ORIGINAL ARTICLE



Check for updates

Species diversity of eukalyptorhynch flatworms (Platyhelminthes, Rhabdocoela) from the coastal margin of British Columbia: Polycystididae, Koinocystididae and Gnathorhynchidae

Niels W. L. Van Steenkiste and Brian S. Leander

Beaty Biodiversity Research Centre, Departments of Botany and Zoology, University of British Columbia, Vancouver, BC, Canada

ABSTRACT

Kalyptorhynchs are abundant members of meiofaunal communities worldwide, but knowledge on their overall species diversity and distribution is poor. Here we report twenty species of eukalyptorhynchs associated with algae and sediments from the coastal margin of British Columbia. Two species, *Paulodora artoisi* sp. nov. and *Limipolycystis castelinae* sp. nov., are new to science and described based on their unique stylet morphology. New observations on two morphotypes of *Phonorhynchus helgolandicus* and two morphotypes of *Scanorhynchus forcipatus* suggest that the different morphotypes represent different species; accordingly, *Phonorhynchus contortus* sp. nov., *Phonorhynchus velatus* sp. nov. and *Scanorhynchus herranzae* sp. nov. are described here as separate species. Furthermore, we report on the occurrence and morphology of *Polycystis hamata*, *Polycystis naegelii*, *Austrorhynchus pacificus*, *Austrorhynchus californicus*, *Paraustrorhynchus pacificus*, *Alcha evelinae*, *Duplacrorhynchus minor*, *Yaquinaia microrhynchus*, *Gyratrix hermaphroditus* s. I., *Scanorhynchus forcipatus*, *Rhinolasius dillonicus*, *Itaipusa biglandula*, *Utelga heinckei*, *Neognathorhynchus suecicus* and *Zonorhynchus seminascatus*.

ARTICLE HISTORY

Received 11 June 2018 Accepted 23 January 2019 Published online 26 February 2019

SUBJECT EDITOR Danny Eibye-Jacobsen

KEYWORDS

Flatworms; Pacific Ocean; Kalyptorhynchia; species discovery; microturbellaria; meiofauna

Introduction

Kalyptorhynchs comprise an important group of predatory microturbellarians in marine habitats around the globe. While several studies have shown that they comprise a species-rich component of meiofaunal communities (e.g. Fonseca et al. 2017), we know very little about their occurrence and biodiversity in many parts of the world. Coastal areas of the Northeast Pacific Ocean are among the most productive and harbour high levels of biodiversity, yet meiofauna is greatly underrepresented in biodiversity surveys of this region. A number of studies from the previous century report on kalyptorhynchs in the Northeast Pacific Ocean (Schockaert and Karling 1970; Karling 1977, 1980, 1982, 1983, 1986, 1989; Karling and Schockaert 1977; Ax and Armonies 1990); however, the study area in these works is mostly confined to a few localities in Alaska, Oregon and California. With numerous islands, inlets, and about 25,000 km of coastline, the coastal margin of British Columbia represents an important, but poorly explored part of the Northeast Pacific Ocean. Recently, six kalyptorhynchs were reported from the west coast of Vancouver Island and Vancouver (Rundell and Leander 2014), but this is only a tiny fraction of the actual number of species in British Columbia.

Of the 39 kalyptorhynch species described from the Northeast Pacific Ocean, 28 are eukalyptorhynchs (with an undivided proboscis) and 11 are schizorhynchs (with a split proboscis). Eukalyptorhynchia comprises the majority of known kalyptorhynch species and consists of several families. A recent molecular phylogenetic analysis based on 18S and 28S rDNA sequences by Tessens et al. (2014) has changed our understanding of the evolutionary relationships between most of the known eukalyptorhynch (sub)families and genera. Based on this phylogenetic framework, a new classification was proposed. Polycystididae, Koinocystididae and Gnathorhynchidae (sensu Tessens et al. 2014) are the most species-rich groups, and representatives of these taxa are common in marine sediments and on intertidal seaweeds. The members of the Polycystididae encompass the bulk of eukalyptorhynch species and are characterized by an impressive

CONTACT Niels W. L. Van Steenkiste inite_van_steenkiste@hotmail.com inite@hotmail.com inite@hotmail.co

diversity and complexity of atrial organs (Artois and Schockaert 2003, 2005). Members of the Koinocystididae have a very large proboscis with a typical sphincter at the base of the cone, a complex copulatory organ usually adorned with sclerotized structures, and a copulatory bursa (Brunet 1972; Karling 1980). Members of the Gnathorhynchidae can easily be recognized by their armed proboscis featuring a pair of sclerotized hooks (Den Hartog 1968).

In order to improve knowledge about the overall diversity of microturbellarians in the Northeast Pacific Ocean, we have been surveying intertidal and subtidal sediments and intertidal algae from the coast of British Columbia since 2015. Contributions on dalytyphloplanids can be found in Van Steenkiste and Leander (2018), Van Steenkiste et al. (2018) and Stephenson et al. (2019). In this work, we focus on the Polycystididae, Koinocystididae and Gnathorhynchidae. We provide an overview of all 30 species of Polycystididae, Koinocystididae and Gnathorhynchidae currently known from the Northeast Pacific Ocean, including the new records and species described in this contribution.

Material and methods

Collection and morphological examination of the taxa

Specimens were collected in 2015–2018 from beaches, rocky intertidal zones and estuarine mudflats along the Pacific coast of British Columbia, Canada (Figure 1). Sampling locations are in several regional marine ecozones, such as the Juan de Fuca Strait (Victoria), the Vancouver Island Shelf (Bamfield), the Strait of Georgia (Vancouver, Surrey, Nanaimo), and the North Coast Fjords (Calvert Island). Intertidal samples were taken by hand, subtidal samples were all taken with the aid of a small handheld meiobenthic dredge (± 10 L), except for the Hunter Island sample which was taken with a Ponar grab sampler. *Alcha evelinae* Marcus, 1949 was also collected in Curaçao during a sampling campaign in 2016.

Live animals were isolated from a few scoops of sand or a handful of algae using the MgCl₂ decantation method (Schockaert 1996). Alcha evelinae, Rhinolasius dillonicus Karling, 1980 and Itaipusa biglandula Reygel et al., 2011 were collected from mud spread out in a large tray (±10 L) using the oxygen depletion method (Schockaert 1996). Specimens were studied alive with the aid of a stereoscope and DIC optics, and photographed under different magnifications. Specimens with sclerotized parts (e.g. proboscis hooks, stylet, cirrus), were subsequently whole mounted with lactophenol for preservation. These hard parts were then photographed, measured and drawn to aid in the identification and description of the animals. Most pictures were taken with a Zeiss Axioplan 2 microscope equipped with a Zeiss Axiocam 503 colour camera. Some pictures were taken with a Leica DMIL inverted microscope equipped with a Leica MC170 HD camera. Pictures of all whole mounts presented in the figures were produced in Helicon Focus (HeliconSoft) by stacking series of micrographs. Measurements were taken from whole-mounted and live specimens using Zeiss ZEN 2 software. All measurements were



Figure 1. Sampling locations of eukalyptorhynchs in this study. (a) Position of British Columbia along the Pacific Coast of North America. (b) Sampling locations on the coastal margin of British Columbia.

Schockaert (2003, 2005). The examined material is thoroughly compared to the existing primary literature for species identification and differential diagnosis (Schockaert and Karling 1970; Karling and Schockaert 1977; Karling 1956a, 1956b, 1977, 1980, 1982, 1986; Artois and Tessens 2008; Reygel et al. 2011; Artois et al. 2012). Listings of synonymies for each species are only mentioned when relevant taxonomic changes occur. The holotypes of Paulodora artoisi sp. nov., Phonorhynchus contortus sp. nov., Phonorhynchus velatus sp. nov. and Scanorhynchus herranzae sp. nov. are deposited in the Swedish Museum of Natural History (SMNH, Stockholm, Sweden). The holotype of Limipolycystis castelinae sp. nov. and all other whole mounts are deposited in the Beaty Biodiversity Museum (BBM, University of British Columbia, Vancouver, Canada).

we use the terminology proposed by Artois and

Results and discussion

Species diversity in the Northeast Pacific Ocean

Table I lists all 30 species of Polycystididae, Koinocystididae and Gnathorhynchidae currently known from the Northeast Pacific Ocean, including the new species and records of this study. Most species belong to the Polycystididae (18); Koinocystididae (9) and Gnathorhynchidae (3) count fewer species. Of these, 19 are reported from British Columbia, 6 of which have only been found there so far. Twenty-one species seem to be confined to the Northeast Pacific as they have not been reported from any other part of the world. The nominal species Polycystis naegelii Kölliker, 1845, Alcha evelinae, Gyratrix hermaphroditus Ehrenberg, 1831 s. l., Gyratrix proaviformis Karling & Schockaert, 1977, Scanorhynchus forcipatus Karling, 1955, Utelga heinckei (Attems, 1897), Utelga pseudoheinckei Karling, 1980 and Neognathorhynchus suecicus Karling, 1956 seem to have widespread distributions. However, G. hermaphroditus s. l. is known to be a (pseudo-cryptic) species complex, and it cannot be excluded that some of the other above-mentioned nominal species also consist of multiple species (see remarks and discussion on P. naegelii, Alcha evelinae and G. hermaphroditus s. l.). Itaipusa biglandula has only been found in two distant locations in the Pacific Ocean (British Columbia and the Galápagos Islands).

All kalyptorhynchs are hermaphroditic and have complex male and female genital systems. In most genera, species differ from each other in the morphology of traits involved in sexual reproduction (e.g. stylet, prostate vesicle, seminal receptacle, female duct) and feeding (proboscis). This makes kalyptorhynchs an interesting group to study the relations between feeding strategies, sexual reproduction, sexual selection and speciation. Increasing knowledge on species diversity and morphology from poorly sampled regions will provide valuable insights into the evolution, biogeography and ecology of meiofauna in general and microturbellarians in particular. As has also been demonstrated in other meiofaunal taxa (e.g. kinorhynchs, Herranz et al. 2018; schizorhynchs, Rundell and Leander 2014; thalassotyphloplanids, Van Steenkiste and Leander 2018; dalytyphloplanids, Stephenson et al. 2019), the diversity of rhabdocoels in the Northeast Pacific is only partly known. This region thus offers an exciting potential for species discovery and exploration.

Taxonomy

Polycystididae von Graff, 1905 Polycystidinae Schockaert & Karling, 1970

Polycystis Kölliker, 1845

Polycystis hamata Karling, 1986 (Figure 2a,b)

Material examined

Observations on at least ten live animals. Seventeen whole mounts (Victoria: BBM MI4124–4127; Calvert Island: BBM MI4128–4134; Wizard Islet, Bamfield: BBM MI4135–4139; Grappler Inlet, Bamfield: BBM MI4140).

Diagnosis

Species of *Polycystis*. Prostate stylet type I 25–59 μ m long with a proximal funnel, a 25–55 μ m-wide, partly toothed, distal collar, and distinctive hooked spur.

