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Analysing long-term change in small benthos: geomorphological dynamics affects method selection

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Abstract

In the tidal inlets of the northern Wadden Sea, species composition of selected taxa of the small benthos is compared to a study performed some 35 years before, using the same methods and sampling the same sites. Site-by-site comparisons suggest a dramatic change in community composition at a local scale. However, geomorphology is highly dynamic in this area, and sediment composition, water depth, or both, had changed during the intermediate decades in most of the sites. Since most of the species are limited to a single sediment type, a habitat approach was used for an alternative analysis of the data. This contradicted the idea of dramatic change but revealed relatively high stability of species composition at a regional scale, indicating that local change cannot be up-scaled to larger areas in this highly dynamic environment. Instead, a habitat approach is more adequate though increasing environmental dynamics requires increasing sampling effort. As a by-product of this study, 8 new taxa of Platyhelminthes are described: *Karlingia septentrionalis* n. sp., *Paracalviria diadema* n. sp., *Kataplana macrobursalia* n. sp., *Adenorhynchus compositus* n. sp., *Litucivis simplex* n. sp., *Scoliopharyngea magnaspina* n. sp., *Promesostoma convolutum* n. sp., and *Gnathorhynchus rostellatus indivisus* n. spp.

Keywords: Benthos, Geomorphology, Coastal dynamics, Patchiness, LTR, North Sea, Platyhelminthes

Background

Due to the natural variability of environmental and climatic factors as well as to human interference, habitats and their associated communities are subject to change over time. Where sound background data are available, the degree of change can be analysed by repetition of a previous study using the same methods, and sampling the same sites, which may be an efficient method to reduce random variability when temporal changes are the target [1]. This worked quite well in the analysis of temporal change in the small benthos of a semi-exposed tidal beach that had been morphologically stable over the past decades [2]. However, problems may arise where geomorphology is highly dynamic. The tidal inlets of the Wadden Sea are such a highly dynamic zone, where dislocations of the tidal channels and interspersed sand banks result in bathymetric changes up to 20 m within 10 years [3]. This caused no major problems in analyses of historic change in the larger epibenthic fauna [4, 5] because dredging always integrates over the dredged distance and the habitat types therein, and because mobility determines the spatial scales over which the densities of benthic organisms are associated with substrate variability [6]. But an attempt to re-sample previous sites for studies on small-sized infauna with limited mobility gave distorted results because sediment composition, water depth, or both, strongly differed from previous conditions. Since species vary in the preferred ranges of environmental factors, a site characterised by "fine sand, 12 m depth" in a previous

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survey cannot be expected to harbour the same species today, when we found gravel in 20 m water depth at the same geographical coordinates. Thus, an alternative approach to analyse temporal change in sediment-dwelling animals is needed for geomorphological dynamic areas. In this study, a habitat-based approach was used which compensated for the spatial shift of single habitat types and thus indicated a far higher stability of regional community composition.

Materials and methods

Comprehensive studies on meiobenthic species are extremely scarce, in particular from subtidal areas. Two of these rare studies covered the eastern North Sea. This is a shallow coastal area with a chain of barrier islands separating the North Sea from the back-barrier Wadden Sea. Sylt is the largest of the barrier islands; it is connected to the mainland by a railway dam. A similar dam connects the neighbouring Danish island of Rømø to the mainland. These dams separate Sylt-Rømø bight from the adjoining Wadden Sea, with List deep as a single connection to the North Sea (Fig. 1). Mean tidal range is 1.8 m creating a mosaic of tidally emergent flats and continuously submerged areas along the tidal channels as typical for the northern Wadden Sea. A sandy bar 'Salzsand' also

occurs west of the island, but it never emerged during historical times.

In the years 1982 and 1983, Wehrenberg and Reise [7] analysed the platyhelminth community structure with emphasis on species richness, abundance, and diversity. At the same time (1982 to 1984), Noldt [8, 9] studied the spatial distribution of Kalyptorhynchia and described many new species. Both studies included some 40 sampling sites along the tidal channels List deep, Lister Ley, and the North Sea (around 55.0° to 55.1° N, 008.2° to 008.5° E; Fig. 1). In the studied North Sea area, sediments are mostly composed of fine sands and water depth gradually slopes down to some 12 m at the most remote site studied (some 10 km west of the islands). Along the tidal inlets, however, sediment composition is highly variable, from very fine sand to gravel, and water depth reaches down to nearly 40 m. A general description of the study area is given in Wehrenberg and Reise [7]), but only Noldt [8, 9] gave detailed information on the coordinates, sediment type, and water depth of his sites. Therefore, his data are used as a baseline to detect temporal change in species composition over the past 35 years. However, Noldt did not report on the sampling dates or the number of replicates in space or time. Therefore, this comparison is only based on presence-absence data of species.
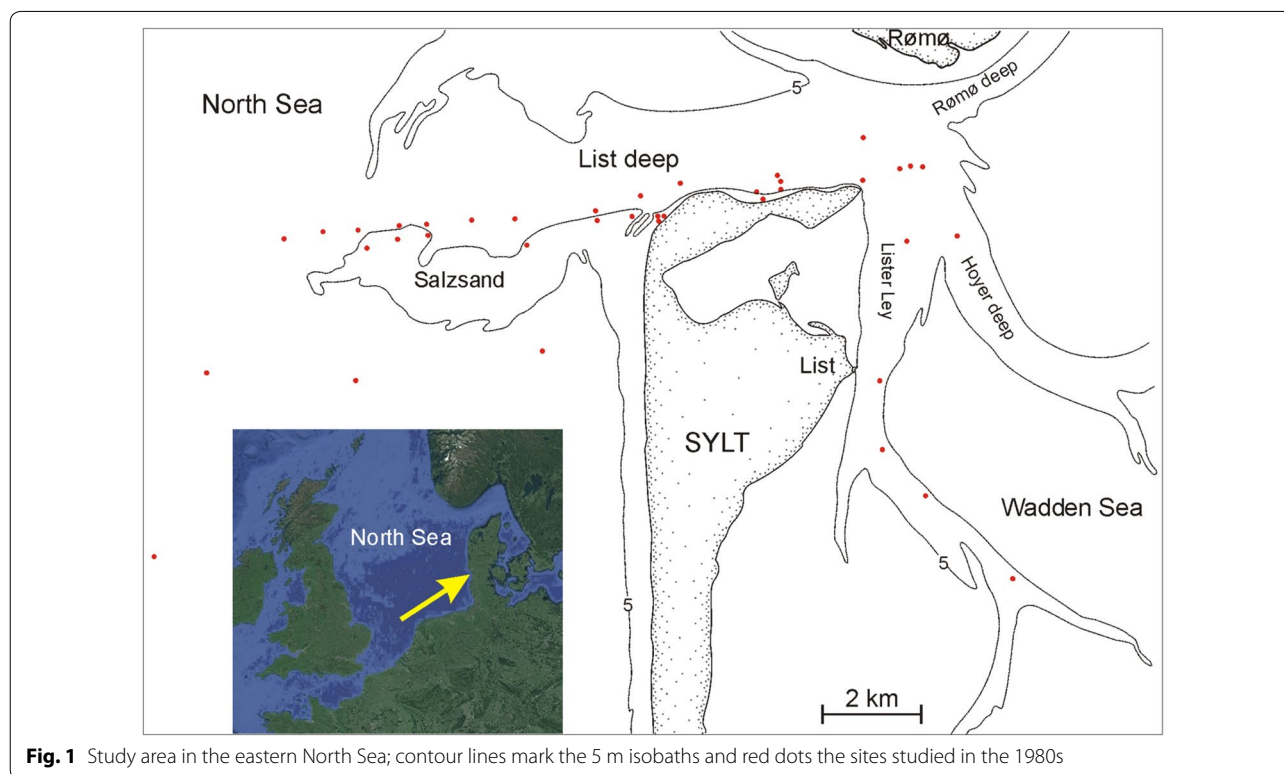

