Segments 6 to 8, lateral view. **E.** Segments 8 to 11, lateral view. Abbreviations: see Material and methods.

and middorsally, on this and following seven segments. Cuticular hairs more densely distributed across tergal plate, but otherwise as on preceding segment. Posterior segment margin straight, terminating in pectinate fringe with pointed fringe tips, longer than as on preceding segments.

SEGMENT 4. With spine in middorsal position (Figs 29A, 31D). Segment without sensory spots, but with glandular cell outlets type 1 in paradorsal and ventromedial positions. Pachycycli, pectinate fringe and cuticular hairs as on preceding segment.

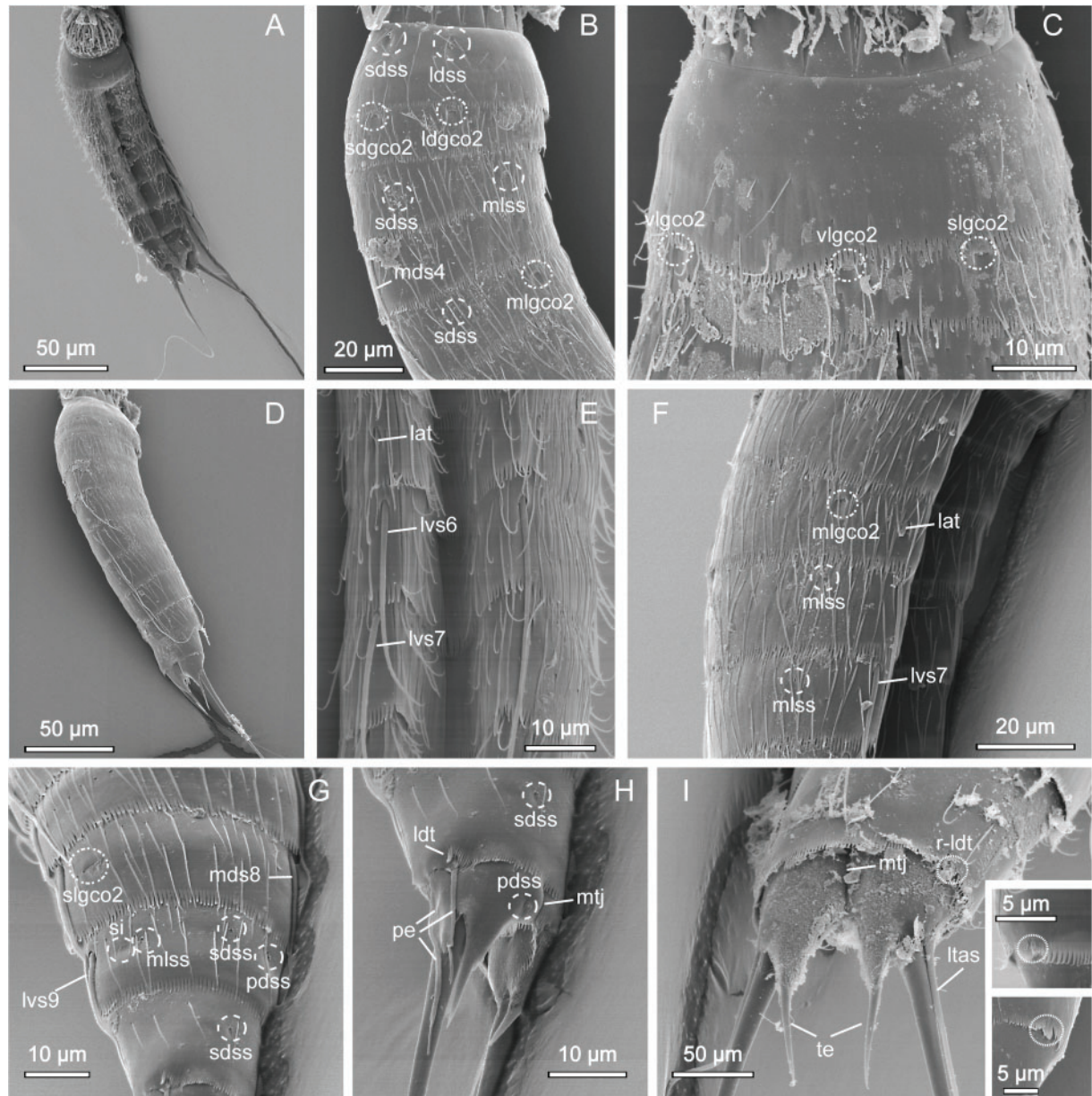


Fig. 31. Scanning electron micrographs showing overviews and details of *Echinoderes galadriellae* sp. nov. **A.** Ventral overview. **B.** Segments 1 to 5, dorsolateral view. **C.** Segments 1 to 2, lateroventral view. **D.** Dorsal overview. **E.** Segments 5 to 7, ventral view. **F.** Segments 4 to 7, lateral view. **G.** Segments 8 to 10, dorsolateral view. **H.** Segments 10 to 11 of male, dorsolateral view. **I.** Segments 10 to 11 of female, dorsal view with insets showing close-up of reduced laterodorsal tubes on segment 10. Abbreviations: see Material and methods.

Table 20. Measurements from light microscopy of *Echinoderes galadrielae* sp. nov. (in μm) from the Hikurangi Margin, including number of measured specimens (n) and standard deviation (SD). Left part of the table shows ranges for *E. galadrielae* sp. nov., right part shows ranges for *Echinoderes* sp. aff. *E. galadrielae*/*E. beringiensis* with shorter tergal extensions.

Character	<i>E. galadrielae</i> sp. nov.				<i>E. sp. aff. E. galadrielae/beringiensis</i>			
	n	Range	Mean	SD	n	Range	Mean	SD
TL	4	210–235	224	8.0	7	196–211	208	8.3
MSW-8	4	47–50	49	1.5	6	41–48	44	2.9
MSW-8/TL	4	21–23%	22%	0.7%	6	20–23%	21%	1.1%
SW-10	4	41–43	42	0.5	6	32–38	34	1.9
SW-10/TL	4	18–20%	19%	0.4%	6	16–18%	17%	0.7%
S1	4	26–28	27	0.9	7	22–25	23	0.9
S2	4	24–25	25	0.6	7	19–24	21	1.6
S3	4	24–26	25	0.9	7	20–27	23	2.2
S4	4	25–28	27	1.2	7	25–31	26	2.3
S5	4	30–37	34	2.8	7	24–32	28	2.6
S6	4	33–41	36	3.8	7	28–35	30	2.3
S7	4	37–43	40	2.5	7	29–35	32	2.1
S8	4	38–42	40	1.6	7	32–37	35	2.2
S9	4	36–41	38	1.9	7	30–35	32	1.4
S10	4	30–35	33	2.5	7	24–32	29	3.4
S11	4	37–40	38	1.4	6	24–30	27	3.9
MD4 (ac)	3	25–31	29	2.4	7	29–46	40	5.6
MD5 (ac)	3	33–36	36	2.7	6	45–61	53	6.0
MD6 (ac)	4	46–55	51	3.3	6	58–64	60	2.3
MD7 (ac)	3	54–56	55	0.9	6	61–75	69	5.2
MD8 (ac)	4	62–69	66	2.5	6	77–87	81	3.7
LV6 (ac)	4	29–37	32	3.4	7	32–44	37	4.4
LV7 (ac)	3	45–47	46	0.8	7	30–46	42	6.1
LV8 (ac)	4	45–49	47	1.6	7	38–52	44	7.9
LV9 (ac)	4	41–44	43	1.2	6	36–43	38	3.3
TE	4	28–33	32	2.2	7	14–21	18	2.8
TE/TL	4	13–15%	14%	0.9%	7	7–10%	9%	1.5%
LTS	4	178–214	199	13.4	7	181–254	220	32.2
LTS/TL	4	76–94%	87%	8.0%	7	86–125%	106%	15.1%
LTAS	4	50–60	55	3.6	4	35–55	42	8.6

SEGMENT 5. With spine in middorsal position and tubes in lateral accessory positions (Figs 29A–B, 30C, 31E–F). Glandular cell outlets type 2 present in midlateral positions, being similar in size and shape to those on segment 2. Sensory spots located subdorsally, and glandular cell outlets type 1 present in paradorsal and ventromedial positions. Segment otherwise as segment 4.

SEGMENT 6. With spines in middorsal and lateroventral positions (Figs 29A–B, 30A, C, 31A, D, F). Sensory spots present in paradorsal, midlateral and ventromedial positions (Figs 29A–B, 30C, 31F). Glandular cell outlets type 1 present in paradorsal and ventromedial positions (Figs 29A–B, 30C). Tips of pectinate fringe of posterior segment margin as on preceding segments. Cuticular hairs and posterior segment margin as on preceding segment.

Table 21. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes galadrielae* sp. nov.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1		ss	ss					gco1	
2	gco1,ss		gco2	ss,gco2,ss		gco2			gco2	gco1,ss
3	gco1		ss		ss					gco1
4	ac	gco1								gco1
5	ac	gco1	ss		gco2		tu			gco1
6	ac	gco1,ss			ss			ac		gco1,ss
7	ac	gco1,ss			ss			ac		gco1
8	ac	gco1,ss				gco2		ac		gco1
9		gco1,ss	ss		ss	si		ac	ss	gco1
10	gco1 × 2		ss	tu(♂)					ss	gco1
11	gco1 × 2	ss			pe × 3(♂)		ltas(♀)	lts		

SEGMENT 7. With spines in middorsal and lateroventral positions (Figs 29A–B, 31D–F). Sensory spots present in paradorsal and midlateral positions (Figs 29A–B, 31F), and glandular cell outlets type 1 in paradorsal and ventromedial positions (Figs 29A–B, 30E). Cuticular hair covering as on preceding segment. Segment otherwise as segment 6.

SEGMENT 8. With spines in middorsal and lateroventral positions (Figs 29A–B, 30E, 31D, G). Glandular cell outlets type 2 located in sublateral positions; gland very conspicuous, larger than those on segments 2 and 5 (Figs 30D–E, 31G). Sensory spots present in paradorsal positions, and glandular cell outlets type 1 in paradorsal and ventromedial positions (Fig. 30E). Pectinate fringe of posterior segment margin as on preceding segment.

SEGMENT 9. With spines in lateroventral positions (Figs 29B, 31A, G). Sensory spots located in paradorsal, subdorsal, midlateral and ventrolateral positions; subdorsal pair situated more anterior than others (Figs 29A–B, 31G). Glandular cell outlets type 1 present in paradorsal and ventromedial positions. Small, rounded sieve plates located in sublateral positions (Figs 30E, 31G). Pectinate fringe as on preceding segment. Cuticular hair covering and posterior segment margin similar to those on preceding segment.

SEGMENT 10. With sensory spots in subdorsal and ventrolateral positions (Fig. 31G–H). Glandular cell outlets type 1 in ventromedial positions and as pair in middorsal position (Fig. 30E). Males with very short laterodorsal tubes, emerging through slit-like, fringed opening; females with similar slit-like, fringed opening, but with tubes being even further reduced, and either not visible at all or only visible as plate-like projection emerging through opening (Fig. 31H–I). Cuticular hairs very scarce on both tergal and sternal plates (Fig. 31A, G–I). Pectinate fringe of posterior margin on dorsal and lateral sides with markedly shorter fringe tips as on preceding segments, but with longer tips on paraventral areas. Margins of sternal plates extend midventrally.

SEGMENT 11. With pair of lateral terminal spines (Fig. 29A). Females with lateral terminal accessory spines (Figs 29A, 30A, 31I); males with three pairs of penile spines (Figs 29C, 31H), with dorsal- and ventralmost penile spines being slender and tubular, with abrupt narrowings about ¼ from their distal tips; median ones stout and triangular. Sensory spots present in paradorsal positions, near posterior margins of sternal plate (Fig. 31H). A pair of glandular cell outlets type 1 present in middorsal position. Segment devoid of cuticular hairs, but has small patches with short and tiny hair-like extensions in

paradorsal positions. Short fringes covering margins of sternal plates. Segment composed of two tergal and two sternal plates (Fig. 31H–I) Tergal extensions significantly elongated and posteriorly projecting (Figs 30A, 31H–I); sternal extensions short and rounded.