Description

Large, plump animals between 1.3 and 4 mm long, caudally and anteriorly tapering. Adults usually opaque white, sometimes with various colouration and coloured vesicles (Figure 2a). General appearance and internal organization as described by Karling (1986). Prostate stylet type I is 42–59 µm long ($\bar{x} = 51$ µm; n = 17) with a 44–52 µm-wide ($\bar{x} = 48$ µm; n = 17), partly toothed, distal collar and a distinctive hooked

Table I. Checklist of Polycystididae,	Koinocystididae and	Gnathorhynchidae in	the Northeast	Pacific Ocean including the new
records.				

Таха	Distribution in the Northeast Pacific	Distribution in other localities	Reference
Polycystididae Von Graff, 1905			
Polycystidinae Schockaert & Karling, 1970			
Polycystis californica Artois & Tessens,	California		Karling (1986); Artois and Tessens
2008	Camorina		(2008)
Polycystis hamata Karling, 1986	California, Oregon, British		This study
	Columbia		·
Polycystis naegelii Kölliker, 1845	British Columbia	W Atlantic, E Atlantic, NE Atlantic;	This study
		Mediterranean and Black Sea	
Paulodora artoisi sp. nov.	British Columbia		This study
Austrorhynchus pacificus Karling, 1977	California, Oregon, British		This study
	Columbia		
Austrorhynchus californicus Karling,	California, Oregon, British		This study
1977	Columbia Colifornia British Columbia		This study
Paraustrorhynchus pacificus Karling &	California, British Columbia		This study
Schockaert, 1977	California Duitich Calumphia	C Desife C Desife W/ Atlantic CW/ Atlantic	The in a standard
Alcha evelinae Marcus, 1949	California, British Columbia	E Pacific, C Pacific; W Atlantic, SW Atlantic;	This study
Duplacrorhynchus minor Schockaert &	California, British Columbia	W Indian Ocean	This study
Karling, 1970	California, British Columbia		
Duplacrorhynchus major Schockaert &	Oregon, Alaska		Schockaert and Karling (1970);
Karling, 1970	oregon, Alaska		Ax and Armonies (1990)
Yaquinaia microrhynchus Schockaert &	Oregon, British Columbia		This study
Karling, 1970	oregon, british columbia		This study
Phonorhynchus contortus sp. nov.	California, Oregon, British		This study
<i>,</i>	Columbia		,
Phonorhynchus velatus sp. nov.	California, British Columbia		This study
Gyratricinae von Graff, 1905			
Gyratrix hermaphroditus Ehrenberg,	California, Oregon, British	Cosmopolitan, euryhaline	This study
1831 s. l.	Columbia, Alaska		
Gyratrix proaviformis Karling &	Oregon	Mediterranean	Karling and Schockaert (1977);
Schockaert, 1977			Tessens et al. (2014)
Typhlopolycystidinae Evdonin, 1977			
Limipolycystis castelinae sp. nov.	British Columbia		This study
Scanorhynchinae Tessens et al., 2014			
Scanorhynchus forcipatus Karling, 1955	California, British Columbia	NE Atlantic	This study
Scanorhynchus herranzae sp. nov.	California, British Columbia		This study
Koinocystididae Meixner, 1924	California Britich Columbia		This study
Rhinolasius dillonicus Karling, 1980 Itaipusa biglandula Reygel et al., 2011	California, British Columbia British Columbia	E Pacific	This study This study
Itaipusa bispina Karling, 1980	California, Oregon	E Pacific	Karling (1980)
Itaipusa curvicirra Karling, 1980	California, Oregon		Karling (1980)
Utelga heinckei (Attems, 1897)	British Columbia	E Pacific; NW Atlantic, NE Atlantic;	This study
otelga hemener (Attems, 1057)	british columbia	Mediterranean and Black Sea	This study
Utelga pseudoheinckei Karling, 1980	California	NE Atlantic; Mediterranean and Black Sea	Karling (1980)
Utelga montereyensis Karling, 1980	California		Karling (1980)
Neoutelga inermis Karling, 1980	California		Karling (1980)
Groveia unicornis Karling, 1980	California		Karling (1980)
Gnathorhynchidae Meixner, 1929			-
Neognathorhynchus suecicus Karling,	British Columbia	NE Atlantic	This study
1956			
Prognathorhynchus dividibulbosus Ax &	Alaska		Ax and Armonies (1990)
Armonies, 1990			
Uncinorhynchus pacificus Karling, 1989	Oregon		Karling (1989)

Note: References for the species treated in this study can be found in the text.

spur (Figure 2b). The relative size of the spur varies somewhat between individuals.

Distribution

New localities: Clover Point, Victoria, British Columbia, Canada (48°24'12"N, 123°21'03"W), algae in rocky lower intertidal (May 6, 2015; January 28, 2018). Meay Inlet, Calvert Island, British Columbia, Canada (51° 39'52"N, 128°05'47"W), algae in rocky lower intertidal (June 6, 2015; April 10, 2016). Wizard Islet, Bamfield, British Columbia, Canada (48°51′30″N, 125°09′33″W), algae in rocky lower intertidal (June 1, 2015). Grappler Inlet, Bamfield, British Columbia, Canada (48°50′17″N, 125°08′04″W), algae in rocky lower intertidal (August 30, 2015).

Known distribution: Northeast Pacific Ocean: Hopkins Marine Station, Pacific Grove, California and Whale Cove, Yaquina Head and Newport, Oregon (Karling 1986).



Figure 2. *Polycystis hamata.* (a) Live specimen slightly squeezed under cover slip. (b) Prostate stylet type I from a whole-mounted specimen. *Polycystis naegelii.* (c) Prostate stylet type I from a whole-mounted specimen. *Paulodora artoisi* sp. nov. (d) Live specimen slightly squeezed under cover slip. (e) Detail of the atrial organs in the live specimen. (f) Prostate stylet type I from the whole-mounted specimen (holotype). Abbreviations: b, bursa; co, copulatory organ; de, ejaculatory duct; e, eye; o, ovary; p, proboscis; ph, pharynx; pv1, prostate vesicle type I; st1, prostate stylet type I; t, testis; vi, vitellaria; vs, seminal vesicle. Scale bars; a, $d = 100 \ \mu m$; b-c, $e-f = 20 \ \mu m$.

Comparisons

This species closely resembles other species of *Polycystis*, but can be recognized by the distinctive hooked spur on the prostate stylet type I.

Remarks

One individual was observed carrying a large stalked egg. *Polycystis hamata* can be very abundant on algae in the intertidal.

Polycystis naegelii Kölliker, 1845 (Figure 2c)

Material examined

Observations on one live animal. One whole mount (Bamfield: BBM MI4141).

Diagnosis

Species of *Polycystis*. Prostate stylet type I with a distinctive, very long spur.

Description

Morphology as other species of *Polycystis*. Unmistakable prostate stylet type I with a distinctive long spur (Figure 2c). The prostate stylet type I is 74 μ m long, the distal collar is 45 μ m wide. The spur measures 180 μ m.

Distribution

New locality: Wizard Islet, Bamfield, British Columbia, Canada (48°51′30″N, 125°09′33″W), algae in rocky lower intertidal (June 1, 2015).

Known distribution: Northeast Atlantic Ocean: North Sea, Bay of Biscay, English Channel, Isles of Scilly, Firth of Clyde (von Graff 1913 and references therein; Faubel and Warwick 2005). Mediterranean, Sea of Marmara and Black Sea (von Graff 1913 and references therein; Ax 1959; Mack-Fira 1974; Tessens et al. 2014). East Atlantic Ocean: Madeira and Canary Islands (von Graff 1913 and references therein). West Atlantic Ocean: Bermuda (Karling 1978).

Comparisons

This species closely resembles other species of *Polycystis*, but can be recognized by the very long spur on the prostate stylet type I.

Remarks

Polycystis naegelii co-occurs at the same locality with P. hamata and can only be distinguished from the latter species after careful observation of the stylet. Polycystis naegelii is widespread in the Atlantic Ocean, but this is the first record of this species in the Pacific Ocean. Some variation in stylet morphology and biometrics has been reported for different populations (e.g. von Graff 1913; Karling 1978). No measurements are available for many of the older records of this species, but the prostate stylet type I in the specimens from Bermuda only measures 70-80 µm including the spur (Karling 1978). Based on its wide geographical distribution and morphological variation between populations, it is possible that the nominal species P. naegelii consists of a complex of closely related species (see also remarks on Alcha evelinae). A thorough revision of this taxon is necessary, including morphological and molecular data of different geographic populations.

Paulodora Marcus, 1948

Paulodora artoisi sp. nov. (Figure 2d,f)

Material examined

Holotype: One whole mount (Calvert Island: SMNH type-9108). *Other material:* Images of the live type specimen.

Diagnosis

Species of *Paulodora* with a sickle-shaped, 139 μ m-long prostate stylet type I. Outer stylet with a 26 μ m-long, 36 μ m-wide proximal funnel, a more or less straight to slightly curved section with an inconspicuous protrusion, a 90° curve, and a more or less straight tube that ends in a sharp point. Inner stylet starts at distal part of the funnel and runs along the concave side of the curve.

Description

Animal about 1.1 mm long, with a dark yellow parenchymatous colouration (Figure 2d). Proboscis and pharynx are 200 and 170 μ m long, respectively, both are typical for Polycystididae. Proboscis cone and bulb about the same length. Paired eyes just behind the proboscis. Pharynx situated in the first body half, somewhat elongated with posterior pharyngeal teeth. Paired testes on each side of the body, stretching from the proboscis to behind the pharynx (Figure 2d). Paired seminal vesicles large and filled with sperm. The remainder of the male genital system is composed of a prostate vesicle type I, prostate stylet type I and an ejaculatory duct (Figure 2e). The prostate vesicle type I is relatively small, more or less globular, and filled with two types of prostate secretions; a peripheral lighter secretion and more centrally located denser secretion. The ejaculatory duct runs partly alongside the prostate vesicle type I, but its connection to the seminal vesicles could not be seen. The double-walled, 139 µm-long prostate stylet type I is sickle-shaped and consists of an inner and outer stylet (Figure 2f). The proximal part of the outer stylet forms a robust, 26 µm-long funnel that envelops the distal part of the prostate vesicle type I. The proximal opening of the funnel is about 36 µm wide. The inner stylet starts at the distal part of the funnel and receives the secretions of the prostate glands. Sperm of the ejaculatory duct empties in an inconspicuous protrusion of a more or less straight to slightly curved section of the outer stylet just distal of the funnel (arrow in Figure 2f). From there on, the outer stylet makes a sharp, 90° curve, and runs more or less straight to gradually taper off in a sharp point. The inner stylet runs along the concave side of the curve, but its course in the distal straight 1/3 of the stylet is not fully clear. In the live animal, two ovaries and a tissue mass with sperm vesicles (most likely the bursa) are visible posterior to the male system. At least on one ovary, a 'nozzle-like' structure could be observed (arrow in Figure 2e).

Distribution

Type locality: Meay Inlet, Calvert Island, British Columbia, Canada (51°39′52″N, 128°05′47″W), algae in rocky lower intertidal (June 6, 2015).

Etymology

Species epithet in honour of Prof. Dr. Tom Artois, Ph.D. supervisor of NVS, and one of the world's foremost rhabdocoel experts.