Fig. 1 Study area in the eastern North Sea; contour lines mark the 5 m isobaths and red dots the sites studied in the 1980s

In 2017/2018 I re-visited the study area. Sampling and extraction followed the previous procedures [8, 9]: sediment cores were retrieved from the seafloor with a modified Reineck box-corer (described in [7]) and either subsampled using tubes of 10 cm^2 opening area, or the entire grab (200 cm^2 opening area) was transferred into a bucket. Specimens were separated from the sediment by decantation after anaesthetisation with MgCl$_2$-solution (SMB-method [10]). However, the means of nautical navigation changed: we now used GPS while Decca-navigation with a lower precision was used in the 1980. Thus, there may be deviations in exact re-localisation of some of the previous sites. Other sites, however, could be exactly re-localised because they were well documented positions of fixed nautical marks; some of these marks even kept a stable position until today.

Originally I planned to re-sample all of the 40 sites that had been studied previously, with site-by-site analyses of the local species spectra. However, when major differences between actual and previous properties of the sites became apparent (Table 1) this intermediate analysis was inserted. It covers a subset of 15 repeated sites. I studied all of the platyhelminth taxa, but as the baseline data are restricted to Kalyptorhynchia, this intermediate evaluation is restricted to this taxon while the results on other taxa will be published later.

For statistical analysis, a species/site matrix was compiled from the localities given by Noldt and compared to a corresponding matrix from the data on Kalyptorhynchia compiled during this study (see Additional file 1: Table S1). Similarity between corresponding sites was calculated by Sørensen's percentage similarity index and by Jaccard's index, both according to Pilou [11].

For the alternate analysis, the sites were categorised according to sediment type (fine, medium, and coarse sand, following the categories used by Noldt) and water depth (< 10 m and > 10 m) and the species spectra joint within corresponding categories. This analysis was calculated twice, for the subset of the 15 sites studied during both periods, and a second time for all sites studied in each of the periods (data in Additional file 1: Tables S4–S6).

Results

Site-by-site comparison of the species spectrum between 1982 and 1984 and 2018 suggests very different communities with average similarities of species composition of only 8% (Sørensen's similarity) and 5.1% (Jaccard's index; Table 2). Between surveys, water depth changed in 12, sediment composition in eight, and both in at least four of the 15 sites (Table 1).

The alternate habitat approach indicated higher similarity values. Overall Sørensen similarity increased to 47% and Jaccard's index to 31% for the set of 15 joint sites (Table 3). However, this increase was only due to the habitat types represented by the relatively highest number of sites (medium sand and shallow-water fine sand).

Extending the data set to all sites studied in both periods increased overall Sørensen similarity to 57% and Jaccard's index to 55% (Table 4). Again, highest similarity values occurred in the habitat types studied

Table 1 Coordinates, water depth, and sediment type of the sites sampled by Noldt [8, 9] and repeated during this study

Noldt 1982–1984					This study		
Site no.	° N	° E	Depth m	Sediment	Sample-ID	Depth m	Sediment
1	55.0353	8.2139	13	Fine sand	20180409	14	Fine sand
3	55.0506	8.2942	8	Fine sand	20180807-3	10	Fine sand
4	55.0419	8.3517	7	Medium sand	20180807-4	7	Medium sand
5	55.0789	8.2919	8	Fine sand	20181010-5	8	Medium sand
6	55.0775	8.3036	6	Fine sand	20181108-6	8	Fine sand
26	55.0561	8.4433	3	Medium sand	20180821	4	Medium sand
27	55.0539	8.4433	8	Medium sand	20180828	7	Medium sand
29	55.0483	8.4822	9	Medium sand	20180312	10	Coarse sand
30	55.0550	8.4736	4	Coarse sand	20181022	24	Coarse sand
31	55.0472	8.4828	28	Coarse sand	20180920	20	Medium sand
32	55.0478	8.4794	20	Medium sand	20180326	20	Medium sand
34	55.0319	8.4889	12	Medium sand	20180221	16	Medium sand
35	55.0350	8.4725	4	Medium sand	20180219	5	Fine sand
37	55.0144	8.4419	12	Fine sand	20180207-1	20	Gravel and stones
39	54.9911	8.4472	12	Medium sand	20180213	14	Medium sand

Table 2 Number of Kalyptorhynchia species in 15 sites of the northern Wadden Sea tidal inlets, studied 1982–1984 and 2018, and similarity of species composition between sites

Site	No. of Kalyptorhynchia species					Similarity	
	1982–1984 total	2018 total	Present in both periods	Present only in 1982–1984	Present only in 2018	Sørensen's index (%)	Jaccard's index (%)
1	2	7	0	2	7	0	0
3	2	5	0	2	5	0	0
4	1	11	0	1	11	0	0
5	20	3	1	19	2	9	5
6	4	1	0	4	1	0	0
26	11	2	0	11	2	0	0
27	12	1	1	11	0	15	8
29	2	0	0	2	0	0	0
30	2	0	0	2	0	0	0
31	4	0	0	4	0	0	0
32	3	7	1	2	6	20	11
34	12	5	1	11	4	12	6
35	14	8	7	7	1	64	47
37	4	0	0	4	0	0	0
39	5	2	0	5	2	0	0
Average	6.5	3.5	0.7	5.8	3.0	8.0	5.1
All sites	53	34	21	31	14		

Table 3 Number of Kalyptorhynchia species in 15 sites of the northern Wadden Sea tidal inlets studied 1982-84 and 2018 classified with habitat types, and similarity of species composition between habitat types

Sediment type	Depth range	No of sites		Number of Kalyptorhynchia species				Similarity	
		1982–1984	2018	1982–1984 total	2018 total	Combined total	present in both periods	Sørensen's similarity	Jaccard's index
Fine sand	>10 m	3	3	22	8	24	6	40	25
	>10 m	2	1	6	12	17	1	11	6
	Total	5	4	26	17	33	10	47	30
Medium sand	>10 m	5	4	30	17	41	6	26	15
	>10 m	3	4	13	10	19	4	35	21
	Total	8	8	35	25	49	11	37	22
Coarse sand	>10 m	1	0	2	0	2	0	0	0
	>10 m	1	3	4	0	4	0	0	0
	Total	2	3	6	0	6	0	0	0
All types	Total	15	15	53	34	68	21	47	31

most intense in both surveys while types represented by few sites often had no species in common.