Distribution

Hikurangi Margin, from slope, through canyon, and seamount habitats, 1013–1495 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Taxonomic remarks on *Echinoderes galadrietae* sp. nov.

Echinoderes galadrietae sp. nov. displays a very common spine pattern, with five middorsal ones on segments 4 to 8, and lateroventral spines on segments 6 to 9, which is shared with almost 50 species of *Echinoderes*. However, what makes *E. galadrietae* differ from most of its congeners is the presence of tubes on segment 5 in lateral accessory positions rather than in lateroventral positions. Such tube displacement is actually a very uncommon trait, observed for only four other species, i.e., *E. bathyalis* Yamasaki *et al.*, 2018, *E. drogoni* Grzelak & Sørensen, 2017 in Grzelak & Sørensen (2018), *E. ferrugineus* Zelinka, 1928 and *E. beringiensis* Adrianov & Maiorova, 2022 (Grzelak & Sørensen 2018; Yamasaki *et al.* 2018c; Yamasaki & Dal Zotto 2019; Adrianov & Maiorova 2022). *Echinoderes galadrietae* can easily be distinguished from *E. bathyalis* though, by its number and positions of glandular cell outlets type 2: *E. galadrietae* has four pairs of those glands on segment 2, and one pair midlaterally on segment 5 and sublaterally on segment 8, whereas *E. bathyalis* shows only one pair on segment 2, an absence of glands on segment 5 and lateral accessorially on segment 8 (Yamasaki *et al.* 2018c). Moreover, *E. bathyalis* possesses markedly different tergal extensions, and all its acicular spines are longer.

Echinoderes ferrugineus and *E. galadrietae* sp. nov. share the same number and arrangement of type 2 glands on segments 2, 5 and 8 (on the latter segment in midlateral rather than sublateral position though), but *E. ferrugineus* has two additional pairs of glandular cell outlets type 2 on segment 4, in subdorsal and midlateral positions (Yamasaki & Dal Zotto 2019). Moreover, in addition to its very different tergal extensions, *E. ferrugineus* also differs by being larger (304 μm vs 224 μm), and having markedly shorter lateroventral and lateral terminal spines (for details see Yamasaki & Dal Zotto 2019).

Among the abovementioned species, two Arctic ones, *E. drogoni* and *E. beringiensis*, show the closest resemblance to *E. galadrietae* sp. nov. The three species share several features, including tube and spine patterns, number and arrangement of glandular cell outlets type 2 and most sensory spots. They also share another very characteristic and uncommon feature, which is the middorsal division of the tergal plate of segment 11 (Grzelak & Sørensen 2018; Adrianov & Maiorova 2022). Nevertheless, despite overall similarity, *E. galadrietae* can easily be distinguished from both *E. drogoni* and *E. beringiensis* by its elongated tergal extensions.

Such long and conspicuous tergal extensions, constituting almost 15% of the total trunk length, is in fact the most prominent trait of *E. galadrietae* sp. nov. Longer tergal extensions (TE/TL \sim 20%) are known only for two other species, i.e., *E. balerioni* Grzelak & Sørensen, 2019 and *E. cernunnos* Sørensen *et al.*, 2012 (see Sørensen *et al.* 2012; Grzelak & Sørensen 2019). *Echinoderes balerioni* can easily be discriminated from *E. galadrietae* by its three middorsal spines on segments 4, 6 and 8 and the lack of glandular cell outlets type 2. In contrast, *E. cernunnos* – a species described from Korean waters – shows a much closer resemblance to the new species. The spine and glandular cell outlets type 2 distributions are almost identical with those in *E. galadrietae*, and a re-examination of the paratypes (NHMD-099881 to 099882) and photos of the holotype (INBRIV-0000245082) of *E. cernunnos* revealed that both species also have their tubes on segment 5 displaced to lateral accessory positions. The most conspicuous difference between the species is the presence of midlateral glandular cell outlets type 2 on segment 7 in *E. cernunnos*, which are absent in *E. galadrietae*. Interestingly, *E. cernunnos* is also one

of the few known congeners (together with abovementioned *E. drogoni* and *E. juliae* Sørensen *et al.*, 2018) with a middorsal fissure on segment 11 (Sørensen *et al.* 2012, 2018; Grzelak & Sørensen 2018) and is also characterised by tergal extensions not only similar in length, but also in their horn-like shape (compare Sørensen *et al.* 2012: fig. 6f–h with Fig. 31H–I in the present study). Nonetheless, despite several similarities and the fact that *E. galadriela* and *E. cernunnos* share several rare character traits, telling them apart should not be a problem. Except for the different distribution of sensory spots, the easiest way is to focus on segment 7, which has glandular cell outlets type 2 in *E. cernunnos*, and on the lateral terminal spines, which are markedly longer in *E. galadriela* (LTS/TL=87% in *E. galadriela* vs LTS/TL=23% in *E. cernunnos*) (Sørensen *et al.* 2012).

Hence, in summary, *E. galadriela* sp. nov. appears to share a number of traits with *E. drogoni*, *E. cernunnos*, and *E. beringiensis*, including general spine pattern, lateral displacement of the tubes on segment 5, glandular cell outlet type 2 patterns on segments 2, 5 and 8, and middorsal division of the tergal plate of segment 11. This combination of rather unusual characters suggests that the four species are closely related and represent a clade within *Echinoderes*. Following previous attempts to identify such species groups within the genus (see, e.g., Yamasaki 2016; Sørensen *et al.* 2018, 2020), we propose that these four species should be considered as a monophyletic entity and referred to as the *E. cernunnos* species group.

Species with uncertain identities

Echinoderes* sp. aff. *E. galadriela*/*E. beringiensis

Fig. 32; Table 20

Material examined

NEW ZEALAND • 1 ♀; Hikurangi Slope, stn TAN1004/4; 41.6837° S, 175.6642° E; 1046 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159427. Mounted for LM in Fluoromount G on glass slide • 2 ♂♂; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀; Hikurangi Slope, stn TAN1004/76; 41.6833° S, 175.6500° E; 1282 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921503. Mounted for LM in Fluoromount G on HS slide • 1 ♂; same collection data as for preceding; personal reference collection of MVS. Mounted for SEM • 1 ♀, 1 ♂; Pahaua Canyon, stn TAN1004/12; 41.5508° S, 175.7250° E; 1350 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921498 to 921499. Mounted for LM in Fluoromount G on glass slides • 2 ♂♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Honeycomb Canyon, stn TAN1004/53; 41.4563° S, 175.8970° E; 948 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921500. Mounted for LM in Fluoromount G on glass slide • 1 ♂; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8977° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921502. Mounted for LM in Fluoromount G on HS slide • 1 ♀; Seamount 310, stn TAN1004/69; 41.3353° S, 176.1882° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921501. Mounted for LM in Fluoromount G on glass slide.

Distribution

Hikurangi Margin, from slope, through canyon, and seamount habitats, 670–1350 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Brief description and remarks

The examined specimens closely follow the morphology of *E. galadrietae* sp. nov. in terms of distribution of spines, tubes, glandular cell outlets, and even the middorsal division of the tergal plate of segment 11. However, *E. galadrietae* and *E. aff. E. galadrietae/E. beringiensis* differ at two important points, i.e., spine morphometrics (see Table 20) and the shape of the tergal extensions (compare Figs 30A, 31D, I with Fig. 32). Middorsal spines were in general longer in this current set of specimens, while the lateroventral ones were shorter than in *E. galadrietae*. The unidentified specimens have also markedly longer lateral terminal spines, which in most cases exceed the trunk length, resulting in markedly higher LTS/TL ratio in this species compared to *E. galadrietae* (average LTS/TL: 106% vs 87%, respectively). The most conspicuous difference between *E. galadrietae* and these unidentified specimens is expressed in the tergal extensions, which are exceptionally long in *E. galadrietae* (Figs 29–31). This stands in strong contrast to the short, triangular tergal extensions in the unidentified specimens (Fig. 32). These tergal extensions are much more similar to those in *E. beringiensis* as well as many other species of *Echinoderes*.

We would, on the other hand, hesitate in identifying the specimens as *E. beringiensis*, since they differ in the distribution of sensory spots and lack the midlateral glandular cell outlets type 2 that characterizes females of *E. beringiensis* (see Adrianov & Maiorova 2022). In addition, *E. beringiensis* has a longer trunk (TL: 331 μm vs 208 μm , respectively) and has proportionally shorter lateral terminal spines (LTS/TL: 50% vs 106%, respectively). In conclusion, these enigmatic specimens appear to represent an intermediate between *E. galadrietae* sp. nov. and *E. beringiensis*, and it would require a molecular comparison to unveil their true identity.

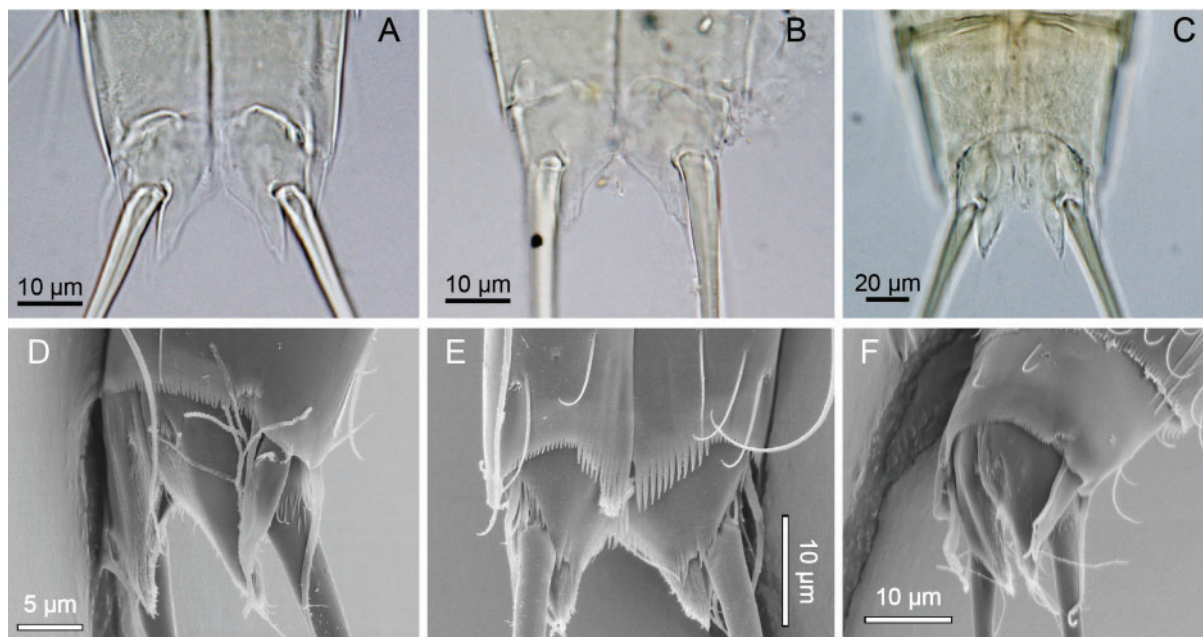


Fig. 32. Segment 11 and morphological variations of tergal extensions in *Echinoderes* sp. aff. *E. galadrietae/E. beringiensis*. **A–C.** Light micrographs. **D–F.** Scanning electron micrographs.

Echinoderes sp. aff. *E. balerioni*

Fig. 33; Tables 22–23

Material examined

NEW ZEALAND • 1 ♂; Seamount 310, stn TAN1004/69; 41.3353° S, 176.1882° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921971. Mounted for LM in Fluoromount G on HS slide.

Distribution

Seamount 310, 670 m depth. See Fig. 1 for geographic location of station and Table 1 for station and specimen information.

Brief description and remarks

Echinoderes with middorsal spines on segments 4, 6, and 8 and spines in lateroventral positions on segments 6 to 9. Tubes present in subdorsal, sublateral, and ventrolateral positions on segment 2, lateroventral positions on segment 5, and lateral accessory positions on segment 8. Tergal extensions conspicuously long and spiniform.