Comparisons

The combination of several morphological characters, including the polycystidid-type proboscis and

pharynx, paired testes, ovaries and seminal vesicles, the presence of a prostate vesicle type I and prostate stylet type I, the absence of accessory glands type I, the proximal entry of the ejaculatory in the prostate stylet type I, and the likely presence of ovarian 'nozzles' (sclerotic, umbrella-shaped elements between the bursal system and each ovary; see Artois and Schockaert 2005), indicates this specimen is a representative of the genus Paulodora (see Artois and Tessens 2008 for a recent discussion on this genus). The fifteen recognized species of this genus can be distinguished from each other based on the detailed morphology of the prostate stylet type I. Four species, P. drepanophora Artois & Tessens, 2008, P. hamifer Artois & Tessens, 2008, P. schockaerti Artois & Tessens, 2008, and P. subcontorta (Schockaert, 1982), have a sickleshaped or hook-shaped prostate stylet type I. The first three species also have a protrusion just distal from the proximal funnel where the ejaculatory duct empties into the outer stylet, very pronounced and flap-like in P. drepanophora, semitubular and folded in P. hamifer and P. schockaerti. Paulodora subcontorta lacks such a protrusion and thus has a prostate stylet type I more similar to P. artoisi sp. nov. However, the prostate stylet type I of P. subcontorta has a blunt distal tip and the curvature of the entire stylet is more gentle than in P. artoisi sp. nov. Based on its stylet morphology, P. artoisi sp. nov. can easily be recognized from other species of Paulodora.

Remarks

Paulodora artoisi sp. nov. is the first Paulodora species recorded from a temperate location of the Pacific Ocean. Most species of Paulodora are found in tropical seas or the Mediterranean (Artois and Tessens 2008). Paulodora contorta (Schockaert & Karling, 1975) is the only other species that is also found in temperate waters (Norwegian Sea). Paulodora asymmetrica Artois & Schockaert, 2001 from the Galápagos Islands is the only other species from the Pacific Ocean.

Austrorhynchus Karling, 1952

Austrorhynchus pacificus Karling, 1977 (Figure 3a,b)

Material examined

Observations on at least five live animals. Seven whole mounts (Victoria: BBM Ml4142–4146; Meay Inlet, Calvert Island: BBM Ml4147; Little Wolf Beach, Calvert Island: BBM Ml4148).

Diagnosis

Slightly amended from Karling (1977). Species of *Austrorhynchus*. Prostate stylet type II 22–44 μ m without a hook, with basal funnel and tube of equal length. Prostate stylet type III 87–116 μ m with S-shaped basal line and weakly differentiated style. Curving comb and flagellum with fine teeth.

Description

Animals between 0.6 and 0.9 mm long, caudally rounded, anteriorly tapering. Mostly transparent with some light brown colouration (Figure 3a). General appearance and internal organization as in other species of *Austrorhynchus*. Prostate stylet type II and prostate stylet type III (stylet and A-organ in Karling, 1977, respectively; see Artois & Schockaert, 2003 for current terminology) correspond to those of *A. pacificus* as described by Karling (1977) (Figure 3b). Prostate stylet type II is 33–43 µm long ($\bar{x} = 40 \ \mum; n = 6$) and consists of a 16–25 µm-long proximal funnel ($\bar{x} = 23 \ \mum; n = 6$) and a 16–19 µm-long distal tube ($\bar{x} = 18 \ \mum; n = 6$). Prostate stylet type III measures 90–109 µm ($\bar{x} = 102 \ \mum;$ non-axial: 74–82 µm, $\bar{x} = 77 \ \mum; n = 6$) from the base of the foot to the tip of the flagellum. The combed plate is 33–43 µm wide ($\bar{x} = 38 \ \mum; n = 6$).

Distribution

New localities: Clover Point, Victoria, British Columbia, Canada (48°24'12"N, 123°21'03"W), algae in rocky lower intertidal (September 2, 2015; March 3, 2016). Meay Inlet, Calvert Island, British Columbia, Canada (51°39'52"N, 128°05'47"W), algae in rocky lower intertidal (June 6, 2015). Little Wolf Beach, Calvert Island, British Columbia, Canada (51°39'53"N, 128°07'44"W), algae in rocky lower intertidal (April 7, 2016).

Known distribution: Northeast Pacific Ocean: Point Pinos, Pacific Grove, California and Newport area, Oregon (Karling 1977).

Comparisons

This species closely resembles *A. californicus* Karling, 1977, and *A. hawaiiensis* Karling, 1977, but differs in lacking a hook in the prostate stylet type II (see Karling 1977).

Remarks

Our measurements fall completely within the range of the measurements for the specimens from California and Oregon studied by Karling (1977).

Austrorhynchus californicus Karling, 1977 (Figure 3c,d)



Figure 3. *Austrorhynchus pacificus.* (a) Live specimen slightly squeezed under cover slip. (b) Prostate stylet type II and prostate stylet type III from a whole-mounted specimen. *Austrorhynchus californicus.* (c,d) Prostate stylet type II and prostate stylet type III from whole-mounted specimens. *Paraustrorhynchus pacificus.* (e) Live specimen slightly squeezed under cover slip. (f) Detail of blue and brown pigment in live specimen. (g) Prostate stylet type II and prostate stylet type III from a whole-mounted specimen. *Alcha evelinae.* (h,i) Prostate stylet type III from whole-mounted specimens from British Columbia. (j) Prostate stylet type III from a whole-mounted specimen from Curaçao. Abbreviations: c, comb; e, eye; f, flagellum; o, ovary; p, proboscis; ph, pharynx; st2, prostate stylet type III; t, testis; vs, seminal vesicle. Scale bars; a, $e-f = 100 \ \mum; b-d, q-j = 20 \ \mum.$

Material examined

Observations on one live animal. Two whole mounts (Bamfield: BBM MI4149; Calvert Island: BBM MI4150).

Diagnosis

Slightly amended from Karling (1977). Species of Austrorhynchus. Prostate stylet type II 35–50 μ m, with basal funnel, hook and tube of equal length. Prostate stylet type III 87–130 μ m with triangular, proximally

pointed plate and weakly differentiated style. Transversal curving comb and flagellum with fine teeth.

Description

The prostate stylet type II is 44–49 µm long ($\bar{x} = 46$ µm; n = 2) with a 20–23 µm-long proximal funnel ($\bar{x} = 22$ µm; n = 2), a 24–26 µm-long distal tube ($\bar{x} = 25$ µm; n = 2) and a 24 µm-long distal hook ($\bar{x} = 24$ µm; n = 2) at the transition of funnel to tube (Figure 3c-d). Prostate stylet type III 98–112 µm long ($\bar{x} = 105$ µm; non-

axial: 81–89 μ m, \bar{x} = 85 μ m; n = 2) from the base of the foot to the tip of the flagellum. Combed plate 35 μ m wide (n = 1).

Distribution

New localities: Bamfield, British Columbia, Canada (48° 51'18"N, 125°09'45"W), coarse sand and pebbles at 15–20 m depth between Wizard Islet and Helby Island (August 31, 2015). Meay Inlet, Calvert Island, British Columbia, Canada (51°39'52"N, 128° 05'47"W), algae in rocky lower intertidal (June 6, 2015).

Known distribution: Northeast Pacific Ocean: Monterey Bay, California and Newport area, Oregon (Karling 1977).

Comparisons

This species closely resembles *A. hawaiiensis*, but differs in having a triangular rather than square prostate stylet type III plate, and in having finer teeth on the comb and flagellum (see Karling 1977).

Remarks

Measurements correspond to the ones from the Californian and Oregonian specimens. *Austrorhynchus californicus* and *A. pacificus* co-occur in at least one locality in California and Oregon and were also found in the same locality in British Columbia (Calvert Island). They can only be distinguished from each other after careful examination of the prostate stylets.

Paraustrorhynchus Karling & Schockaert, 1977

Paraustrorhynchus pacificus Karling & Schockaert, 1977 (Figure 3e–q)

Material examined

Observations on at least six live animals. Three whole mounts (Bamfield: BBM MI4151; Calvert Island: BBM MI4152– 4153).

Diagnosis

As in Karling and Schockaert (1977).

Description

Animals about 0.7–0.9 mm long, with subepidermal blue and brown pigment granules arranged in alternating patchy bands in at least two adult specimens (Figure 3e) and one subadult specimen from Calvert Island, and in one subadult specimen from Bamfield (Figure 3f). One subadult specimen and one adult specimen from Calvert Island seemed to lack the blue pigmentation. Ovaries with brown pigmentation in all specimens. Posterior body half often filled with orange-red lipid vesicles (Figure 3f). General appearance and internal organization as described by Karling and Schockaert (1977). The curved, doublewalled prostate stylet type II is 113–125 μ m long (\bar{x} = 119 μ m; n = 2). The prostate stylet type III consists of two long plates connected to each other by a proximal, sclerotized base (Figure 3g). A strong muscle arch inserts on this broad base. The bi-lobed, partly smooth, partly finely toothed plate measures 120-131 μ m ($\bar{x} = 125 \mu$ m; n = 2), while the other, coarsely toothed plate is 126–152 μ m long (\bar{x} = 139 μ m; n = 2).

Distribution

New localities: Deer Group Islands, Bamfield, British Columbia, Canada (48°52′22″N, 125°09′44″W), pebbles and shell hash at 6–10 m depth (June 3, 2015; August 29, 2015). Meay Inlet, Calvert Island, British Columbia, Canada (51°39′52″N, 128°05′47″W), algae in rocky lower intertidal (June 6, 2015; July 26, 2017). *Known distribution:* Northeast Pacific Ocean: Monterey Bay and Point, Pinos, Pacific Grove, California (Karling and Schockaert 1977).

Comparisons

This species differs from other species of *Paraustrorhynchus* in the morphology of its prostate stylets. For a thorough comparison between all known species of *Paraustrorhynchus*, we refer to Lin et al. (2019).

Alcha Marcus, 1949

Alcha evelinae Marcus, 1949 (Figure 3h-j)

Material examined

Observations on at least four live animals. Two whole mounts from British Columbia (Surrey: BBM Ml4154–4155), two whole mounts from Curaçao (Piscadera Bay: BBM Ml4156–4157).

Diagnosis

As in Karling and Schockaert (1977), but prostate stylet type III with triangular or bowtie-shaped basal frame.

Description

Animals about 0.6-0.7 mm long. General appearance as in Karling and Schockaert (1977). The small prostate stylet type III measures 33-40 µm $(\bar{x} = 37 \ \mu m; n = 2)$ for the British Columbia specimens and 35–36 μ m (\bar{x} = 36 μ m; n = 2) for the specimens from Curaçao. The prostate stylet type III in the Curaçaon specimens (Figure 3j) looks almost exactly as the prostate stylet type III in the Brazilian specimen studied by Karling and Schockaert (1977). The prostate stylet type III of the British Columbia specimens also has most elements described by the latter authors (Figure 3h-i). It consists of a broad proximal base and several overlapping plates with finely toothed edges. The plates are supported by two more heavily sclerotized tongue-like projections. On one of these projections, the toothed plate folds over. One plate also has a distal smooth lobe as observed in specimens from other locations. However, the base of prostate stylet type III in the British Columbia specimens seems to be slightly different from the descriptions, illustrations and figures in Marcus (1949), Karling and Schockaert (1977) and Jouk and De Vocht (1989). In specimens from other locations, the base is irregular triangular with a lateral projection, while in the British Columbia specimens it is more bowtie-shaped with a less conspicuous lateral projection.