Discussion

Species spectrum

As an effect of climate change, spatial shifts of species distributional ranges are expected or already documented [12]. Until now, 96 species of Kalyptorhynchia have been recorded from the Sylt subtidal (species list in Additional file 1) and 88 of them were already known from the Sylt subtidal prior to this study. *Gnathorhynchus rostellatus indivisus* n. ssp. is described in this study and two species were described in its 2018 predecessor [2]; their geographical distribution outside the Sylt area is unknown. Among the remaining five species recorded for the first time near Sylt, *Utelga heinckei* is well known from the

Table 4 Number of Kalyptorhynchia species in habitat types of the northern Wadden Sea tidal inlets studied 1982–1984 and 2018–2019, and similarity of species composition between sites

Sediment type	Depth range	No of sites		Number of Kalyptorhynchia species				Similarity	
		1982–1984	2015–2019	1982–1984 total	2015–2019 total	Combined total	Present in both periods	Sørensen's similarity (%)	Jaccard's index (%)
Fine sand	> 10 m	6	56	40	29	52	17	46	33
	> 10 m	4	12	9	19	25	3	40	12
	Total	10	68	45	35	61	19	46	31
Medium sand	> 10 m	18	29	53	51	73	31	54	42
	> 10 m	8	4	26	10	32	4	24	13
	Total	26	33	58	54	74	38	57	51
Coarse sand	> 10 m	1	12	2	4	6	0	0	0
	> 10 m	3	6	6	1	7	0	0	0
	Total	4	18	8	5	12	1	20	8
All types	Total	40	119	73	63	88	48	57	55

island of Helgoland (some 50 km south of Sylt) while *Cheliplana rubescens* was described from the Mediterranean [13] but intermittently has also been found in Swedish waters [14]; their natural ranges seem to enclose the North Sea. Thus, only three species are potential invaders to the North Sea, viz. *Uncinorhynchus westbladi*, *Paracrorhynchus axi*, and *Cheliplanilla implicata*. The first two species hitherto have not been recorded outside the Baltic Sea; however, when the Baltic came into existence only a few 1000 years ago (after the last quaternary glaciation), its species invaded via the North Sea and derived from the same Northern Atlantic species pool as the North Sea fauna. Thus, these two species are not invaders but either part to the regular North Sea fauna, or are relicts left after the last glaciation. Among the Kalyptorhynchia studied here, this leaves *Cheliplanilla implicata* the only candidate for a potential invader or species that enlarged its distributional ranges in a northward direction, respectively. Up to now, it had only been found in the Mediterranean.

Species composition

After 35 years, only two out of 15 sites had the same sediment type and water depth as before, though it is not clear whether they had been stable over the intermediate period or just happened to return to the previous state. Paralleling these changes, site-by-site comparisons indicated a strong change in local faunal composition. This, once more, demonstrates the well-known importance of sediment composition for meiofauna in general [15] which makes it a meaningful habitat descriptor for Kalyptorhynchia, as well. Contrary to this, it is not clear whether the division of water depth is really significant within the depth range (maximum 40 m) present in this tidal area, and whether the division in two categories (> 10 m and < 10 m) is meaningful. In medium and coarse sands, at least, a number of species apparently switched depth levels between the surveys; this caused the similarity values for the totals of the depth categories to be higher than those for either depth level (Tables 3, 4). Further studies are needed to adequately check for a significant depth effect on meiofaunal species composition within these (altogether shallow) coastal waters.

Though habitat types changed in most sites, the spatial distance to the next patch with a habitat type as before was < 200 m in all sites studied so far, and all habitat types studied in the 1982–1984 period were still present in 2017/2018 in the studied area. This is why the habitat approach indicated a far higher similarity of faunal composition than the site-by-site approach. Thus, these approaches act at different spatial scales. A site is a rather small spatial unit, of a few to tens of m in diameter, mainly depending on navigational capabilities and water depth. Where geomorphological dynamics are high, such a small area may easily change its characteristics with consecutive changes in the associated fauna. Thus, the site-by-site approach is best suited to reveal change at very small spatial scales. The habitat approach is not sensitive to the exact coordinates of sites within a given study area, or to the arrangement of sample sites (random, along transects, or in a grid pattern). It only needs a number of samples high enough to record all habitat types with a sufficient number of replicates. In the present study, this requirement was not fulfilled for coarse sediment types; the respective data not very trustworthy, accordingly.

Adequate replication may be a special problem in areas with a high dynamics in geomorphology. In the

cores evaluated during this study, abundance of Platyhelminthes varied between 0 and 94 individuals 10 cm^{-2} (mean 15.5), and species richness between 0 and 22 in sediment cores of 10 cm^2 (mean 5.9) and between 1 and 46 in cores of 200 cm^2 (mean 18.9, see Additional file 1). Besides seasonal effects, the dynamics of geomorphology is likely to contribute to this high heterogeneity. Where large quantities of the sediment are eroded or deposited, the fauna will need some time for re-settlement or adjustment to the new conditions. Thus, highly dynamic sediments may best be described as a mosaic of patches, each one with an individual history of disturbance. High spatial and temporal variability of the fauna is a consequence of environmental dynamics. In quantitative studies, this variability calls for a high number of replicates [16].

Where environmental parameters are patchy on small spatial scales and highly variable on short temporal scales, single sites (defined by their coordinates) may harbour different habitat types over time. In this case, the need to re-locate a population becomes a special problem. Re-sampling an original site (defined by its coordinates) equals a site-by-site comparison as tried above, with a low chance for success. Therefore, geographical coordinates can only indicate an area where suitable habitat for the species may occur, and a more detailed description of the habitat type may be superior to a high precision of coordinates. In addition, sites with similar physical habitat descriptors (like sediment composition and water depth) may still differ in their successional state after the last disturbance. Therefore, where the option to re-locate a population is required (e.g., in species descriptions), further information on the physical and biotic properties of the locality may give hints to the successional state of a locality and help to re-locate a population. Among the biotic properties, naming the numerical abundant species accompanying the target species may be particular useful, because this information may help to recognise the community typically associated with the respective successional state.