Adult with head, neck and eleven trunk segments. Overview of measurements and dimensions in Table 22. Only a single specimen was available for LM examination, and thus some cuticular structures such as sensory spots or glandular cell outlets might not have been identified. Therefore, lack of information about structures reported in Table 23 should not necessarily be understood as a confirmation of their absence.

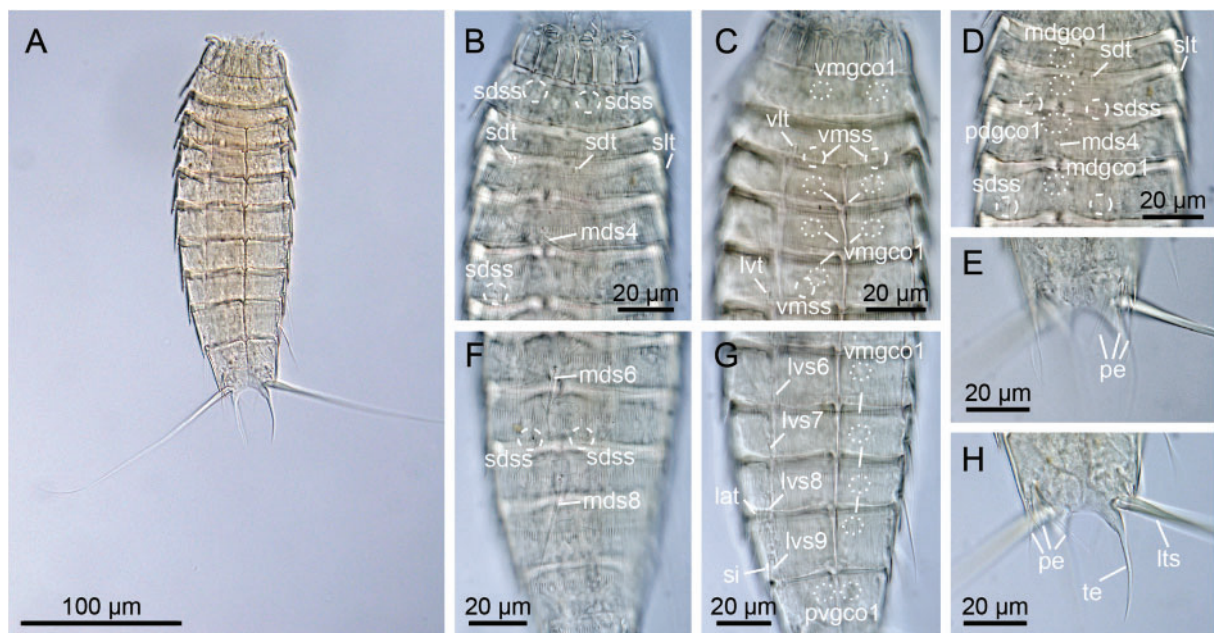


Fig. 33. Light micrographs showing overview and details of *Echinoderes* sp. aff. *E. balerioni*, ♂ (NHMD-921971). **A.** Ventral overview. **B.** Segments 1 to 5, dorsal view. **C.** Segments 1 to 5, ventral view. **D.** Segments 2 to 5, dorsal view. **E.** Segments 10 to 11, dorsal view. **F.** Segments 6 to 10, dorsal view. **G.** Segments 6 to 10, ventral view. **H.** Segments 10 to 11, ventral view. Abbreviations: see Material and methods.

Table 22. Measurements from light microscopy of *Echinoderes* sp. aff. *E. balerioni* (in μm) from the Hikurangi Margin with a comparison of measurements for *E. balerioni* from its type locality.

Character	<i>E. aff. E. balerioni</i> present study	<i>E. balerioni</i> Grzelak & Sørensen, 2019
	NHMD-921971 (♂)	NHMD-202793 (♂)
TL	227	300
MSW-6	47	64
MSW-6/TL	20.7%	21.3%
SW-10	39	52
SW-10/TL	17.2%	17.3%
S1	24	32
S2	21	30
S3	22	31
S4	23	36
S5	24	39
S6	28	45
S7	31	46
S8	34	48
S9	31	47
S10	33	43
S11	52	73
MD4 (ac)	23	23
MD6 (ac)	28	32
MD8 (ac)	50	35
LVS6 (ac)	29	34
LVS7 (ac)	28	40
LVS8 (ac)	33	47
LVS9 (ac)	35	52
TE	40	55
TE/TL	17.6%	18.3%
LTS	148	181
LTS/TL	65.2%	60.3%

Segments 1 and 2 composed of complete cuticular rings. Segment 1 with sensory spots in subdorsal positions, and with glandular cell outlets type 1 in middorsal and ventrolateral positions (Fig. 33B–C). Posterior segment margin of this and following nine segments with well-developed pectinate fringe tips. Segment 2 with three pairs of tubes in subdorsal, sublateral and ventrolateral positions (Fig. 33B–D). Sensory spots observed in ventromedial positions and glandular cell outlets type 1 in middorsal position only. Cuticular hairs on this and following segments abundant, distributed evenly around segment. Segments 3 to 11 consists of one tergal and two sternal plates. Segment 3 with sensory spots in subdorsal positions, and glandular cell outlets type 1 in middorsal and ventromedial positions. Segment 4 with relatively short (23 μm) middorsal spine (Fig. 33B), and glandular cell outlets type 1 located paradorsally and ventromedially; no sensory spots observed. Pectinate fringe with longer fringe tips than on preceding segments. Segment 5 with lateroventral tubes (Fig. 33C); sensory spots present in subdorsal, midlateral and ventromedial positions, and glandular cell outlets type 1 located middorsally and ventromedially (Fig. 33B–D). Segment 6 with spines in middorsal and lateroventral positions (Fig. 33F–G), paradorsal, midlateral and ventromedial sensory spots, and glandular cell outlets type 1 located paradorsally and ventromedially (Fig. 33G). Segment 7 with spines in lateroventral positions,

Table 23. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes* sp. aff. *E. balerioni*.

Position segment	MD	PD	SD	ML	SL	LA	LV	VL	VM	PV
1	gcol		ss						gcol	
2	gcol		tu		tu			tu	ss	
3	gcol		ss						gcol	
4	ac	gcol							gcol	
5	gcol		ss	ss			tu		gcol,ss	
6	ac	gcol,ss		ss			ac		gcol,ss	
7	gcol		ss	ss			ac		gcol	
8	ac	gcol,ss				tu	ac		gcol	
9		gcol,ss	ss			si	ac	ss	gcol	
10	gcol × 2									gcol
11				pe × 3			lts			

subdorsal and midlateral sensory spots, and glandular cell outlets type 1 present in middorsal and ventromedial positions (Fig. 33F–G). Segment 8 with spines in middorsal and lateroventral positions, and tubes in lateral accessory positions (Fig. 33F–G); sensory spots observed only in paradorsal positions; glandular cell outlets type 1 present in paradorsal and ventromedial positions. Segment 9 with spines in lateroventral positions (Fig. 33G); sensory spots located in paradorsal, subdorsal and ventrolateral positions, and glandular cell outlets type 1 present in paradorsal and ventromedial positions (Fig. 33G); small sieve plate located in lateral accessory positions (Fig. 33G). Segment 10 with glandular cell outlets type 1 located in paraventral positions and with two located middorsally (Fig. 33G); no sensory spots observed. Segment 11 with pair of relatively long lateral terminal spines (Fig. 33A,H). Three pairs of long penile spines present (Fig. 33E, H). Tergal extensions conspicuously long and spiniform (Fig. 33H). No cuticular hairs nor any other cuticular structures visible on this segment.

Echinoderes balerioni is a species described from 880 m depth at the Yermak Plateau, north of Svalbard (Grzelak & Sørensen 2019). There is no other species with acicular spines in middorsal position on segments 4, 6, and 8, three pairs of tubes on segment 2 and conspicuously long tergal extensions. The latter constitutes almost 18.3% of the total trunk length and this is the most prominent feature of *E. balerioni*. The lengths of the tergal extensions in this species are comparable only with those of *E. cernunnos*, *E. yamasakii* and *E. galadrielae* sp. nov. – the species with the longest extensions (Sørensen *et al.* 2012, 2018). However, all three species are easily distinguished from *E. balerioni* by their five middorsal spines on segments 4 to 8 and the presence of glandular cell outlets type 2.

The individual examined for the present study closely follows the morphology of *E. balerioni*, in particular in the appearance of tergal extensions (see Table 22). Most morphometric data, general trunk appearance and other cuticular structures, such as arrangements of spines and tubes (however, see below), also followed those reported for the Arctic specimen (compare Table 23 in present contribution with Grzelak & Sørensen 2019: table 3). Nevertheless, we cannot identify the examined specimen as *E. balerioni* with certainty because of certain morphological differences. Considering the geographical distance between northern Svalbard and New Zealand and the fact that in both cases only a single specimen was available for LM investigation, we cannot be sure whether the observed discrepancies are the result of inter-population variations or indicate the presence of two, closely related species.

Due to the fact that no specimen was available for SEM investigation, Grzelak & Sørensen (2019) did not provide details about sensory spots on segments 2 to 11, and a comparison of their patterns between

the specimens from the Arctic and New Zealand is therefore not possible. The major difference between the specimen from New Zealand and *E. balerioni* from the Arctic is the presence of tubes on segment 2 in the subdorsal rather than the laterodorsal positions. Both specimens also slightly differ in terms of morphometric details. The specimen from New Zealand is smaller (TL: 227 μm vs 300 μm) and has a longer middorsal spine on segment 8 (MDS8: 50 μm vs 35 μm) than *E. balerioni* from the type locality. Nevertheless, differences in trunk length do not result in differences in TE/TL or LTS/TL ratios (Table 22), which confirms the close similarity between specimens. Interestingly, the variation in the arrangement of the tubes on segment 2 might have resulted from inter-population variations. Recently, specimens from the Bering Sea, Alaska, clearly similar to *E. balerioni*, have been investigated by the first author of the present study, and all of them possess tubes on segment 2, in subdorsal, laterodorsal, sublateral and ventrolateral positions (Grzelak, unpubl. obs.). A variation regarding the presence or absence of tubes has previously been observed for several species, e.g., *E. arlis*, *E. daenerysae*, *E. eximus*, *E. rhaegali* and *E. dalzottoi* sp. nov., and it occurred within the same population, randomly and independently of developmental stage or sex (Grzelak & Sørensen 2018, 2019; present study). However, uncovering this variation would require a certain number of specimens, which is why the very low number of individuals of *E. balerioni* from the Arctic and the single one examined in the present study hamper proper comparison, and leave us uncertain about the specimen's identity. Nevertheless, our results, as well as the observations made by Grzelak for Alaskan specimens, stress the necessity of further investigations of this interesting species, both in terms of intra- or interspecific variation and its geographical distribution.

Echinoderes sp. aff. *E. lupherorum*

Figs 34–35; Tables 24–25

Material examined

NEW ZEALAND • 1 ♂; Hikurangi Slope, stn TAN1004/4; 41.6837° S, 175.6642° E; 1046 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159428. Mounted for LM in Fluoromount G on glass slide • 1 ♂; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921636. Mounted for LM in Fluoromount G on HS slide • 1 ♀; Hikurangi Slope, stn TAN1004/44; 41.5258° S, 175.8003° E; 728 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 2 ♂♂; Hikurangi Slope, stn TAN1004/76; 41.6833° S, 175.6500° E; 1282 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Hikurangi Slope, stn TAN1004/128; 42.0485° S, 174.7000° E; 1420 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921635. Mounted for LM in Fluoromount G on HS slide • 1 ♂; Pahaua Canyon, stn TAN1004/22; 41.5100° S, 175.7187° E; 1188 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159429. Mounted for LM in Fluoromount G on HS slide • 1 ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NIWA-159430. Mounted for LM in Fluoromount G on HS slide • 3 ♀♀, 2 ♂♂; same collection data as for preceding; personal reference collection of MVS. Mounted for SEM • 1 ♀; Honeycomb Canyon, stn TAN1004/62; 41.4760° S, 175.9477° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀; Campbell Canyon, stn TAN1004/126; 42.1422° S, 174.5492° E; 1495 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921634. Mounted for LM in Fluoromount G on HS slide • 1 ♀; Seamount 310, stn TAN1004/69; 41.3353° S, 176.1882° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921632. Mounted for LM in Fluoromount G on glass slide • 1 ♂; Seamount 310, stn TAN1004/72; 41.3657° S, 176.1958° E; 985 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921633. Mounted for LM in Fluoromount G on glass slide • 1 ♀; same collection data as for preceding; personal reference collection of MVS. Mounted for SEM.