Distribution

New locality in British Columbia: Mud Bay Park, Surrey, British Columbia, Canada (49°05′09″N, 122°51′39″W), algae in intertidal mudflat (July 29, 2015).

Other new locality: Piscadera Bay, Curaçao (12°07′20″N, 68°58′09″W), algae growing on the dock and rocks (April 26, 2016).

Known distribution: Southwest Atlantic Ocean: Brazil (Marcus 1949); Northeast Pacific Ocean: Hopkins Marine Station and Point Pinos, Pacific Grove, California (Karling and Schockaert 1977); East Pacific Ocean: Mexico (Artois and Tessens 2008); Central Pacific Ocean: Hawaii (Tessens et al. 2014); West Indian Ocean: Kenya (Jouk and De Vocht 1989; Artois and Tessens 2008).

Comparisons

Monotypic genus. The male atrial system only has a prostate stylet type III, which is a unique feature among Polycystidinae (sensu Tessens et al. 2014).

Remarks

Alcha evelinae has previously been reported from distant localities in tropical, subtropical and temperate coastal areas. Its presence in British Columbia is the northernmost record of this species to date. As is also the case for other nominal rhabdocoel species (e.g. Astrotorhynchus bifidus (McIntosh, 1875) s. l. in Van Steenkiste et al. 2018), it cannot be excluded that A. evelinae is potentially a complex of (pseudo-)cryptic species. However, detailed diagnostic features associated with the stylet are currently hard to assess on whole mounts because of their small size and overlapping structures. Until molecular data and a more thorough revision of the (stylet) morphology of different populations become available, we classify the specimens from British Columbia and Curaçao as Alcha evelinae.

Duplacrorhynchus Schockaert & Karling, 1970

Duplacrorhynchus minor Schockaert & Karling, 1970 (Figure 4a–c)

Material examined

Observations on three live animals (Vancouver).

Diagnosis

As in Schockaert and Karling (1970), but with some sclerotization in the cirrus of the male atrial system.

Description

Live specimens about 0.5 mm long. External and internal morphology as described by Schockaert and Karling (1970), with brown pigment in the parenchyma (Figure 4a-c) and clearly visible excretory canals. Proboscis about 80 μ m long and 50 μ m wide. Barrel-shaped pharynx about 85 μ m long and at about 40% of the body length. Paired testes beside and behind the pharynx, paired ovaries posterior to the male copulatory organ (Figure 4a). This copulatory organ consists of extra- and intracapsular seminal vesicles, a prostate vesicle type IV (pv4), a cirrus, and several muscular constrictions (Figure 4b, c; black arrows indicate constrictions). A septum



Figure 4. *Duplacrorhynchus minor*. (a) Live specimen slightly squeezed under cover slip. (b,c) Detail of the atrial organs in a live specimen. *Yaquinaia microrhynchus*. (d) Two live specimens slightly squeezed under cover slip (left) and free-swimming under cover slip (right). (e,f) Detail of the atrial organs in a live specimen. Abbreviations: b, bursa; ci, cirrus; co, copulatory organ; e, eye; evs, external seminal vesicle; fd-I, female duct type I; ivs, internal seminal vesicle; lo, left ovary; lod, left oviduct; mo, morula-shaped organ; o, ovary; p, probosics; pv4, prostate vesicle type IV; ph, pharynx; ro, right ovary; rod, right oviduct; rs, seminal receptacle; s, septum; scn, sclerotized nobs; st4, prostate stylet type IV; t, testis; vi, vitellaria; vs, seminal vesicle. Scale bars; a, d = 100 μ m; e = 50 μ m; b-c, f = 20 μ m.

surrounds the cirrus, prostate vesicle type IV and the intracapsular part of the seminal vesicle. The latter is separated from the extracapsular part by a weak constriction. A second constriction surrounded by a muscular sphincter is present somewhat distal from the first constriction. In the prostate vesicle type IV, prostate secretion from the prostate glands is discharged in the most distal part of the seminal vesicle. The latter connects to the cirrus through a third constriction and sphincter (Figure 4c). The 80 µm-long cirrus is muscular and seems slightly sclerotized in its proximal half. In its distal half, some sclerotized knobs are present (white arrow in Figure 4b,c). The female system is situated posterior to male system. The oviducts merge to form the common oviduct (sensu Artois and Schockaert 2005), which is locally enlarged to form the conspicuous morula-shaped appendage (Figure 4b,c). Distally, it connects to a large seminal receptacle at its posterior end and to the proximal part of the female duct type I at its anterior end. Both transition zones are surrounded by a sphincter. The female duct type I is wide and muscular and

seems to have some sclerotization. A uturus and its associated glands is also present (Figure 4c).

Distribution

New locality: Spanish Banks beach, Vancouver, British Columbia, Canada (49°16′42″N, 123°13′18″W), algae in rocky lower intertidal (September 18, 2015).

Known distribution: Northeast Pacific Ocean: Nicks Cove, Tomales Bay and Elkhorn Slough, California (Schockaert and Karling 1970).

Comparisons

The morphology of our specimens almost completely agrees with *D. minor* as described by Schockaert and Karling (1970). Some minor differences are present between the Californian and British Columbia specimens. Schockaert and Karling (1970) do not mention sclerotized knobs in the distal part of the cirrus in *D. minor*. Interestingly, sclerotized cirrus spines are described for *Duplacrorhynchus major* Schockaert and

Karling, 1970, a closely related species also present in the Northeast Pacific. Both D. minor and D. major have the unique morula-shaped appendage in the common oviduct. The latter species, however, is about double the size of D. minor and also has a large female bursa in its female system, a character clearly absent in our specimens. Some of the constrictions in the male and female system are also not mentioned in Schockaert and Karling (1970). The specimens from California were mostly described based on histological sections, while our specimens are described from observations on live animals. Possibly, fixation of tissues for histological sections could induce contraction or relaxation of certain muscles and explain some of these differences between the observations between live and fixed specimens. For now, we prefer to assign our specimens to D. minor until more material for detailed morphological studies and DNA taxonomy can be acquired from both populations.

Remarks

See remarks on *Yaquinaia microrhynchus* Schockaert & Karling, 1970.

Yaquinaia Schockaert & Karling, 1970

Yaquinaia microrhynchus Schockaert & Karling, 1970 (Figure 4d–f)

Material examined

Observations on four live animals (Victoria).

Diagnosis

As in Schockaert and Karling (1970).

Description

Animals about 0.8–0.9 mm long. General appearance and internal organization exactly as described by Schockaert and Karling (1970), but with bright orange-red pigment in the parenchyma (Figure 4d– f). Relatively small proboscis 80 µm long and 40 µm wide when relaxed, and 52 µm long and 50 µm wide when contracted. Globular pharynx with diameter 100–127 µm ($\bar{x} = 112$ µm; n = 4) at about 25% of the body length (Figure 4d). Male copulatory organ with a 77–184 µm-long seminal vesicle ($\bar{x} = 113$ µm; n = 4), depending on the amount of sperm it contains, and a 115–117 µm-long distal part ($\bar{x} = 116$ µm; n = 4) consisting of a prostate vesicle type IV and a septumenclosed flexible duct with a proximal sclerotized funnel-shaped prostate stylet type IV (Figure 4f). Female system with muscular female duct type I, small seminal receptacle and large syncytial bursa with the characteristic sclerotized knobs around its entrance (Figure 4e,f).

Distribution

New locality: Clover Point, Victoria, British Columbia, Canada (48°24′12″N, 123°21′03″W), algae in rocky lower intertidal (March 20, 2015; September 2, 2015; March 3, 2016).

Known distribution: Northeast Pacific Ocean: Yaquina River, Newport, Oregon (Schockaert and Karling 1970).

Comparisons

The monotypic genus *Yaquinaia* was originally classified within Duplacrorhynchinae based on the similarity of the male atrial organs with those of species of *Duplacrorhynchus* (Schockaert and Karling 1970). Schockaert and Karling (1970) and Artois and Schockaert (2005) also mention the occurrence of a ring of sclerotized knobs at the entrance of the bursa in species of *Parachrorhynchus*. Hence, a close relationship to either one of these genera is not unlikely. However, *Y. microrhynchus* differs from species of *Duplacrorhynchus* and *Parachrorhynchus* by having a prostate stylet type IV rather than a cirrus.

Remarks

In a molecular phylogenetic analysis of the Kalyptorhynchia, including two species of *Duplacrorhynchus* and one representative of *Parachrorhynchus*, Tessens et al. (2014) showed that Duplacrorhynchinae and *Duplacrorhynchus* are not monophyletic. Future inclusion of molecular data of more representatives of 'Duplacrorhynchinae' in a phylogenetic analysis, including the type species *D. minor* and *Y. microrhynchus* will provide us with a better understanding of the evolutionary relationships among duplacrorhynchs.

Phonorhynchus von Graff, 1905

Phonorhynchus contortus sp. nov. (Figure 5a–c)

Syn. *Phonorhynchus helgolandicus* (Mecznikow, 1865) form '*contorted*' in Karling (1982)



Figure 5. *Phonorhynchus contortus* sp. nov. (a) Live specimen slightly squeezed under cover slip. (b,c) Prostate stylet type I and prostate stylet type II from whole-mounted specimens (b = holotype; c = paratype). *Phonorhynchus velatus* sp. nov. (d) Prostate stylet type I and prostate stylet type II from a whole-mounted specimen (holotype). *Gyratrix hermaphroditus*. (e) Prostate stylet type II and prostate stylet type III from a whole-mounted specimen. *Scanorhynchus forcipatus*. (f) Two specimens slightly squeezed under cover slip. (g,h) Prostate stylet type II and prostate stylet type II and prostate stylet type II and prostate stylet type III from whole-mounted specimens. (i) Detail of head and proboscis. *Scanorhynchus herranzae* sp. nov. (j) Detail of head and proboscis. (k) Prostate stylet type II and prostate stylet type III from the whole-mounted specimen (holotype). Abbreviations: b, bursa; e, eye; o, ovary; p, proboscis; ph, pharynx; st1, prostate stylet type II; st2, prostate stylet type II; st3, prostate stylet type III; t, testis; vs, seminal vesicle. Scale bars: a, f = 100 µm; i–j = 50 µm; b–e, g–h, k = 20 µm.

Material examined

Holotype: One whole mount (Victoria: SMNH type-9109).

Paratypes: Ten whole mounts (Victoria: BBM MI4158–4161; Meay Inlet, Calvert Island: BBM MI4162–4163; North Beach, Calvert Island: BBM MI4164; Quadra Island: BBM MI4165).

Other material: Observations on at least four live animals.

Diagnosis

Species of *Phonorhynchus* with curved and slightly twisted, $72-92 \mu$ m-long prostate stylet type I with proximal funnel, ring and axial tube. One of the tube's

edges broad and wing-shaped. Needle-shaped prostate stylet type II with proximal funnel about 72–92 μ m long (see Karling 1982).