For long-term ecological research, temporal variability of habitat types within a given spatial unit requires precautions as well. Either, both the distribution of habitat types, and the community composition within the habitat types should be monitored; the blending of both aspects is called biotope monitoring [17]. This approach uses predefined habitat types, e.g. based on sediment composition and bathymetry; these factors are significant for many benthic species, and they are accessible to remote sensing allowing rapid classification of larger areas. However, as remote sensing capabilities increase, todays pre-defined habitat types might be judged insufficient in the future. Therefore, post hoc classification of habitat types may be a more forward-looking approach. This includes measurements of water depth and sediment data (and as many as possible of other factors that may be significant for the studied taxa [18]) and statistically treat them as co-variants. Besides the possibility to adapt habitat type classification to the progress in remote sensing techniques, measuring environmental data directly may increase the sensitivity to detect effects of environmental change. In particular, changes rising little by little may become recognised already before they accumulated to a threshold value switching the site to another habitat type. In addition, measuring environmental factors from each of the replicate cores of a site (instead of taking a separate core for these measurements) will improve statistical analyses by reducing unexplained variance among the replicates. This, again, is most useful in spatially heterogeneous and/or geomorphological dynamic areas.

Descriptions of new taxa

Besides eight species of Platyhelminthes recently described [19], the number of undescribed subtidal species recorded during this study meanwhile accumulated to some 40. Seven of them were frequent enough for a description (Table 5). In addition, samples collected to verify the species identity of intertidal and subtidal *Hangethellia calceifera* revealed a new species, *Vannuccia diadema* n. sp. from the intertidal. All type material is deposited in the Platyhelminth collection of AWI Wadden Sea Station Sylt.

Karlingia septentrionalis n. sp. (Fig. 2)
Type locality
Wadden Sea near Sylt, sand bank in tidal inlet 'Lister Ley', medium to fine sand, 4 to 6 m water depth (55.0360° N, 008.4747° E, 11 Mar 2019, 3 individuals; 55.0370° N, 008.4739° E, 23 May 2019, 5 individuals). The specimens were accompanied by high densities of *Archimonocelis oostenendensis*, *Subulagera rubra*, *Promesostoma convolutum,* and *Litucivis serpens*.

Material
Life observations including drawings and photographs. Eight whole mounts, one designated holotype (AWI Sylt P2019-101), and 7 paratypes (AWI Sylt P2019-102 to 108).

Etymology
The species name refers to the northern locality ('septentrionalis' = Latin for 'northern'), as opposed to the only other species *Karlingia lutheri* (Marcus, 1948) from Brazil.

Table 5 Systematic classification of the new taxa

Platyhelminthes Rhabditophora

  Macrostomorpha

    Dolichomacrostomidae

    Karlingiinae

    Karlingia Ferguson, 1954

      Karlingia septentrionalis n. sp.

  Proseriata

    Calviriidae

    Paracalviria Schockaert, Curini-Galletti, De Ridder & Artois, 2011

      Paracalviria diadema n. sp.

  Otoplanidae

    Parotoplaninae

    Kataplana Ax, 1956

      Kataplana macrobursalia n. sp.

  Rhabdocoela

    Neotyphloplanida

    Promesostomidae

    Adenorhynchus Meixner, 1938

      Adenorhynchus compositus n. sp.

    Litucivis Ax & Heller, 1970

      Litucivis simplex n. sp.

    Scoliopharyngia Ehlers, Mueller & Franke, 1994

      Scoliopharyngea magnaspina n. sp.

    Promesostoma Graff, 1882

      Promesostoma convolutum n. sp.

  Kalyptorhynchia

    Eukalyptorhynchia

    Gnathorhynchidae

    Gnathorhynchus Meixner, 1929

      Gnathorhynchus rostellatus Brunet, 1973

        Gnathorhynchus rostellatus indivisus n. spp.

Diagnosis

Karlingia with an accessory gland organ lacking a gland stylet.

Description

Up to 3 mm long specimens with a body diameter of 200–250 μm in free creeping animals; body whitish without eye pigmentations. The pharynx is large and far frontal in the end of the first tenth of the body. Both body ends softly rounded but frontal end may be conically stretched in specimens that fumble around. Adhesive glands scattered over the entire body. Genital opening positioned in the beginning of the last tenth of the body. In juveniles and adolescent individuals the intestine reaches back almost to the genital opening while it is limited by the largest oocytes in adults. An intestinal muscle ring is not developed.

Male organs

The unpaired testis lies laterally in the beginning of the second half of the body; it is inversely pear-shaped with a rather wide deferent duct. Throughout its length the seminal duct was filled with a mixture of sperm and granular secretions that both originate from the testis. Distally the seminal duct is swollen to a drop-shaped seminal vesicle that joins the vesicula granulorum from the caudal side. The vesicula granulorum is inversely pear-shaped (about 110 μm long and 70 μm maximum diameter), with a strong muscle cover; most of its interior space is filled by tube-shaped cells that only leave a small ejaculatory duct along the central axis. Distally it merges to the penis stylet with extends into the genital atrium from the caudal side.

The penis stylet is boot-shaped (total length 75 μm), with a bootleg of 50 μm and a foot-part of 41 μm. The bootleg starts with a proximal opening of 30 μm diameter and it tapers to 9 μm at the heel. The foot-part carries a heel-spur of some 20 μm length which is sharply bent at an angle of nearly 180° to recline the ankle region. Another spur of some 8 μm length occurs at the tip of the sole; however, it is bent aside at a right angle and therefore only occasionally visible. The stylet opening is an oval hole from the mid dorsum of the foot to the tip of the sole.

Right to the penis stylet the accessory gland organ enters the genital atrium laterally. It consists of two parts, bright voluminous cells (without an external sheath visible in life observation), and a dark conical cluster of fine tubes that enters the genital atrium. An accessory stylet was not observed.

Female organs

The unpaired ovary starts laterally in the beginning of the second half of the body, opposed to the testis. The bursa seems to be squeezed between the largest egg cells and the accessory glandular organ, in life organisms. The mid-piece of the sclerotized bursal apparatus (55 μm long and 30 μm wide) looks like a barrel indented at one side. The mouth-piece is a short (about 10 μm) fine tube (1.5 μm in diameter) with the typical two disk-shaped thickenings. The spermatic tube (total length up to 230 μm) starts with a diameter of 2 μm at the mid-piece and enlarges to 8 μm in its most distal part where the walls become faint until they are no more visible.