Distribution

Hikurangi slope, seamount, Honeycomb Canyon, Pahaua Canyon, Campbell Canyon, 670–1495 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Brief description and remarks

Echinoderes with middorsal spines on segments 4 to 8, and spines in lateroventral positions on segments 6 to 9. Tubes present in lateroventral positions on segment 2 and 5, and in midlateral positions on segment 10. Minute glandular cell outlets type 2 present in subdorsal positions on segment 2, and in laterodorsal positions on segments 8 and 9. Tergal extensions of segment 11 long, constituting 6% of the trunk length. Males with three pairs of penile spines, females with lateral terminal accessory spines and papillae in ventrolateral positions on segment 7 and in ventromedial positions on segment 8.

General. Adults with head, neck and eleven trunk segments (Figs 34–35). Overview of measurements and dimensions in Tables 24. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 25.

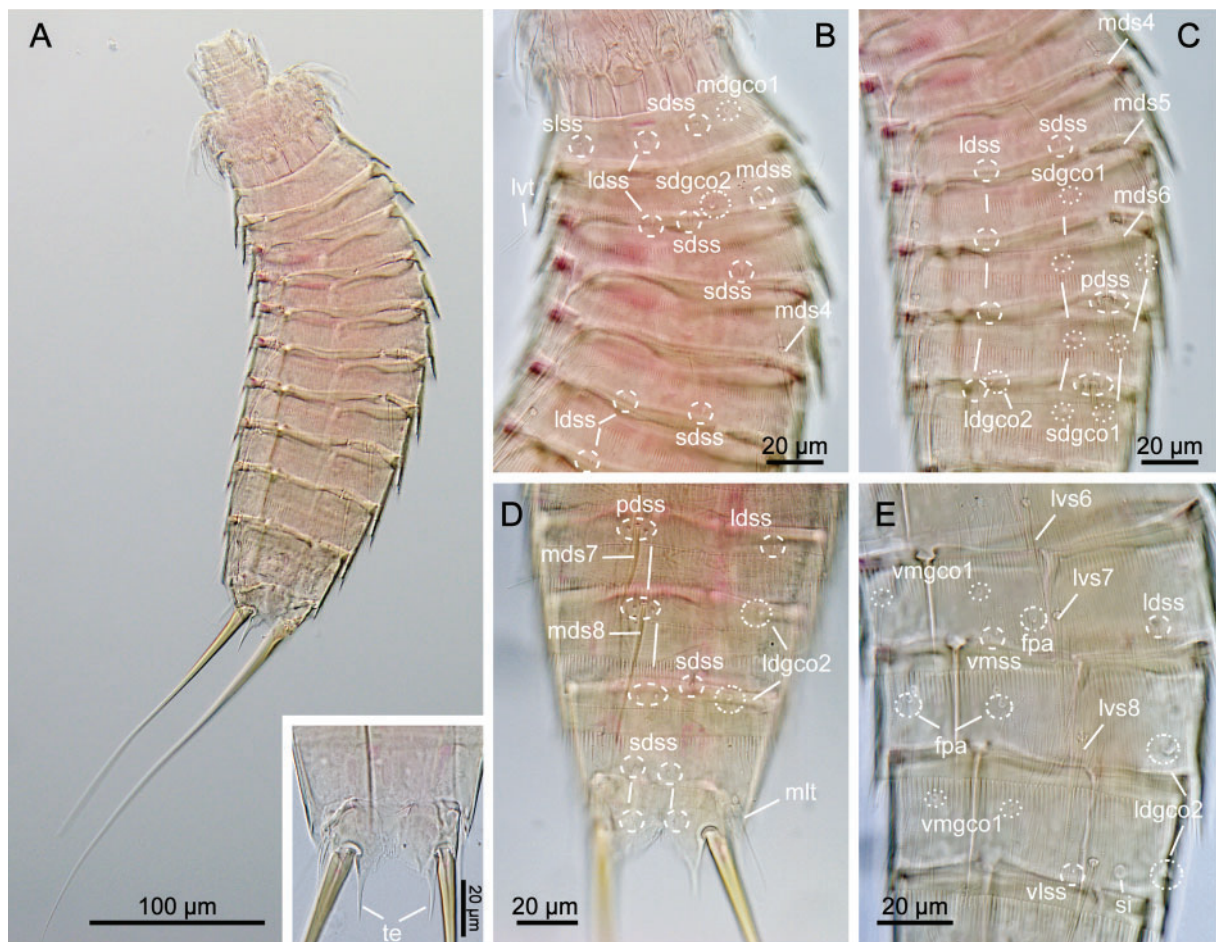


Fig. 34. Light micrographs showing overview and details of *Echinoderes* sp. aff. *E. lupherorum*. **A–C.** ♂ (NHMD-921636). **D.** ♂ (NHMD-921635). **E.** ♀ (NHMD-921632). **A.** Lateroventral overview, with inset showing close-up of segment 11. **B.** Segments 1 to 6, dorsolateral view. **C.** Segments 4 to 9, dorsolateral view. **D.** Segments 8 to 11, dorsal view. **E.** Segments 6 to 9, lateroventral view. Abbreviations: see Material and methods.

Segments 1 and 2 composed of complete cuticular rings. Segment 1 with glandular cell outlets type 1 in middorsal and ventrolateral positions and sensory spots in subdorsal, laterodorsal, sublateral, and ventromedial positions (Figs 34B, 35B–C). Posterior segment margin of this and following nine segments with pectinate fringe with well-developed tips. Cuticular hairs relatively long, evenly distributed around segment. Segment 2 with lateroventral tubes and pair of glandular cell outlets type 2 in subdorsal positions (Figs 34B, 35B–C). Sensory spots present in middorsal, subdorsal, laterodorsal and ventromedial positions. Glandular cell outlets type 1 observed only in middorsal position. Cuticular hairs on this and following eight segments densely covering tergal plates and lateral halves of sternal plates; paraventral and ventromedial areas hairless (Fig. 35A, D). Segments 3 to 11 consists of one tergal and two sternal plates. Segments 3 with sensory spots in subdorsal positions and glandular cell outlets type 1 in middorsal and ventromedial positions. Segment 4 with middorsal spine, and sensory spots and glandular cell outlets type 1 located ventromedially. Segment 5 with middorsal spine, lateroventral tubes, sensory spots present in subdorsal and laterodorsal positions and glandular cell outlet type 1 located subdorsally and ventromedially. Segment 6 and 7 with spines in middorsal and lateroventral positions, sensory spots in paradorsal, laterodorsal and ventromedial positions, and glandular cell outlets

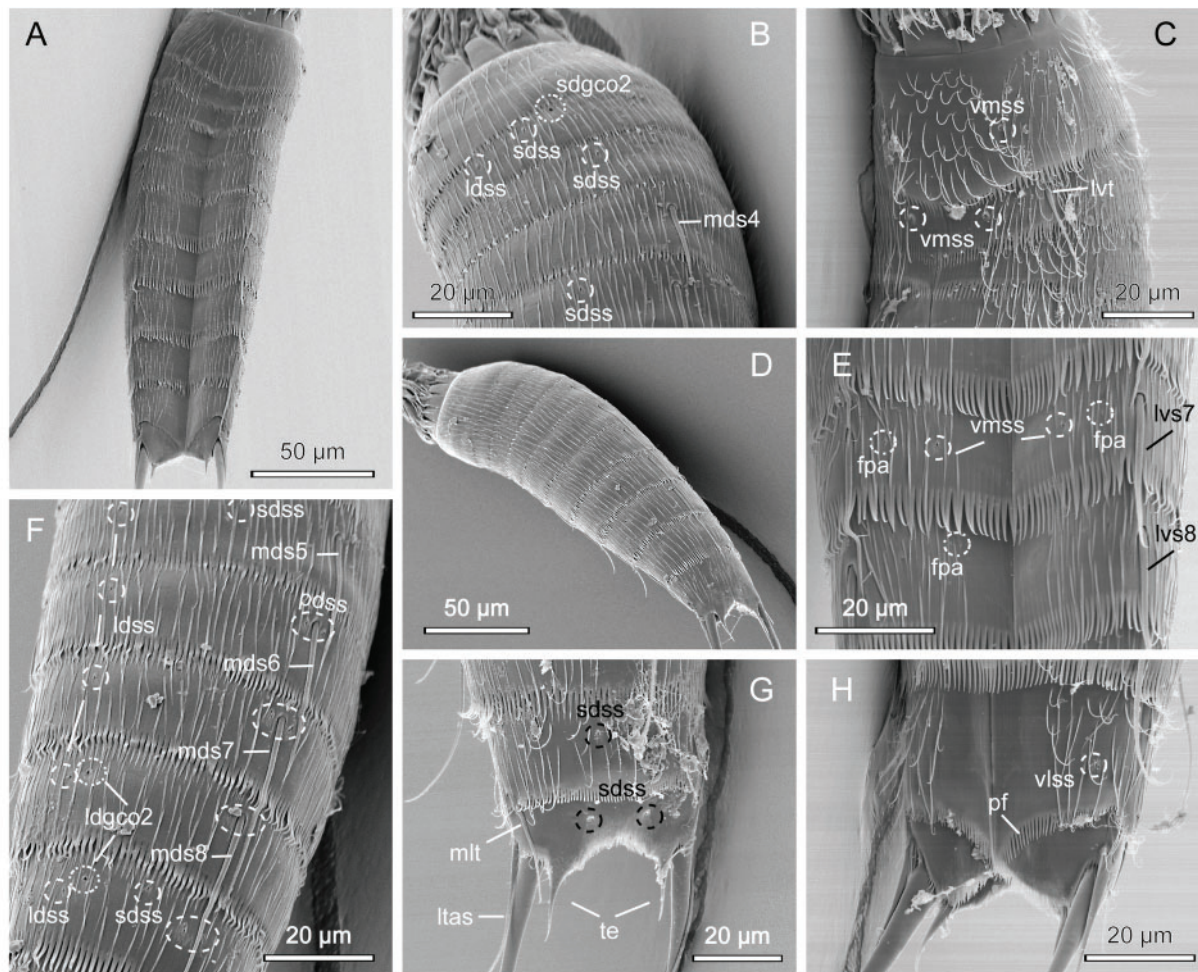


Fig. 35. Scanning electron micrographs showing overviews and details of *Echinoderes* sp. aff. *E. lupherorum*. **A.** Ventral overview. **B.** Segments 1 to 5, dorsolateral view. **C.** Segments 1 to 3, lateroventral view. **D.** Laterodorsal overview. **E.** Segments 7 to 8, ventral view. **F.** Segments 5 to 9, laterodorsal view. **G.** Segments 10 to 11 of female, dorsal view. **H.** Segments 10 to 11 of female, ventral view. Abbreviations: see Material and methods.

Table 24. Measurements from light microscopy of *Echinoderes* sp. aff. *E. lupherorum* (in µm) from the Hikurangi Margin with comparison of measurements for *E. lupherorum* from its type locality, including number of measured specimens (n) and standard deviation (SD).