Description

Animals between 0.8–1.4 mm long, mostly transparent with some light brown colouration (Figure 5a). General appearance, internal organization and morphology of the prostate stylets as described by Karling (1982). Prostate stylet type I is 80–92 µm long ($\bar{x} = 86 \text{ µm}$; n = 11), prostate stylet type II is slightly shorter measuring 74–85 µm ($\bar{x} = 78 \text{ µm}$; n = 11). Female duct type I, bursa, and muscular sphincter with ring of sclerotized denticles at the posterior end of the female duct type I clearly visible in live animals.

Distribution

New localities: Clover Point, Victoria, British Columbia, Canada (48°24'12"N, 123°21'03"W), algae in rocky lower intertidal (March 14, 2015; May 6, 2015; January 28, 2018). Meay Inlet, Calvert Island, British Columbia, Canada (51°39'52"N, 128°05'47"W), algae in rocky lower intertidal (June 6, 2015; April 10, 2016). North Beach, Calvert Island, British Columbia, Canada (51° 39'58"N, 128°08'18"W), coarse sand in the subtidal (April 11, 2016). Quadra Ecological Observatory, Quadra Island, British Columbia, Canada (50°06'53"N, 125° 13'13"W), algae in rocky lower intertidal (April 26, 2017). *Known distribution:* Northeast Pacific Ocean: White Gulch, Dillon Beach, California and Yaquina River, Newport, Oregon (Karling 1982).

Etymology

The species epithet refers to the name of the morphotype 'contorted' as designated by Karling (1982).

Comparisons

See Phonorhynchus velatus sp. nov.

Phonorhynchus velatus sp. nov.

(Figure 5d)

Syn. *Phonorhynchus helgolandicus* (Mecznikow, 1865) form '*veil*' in Karling (1982)

Material examined

Holotype: One whole mount (Bamfield: SMNH type-9110).

Paratypes: One whole mount (Nanaimo: BBM MI4168). *Other material:* Observations on two live animals.

Diagnosis

Species of *Phonorhynchus* with twisted, lamellar, 80– 113 μ m-long prostate stylet type I with proximal funnel, ring and axial tube. Stylet provided with very broad lamellar wing with irregular holes and ridges. Extremely long, needle-shaped and flexible prostate stylet type II with proximal funnel about 145–217 μ m long (see Karling 1982).

Description

Animals measure 0.7–0.8 mm and have a brownish parenchymatous colouration. With relatively small proboscis and a pair of conspicuously large eyes. Prostate stylet type I and prostate stylet type II as described by Karling (1982) and measuring 102–113 μ m ($\bar{x} =$ 108 μ m; n = 2) and 180–217 μ m ($\bar{x} =$ 199 μ m; n = 2), respectively.

Distribution

New localities: Departure Bay, Nanaimo, British Columbia, Canada (49°11′43″N, 123°57′32″W), coarse sand and shell hash in the low intertidal (April 12, 2015). Deer Group Islands, Bamfield, British Columbia, Canada (48°52′22″N, 125°09′44″W), pebbles and shell hash at 6–10 m depth (June 3, 2015).

Known distribution: Northeast Pacific Ocean: Pacific Grove and Elkhorn Slough, California (Karling 1982).

Etymology

The species epithet refers to the name of the morphotype '*veil*' as designated by Karling (1982).

Comparisons

Karling (1982) recognizes 5 different morphotypes or 'forms' of *Phonorhynchus helgolandicus* based on the morphology of the prostate stylet type I and prostate stylet type II. Several of these forms co-occur regionally (e.g. '*contorted*' and '*veil*' in the Northeast Pacific Ocean) or locally (e.g. '*umbrella*' and '*winged*' in Arctic Alaska). However, Karling (1982) argues that 'stable characteristics' for the recognition of separate species should be backed up by a larger number of specimens and a better knowledge on their distribution. The new specimens from British Columbia corresponding to Karling's forms '*contorted*' and '*veil*', provide further evidence that *P. helgolandicus* s. I. is composed of at least two separate species in the Northeast Pacific Ocean. *P. contortus* sp. nov. and *P. velatus* sp. nov. can easily be recognized based on the prostate stylet type I and prostate stylet type II. Although the other forms '*umbrella*', '*winged*' and '*spatula*' can also be recognized based on these features, we prefer to refrain from formally recognizing these as separate species until additional material becomes available.

Gyratricinae von Graff, 1905

Gyratrix Ehrenberg, 1831

Gyratrix hermaphroditus Ehrenberg, 1831 s. l. (Figure 5e)

Material examined

Observations on several live animals. One whole mount (Surrey: BBM MI4169).

Diagnosis

Species of Gyratrix with a long stalk on the stylet sheath.

Description

Details on the morphology of *G. hermaphroditus* s. l. can be found in a vast amount of literature (see references in Artois and Tessens 2008). The stylet, sheath and stalk of a specimen from Surrey measure 80, 25 and 63 μ m, respectively (Figure 5e).

Distribution

New localities: Mud Bay Park, Surrey, British Columbia, Canada (49°05′09″N, 122°51′39″W), mud and algae in

intertidal mudflat (October 26, 2015). Clover Point, Victoria, British Columbia, Canada (48° 24'15"N, 123°21'04"W), sediment in sea grass bed about 2–3 m deep (March 14, 2015). Departure Bay, Nanaimo, British Columbia, Canada (49° 11'43"N, 123°57'32"W), coarse sand and shell hash in the low intertidal (April 12, 2015). Bamfield, British Columbia, Canada (48°51'18"N, 125°09'45"W), coarse sand and pebbles at 15–20 m depth between Wizard Islet and Helby Island (June 3, 2015).

Known distribution: Northeast Pacific Ocean: Pacific Grove and Elkhorn Slough, California and Yaquina Head and Newport, Oregon (Karling and Schockaert 1977), Trevor Channel, Barkley Sound, British Columbia (Rundell and Leander 2014), Lowell Point, Seward, Alaska (Ax and Armonies 1990); cosmopolitan, euryhaline.

Comparisons

The nominal species *G. hermaphroditus* s. l. is a complex of numerous (pseudo-)cryptic species and closely related to *G. proavus* Meixner, 1929, and *G. proaviformis*. The latter species also occurs in the Northeast Pacific Ocean (Karling & Schockaert, 1977). However, members of *G. hermaphroditus* s. l. differ distinctly from *G. proavus* and *G. proaviformis* in having a long stalk on the stylet sheath. For a recent discussion on *G. hermaphroditus* s. l., we refer to Artois and Tessens (2008).

Typhlopolycystidinae Evdonin, 1977 Limipolycystis Schilke, 1970 Limipolycystis castelinae sp. nov. (Figure 6)



Figure 6. *Limipolycystis castelinae* sp. nov. (a) Live specimen slightly squeezed under cover slip. (b) Seminal receptacle (left) and accessory stylet type II (right) based on observations in the live specimen. (c,d) Detail of the atrial organs in the live specimen. Abbreviations: acg2, accessory glands type II; ast2, accessory stylet type II; e, eye; fd-I, female duct type I; o, ovary; p, proboscis; ph, pharynx; rs, seminal receptacle; t, testis; vi, vitellaria; vs, seminal vesicle. Scale bars: $a = 100 \mu m$; $b-d = 20 \mu m$.

Material examined

Holotype: The type specimen was used for genomic DNA extraction; therefore, the DNA extract becomes the holotype (Hunter Island: BBM MI4170). *Other material:* Images of the live type specimen.

Diagnosis

Species of *Limipolycystis* with two small eyes. Accessory stylet type II 89 μ m long, mostly straight and tubular, with short asymmetrical proximal funnel perpendicular to the stylet's axis, diagonal ridge, subterminal opening and sharp distal point. Tripartite seminal vesicle with funnel, vesicle and blind tube.

Description

Animal about 0.8 mm long and transparent (Figure 6a). The 80 µm-long proboscis is relatively small. Paired eyes just behind the proboscis. Pharynx situated in the first body half, somewhat elongated, about 120 µm long and 80 µm wide. Single testis and ovary caudal from the male copulatory organ (Figure 6c,d). The latter consists of accessory glands type II and a seminal vesicle emptying in the accessory stylet type II. The prostate vesicle type III could not be observed in the live specimen. The accessory stylet type II is 89 μm long (84 μm non-axial) and consists of short asymmetrical proximal funnel with an 11 µm-wide opening (Figure 6b–d). The funnel bends over 90° and continues as a straight tube that distally tapers into a sharp point. The distal opening of the accessory stylet type II is subterminal on one side before the distal point (arrow in Figure 6b). From the funnel, a ridge runs down the stylet which diagonally crosses to the other side in the second half of the stylet. An elongated, tripartite seminal receptacle can be observed close to the ovary. It consists of a funnel, a vesicular part and a narrower, more tubular part (Figure 6b). The funnel connects to an enlarged portion of the female system (likely a bursa), while the tubular part ends closer to the ovary (Figure 6c,d). The clear delineation of the seminal receptacle suggests it is weakly sclerotized. Parts of the female duct are also visible between the accessory stylet type II and the seminal receptacle.

Distribution

Type locality: Hunter Island, British Columbia, Canada (51°54′29″N, 128°05′30″W), medium sand at 38 m depth in the central inlet (April 10, 2016).

Etymology

Species epithet in honour of Dr. Magalie Castelin, former colleague and friend of NVS, and malacologist at the Muséum national d'Histoire naturelle (Paris).

Comparisons

The specimen shows the typical characteristics of representatives of the genus Limipolycystis, including a relatively small proboscis, the caudal position of a single testis, the presence of an accessory stylet type II, and the absence of a prostate stylet. A detailed taxonomic account and discussion on this taxon and its representatives is given in Artois et al. (2012). The genus Limipolycystis currently has six other species which can be distinguished from each other based on the morphology of the accessory stylet type II. The accessory stylet type II of L. castelinae sp. nov. is unique because it is straight, distally needle-shaped, and has a proximal funnel bend over 90°. The small proximal accessory stylet type II opening of L. friedae Artois et al., 2012 is also bent, but is not funnelshaped and the remainder of the stylet is slightly curved with a blunt distal point. Limipolycystis wallbergi Artois et al., 2012 also has a more or less straight accessory stylet type II, but the proximal funnel is not bend and its distal point ends in a tiny hook. All other species of Limipolycystis (L. falx Artois et al., 2012, L. libra Artois et al., 2012, L. sicilicula Artois et al., 2012 and L. curvitubo Schilke, 1970) have a curved or sickle-shaped accessory stylet type II. The relative size of the proboscis of L. castelinae sp. nov. is very small compared to other species. It is about 1/10 of the body length, while for its congeners a relative proboscis size of about 1/5 of the body length is reported. Artois et al. (2012) report on the variation in the shape of the seminal receptacle among different species of Limipolycystis. In most species, it consists of a simple, sclerotized tube that can be enlarged to a funnel or vesicle close to the bursa. The seminal receptacle of L. castelinae sp. nov. is very similar to the one of L. falx, the latter also consisting of a funnel-shaped, vesicular and tubular part. The tubular part of L. castelinae sp. nov. seems to be more robust than in L. falx.

Remarks

Limipolycystis castelinae sp. nov. is the first species of *Limipolycystis* outside of European marine waters. All other species but one occur in subtidal sediments in the Western Mediterranean (Artois et al. 2012).