Discussion

Karlingiinae are diagnosed as Dolichomacrostomidae with unpaired gonads bearing a penis stylet, an accessory gland organ with a gland stylet, and a bursal organ; the gut does not extend caudally over the genitalia; eyes, a
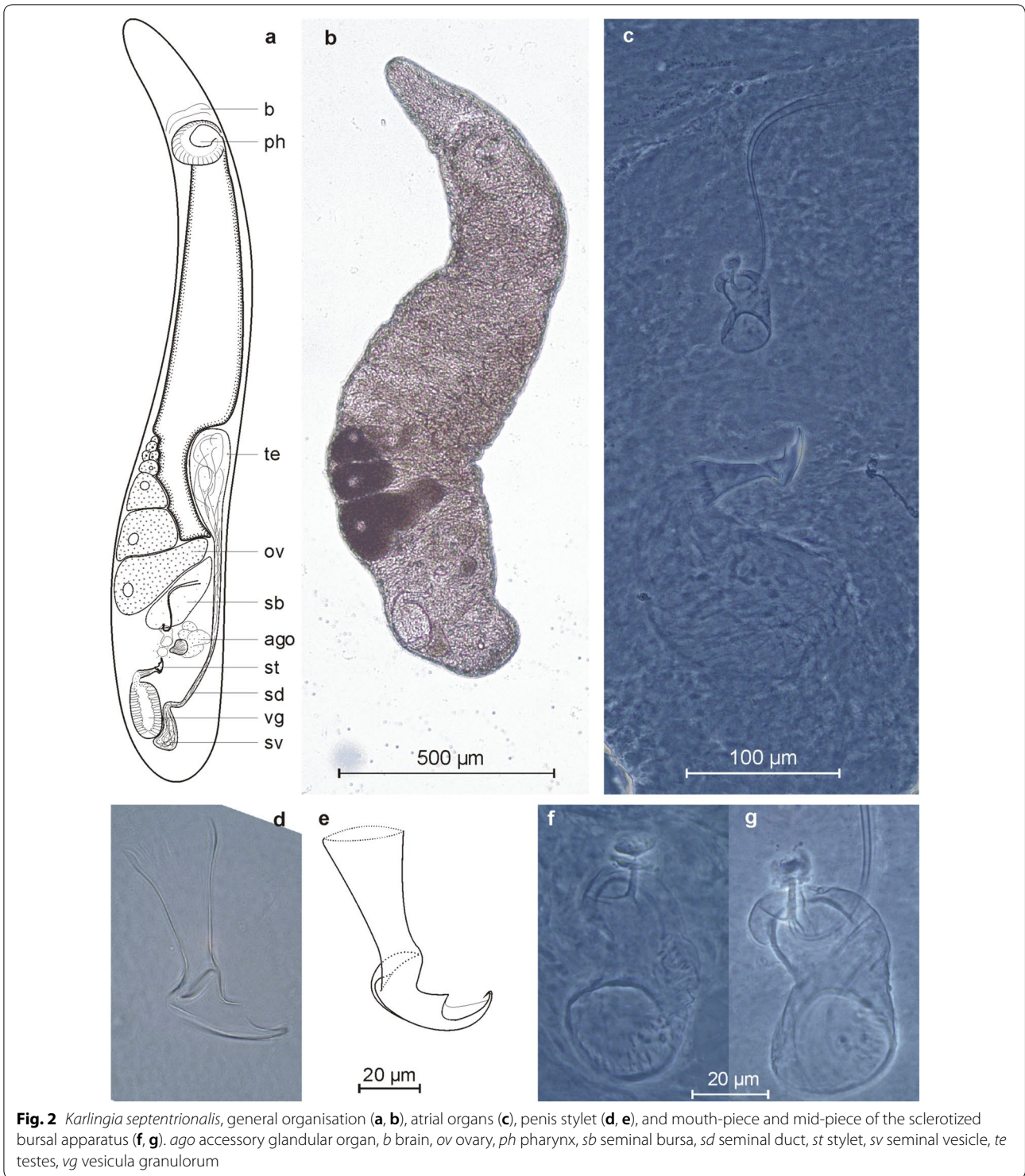
Fig. 2 *Karlingia septentrionalis*, general organisation (**a**, **b**), atrial organs (**c**), penis stylet (**d**, **e**), and mouth-piece and mid-piece of the sclerotized bursal apparatus (**f**, **g**). *ago* accessory glandular organ, *b* brain, *ov* ovary, *ph* pharynx, *sb* seminal bursa, *sd* seminal duct, *st* stylet, *sv* seminal vesicle, *te* testes, *vg* vesicula granulorum

muscle ring, and caudal sensory organs are absent [20]. Following this diagnosis, *Acanthomacrostomum* Papi & Swedmark, 1959 and *Karlingia* Ferguson, 1954 are the only genera in this subfamily while *Paramyozonaria* Rieger, 1971 is more likely to belong to the subfamily Myozonariinae [20]. These genera differ in the presence (*Acanthomacrostomum*) or absence (*Karlingia*) of an endoskeleton [21]. Accordingly, the new species was preliminary classified with *Karlingia*; the decision whether

or not the lack of an accessory gland stylet justifies a new genus is postponed until we know more of the relatives.

Paracalviria diadema n. sp. (Fig. 3)
Type locality
Lister Haken, a sheltered sandy hook north of List, 0.2 m below mean high tide level (55.0254° N, 008.4330° E, 23 Apr 2019). All individuals came from a single out of six replicate sediment cores with a very unusual sediment composition of very coarse sand with bivalve shells, mixed with some 2% (by volume) of mud. A second set of six cores collected a few days later failed to supply additional specimens. The species occurred together with *Praebursoplana reisingeri*, *Parotoplana papii*, *Balgetia semicirculifera*, *Provortex psammophilus*, and *Karkinorhynchides purpureus*.

Material
Life observations and photographs on five individuals. Three whole mounts, the specimen most advanced in maturity designated holotype (AWI Sylt P2019-111), and a less advanced one paratype (AWI Sylt P2019-112).

Etymology
The species name refers to the arrangement of the cirrus spines, from Latin diadema = coronet.

Diagnosis
Paracalviria with a coronet-shaped cirrus of atrial spines regularly varying in size and shape.