Character	<i>E. aff. E. lupherorum</i> present study				<i>E. lupherorum</i> Sørensen <i>et al.</i> , 2018
	n	Range	Mean	SD	Range
TL	6	250–339	307	33.1	331–415
MSW-8	3	63–67	65	2.1	75–81
MSW-8/TL	3	21–26%	24%	3.4%	19.3–23.9%
SW-10	3	48–57	54	5.1	65–71
SW-10/TL	3	16–22%	19%	3.3%	15.7–20.2%
S1	5	34–38	35	2.0	35–42
S2	5	29–36	33	2.8	33–37
S3	5	32–39	36	3.2	39–43
S4	5	38–47	42	4.4	42–47
S5	5	40–50	45	6.1	42–52
S6	5	38–57	49	9.6	50–57
S7	5	38–56	50	7.6	54–60
S8	5	43–55	49	5.1	54–62
S9	5	46–53	50	2.8	59–62
S10	5	38–48	43	3.9	44–51
S11	6	43–47	44	2.3	53–58
MD4 (ac)	6	27–33	31	2.0	31–36
MD5 (ac)	6	36–39	38	1.4	40–48
MD6 (ac)	5	38–50	46	4.5	50–67
MD7 (ac)	5	53–60	57	4.6	54–83
MD8 (ac)	5	62–81	71	8.3	90–128
LV6 (ac)	6	28–37	32	3.1	32–43
LV7 (ac)	6	38–44	42	2.1	45–53
LV8 (ac)	6	40–50	46	3.4	53–68
LV9 (ac)	6	45–56	53	4.1	54–74
TE	6	16–20	18	1.3	24–28
TE/TL	6	5–6%	6%	0.6%	6.0–8.2%
LTS	5	253–283	270	12.8	324–355
LTS/TL	5	82–108%	91%	11.6	80.5–100.9%
LTAS	1	54	n/a	n/a	62–83

type 1 in subdorsal and ventromedial positions (Figs 34C–D, 35F); females with papillae located in ventrolateral positions on segment 7 (Figs 34E, 35E). Segment 8 with middorsal spine, lateroventral spines, small glandular cell outlets type 2 in laterodorsal positions, sensory spots in paradorsal and laterodorsal positions and glandular cell outlets type 1 located subdorsally and ventromedially; females with papillae in ventromedial positions (Figs 34D–E, 35E–F). Segment 9 with lateroventral spines, small glandular cell outlets type 2 present in laterodorsal positions, four pairs of sensory spots, located in paradorsal, subdorsal, laterodorsal and ventrolateral positions, and glandular cell outlets type 1 present in subdorsal and ventromedial positions (Figs 34D–E, 35F); small sieve plate located in sublateral positions (Fig. 34E); on this and previous segment glandular cell outlets type 2 and laterodorsal sensory spots located close to midlateral line. Segment 10 with distinct, long midlateral tubes, sensory spots in subdorsal and ventrolateral positions and two glandular cell outlets type 1 located middorsally and

Table 25. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes* sp. aff. *E. lupherorum*.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM
1	gco1		ss	ss		ss			gco1	ss
2	gco1,ss		gco2,ss	ss				tu		ss
3	gco1		ss							gco1
4	ac									gco1,ss
5	ac		gco1,ss	ss				tu		gco1
6	ac	ss	gco1	ss				ac		gco1,ss
7	ac	ss	gco1	ss				ac	pa(♀)	gco1,ss
8	ac	ss	gco1	gco2,ss				ac		gco1,pa(♀)
9		ss	gco1,ss	gco2,ss		si		ac	ss	gco1
10	gco1 × 2		ss		tu				ss	gco1
11			ss		pe × 3 (♂)		ltas(♀)	lts		

in ventromedial positions (Figs 34D, 35G–H). Segment 11 with a pair of long lateral terminal spines nearly reaching trunk length (Table 24) and subdorsal sensory spots. Cuticular hairs not present. Females with lateral terminal accessory spines, males with three pairs of penile spines. Tergal extensions long, constituting 6% of trunk length; sternal extensions shorter and rounded (Figs 34A, 35G–H).

Echinoderes lupherorum Sørensen *et al.*, 2018 is one of the deep-sea species originally described from the abyssal plain off southern Oregon, in the Northeast Pacific, at a depth of 2719–3675 m (Sørensen *et al.* 2018). With five additional species, i.e., *E. kohni* Varney *et al.*, 2019, *E. microaperturus* Sørensen *et al.*, 2012, *E. spinifurca* Sørensen *et al.*, 2005, *E. sylviae* Landers & Sørensen, 2018 and *E. yamasakii* Sørensen *et al.*, 2018, it constitutes the *E. spinifurca* species group, which is characterized by conspicuous, spinous tergal extensions (Sørensen *et al.* 2005, 2012, 2018; Landers & Sørensen 2018; Varney *et al.* 2019). Additionally, the group shares other morphological features, e.g., the presence of five middorsal spines, the presence of lateroventral/ventrolateral tubes on segment 2 and midlateral tubes on segment 10, with all tubes being long and very well developed, and the presence of the female papillae on sternal plates of segments 6, 7 and/or 8. Within the group, the species are most easily distinguished by the length of their tergal extensions and the presence of glandular cell outlets type 2. *Echinoderes spinifurca* and *E. sylviae* stand out as the species without type 2 glands on segment 2 (although the latter species has glands on segments 8 and 9), while *E. yamasakii* is known as the species with the longest tergal extensions (see Varney *et al.* 2019 for details). The remaining three species, including *E. lupherorum*, show the greatest similarity, including an identical pattern of cuticular structures, a very similar arrangement of sensory spots and a medium length of tergal extensions (*E. microaperturus* TE/TL=5%, *E. lupherorum* TE/TL=7.2%, *E. kohni* TE/TL=8.3%) (Varney *et al.* 2019)

The individuals examined for the present study show the closest resemblance to *E. lupherorum*. They closely follow the morphology of *E. lupherorum*, including all taxonomically significant characters and all spine dimensions. Although the spines at first sight appear longer in the East Pacific specimens of *E. lupherorum*, the relative lengths of the spines in the specimens from New Zealand are almost identical after accounting for the difference in trunk length (New Zealand specimens are slightly smaller with TL=307 µm than Pacific ones with TL=371 µm) (see Sørensen *et al.* 2018: table 12 and Table 24 in the present study for details). The most conspicuous difference between *E. lupherorum* from the type locality and the specimens in the present study are the lengths of the tergal extensions, which are shorter in New Zealand individuals (TE/TL=7.2% vs 6%, respectively). We also notice subtle differences in sensory spot distribution, which can be seen in the shift of the midlateral sensory spots present in *E. lupherorum*

towards laterodorsal positions in our specimens, and the lack of sublateral and ventromedial sensory spots on segment 1 in the East Pacific specimens that, in contrast, are present in the latter.

We were not able to compare the glandular cell outlets type 1 distribution. In *E. lupherorum* from the East Pacific, the presence of this type of glands, particularly on the dorsal side, could not be confirmed due to a thin cuticle (Sørensen *et al.* 2018), and a re-examination of the type material did not provide any new information. This is unfortunate as specimens from New Zealand show a rather rare pattern of glandular cell outlets type 1 on the dorsal side, namely the presence of type 1 outlets in the middorsal positions on segments 1 to 3 and the subdorsal positions on segments 4 to 9. This pattern has so far been connected with the *E. dujardinii* species group, and *E. worthingi* – a species also closely related to the *E. dujardinii* group (Sørensen *et al.* 2020). Nevertheless, a very similar distribution pattern of dorsal glands has also been observed for *E. kohni* (with the exception of segment 3 glands that are present as a pair in subdorsal positions rather than as an unpaired one in middorsal position) (Varney *et al.* 2019). This may indicate that species belonging to the *E. spinifurca* group also have an uncommon distribution pattern of glandular cell outlets type 1.

To summarize, even though we can observe some minor differences between the East Pacific and New Zealand populations of *E. lupherorum*, these are too minor to distinguish and describe a new species without support from molecular data. Molecular approaches appear to be increasingly necessary in taxonomic research of *Echinoderes* nowadays, since the differential characters appear to become increasingly more subtle the more species we examine.

Echinoderes* sp. aff. *E. unispinosus

Figs 36–37; Tables 26–27

Material examined

NEW ZEALAND • 1 ♂; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921792. Mounted for LM in Fluoromount G on HS slide • 1 ♀, 1 ♂; same collection data as for preceding; personal reference collection of MVS. Mounted for SEM.

Distribution

Hikurangi slope, 1121 m b.s.l. See Fig. 1 for geographic location of station and Table 1 for station and specimen information.

Brief description and remarks

Echinoderes with middorsal spine on segment 4 and spines in lateroventral positions on segments 6 and 7. Glandular cell outlets type 2 present in midlateral positions on segment 1, subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, lateral accessory positions on segment 5, and midlateral positions on segment 8. Males with three pairs of penile spines and glandular cell outlets type 2 in laterodorsal positions on segment 10; females with lateral terminal accessory spines only.

General. Adults with head, neck and eleven trunk segments. Overview of measurements and dimensions in Tables 26. Distribution of cuticular structures, i.e., sensory spots, glandular cell outlets, spines and tubes, summarized in Table 27.

Segments 1 and 2 composed of complete cuticular rings. Segment 1 with glandular cell outlets type 2 in midlateral positions, sensory spots in subdorsal and laterodorsal positions, and with glandular cell outlets type 1 in middorsal and ventrolateral positions (Figs 36B–C, 37B–C). Posterior segment margin

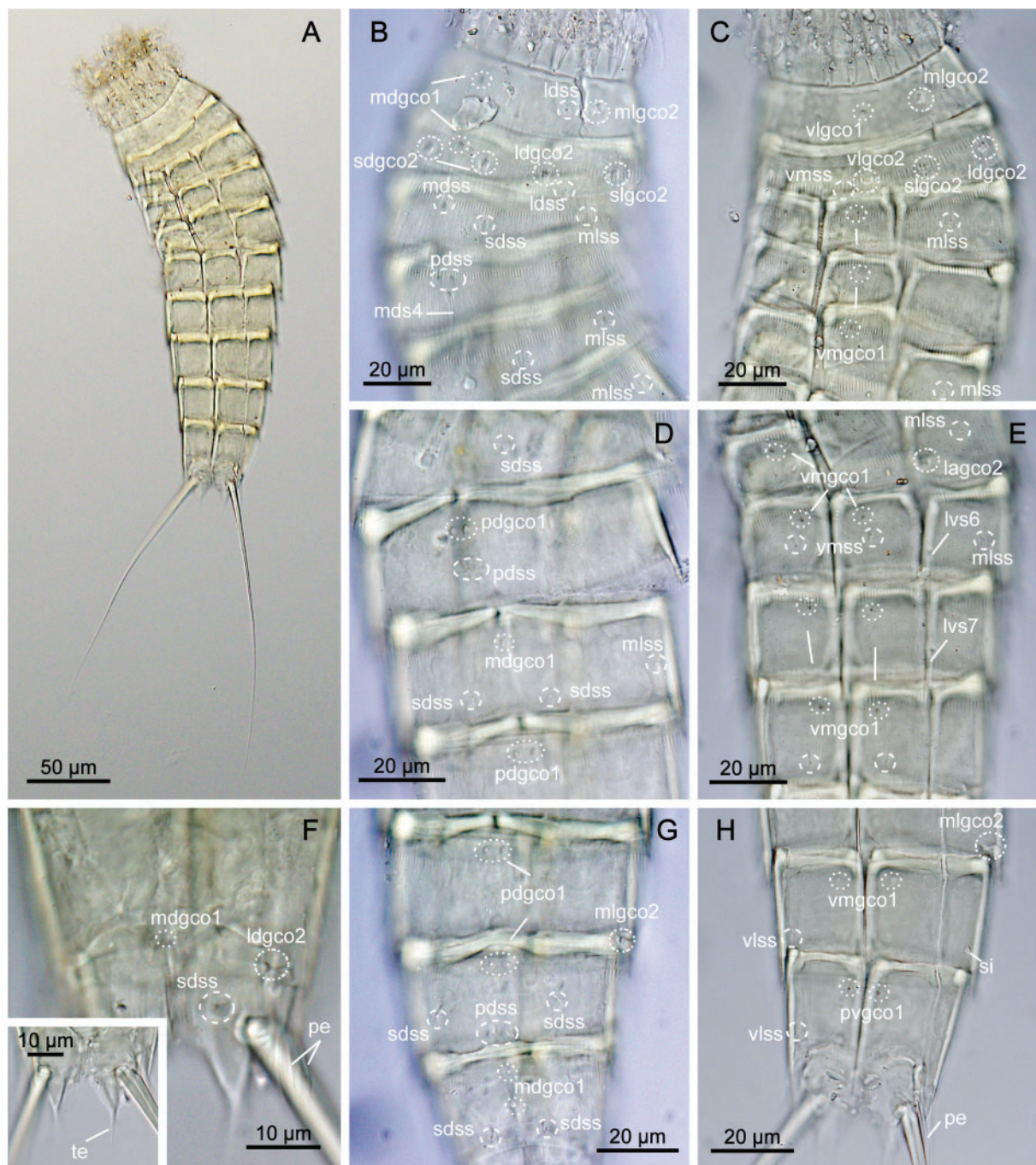


Fig. 36. Light micrographs showing overview and details of *Echinoderes* sp. aff. *E. unispinosus*, ♂ (NHMD-921792). **A.** Lateroventral overview. **B.** Segments 1 to 5, dorsolateral view. **C.** Segments 1 to 5, lateroventral view. **D.** Segments 5 to 8, dorsal view. **E.** Segments 5 to 8, lateroventral view. **F.** Segments 10 to 11, dorsal view, with inset showing close-up of tergal extensions of segment 11. **G.** Segments 8 to 10, dorsal view. **H.** Segments 8 to 11, lateroventral view. Abbreviations: see Material and methods.