	S. forcipatus (NE Atlantic)	<i>S. forcipatus</i> (1960 morphotype California)	S. forcipatus (Calvert Island)	S. <i>herranzae</i> sp. nov. (1969 morphotype California)	S. herranzae sp. nov. (Calvert Island)
Ratio proboscis/total body length	1/12	'markedly smaller'	1/17	1/6	1/7
Prostate stylet type II axial (non-axial)	45 (40 μm)	62 μm (47 μm)	65–72 μm (46–48 μm)	110 (87 μm)	130 μm (77 μm)
Ratio funnel/non-axial prostate stylet type II	1/3–2/5	1/3	1/3	2/3	1/2
Prostate stylet type III axial (non-axial)	?–62 μm (48–60 μm)	73 μm (72 μm)	64–75 μm (63–72 μm)	189 (174 μm)	118 μm (110 μm)

Table II. Measurements on the proboscis and prostate stylets in different populations of *Scanorhynchus forcipatus* and *Scanorhynchus herranzae* sp. nov. including the new specimens and records from the literature (Karling 1955; Schilke 1970; Karling and Schockaert 1977; Noldt 1989).

Limipolycystis curvitubo is described from intertidal sediments from the North Sea (Schilke 1970).

Scanorhynchinae Tessens et al., 2014

Scanorhynchus Karling, 1955

Scanorhynchus forcipatus Karling, 1955 (Figure 5f–i; Table II)

Material examined

Observations on three live animals. Three whole mounts (Calvert Island: BBM MI4171–4173).

Diagnosis

Species of *Scanorhynchus* with relatively small proboscis about 1/12–1/17 of the body length. Prostate stylets relatively slender. Prostate stylet type II 45–72 μ m long (non-axial: 40–48 μ m) with 13–15 μ m-wide proximal funnel. Ratio funnel/non-axial length of prostate stylet type II about 1/3–2/5. Prostate stylet type III 62–75 μ m long (non-axial: 48–72 μ m) with well-developed stalk.

Description

Animals about 0.9–1.2 mm long, with brown colouration (Figure 5f). The proboscis is relatively small and slender and is about 70 µm long and 25 µm wide (Figure 5i). With paired eyes, and globular pharynx at about 40% of the body length. Internal anatomy as described by Karling (1955). The sclerotized parts of the male copulatory system measure 67–75 µm (nonaxial: $\bar{x} = 70$ µm; n = 3) in total (Figure 5g,h). They consist of a 65–72 µm-long prostate stylet type II ($\bar{x} =$ 68 µm; non-axial: 46–48 µm, $\bar{x} = 47$ µm; n = 3) with a 13–15 µm-wide proximal funnel, and a 64–75 µmlong prostate stylet type III ($\bar{x} = 69$ µm; non-axial: 63– 72 µm, $\bar{x} = 66$ µm; n = 3).

Distribution

New localities: North Beach, Calvert Island, British Columbia, Canada (51°39'52"N, 128°08'46"W), coarse sand in the lower intertidal (June 7, 2015). North Beach, Calvert Island, British Columbia, Canada (51° 39'51"N, 128°08'20"W), fine sand at 3 m depth just off North Beach (April 9, 2016).

Known distribution: Northeast Atlantic Ocean: North Sea (Karling 1955; Schilke 1970; Hoxhold 1974; Dittmann and Reise 1985; Noldt 1989), Skagerrak (Karling 1955), Kattegat (Tessens et al. 2014), Irish Sea (Boaden 1966). Northeast Pacific Ocean: Monterey Bay, California (Karling and Schockaert 1977).

Comparisons

See Scanorhynchus herranzae sp. nov.

Scanorhynchus herranzae sp. nov.

(Figure 5j,k; Table II)

Syn. *Scanorhynchus forcipatus*, '1969' morphotype in Karling and Schockaert (1977)

Material examined

Holotype: One whole mount (Calvert Island: SMNH type-9111).

Other material: Images of the live type specimen.

Diagnosis

Species of *Scanorhynchus* with relatively large proboscis about 1/7-1/6 of the body length. Prostate stylets large and robust. Prostate stylet type II 110–130 µm long (non-axial: 77–87 µm) with a very broad 35 µm-wide proximal funnel. Ratio funnel/non-axial length of prostate stylet type II about 1/2-2/3. Prostate stylet type III 118–189 µm long (non-axial: 110–174 µm) with well-developed, broad stalk.

Description

See description of '1969' morphotype of S. forcipatus in Karling and Schockaert (1977). The following description applies to the specimen from Calvert Island, British Columbia. Animal about 1 mm long, and mostly transparent. The proboscis is about 140 µm long and 130 µm wide (Figure 5j). Paired eyes, and globular pharynx at about 50% of the body length. Apart from the prostate stylet type II, prostate stylet type III, prostate vesicle type II, prostate vesicle type IV and the seminal vesicle, no further details on the internal morphology were visible in the live animal. The prostate stylet type II and prostate stylet type III are reminiscent of the ones of S. forcipatus, but are double the size and more robust (Figure 5k). The prostate stylet type II measures 130 µm (non-axial: 77 µm) and has a very broad, 37 µm-wide proximal funnel. The prostate stylet type III is 118 μm long (non-axial: 110 μm).

Distribution

Type locality: West Beach, Calvert Island, British Columbia, Canada (51°39′16″N, 128°08′53″W), mixed fractions of coarse sand, fine sand and algae at 10 m depth just off West Beach (June 3, 2015).

Known distribution: Northeast Pacific Ocean: Monterey Bay, California (Karling and Schockaert 1977).

Etymology

Species epithet in honour of Dr. María Herranz-Matesanz, colleague and friend of NVS, and one of the world's foremost kinorhynch experts.

Comparisons

Based on the size and morphology of the prostate stylet type II and prostate stylet type III and the relative size of the proboscis, Karling and Schockaert (1977) report on the occurrence of two different morphotypes of S. forcipatus in California. Their '1960' morphotype closely corresponds with the original description of S. forcipatus based on specimens from Europe, and with the intertidal specimens from Calvert Island. This 1960 morphotype has a relatively small and slender prostate stylet type II and prostate stylet type III (non-axial: 47 and 72 µm, respectively), and the ratio funnel/non-axial length of prostate stylet type II is about 1/3. This overall appearance and these measurements are almost identical to the ones from our intertidal Calvert Island specimens and only slightly different from

the Northeastern Atlantic specimens (non-axial: 48-60 µm for prostate stylet type III; ratio funnel/nonaxial length of prostate stylet type II about 2/5). Karling and Schockaert (1977) provide no measurements for the proboscis of the 1960 morphotype, but report it is 'markedly small'. The ratio proboscis/total body length is about 1/17 and 1/12 for the intertidal Calvert Island specimens and the European specimens, respectively. In contrast, the 1969 morphotype from California has a much larger and more robust prostate stylet type II and prostate stylet type III (non-axial: 87 and 174 µm, respectively), and the ratio funnel/total length of prostate stylet type II is about 2/3. The ratio proboscis/total body length is about 1/6. These measurements and relative proportions are more similar to the subtidal specimen from Calvert Island, although the prostate stylet type II, prostate stylet type III and relative proboscis size are somewhat larger in the 1969 morphotype.

Remarks

From the discussion above, it is clear that the sympatric 1960 and 1969 morphotypes from California also seem to co-occur in British Columbia. This provides further evidence for the existence of two morphologically distinct species of Scanorhynchus in the Northeast Pacific Ocean. Karling and Schockaert (1977) recognized that the 1969 morphotype is clearly distinct from the European specimens (and thus the 1960 morphotype) to warrant the erection of a new species. They refrained from doing so as they considered both morphotypes from California to belong to the same population. However, in the last decade, there is increasing evidence for meiofaunal species complexes with morphologically and genetically distinct species that can cooccur on local and regional scales (e.g. Van Steenkiste et al. 2018). Therefore, we see no reason to assume that these co-occurring, but morphologically distinct populations belong to the same species, and consequently assign the 1969 morphotype and the subtidal specimen from Calvert Island to a new species.

Koinocystididae Meixner, 1924

Rhinolasius Marcus, 1951

Rhinolasius dillonicus Karling, 1980 (Figure 7a,b)

Material examined

Observations on one live animal (Surrey).



Figure 7. *Rhinolasius dillonicus.* (a) Live specimen slightly squeezed under cover slip. (b) Detail of the atrial organs in the live specimen. *Itaipusa biglandula.* (c) Live specimen slightly squeezed under cover slip. (d,f) Detail of the atrial organs in a live specimen. *Utelga heinckei.* (g) Hooks associated with the male copulatory organ from a whole-mounted specimen. *Neognathorhynchus suecicus.* (h) Proboscis and proboscis hooks from a whole-mounted specimen. (i) Stylet from a whole-mounted specimen. Abbreviations: b, bursa; bs, bursal stalk; ci, cirrus; co, copulatory organ; e, eye; fd, female duct; gl, gland; gp, gonopore; i, intestine; o, ovary; p, probosics; ph, pharynx; pp, penis papilla; pv, prostate vesicle; rs, seminal receptacle; sph, sphincter; st4, prostate stylet type IV; t, testis; u, uterus; vi, vitellaria; vs, seminal vesicle. Scale bars; a, $c = 100 \mu m$; b, $d-i = 20 \mu m$.

Diagnosis

Slightly amended from Karling (1980). Species of *Rhinolasius*, about 0.6–0.7 mm long, with paired eyes and faint orange colouration. Common genital pore at about 80%. Tubiform, 120–200 μ m-long copulatory organ with a straight 50–100 μ m-long cirrus lined with 4 μ m-long spines. Bursa with 3–5 μ m-long teeth and short, sclerotized stalk.

Description

Animal 0.7 mm long, transparent but with very faint orange colouration (Figure 7a). Conical, relatively broad proboscis measuring 80 μ m when slightly contracted. Paired eyes, and globular pharynx with diameter 130 μ m at about 40% of the body length. Intestine contains the remains of a nematode (Figure 7a). Morphology of the atrial organs (Figure 7b) as described by Karling (1980). Paired testes lateral and postero-lateral of the pharynx. The muscular male copulatory organ measures 120 μ m. In its proximal part, two muscular extracapsular seminal vesicles merge. Prostate glands enter on both sides and form the prostate vesicle which fills the proximal half of the copulatory organ. The distal half consists of a 50 μ mlong cirrus with 4 μ m-long spines. The characteristic bursa is completely lined with 3 μ m-long teeth and has a short, sclerotized bursal stalk. The female duct connects the paired ovaries and vitellaria to a seminal receptacle. The latter connects to the common genital atrium through a strong sphincter. The uterus could not be observed in the live specimen.

Distribution

New locality: Mud Bay Park, Surrey, British Columbia, Canada (49°05′09″N, 122°51′39″W), mud and algae in intertidal mudflat (October 26, 2015).

Known distribution: Northeast Pacific Ocean: Nicks Cove, Tomales Bay, California (Karling 1980).

Comparisons

This species can easily be distinguished from the only other species in this genus, *Rhinolasius sartus* Marcus, 1951, by the distinctive teeth in the bursa. These are lacking in the bursa of *R. sartus* (see Karling 1980).