Description
Stretched maturing specimens 13 to 15 mm long and 150 μm in diameter (measured from whole mounts), fully grown specimens possibly even longer; contracted with a slightly salmon colour but whitish when sprawled. Both body ends gently rounded, without prominent tactile cilia. Body uniformly covered with cilia of 5–6 μm length, only lacking in the frontal end where the glands of the frontal organ open. Epidermal glands inconspicuous in life animals but tube-shaped glands are seen in the whole mounts; in the paratype they are partly everted, ending in a roundish knob in level with the cilia; in the holotype they are everted to form oval to tube-shaped protrusions up to 20 μm length and 3–6 μm in diameter. Adhesive papillae were not seen. Sub-epidermal musculature with strong longitudinal and inconspicuous circular muscles. The encapsulated brain is oval (60 × 85 μm) with the statocyst (23 μm in diameter, with four statoliths) directly in front of the brain. With a pre-cerebral gut diverticulum above the brain, reaching to about half the distance between the statocyst and the frontal end; without a lumen. The pharynx lies in the end of the frontal body

half and the genital openings in the beginning of the last sixth of the body.

As the specimens were just maturing, only parts of the genital organs could be observed. The male atrium includes a cirrus of some 120 spines in a very special arrangement; frontal of the cirrus there is a longish muscular bag of some 600 μm length that contained a few granular secretions, presumably the pre-penial glandular complex. Further prostatic glands or a prostatic vesicle could not be seen. Paired very long seminal vesicles were seen in the caudal end of one specimen, however, as the specimen was preserved in a twisted position it is not clear whether the paired condition holds true over the entire length of the vesicles; they might be fused more distally. The seminal ducts towards the copulatory organ could not be seen, nor testis vesicles. Among the female organs, I could only see the short but strongly muscular female genital canal caudally of the male genital atrium, and parts of the vitelloducts starting from the female genital canal and passing the male copulatory apparatus laterally.

The cirrus (total length 260 μm) contains 3 groups of spines that are arranged in different planes. Proximally some 60 spines are arranged in a horizontal half circle. These spines are 75 to 80 μm long with a slightly bent tip. Ten to 15 μm from the tip they bear a slight triangular projection; presumably only the tips beyond reach into the ejaculatory duct while the shafts are anchored in the surrounding tissue. The most proximal spines in this group are circular in diameter while the tips of the distal ones become continuously more flattened, finally looking like a knife with a slightly bent blade. Under highest magnification this blade seems to be finely serrated. Distally these large spines are followed by the second group of some 20 smaller spines at each side which are oriented dorso-ventrally. These spines bear a sickle-shaped hook at their tip and a fine serration along the shaft below; the hooks and the serration are always oriented towards the lateral body sides. The length of these spines is about 35–40 μm (estimated from a lateral view of the cirrus). The most distal spines are oriented more horizontally again and therefore appear as the third group. They are smaller (30 to 20 μm), bent at their tips, and with a plain shaft. Due to the vertical orientation of spines in the median group it is not clear whether the spine types merge or are strictly separated in shape.

Discussion
Although no fully mature specimens were found, the combination of prominent frontal glands, an encapsulated brain, a pre-cerebral gut diverticulum, a short female duct with oviducts joining behind the male
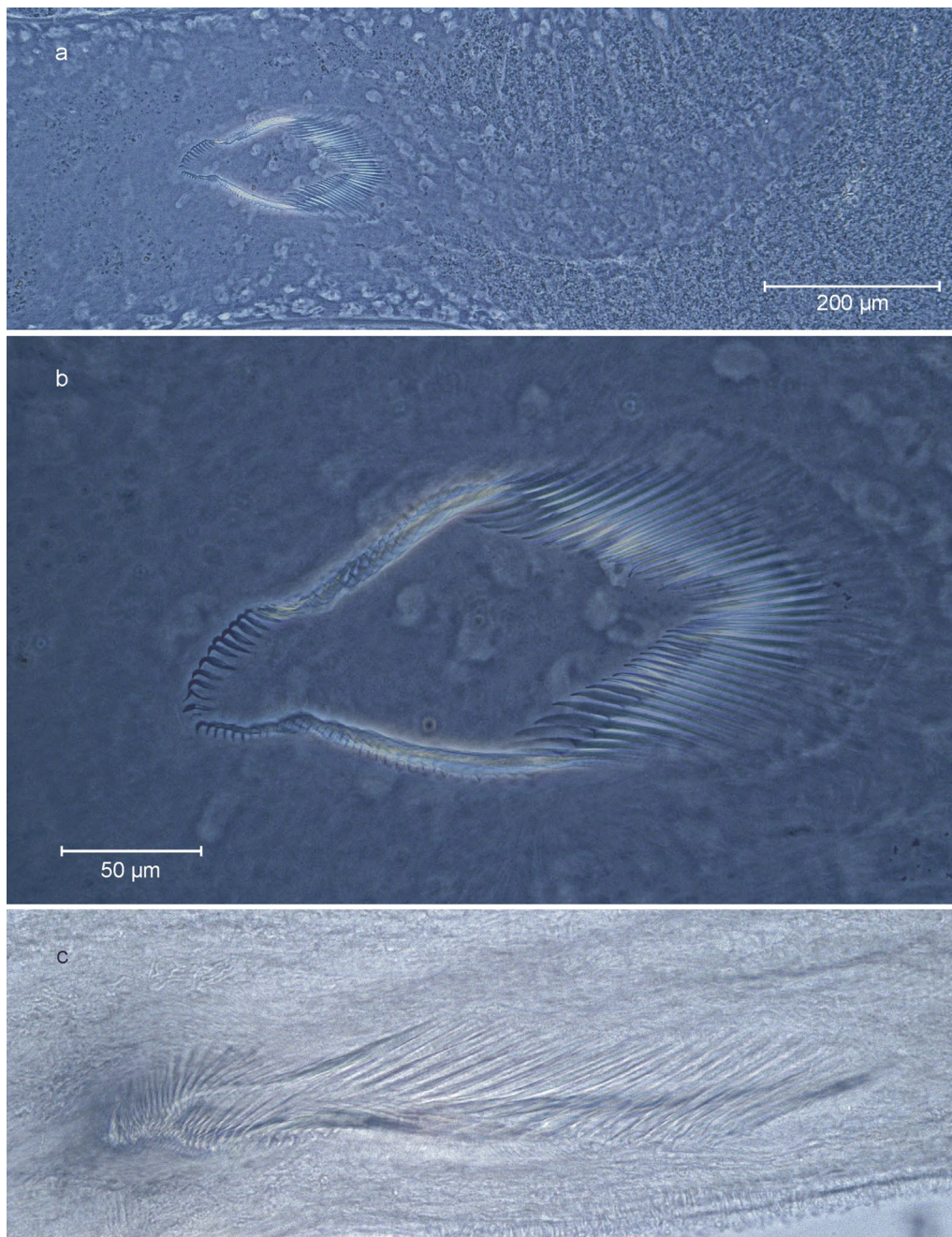
Fig. 3 *Paracalviria diadema*, cirrus. **a**, **b** Dorsal view; **c** lateral view