of this and following nine segments with pectinate fringe with well-developed tips. Cuticular hairs relatively short, lightly scattered on dorsal side, and almost completely absent on lateral and ventral sides. Segment 2 with glandular cell outlets type 2 in subdorsal, laterodorsal, sublateral and ventrolateral positions (Figs 36B–C, 37B–C, E). Sensory spots present in middorsal, laterodorsal and ventromedial positions. Glandular cell outlets type 1 observed only in middorsal position. Cuticular hair covering denser on this and following eight segments (Fig. 37A–H). Segments 3 to 11 consist of one tergal and two sternal plates. Segment 3 with sensory spots in middorsal, subdorsal and midlateral positions, and glandular cell outlets type 1 in ventromedial positions. Segment 4 with short ($> 20 \mu\text{m}$) middorsal spine (Figs 36B, 37D), and glandular cell outlets type 1 located paradorsally and ventromedially; no sensory spots observed. Segment 5 without spines, but with glandular cell outlets type 2 located in lateral accessory positions (Figs 36E, 37D, G); sensory spots present in subdorsal, midlateral and ventromedial positions, and glandular cell outlet type 1 located middorsally and ventromedially. Segment 6 with

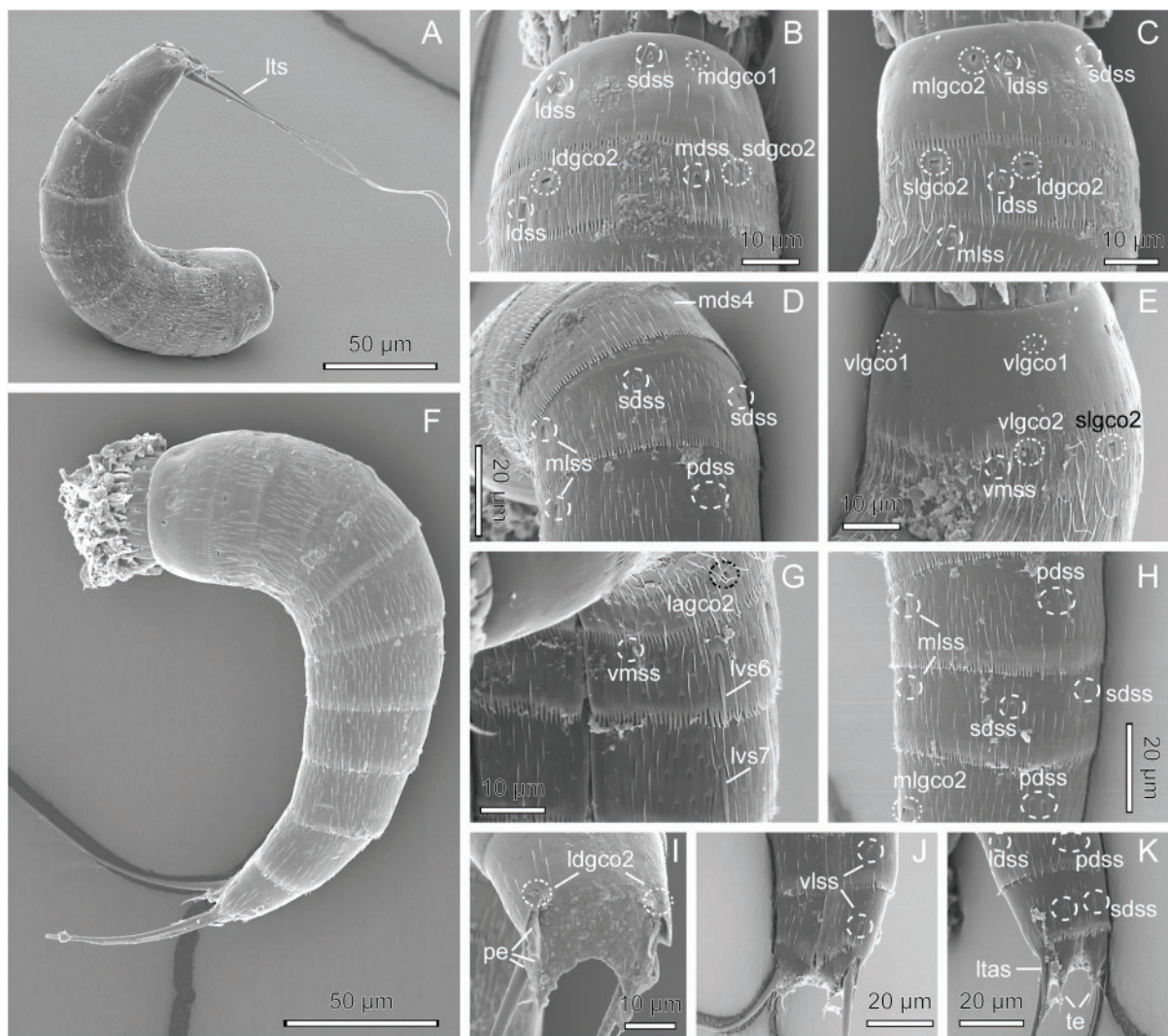


Fig. 37. Scanning electron micrographs showing overviews and details of *Echinoderes* sp. aff. *E. unispinosus*. **A.** Lateral overview. **B.** Segments 1 to 3, subdorsal view. **C.** Segments 1 to 3, lateral view. **D.** Segments 4 to 6, subdorsal view. **E.** Segments 1 to 3, lateroventral view. **F.** Lateral overview. **G.** Segments 5 to 7, lateroventral view. **H.** Segments 6 to 8, laterodorsal view. **I.** Segments 10 to 11 of male, dorsal view. **J.** Segments 9 to 11, ventrolateral view. **K.** Segments 9 to 11 of female, laterodorsal view. Abbreviations: see Material and methods.

Table 26. Measurements from light microscopy of *Echinoderes* sp. aff. *E. unispinosus* (in μm) from the Hikurangi Margin with comparison of measurements for *E. unispinosus* Yamasaki *et al.*, 2018 from its type locality.

Character	<i>E. aff E. unispinosus</i> present study	<i>E. unispinosus</i> Yamasaki <i>et al.</i> , 2018
	NHMD-921792 (♂)	Range
TL	253	265–305
MSW-7	44	44–48
MSW-7/TL	17.4%	15.0–18.2%
SW-10	35	33–38
SW-10/TL	13.8%	11.8–13.9%
S1	27	31–34
S2	24	23–25
S3	26	24–26
S4	29	25–28
S5	32	27–30
S6	33	30–34
S7	35	34–37
S8	36	35–40
S9	34	34–39
S10	36	34–38
S11	19	30–33
MD4 (ac)	19	18–22
LVS6 (ac)	22	15–17
LVS7 (ac)	19	15–19
LTS	177	169–205
LTS/TL	69.9%	60.2–72.9%

spines in lateroventral positions, paradorsal, midlateral and ventromedial sensory spots and glandular cell outlets type 1 located paradorsally and ventromedially (Figs 36D–E, 37D, G–H). Segment 7 with spines in lateroventral positions, subdorsal and midlateral sensory spots, and glandular cell outlets type 1 present in middorsal and ventromedial positions (Figs 36D–E, 37G–H). Segment 8 with glandular cell outlets type 2 in midlateral positions, and sensory spots and glandular cell outlet type 1 in paradorsal and ventromedial positions (Figs 36G–H, 37H). Segment 9 without spines or glandular cell outlets type 2; sensory spots located in paradorsal, subdorsal, laterodorsal and ventrolateral positions, and glandular cell outlets type 1 present in paradorsal and ventromedial positions (Figs 36G–H, 37J–K); small sieve plate located in sublateral positions (Fig. 36H). Segment 10 with sensory spots in subdorsal and ventrolateral positions, and two glandular cell outlets type 1 located middorsally and in paraventral positions (Figs 36G–H, 37J–K). Laterodorsal glandular cell outlets type 2 present in males (Figs 36F, 37I). Segment 11 with lateral terminal spines, subdorsal sensory spots and middorsal glandular cell outlet type 1 (Fig. 36F). Cuticular hairs not present. Females with lateral terminal accessory spines, males with three pairs of penile spines (Figs 36F, H, 37I, K). Tergal extensions relatively long, sternal extensions shorter and rounded (Figs 36F, 37J–K).

Echinoderes unispinosus Yamasaki *et al.*, 2018 is a deep-sea species, known for its wide geographic distribution. It was originally described from the deep-sea plain near Sedlo Seamount in the Northeast Atlantic at a depth of 2875 m (Yamasaki *et al.* 2018b), and was subsequently reported from bathyal

Table 27. Summary of nature and location of sensory spots, glandular cell outlets, tubes and spines arranged by series in *Echinoderes* sp. aff. *E. unispinosus*.

Position segment	MD	PD	SD	LD	ML	SL	LA	LV	VL	VM	PV
1	gco1		ss	ss	gco2				gco1		
2	gco1,ss		gco2	gco2,ss		gco2			gco2	ss	
3	ss		ss		ss					gco1	
4	ac	gco1								gco1	
5	gco1		ss		ss		gco2			gco1,ss	
6		gco1,ss			ss			ac		gco1,ss	
7	gco1		ss		ss			ac		gco1	
8		gco1,ss			gco2					gco1,ss	
9		gco1,ss	ss	ss		si			ss	gco1	
10	gco1 × 2		ss	gco2(♂)					ss		gco1
11	gco1		ss		pe × 3(♂)		ltas(♀)	lts			

depths (2298–3708 m depth) in the Gulf of Mexico (Alvarez-Castillo *et al.* 2020) and cold seep areas in the Mozambique Channel (> 700 m depth) (Cepeda *et al.* 2020). Moreover, very similar specimens, identified as *E. cf. unispinosus*, were found at several localities in the deep sea (2735–3679 m depth) off the Pacific coast of the United States (Sørensen *et al.* 2018).

The combination of spines and glandular cell outlets type 2 makes *E. unispinosus* easily distinguishable from other congeners. *Echinoderes unispinosus* is characterized by having only one, relatively short middorsal spine on segment 4, and lateroventral spines on segments 6 and 7, as well as glandular cell outlets type 2 on segments 1, 2, 5 and 8 and by the lack of any tubes (Yamasaki *et al.* 2018b). The individuals examined for the present study closely follow the morphology of this species. Morphometric data and general appearance are almost identical in New Zealand and Atlantic specimens (see Table 26 in the present contribution and Yamasaki *et al.* 2018: table 4). Subtle differences were noted in the sensory spot distribution though, e.g., the presence of a middorsal sensory spot on segment 3 and subdorsal ones on segment 9, observed in New Zealand specimens only, a lack of ventromedial sensory spots on segment 7 and the displacement of glandular cell outlets type 2 from sublateral to midlateral positions in our specimens (Figs 2G, 3H). However, some of these discrepancies (i.e., distribution of sensory spots on segments 3 and 9) were noted also for the Pacific specimens (Sørensen *et al.* 2018). The only significant difference between *E. unispinosus* from the type locality and specimens from the present study is the presence of laterodorsal glandular cell outlets type 2 in males that were not mentioned in the original description. These structures could potentially have been missed in the original description since Yamasaki *et al.* (2018b) did not have specimens available for SEM and glands in this position on segment 10 may be extremely difficult to visualize in LM. Nevertheless, the specimens found by Sørensen *et al.* (2018) off the US west coast also lacked these structures, indicating that the population from New Zealand might in fact represent a closely related, but yet different species. However, since our material included only three specimens and we cannot confirm whether the subtle differences observed between Atlantic and New Zealand specimens are constant within the population, we hesitate to describe a new species based on this material.