Remarks

Rhinolasius dillonicus is described based on serial sections of only one specimen collected in California by Karling (1980). Based on the characteristic features of its atrial organs (long spiny cirrus, toothed bursa), the specimen from British Columbia unmistakably belongs to this species. As such, this is the second specimen and record of this koinocystidid so far.

Itaipusa Marcus, 1949

Itaipusa biglandula Reygel et al., 2011 (Figure 7c–f)

Material examined

Observations on two live animals (Surrey).

Diagnosis

As in Reygel et al. (2011).

Description

Animals 1.3 mm long, transparent, with two eyes (Figure 7c). Organization and internal morphology mostly as described by Reygel et al. (2011). Large, typical koinocystidid proboscis about 1/6 of the body length (210 μ m), with strong Itaipusa-type juncture sphincter. Syncytial, 8 µm-high, ciliated epidermis with small 3-4 µm-long apical rhabdites, and supported by a thick basement membrane. A second type of 7-8 µm-long, needle-like rhabdites are present subepidermally all over the body. Globular pharynx at about 40% of the body length, followed by a clearly delineated intestine that runs all the way to the posterior end. Oesophageal glands visible right behind the pharynx. Male and female reproductive system in the posterior 1/5 of the body. Male copulatory organ (150 µm) consists of a proximal, globular to oviform prostate vesicle (90 µm), a short muscular duct (30 µm), and a distal, muscular penis papilla (30 µm) protruding in the male genital atrium (Figure 7d). Proximally, the prostate vesicle receives two seminal vesicles and prostate secretion from extracapsular prostate glands. The seminal vesicles are lined with a low nucleated epithelium. The proximal part of the female system (ovaries, vitellaria, proximal part of the female duct) is hardly visible in the live specimens. The distal part consists of a very muscular bursal stalk connecting to a large bursa through a very large, muscular sphincter (Figure 7e). The female duct connects to the bursal stalk through a smaller sphincter. Right before the bursal stalk enters the common genital atrium, a pair of eponymous glandular pouches is present (arrows in Figure 7e-f).

Distribution

New locality: Mud Bay Park, Surrey, British Columbia, Canada (49°05′09″N, 122°51′39″W), mud and algae in intertidal mudflat (July 29, 2015).

Known distribution: East Pacific Ocean: Galápagos Islands (Reygel et al. 2011).

Comparisons

Itaipusa biglandula shows all diagnostic characters of the genus *Itaipusa* and can be easily distinguished from other congeners based on the presence of an unarmed penis papilla and the pair of glandular pouches (see discussion on the genus *Itaipusa* in Reygel et al. 2011).

Remarks

Some minor differences between the British Columbia population and the Galápagos population exist. Reygel

et al. (2011) did not report on subepidermal, needleshaped rhabdites in the Galápagos specimens. In addition, no tubular middle part between the prostate vesicle and the penis papilla is described in the latter population. Possibly, this part was contracted in the serial sections and corresponds with the muscular ejaculatory duct mentioned in the original description. While the British Columbia specimens and the Galápagos specimens were collected in distant geographical locations, the morphological similarities of the speci-

Utelga Marcus, 1949

Utelga heinckei (Attems, 1897) (Figure 7g)

mens indicate conspecificity.

Material examined

Observations on at least five live animals. Five whole mounts (Nanaimo: BBM MI4174–4178).

Diagnosis

Species of *Utelga* with oviform copulatory organ and three uniform, relatively large, (10-)22-40 µm-long hooks.

Description

Animals about 1–1.4 mm long. External and internal morphology as described by Karling (1954, 1980). Copulatory bulb oviform and about 1.5 times longer than wide. The three hooks associated with the male copulatory organ measure 34–40 μ m ($\bar{x} = 37 \mu$ m; n = 5) and are mostly uniform in shape and size (Figure 7g). The genito-intestinal duct connecting the intestine to the muscular bulb and bursa, is surrounded by a strong sphincter muscle.

Distribution

New locality: Departure Bay, Nanaimo, British Columbia, Canada (49°11′43″N, 123°57′32″W), coarse sand and shell hash in the low intertidal (April 12, 2015).

Known distribution: Northeast Atlantic Ocean: North Sea (Attems 1897; Karling 1954; Schilke 1970), Irish Sea (Southern 1936; Boaden 1966), Irish Atlantic coast (Southern 1936), Skagerrak (Karling 1954; Willems et al. 2007). Mediterranean (Brunet 1965). Black Sea (Mack-Fira 1974). Northwest Atlantic Ocean: Massachusetts (Karling 1980). East Pacific Ocean: Galápagos Islands (Reygel et al. 2011).

Comparisons

This species closely resembles *Utelga pseudoheinckei*, but differs in having a more oviform copulatory bulb and much larger cirrus hooks. In *U. pseudoheinckei*, the copulatory bulb is more elongate and the cirrus hooks are relatively small (4–12 μ m). Representatives of the latter species were previously included in *U. heinckei* until Karling (1980) erected *U. pseudoheinckei* for the populations with the abovementioned characters.

Remarks

The maximum length difference between the spines per individual is 3 μ m, with the smallest spine having a slightly smaller base. A similar difference has also been reported for the specimens from the Galápagos Islands (Reygel et al. 2011). Also, the size range of the hooks of the British Columbia specimens corresponds more with the Galápagos specimens (35–40 μ m) than the Atlantic populations (10–35 μ m; see Reygel et al. 2011 for details).

Gnathorhynchidae Meixner, 1929

Neognathorhynchus Karling, 1956

Neognathorhynchus suecicus Karling, 1956 (Figure 7h–i)

Material examined

Observations on at least two live animals. Two whole mounts (Nanaimo: BBM MI4179–4180).

Diagnosis

Species of *Neognathorhynchus* with a $64-80 \mu$ m-long, more or less needle-shaped stylet which is bent proximally (see Karling 1956a).

Description

Animals very slender and about 1 mm long. Morphology as described by Karling (1956a). The proboscis is 46–51 μ m long and 50–51 μ m wide and provided with a pair of sclerotized hooks (n = 2) (Figure 7 h). These 12 μ m-long hooks have a weakly sclerotized, 15 μ m-long axial base and transverse, 7 μ m-long, butterfly wing-like, lateral protrusions. The stylet measures 64–68 μ m (n = 2) and consists of a more or less straight tube with a pointed distal tip and a proximal funnel that is bent over 90° (Figure 7i).



Figure 8. Zonorhynchus seminascatus. (a) Proboscis of slightly squeezed, live specimen. (b) Detail of epidermis and rhabdites in live specimen. (c) Detail of the atrial organs in a live specimen. (d,e) Detail of the male atrial organs in a live specimen. Abbreviations: b, bursa; bs, bursal stalk; ci, cirrus; co, copulatory organ; de, ejaculatory duct; p, proboscis; ph, pharynx; st, stylet; vs, seminal vesicle. Scale bars; a-b, $d-e = 20 \mu m$; $c = 50 \mu m$.

Distribution

New locality: Departure Bay, Nanaimo, British Columbia, Canada (49°11′43″N, 123°57′32″W), coarse sand and shell hash in the low intertidal (April 12, 2015). *Known distribution:* Northeast Atlantic Ocean: North Sea (Schilke 1970; Hoxhold 1974; Noldt 1989; Armonies 2017), Skagerrak (Karling 1956a), Kattegat (Karling 1956a), Irish Sea (Boaden 1966).

Comparisons

This species differs from the only other species in this genus, *Neognathorhynchus lobatus* (Ax, 1952), by having a bent stylet. The stylet of *N. lobatus* is completely straight.

Remarks

The measurements of the stylet from the Pacific specimens correspond more or less with the measurements on animals from the Northeastern Atlantic, although Karling (1956a) reports a stylet length of up to $80 \mu m$.

This is the first time this species is recorded from the Pacific.

Zonorhynchus Karling, 1952

Zonorhynchus seminascatus Karling, 1956 (Figure 8)

Material examined

Observations on two live animals (Nanaimo).

Diagnosis

Species of Zonorhynchus with a 160–183 µm-long cirrus with very fine, sclerotized, hair-like spines and a 56–100 µm-long, needle-shaped stylet. Ejaculatory duct and prostate vesicle about the same length as the cirrus. Seminal vesicles extremely muscular.

Description

Animal about 1.1 mm long, with a very faint orange-red colouration. Morphology as described by Karling

(1956b). Proboscis 127 µm long and 61 µm wide, with a conspicuous belt of glands around the edge of the proboscis cone (Figure 8a). Circular muscles surround the proboscis bulb. Eyes absent. Epidermis with round rhabdites in high density around most of the body (Figure 8b), except for the most anterior part. Pharynx in the anterior body half. Paired testes in the caudal body half, posterior to the seminal vesicles. The paired 350 µm-long seminal vesicles and 240 µmlong copulatory organ are exceptionally large and muscular (Figure 8c). Proximally, the seminal vesicles receive sperm from the testes through the vasa deferentia. Bundles of cell bodies with nuclei (arrows in Figure 8e) are also present here. Most likely, these are the cell bodies of the longitudinal muscle layer of the seminal vesicles. The copulatory organ consists of a proximal prostate vesicle and ejaculatory duct. The latter is coiled and distally ends in a 95 µm-long stylet (Figure 8d). The stylet is a simple needle-like tube and is completely enveloped by a 160 µm-long cirrus that runs all the way from the ejaculatory duct to the distal end of the copulatory bulb. The cirrus is provided with very fine, sclerotized, hair-like spines (Figure 8d). The female system is difficult to observe in the live animal. Only the bursa and muscular bursal stalk (internal vagina) are clearly visible (Figure 8e).

Distribution

New locality: Departure Bay, Nanaimo, British Columbia, Canada (49°11′43″N, 123°57′32″W), coarse sand and shell hash in the low intertidal (April 12, 2015).

Known distribution: Northeast Atlantic Ocean: North Sea (Karling 1956b; Schilke 1970; Dittmann and Reise 1985; Hellwig 1987; Noldt 1989; Krumwiede and Witt 1995), Skagerrak (Karling 1956b; Tessens et al. 2014), Kattegat (Karling 1956b), English Channel (Karling 1956b), Baltic Sea (Karling 1956b), Norwegian Sea (Schmidt 1972), Irish Sea (Boaden 1966).

Comparisons

This species is unmistakable and can easily be distinguished from other species of *Zonorhynchus* because of the large, muscular seminal vesicles and copulatory organ, and the morphology and relative dimensions of the stylet and cirrus. *Zonorhynchus seminascatus* most closely resembles *Z. tvaerminnensis* Karling, 1952, but differs by having a longer ejaculatory duct and prostate vesicle, a more needle-shaped stylet and more muscular seminal vesicles.

Remarks

Zonorhynchus seminascatus was previously only recorded from the Northeast Atlantic Ocean. The size of the copulatory organ (276 μ m), cirrus (183 μ m) and stylet (up to 100 μ m) are in the same order or slightly larger for the Atlantic specimens (see Karling 1956b).