copulatory organ and the female pore behind it, a copulatory organ with atrial needles and an accessory glandular organ point to the family Calviriidae [22]. Among the four known genera, species of *Calviria* Martens & Curini-Galletti, 1993 and *Diskeria* Schockaert, Curini-Galletti, De Ridder & Artois, 2011 bear spines (or a stylet) both in the male atrium and in the accessory organ while *Asilomaria* Karling, 1966 is characterised by the

combination of an unarmed copulatory organ and an armed accessory organ. Thus, the new species conforms most to *Paracalviria* Schockaert, Curini-Galletti, De Ridder & Artois, 2011. In this genus the copulatory organ is equipped with atrial needles in a circle and an unarmed accessory glandular organ in front of the copulatory organ. Like *Paracalviria islandica* Schockaert, Curini-Galletti, De Ridder & Artois, 2011 *P. diadema* is strongly

protandric, has seminal vesicles positioned in the very caudal end of the specimens, and atrial spines arranged in an oval ring. In addition, the unusual epidermal glands observed in *P. diadema* may be equivalent to the large hyaline vacuoles described for *P. islandica*. Therefore I provisionally attribute the new species to the genus *Paracalviria*, with the number, shape, size, and arrangement of atrial spines clearly differing between the species.

Kataplana macrobursalia n. sp. (Figs. 4, 5, 6)
Localities
Subtidal poorly sorted medium sand near the western tip of Salzsand, a shallow sand bar west of the island of Sylt. (1) 55.0799° N, 008.2867° E, 10 Oct 2018, water depth 8.4 m, 10 individuals (type locality). (2) 55.077° N, 008.3020° E, 10 Oct 2018, water depth 5 m, 5 individuals). (3) Wadden Sea near Sylt, sand bank in tidal inlet 'Lister Ley', medium to fine sand, 6 m water depth (55.0370° N, 008.4739° E, 23 May 2019, 4 individuals). The type locality contained a rather poor Platyhelminth assemblage; only unidentified Retronectidae were abundant.

Material
Live observations including drawings and photographs; four whole mounts, one designated holotype (AWI Sylt P2019-115) and three paratypes (AWI Sylt P2019-116 to 118).

Etymology
The species name refers to the extraordinary large sized seminal bursa.

Diagnosis
Species of *Kataplana* with numerous testis follicles, an extraordinary large seminal bursa, and a sclerotic apparatus composed of 30 needles with a regular varying length of their tips.

Description
Unpigmented specimens with a shape as typical for Parotoplanidae; free swimming up to 4 mm long and 150 to 200 μm in diameter. Head end with sensory bristles, a weakly differentiated ciliated furrow, and a prominent median double-row of rhabdites reaching from the frontal end to the statocyst. Behind the statocyst the double row branches into lateral fields reaching backwards well behind the brain. The posterior end of the body is fan-shaped and bears adhesive glands.

The pharynx (about 260 μm long and 160 μm wide) is positioned in the third quarter of the body; its orientation is slightly oblique (i.e. intermediate between the horizontal orientation typical for Otoplaninae and vertical as in most Parotoplaninae). The testes follicles are numerous (about 40 pairs) and arranged in lateral rows reaching from the brain to some 250 μm before the pharynx, followed by the paired germaries. Vitellaria are also numerous, arranged in lateral rows from the germaries to the copulatory organ. However, other than the testes follicles, the vitellaria follicles are not evenly distributed along the rows but they form clusters of several follicles each interrupted by short distances without follicles. Two of these clusters were seen in front of the pharynx, and 3–4 behind the pharynx.

The caudal fifth of the body contains the male copulatory organ and a conspicuous seminal bursa. The copulatory organ consists of a large drop-shaped seminal vesicle (150 μm long and 65 μm wide) and a prostatic vesicle including the stylet needles. Frontal of the stylet needles the genital atrium is enlarged to a pocket. The seminal ducts were only seen during stronger squeezing in a single individual; from this, the seminal vesicle seems to be filled caudally from the ventral side.

The prostatic vesicle directly follows the seminal vesicle. Its epithelium includes a circle of 30 needles composed of a slightly curved shaft and a sickle-shaped tip. Only the shaft is included in the epithelium while the tips extend to the genital atrium. The transition between shaft and tip bears a lateral spine (1–2 μm) assisting in anchoring of the needles in the epithelium. In Un-squeezed specimens the prostatic vesicle has a diameter of 35 to 40 μm and a length of some 75 μm (excluding the tips of the needles).

The size and shape of the stylet needles varies over the circle. The shortest needle has a total length of 58 μm (shaft 50 μm, tip 8 μm). Then the needles get increasingly larger towards both sides of the circle. The largest needles have a total length of 80 μm (shaft 55 μm, tip 25 μm). Thus, the length increase is mainly due to increasingly longer tips of the needles; since the tips extend into the genital atrium, their varying length is easily seen already under lower magnification.

The seminal bursa follows the male copulatory organ caudally. This is a very large pocket almost filling the entire body diameter. Two ciliated ducts leave the seminal bursa at its frontal end but they could only be followed for a short distance and then vanish below the seminal vesicle. Presumably, these ducts connect the bursa with the germo-vitelloducts.