Recorded known species

***Echinoderes juliae* Sørensen et al., 2018**

Figs 38–39; Table 28

Material examined

NEW ZEALAND • 1 ♀, 1 ♂; Hikurangi Slope, stn TAN1004/4; 41.6837° S, 175.6642° E; 1046 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; 1 ♀ NHMD-921717, 1 ♂ NHMD-921715. Mounted for LM in Fluoromount G on glass slides • 1 ♀, 1 ♂; Hikurangi Slope, stn TAN1004/17; 41.6288° S, 175.8682° E; 1514 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; 1 ♀ NHMD-921723, 1 ♂ NHMD-921724. Mounted for LM in Fluoromount G on glass slides • 1 ♂; Hikurangi Slope, stn TAN1004/38; 41.5937° S, 175.8532° E; 1121 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921729. Mounted for LM in Fluoromount G on HS slide • 1 ♀; Hikurangi Slope, stn TAN1004/44; 41.5258° S, 175.8003° E; 728 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♀; Hikurangi Slope, stn TAN1004/76; 41.6833° S, 175.6500° E; 1282 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 2 ♀♀, 2 ♂♂; Pahaua Canyon, stn TAN1004/12; 41.5508° S, 175.7250° E; 1350 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; 2 ♀♀

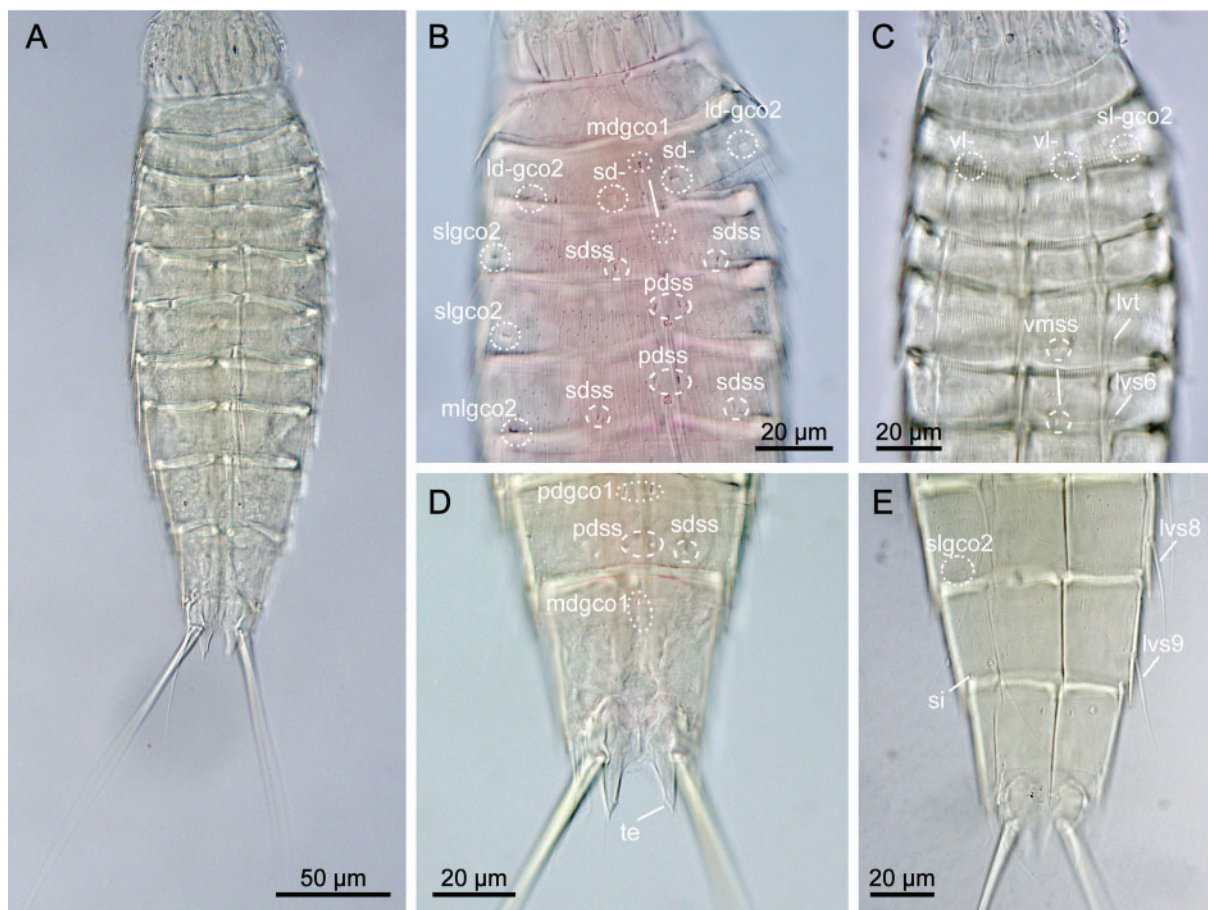


Fig. 38. Light micrographs showing overview and details of *Echinoderes juliae* Sørensen et al., 2018. **A, C.** ♀ (NHMD- 921719). **B, D.** ♂ (NHMD- 921729). **E.** ♂ (NHMD- 921721). **A.** Dorsal overview. **B.** Segments 1 to 5, dorsal view. **C.** Segments 1 to 6, ventral view. **D.** Segments 9 to 11, dorsal view. **E.** Segments 8 to 11, lateroventral view. Abbreviations: see Material and methods.

NHMD-921718-921729, 2 ♂♂ NHMD-921720-921721. Mounted for LM in Fluoromount G on glass slide • 1 ♀; Pahaua Canyon, stn TAN1004/22; 41.5100° S, 175.7187° E; 1188 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921728. Mounted for LM in Fluoromount G on HS slide • 1 ♂; Pahaua Canyon, stn TAN1004/27; 41.4983° S, 175.7043° E; 1013 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 1 ♂; Pahaua Canyon, stn TAN1004/31; 41.4962° S, 175.6828° E; 730 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921725. Mounted for LM in Fluoromount G on glass slide • 2 ♀♀; Honeycomb Canyon, stn TAN1004/58; 41.4080° S, 175.8977° E; 670 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921726 to 921727. Mounted for LM in Fluoromount G on glass slides • 2 ♀♀; same collection data as for preceding; personal reference collection of MVS. Mounted for SEM • 1 ♀; Honeycomb Canyon, stn TAN1004/62; 41.4760° S, 175.9477° E; 1171 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; personal reference collection of MVS. Mounted for SEM • 2 ♀♀; Seamount 766, stn TAN1004/132; 42.1345° S, 174.5850° E; 1453 m b.s.l.; Apr. 2010; NIWA TAN1004 Voyage; soft sediment; NHMD-921730, NHMD-921732. Mounted for LM in Fluoromount G on HS slides.

Distribution

Hikurangi slope, seamount, Honeycomb Canyon, Pahaua Canyon, 670–1514 m b.s.l. See Fig. 1 for a geographic overview of stations and Table 1 for station and specimen information.

Brief description and remarks

Echinoderes with middorsal spines on segments 4 to 8 and spines in lateroventral positions on segments 6 to 9. Tubes present in lateroventral position on segment 5 only. Glandular cell outlets type 2 present in

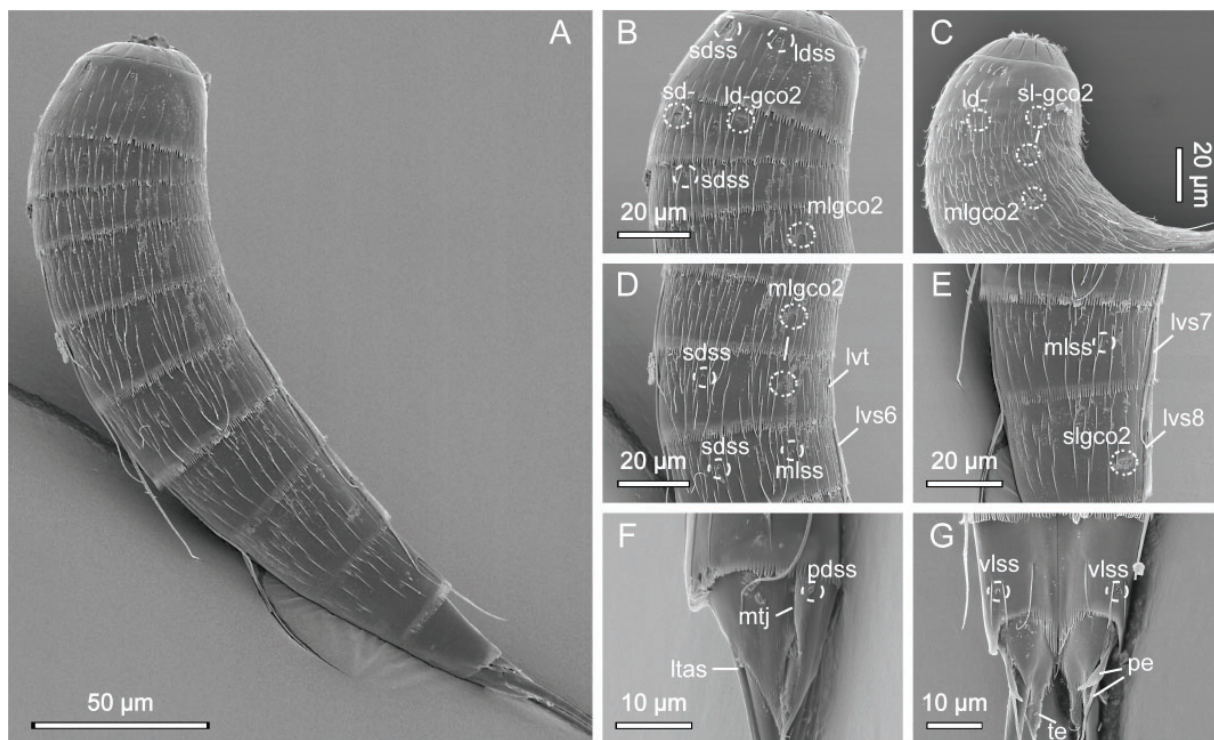


Fig. 39. Scanning electron micrographs showing overviews and details of *Echinoderes juliae* Sørensen *et al.*, 2018. **A.** Lateral overview. **B.** Segments 1 to 4, laterodorsal view. **C.** Segments 1 to 4, lateral view. **D.** Segments 4 to 6, lateral view. **E.** Segments 7 to 8, lateral view. **F.** Segments 10 to 11 of female, dorsal view. **G.** Segments 10 to 11 of male, ventral view. Abbreviations: see Material and methods.

Table 28. Measurements from light microscopy of *Echinoderes juliae* Sørensen *et al.*, 2018 (in μm) from the Hikurangi Margin with comparison of measurements for *E. juliae* from its type locality, including number of measured specimens (n) and standard deviation (SD).

Character	<i>E. juliae</i> present study				<i>E. juliae</i> Sørensen <i>et al.</i> , 2018
	n	Range	Mean	SD	Range
TL	8	227–288	258	20.5	285–327
MSW-7	6	46–53	51	2.5	51–54
MSW-7/TL	6	18–21%	20%	1.1%	15.6–18.6%
SW-10	6	36–40	38	1.6	41–47
SW-10/TL	6	13–16%	15%	1.4%	12.8–15.4%
S1	8	23–33	27	3.0	31–34
S2	8	24–32	26	2.6	28–32
S3	8	23–33	27	3.0	31–36
S4	8	28–36	31	3.1	34–39
S5	8	29–41	33	3.9	37–42
S6	8	29–47	36	5.3	39–45
S7	8	32–48	38	5.4	44–48
S8	8	36–48	41	4.2	44–49
S9	8	35–44	39	3.1	45–52
S10	8	31–41	37	3.6	38–46
S11	5	26–30	28	1.6	31–40
MD4 (ac)	7	37–48	42	4.0	31–44
MD5 (ac)	7	47–57	52	3.4	42–56
MD6 (ac)	7	53–63	56	3.2	59–70
MD7 (ac)	7	55–72	64	8.7	67–78
MD8 (ac)	5	65–87	80	10.2	71–98
LV6 (ac)	8	31–42	38	4.5	33–43
LV7 (ac)	8	35–48	40	4.8	41–48
LV8 (ac)	8	33–47	43	6.2	44–61
LV9 (ac)	8	35–47	41	5.2	40–60
LTS	8	175–213	189	12.2	205–248
LTS/TL	8	65–94%	74%	8.7%	68.8–78.8%
LTAS	4	54–70	62	7.0	128–133

subdorsal, laterodorsal, sublateral and ventrolateral positions on segment 2, in sublateral positions on segments 3 and 8, and in midlateral positions on segments 4 and 5 (Figs 38–39). Tergal extensions long, with flexible tips (Figs 38D, 39G).