Acknowledgments

We are grateful to the Hakai Research Institute, the Bamfield Marine Sciences Centre (BMSC) and the Carmabi Marine Research Institute for hosting sampling campaigns on Calvert Island, Bamfield and Curaçao. María Herranz, Wayne Jacob, Davis Iritani, Noriko Okamoto, Nicholas Irwin, Kevin Wakeman, Rebecca Fiorito and Hostion Ho were of great assistance during sampling in British Columbia.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was funded by the Tula Foundation through the Centre for Microbial Diversity and Evolution (CMDE). The sampling in Curaçao was funded by the Canadian Institute for Advanced Research (CIFAR).

Sampling

Permits for sampling were obtained by the Hakai Research Institute (Calvert Island), the Carmabi Marine Research Institute (Curaçao) and through Fisheries and Oceans Canada (XR 242 2015).

References

- Armonies W. 2017. Long-term change of meiofaunal species composition in a sandy beach, with description of 7 new species of Platyhelminthes. Helgoland Marine Research. 71:12. doi:10.1186/s10152-017-0492-0.
- Artois TJ, Schockaert ER. 2003. Primary homology assessment in the male atrial system of the Polycystididae (Platyhelminthes: Eukalyptorhynchia). Zoologischer Anzeiger. 242:179–190. doi:10.1078/0044-5231-00095.
- Artois TJ, Schockaert ER. 2005. Primary homology assessment of structures in the female atrial system among species of the Polycystididae (Rhabditophora, Eukalyptorhynchia). Invertebrate Biology. 124:109–118. doi:10.1111/j.1744-7410.2005.00013.x.
- Artois TJ, Tessens BS. 2008. Polycystididae (Rhabditophora: Rhabdocoela: Kalyptorhynchia) from the Indian Ocean, with the description of twelve new species. Zootaxa. 1849:1–27.
- Artois T, Willems W, Revis N, Martens P, Schockaert E. 2012. New species of *Limipolycystis* Schilke, 1970 (Rhabdocoela:

Kalyptorhynchia: Polycystididae) from the Western Mediterranean. Zootaxa. 3325:26–36.

- Attems CG. 1897. Beitrag zur Kenntnis der rhabdocoelen Turbellarien Helgolands. Wissenschaftliche Meeresuntersuchungen. 2:219–232.
- Ax P. 1959. Zur Systematik, Ökologie und Tiergeographie der Turbellarienfauna in den ponto-kaspischen Brackwassermeeren. Zoologischer Jahrbucher, Abteilung für Systematik, Geographie und Biologie der Tiere. 87:43– 184.
- Ax P, Armonies W. 1990. Brackish water Plathelminthes from Alaska as evidence for the existence of a boreal brackish water community with circumpolar distribution. Microfauna Marina. 6:7–109.
- Boaden PJS. 1966. Interstitial fauna from Northern Ireland. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven. 2:125–136.
- Brunet M. 1965. Turbellariés calyptorhynques de substrats meubles de la région de Marseille. Recueil des travaux de la station marine d'Endoume. 39:128–218.
- Brunet M. 1972. Koinocystididae de la region de Marseille. Zoologica Scripta. 1:157–174.
- Den Hartog C. 1968. An analysis of the Gnathorhynchidae (Neorhabdocoela, Turbellaria) and the position of *Psittacorhynchus verweyi* nov. gen. nov. sp. in this family. Koninklijke Nederlandse Akademie van Wetenschappen. 71:335–345.
- Dittmann S, Reise K. 1985. Assemblage of free-living Plathelminthes on an intertidal mud flat in the North Sea. Microfauna Marina. 2:95–115.
- Faubel A, Warwick RM. 2005. The marine flora and fauna of the Isles of Scilly: free-living Plathelminthes ('Turbellaria'). Journal of Natural History. 39:1–45. doi:10.1080/ 00222930310001613593.
- Fonseca VG, Sinniger F, Gaspar JM, Quince C, Creer S, Power DM, Peck LS, Clark MS. 2017. Revealing higher than expected meiofaunal diversity in Antarctic sediments: a metabarcoding approach. Scientific Reports. 7:6094. doi:10.1038/s41598-017-06687-x.
- Hellwig M. 1987. Ökologie freilebender Plathelminthen im Grenzraum Watt – Salzwiese lenitischer Gezeitenküsten. Microfauna Marina. 3:157–248.
- Herranz M, Yangel E, Leander BS. 2018. *Echinoderes hakaiensis* sp. nov.: a new mud dragon (Kinorhyncha, Echinoderidae) from the northeastern Pacific Ocean with the redescription of *Echinoderes pennaki* Higgins, 1960. Marine Biodiversity. 48:303–325. doi:10.1007/s12526-017-0726-z.
- Hoxhold S. 1974. Zur Populationsstruktur und Abundanzdynamik Interstitieller Kalyptorhynchia (Turbellaria, Neorhabdocoela). Mikrofauna des Meeresbodens. 41:1–134.
- Jouk PEH, De Vocht AJ-P. 1989. Kalyptorhynchia (Plathelminthes Rhabdocoela) from the Kenyan Coast, with descriptions of four new species. Tropical Zoology. 2:145–157. doi:10.1080/03946975.1989.10539435.
- Karling TG. 1954. Einige marine Vertreter der Kalyptorhynchien-Familie Koinocystididae. Arkiv för Zoologi. 7:165–183.
- Karling TG. 1955. Studien über Kalyptorhynchien (Turbellaria).
 V. Der Verwandtschaftkreis von *Gyratrix* Ehrenberg. Acta Zoologica Fennica. 88:1–39.

- Karling TG. 1956a. Zur Kenntnis einiger Gnathorhynchiden nebst Beschreibung einer neuen Gattung. Arkiv för Zoologi. 9:343–353.
- Karling TG. 1956b. Morphologisch-histologische Untersuchungen an den männlichen Atrialorganen der Kalvptorhynchia (Turbellaria). Arkiv för Zoologi. 9:187–279.
- Karling TG. 1977. Taxonomy, phylogeny and biogeography of the genus Austrorhynchus Karling (Turbellaria, Polycystididae). Mikrofauna des Meeresbodens. 61:153– 165.
- Karling TG. 1978. Anatomy and systematics of marine Turbellaria from Bermuda. Zoologica Scripta. 7:225–248.
- Karling TG. 1980. Revision of Koinocystididae (Turbellaria). Zoologica Scripta. 9:241–269.
- Karling TG. 1982. Anatomy and taxonomy of *Phonorhynchus* Graff (Turbellaria), with special reference to *P. helgolandicus* (Mecznikow). Zoologica Scripta. 11:165–171.
- Karling TG. 1983. Structural and Systematic studies on Turbellaria Schizorhynchia (Platyhelminthes). Zoologica Scripta. 12:77–89.
- Karling TG. 1986. Free-living marine Rhabdocoela (Platyhelminthes) from the N. American Pacific coast. With remarks on species from other areas. Zoologica Scripta. 15:201–219.
- Karling TG. 1989. New taxa of Kalyptorhynchia (Platyhelminthes) from the N. American Pacific coast. Zoologica Scripta. 18:19–32.
- Karling TG, Schockaert ER. 1977. Anatomy and Systematics of some Polycystididae (Turbellaria, Kalyptorhynchia) from the Pacific and S. Atlantic. Zoologica Scripta. 6:5–19.
- Krumwiede A, Witt J. 1995. Zur Verbreitung freilebender Plathelminthen im Weserästuar. Microfauna Marina. 10:319–326.
- Lin Y, Reygel P, Feng W, Chen J, Tessens B, Van Steenkiste NWL, Schockaert ER, Artois TJ, Wang A. 2019. Four new species of the genus *Paraustrorhynchus* (Rhabdocoela: Kalyptorhynchia: Polycystididae). Zootaxa. 4550:357– 373.
- Mack-Fira V. 1974. The Turbellarian fauna of the Romanian littoral waters of the Black Sea and its annexes. In: Riser NW, Morse MP, editor. Biology of the Turbellaria. New York: McGraw-Hill; p. 248–290.
- Marcus E. 1949. Turbellaria Brasileiros (7). Boletins da Faculdade de Filosofia, Ciências e Letras, Universidade de S. Paulo. 14:7–155.
- Noldt U. 1989. Kalyptorhynchia (Plathelminthes) from sublittoral coastal areas near the Island of Sylt (North Sea). II. Eukalyptorhynchia. Microfauna Marina. 5:295–329.
- Reygel PC, Willems WR, Artois TJ. 2011. Koinocystididae and Gnathorhynchidae (Platyhelminthes: Rhabdocoela: Kalyptorhynchia) from the Galapagos, with the description of three new species. Zootaxa. 3096:27–40.
- Rundell RJ, Leander BS. 2014. Molecular examination of kalyptorhynch diversity (Platyhelminthes: Rhabdocoela), including descriptions of five meiofaunal species from the northeastern Pacific Ocean. Journal of the Marine Biological Association of the United Kingdom. 94:499–514.
- Schilke K. 1970. Kalyptorhynchia (Turbellaria) aus dem Eulitoral der deutschen Nordseeküste. Helgoländer wissenschaftliche Meeresuntersuchungen. 21:143–265. doi:10.1007/BF01630522.

- Schmidt P. 1972. Zonierung und jahreszeitliche Fluktuationen der interstitiellen Fauna in Sandstränden des Gebiets von Tromsø. Mikrofauna des Meeresbodens. 12:1–86.
- Schockaert ER. 1996. Turbellarians. In: Hall G, editor. Methods for the examination of organismal diversity in soils and sediments. Wallingford: CAB International; p. 211–225.
- Schockaert E, Karling TG. 1970. Three new anatomically remarkable Turbellaria Eukalyptorhynchia from the North American Pacific coast. Arkiv för Zoologi. 23:237–253.
- Southern R. 1936. Turbellaria of Ireland. Proceedings of the Royal Irish Academy. 43:43–72.
- Stephenson I, Van Steenkiste NWL, Leander BS. 2019. Molecular phylogeny of neodalyellid flatworms (Rhabdocoela), including three new species from British Columbia. Journal of Zoological Systematics and Evolutionary Research. 57:41–56. doi:10.1111/jzs.12243.
- Tessens B, Janssen T, Artois T. 2014. Molecular phylogeny of Kalyptorhynchia (Rhabdocoela, Platyhelminthes) inferred

from ribosomal sequence data. Zoologica Scripta. 43:519–530. doi:10.1111/zsc.12066.

- Van Steenkiste NWL, Herbert ER, Leander BS. 2018. Species diversity in the marine microturbellarian *Astrotorhynchus bifidus* sensu lato (Platyhelminthes: Rhabdocoela) from the Northeast Pacific Ocean. Molecular Phylogenetics and Evolution. 120:259–273. doi:10.1016/j.ympev.2017.12.012.
- Van Steenkiste NWL, Leander BS. 2018. Molecular phylogeny of trigonostomine turbellarians (Platyhelminthes: Rhabdocoela: Trigonostomidae), including four new species from the Northeast Pacific Ocean. Zoological Journal of the Linnean Society. 182:237–257. doi:10.1093/ zoolinnean/zlx046.
- von Graff L. 1913. Das Tierreich 35. Turbellaria II. Rhabdocoelida. Berlin: Verlag von R. Friedländer und Sohn.
- Willems WR, Sandberg MI, Jondelius U. 2007. First report on Rhabdocoela (Rhabditophora) from deep parts of Skagerrak, with the description of four new species. Zootaxa. 1616:1–21.