Echinoderes juliae is one of the deep-sea species originally found on the abyssal plain off Oregon and along the continental rise off California, in the Northeast Pacific at depths of 2702 to 3679 m (Sørensen *et al.* 2018). Recently, its presence was also recorded on the abyssal plain, east of the Atacama Trench in the southeast Pacific at a depth of 2560 m (Grzelak *et al.* 2021).

Despite a significant geographic distance, the Hikurangi Margin individuals examined for the present study follow the morphology and morphometrics of *E. juliae* from the northeast Pacific type locality closely. Differences were only detected for the glandular cell outlets type 2 on segment 4, which are

displaced from sublateral to midlateral positions in the New Zealand specimens (Figs 38B, 39C–D), and the length of the lateral terminal accessory spines, which are twice as long in individuals from the US west coast (see Table 28). Nevertheless, the distribution and arrangement of the other cuticular structures were in line with the original description, and thus we feel confident that the recorded specimens are *E. juliae*.

Discussion

The present study provides the first overview of mud dragon species inhabiting deep waters east of New Zealand. Our material revealed 15 species of *Echinoderes*, of which ten are described as a new species.

Echinoderes is the most widespread and species-rich kinorhynch genus. By mid-2022, it accommodated 137 valid species representing more than 40% of the total Kinorhyncha diversity. *Echinoderes* overwhelms the kinorhynch communities regardless of water depth or latitude (e.g., Dal Zotto & Todaro 2016; Sørensen *et al.* 2018; Grzelak & Sørensen 2019; Landers *et al.* 2020; Grzelak *et al.* 2021). The findings in our study were no different from those observations: out of 204 adult individuals, 194 belonged to the genus *Echinoderes* and only ten specimens to other genera. *Echinoderes* not only dominated in the Hikurangi Margin material, but also shows a high regional diversity, which is comparable to other temperate or tropical regions (Pardos *et al.* 2016a, 2016b; Landers *et al.* 2018, 2019). Also, it was not surprising to find a high number of new species. New Zealand territory has hardly been explored so far in terms of its kinorhynch fauna, thus confirming the notion that the true diversity of Kinorhyncha is severely underestimated due to limited sampling effort.

Different habitats usually harbor distinct communities and therefore contribute to overall deep-sea diversity, as was observed for other meiofaunal taxa (Vanreusel *et al.* 2010). Our results seem to confirm this observation only partially, since many recorded species of *Echinoderes* were not restricted in their distribution regarding habitat type or water depth (Fig. 40). Six species, i.e., *E. sp. aff. E. galadrietae/beringensis*, *E. sp. aff. E. lupherorum*, *E. frodoi* sp. nov., *E. galadrietae* sp. nov., *E. juliae* and *E. samwisei* sp. nov., were present in every surveyed habitat, and three additional species, i.e., *E. aragorni* sp. nov., *E. landersi* sp. nov. and *E. legolasi* sp. nov., occurred in two habitat types. Among all, the canyon communities differed the most from those on seamounts and slopes due to differences in the number of total recorded species and the number of unique species. Canyons supported the highest diversity with twelve out of fifteen recorded species being present in this environment, as well as the highest number of exclusive species (Fig. 40). Among them, *E. gandalfi* sp. nov. was the most abundant species of all recorded during the present study. The dominance of *E. gandalfi* in canyons, a habitat associated with strong hydrodynamic conditions, high sediment transport and accumulation rates (Ingels *et al.* 2009; Rosli *et al.* 2018), may indicate its opportunistic behavior and ability to adapt to and tolerate challenging environmental conditions better than other species. Another species characteristic of this habitat was *E. blazeji* sp. nov. This record seems to be of particular interest, since *E. blazeji* belongs to the *E. coulli* species group, which so far has been considered as typical shallow-water species. There are 17 species in this group (Randsø *et al.* 2019; Yamasaki *et al.* 2020a; ; Cepeda *et al.* 2022; Kennedy *et al.* 2022) and a majority were observed in intertidal marine or brackish water, with the exception of four species that inhabit subtidal, but yet shallow, marine waters (Lundbye *et al.* 2011; Yamasaki 2016; Kennedy *et al.* 2022). Therefore, the occurrence of a representative of the *E. coulli*-group in deep waters probably suggests that physico-chemical properties of the waters are major driving factors affecting the species distribution of the *E. coulli*-group rather than bathymetry per se. Canyons are very heterogeneous habitats, complex systems in terms of topography, hydrography and sedimentology (McClain & Barry 2010; Ingels *et al.* 2011), where also discharges of fresh-brackish water can occur (Hong *et al.* 2019; Paldor *et al.* 2020). Submarine groundwater discharge is a global phenomenon observed at numerous shallow and deep-water sites (Burnett *et al.* 2001; Bratton 2010), thus the presence of *E. blazeji* in Pahaua and Honeycomb canyons may indicate that this process occurs in the investigated region. The last two

species found exclusively in canyons were *E. dalzottoi* sp. nov. and *E. leduci* sp. nov. Both species share a number of morphological features, among which the complete lack of cuticular hairs is the most conspicuous. *Echinoderes dalzottoi* and *E. leduci* co-occur consistently at the stations, indicating that these species not only share morphological traits but also habitat preferences, which may confirm our assumption of a close relationship/association between them.

The slope community was characterized by the presence of ten species (Fig. 40), of which only one was unique for this habitat. *Echinoderes* sp. aff. *E. unispinosus* was present at only one station on the slope, but it is hard to consider this species as an indicator of a particular habitat, not only because it occurred in very low numbers (3 individuals), but also because *E. unispinosus* is known for its wide geographic

A

Species	canyon	seamount	slope
<i>E. sp. aff. balerioni</i>			
<i>E. sp. aff. galadrietae/beringiensis</i>			
<i>E. sp. aff. lupherorum</i>			
<i>E. sp. aff. unispinosus</i>			
<i>E. aragorni</i> sp. nov.			
<i>E. blazeji</i> sp. nov.			
<i>E. dalzottoi</i> sp. nov.			
<i>E. frodoi</i> sp. nov.			
<i>E. galadrietae</i> sp. nov.			
<i>E. gandalfi</i> sp. nov.			
<i>E. juliae</i>			
<i>E. landersi</i> sp. nov.			
<i>E. leduci</i> sp. nov.			
<i>E. legolasi</i> sp. nov.			
<i>E. samwisei</i> sp. nov.			

B

Species	<750 m	750-1000 m	1000-1250 m	1250-1500 m	>1500 m
<i>E. sp. aff. balerioni</i>					
<i>E. sp. aff. galadrietae/beringiensis</i>					
<i>E. sp. aff. lupherorum</i>					
<i>E. sp. aff. unispinosus</i>					
<i>E. aragorni</i> sp. nov.					
<i>E. blazeji</i> sp. nov.					
<i>E. dalzottoi</i> sp. nov.					
<i>E. frodoi</i> sp. nov.					
<i>E. galadrietae</i> sp. nov.					
<i>E. gandalfi</i> sp. nov.					
<i>E. juliae</i>					
<i>E. landersi</i> sp. nov.					
<i>E. leduci</i> sp. nov.					
<i>E. legolasi</i> sp. nov.					
<i>E. samwisei</i> sp. nov.					

Fig. 40. Distribution of species of *Echinoderes* Claparède, 1863 according to (A) habitat type and (B) depth range. Species that occur only in one habitat type or at one depth range are highlighted in the corresponding colours.

distribution and presence in a range of habitats, including cold seeps and seamounts (Sørensen *et al.* 2018; Yamasaki *et al.* 2018b; Cepeda *et al.* 2020; Alvarez-Castillo *et al.* 2020). In contrast, our results are rather in line with observations made for other deep-sea taxa, which suggest that relatively widely distributed species tend to occur at low densities.

The lowest species pool was noted for the seamount habitat (Fig. 40), which is in contrast to observations made by Rosli *et al.* (2018) for nematode diversity. These authors argue that active hydrodynamic conditions occurring on seamounts may increase spatial variation in sedimentation processes and food availability in the sediment, thus supporting more diverse communities in seamount habitats of the Hikurangi region relative to canyon and slope habitats (Rosli *et al.* 2018). Nevertheless, despite the fact that the seamount diversity of *Echinoderes* was the lowest in our study, we noted eight species (Fig. 40), which significantly increases the number of species of *Echinoderes* recorded for this type of habitat. According to Yamasaki *et al.* (2019), fifteen species of *Echinoderes* have been reported from seamounts globally. Of the species recorded in the Hikurangi region, none have previously been observed on other seamounts (Yamasaki *et al.* 2019). Additionally, none of the species from the present study were closely related to other seamount species reported by Yamasaki *et al.* (2019). However, the species composition at the investigated seamounts was not unique and seven out of eight species also occurred in other habitats (Fig. 40). Only *E. sp. aff. E. balerioni* was exclusively present on a seamount. So far, *E. balerioni* has been known only from the Arctic: from the Yermak Plateau north of Svalbard (Grzelak & Sørensen 2019) and the Bering Sea, Alaska (Grzelak, unpubl. obs.).

The results of the present study also provide interesting information about known species of *Echinoderes*. In our material we found *E. juliae*, the second most abundant species in our material, and individuals that closely followed the morphology of *E. lupherorum*, *E. unispinosus*, *E. balerioni* and *E. galadrielaeberingiensis*. The former two species are known from the northeast Pacific, the abyssal plain and the continental rise off California (Sørensen *et al.* 2018) and *E. juliae* was additionally noted in the southeast Pacific (Grzelak *et al.* 2021). *Echinoderes unispinosus* is already considered as one of the species with the widest geographic distribution, as it was described from the Northeast Atlantic and subsequently noted in the Gulf of Mexico, off the Pacific coast of the United States and in the Mozambique Channel in the western Indian Ocean (Sørensen *et al.* 2018; Yamasaki *et al.* 2018b; Alvarez-Castillo *et al.* 2020; Cepeda *et al.* 2020). The least is known to date about *E. balerioni*, considered as an Arctic species (Grzelak & Sørensen 2019). Therefore, if the species reported from New Zealand is conspecific with the abovementioned species, these findings significantly extend its known distribution, and support the suggestions about the capability of deep-sea kinorhynch species to disperse over great distances (Neuhaus & Sørensen 2013; Sørensen *et al.* 2018; Yamasaki *et al.* 2018a, 2019; Grzelak *et al.* 2021), enabled, e.g., through deep-sea currents or thermohaline circulation (Pawłowski *et al.* 2007; Ptatscheck & Traunspurger 2020). Moreover, with the results of the present study it can be concluded that species that were thought to be limited in their range or typical of a particular environment as, e.g., *E. balerioni*, could turn out to have a much wider distribution and known distribution ranges of kinorhynch species should be treated with caution, since the low number of studies limits available information of diversity and distribution patterns of species.

Conclusions

Current information on New Zealand kinorhynchs is still very scarce, and with the exception of the Hikurangi Margin, the kinorhynch fauna in other regions of New Zealand may be considered unexplored. Future research should focus on the coastal areas, the Bay of Plenty which potentially harbours a diverse kinorhynch fauna, and other deep-water habitats to the north, west and south. With the limited knowledge that is currently available, it is difficult to estimate the true kinorhynch biodiversity around New Zealand, but just by looking at the diversity of *Echinoderes* and the number of new species that

have been found only along the Hikurangi Margin, we can expect that New Zealand's territory is a region with a relatively high biodiversity.

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