Discussion
With the existence of an unpaired secondary bursa caudally of the copulatory organ with paired connections to the germo-vitelloducts, the new species fits the diagnosis of *Kataplana* sensu Ax, 1956. Among the *Kataplana*-species described so far, *K. arcuata* Sopott-Ehlers, 1976, *K. celeretrix* Bursea, Smith & Levaitis, 2012,
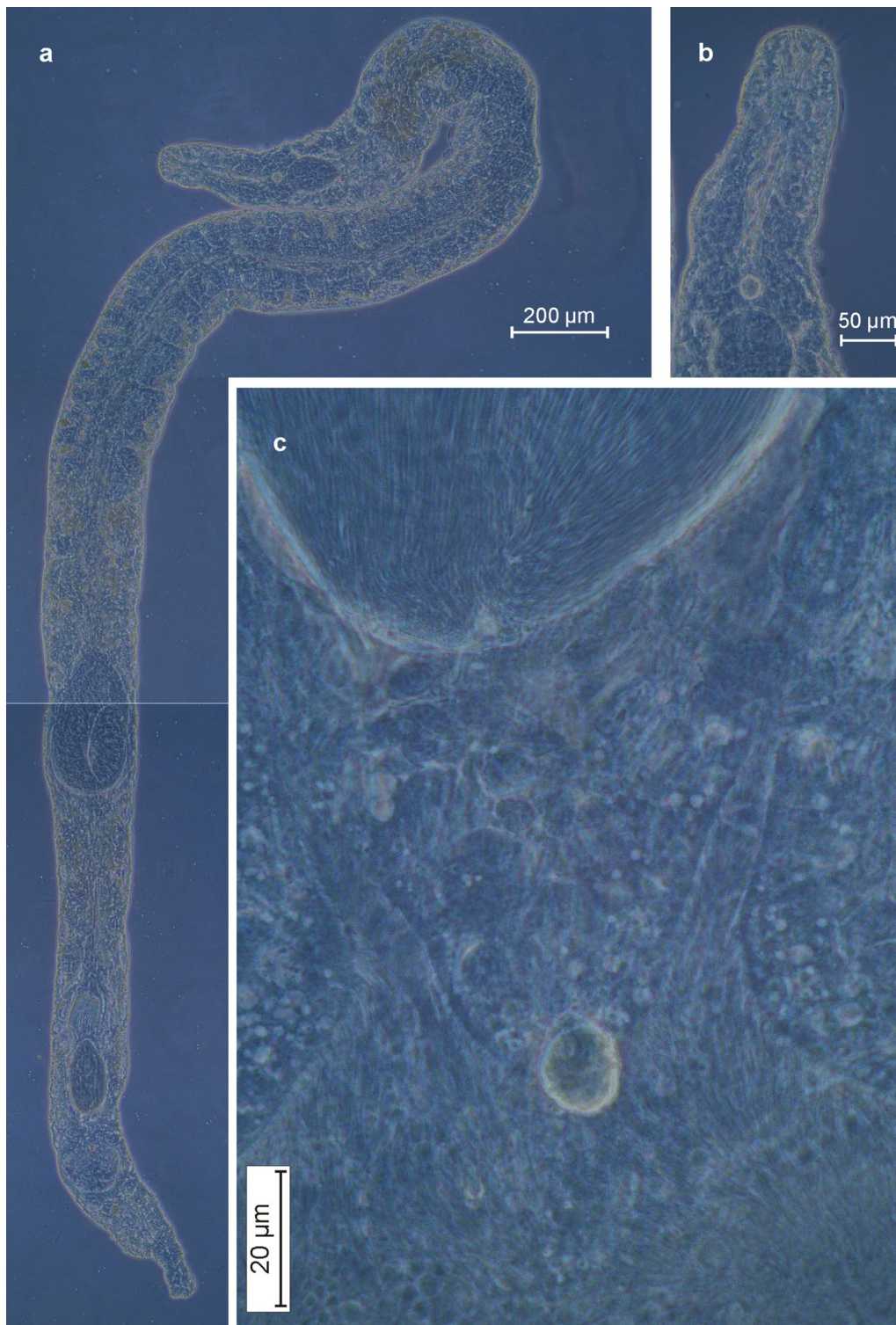
Fig. 4 *Kataplana macrobursalia*. **a** Live individual, **b** frontal end, **c** frontal part of bursa with paired ciliated duct
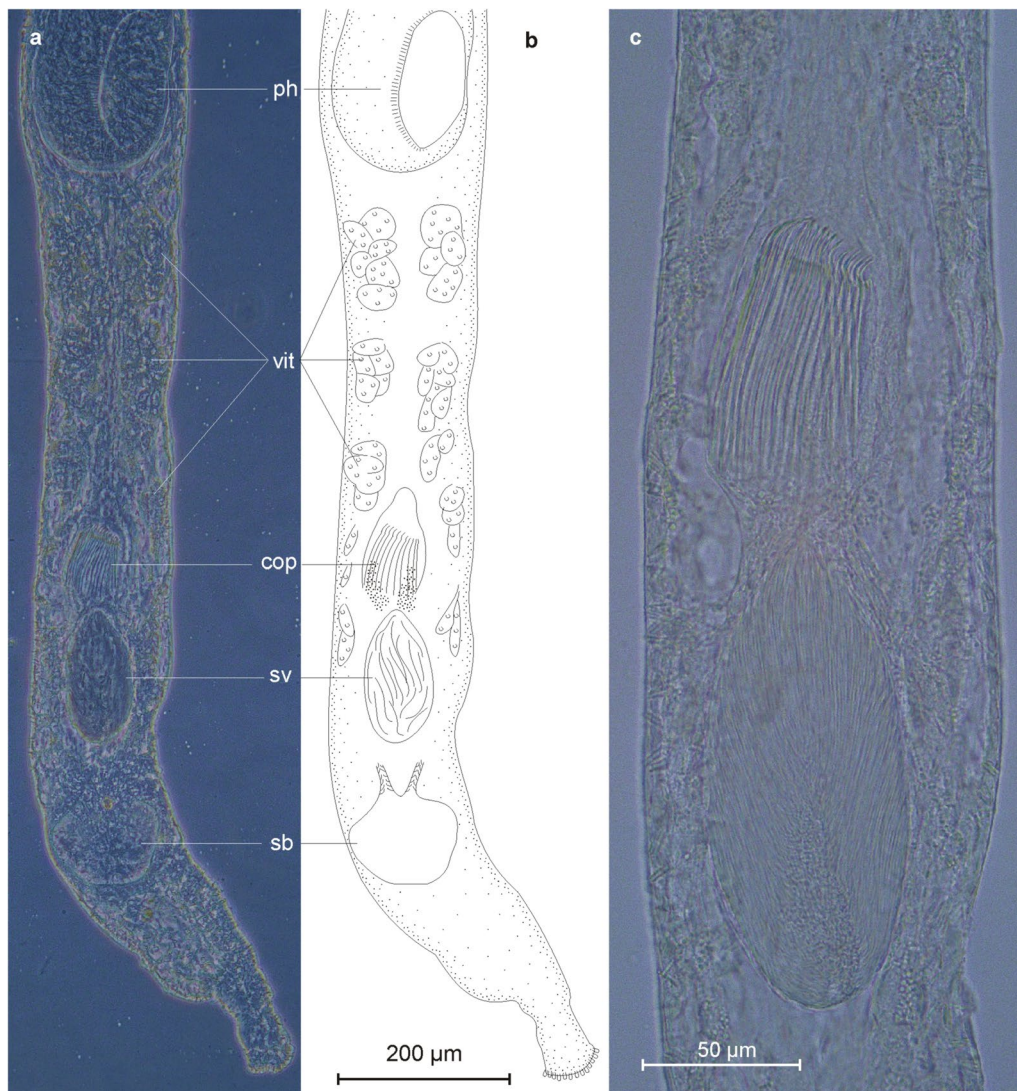
Fig. 5 *Kataplana macrobursalia,* caudal end (**a**, **b**) and copulatory organ (**c**). *cop* copulatory organ, *sb* seminal bursa, *sv* seminal vesicle, *ph* pharynx, *vit* vitellary

and *K. germanica* (Meixner in Ax, 1951) all differ from *K. macrobursalia* in their low number of testes follicles (3 or 4 pairs) and the position and shape of the pharynx (in mid-body, oriented vertically). The most similar species is *Kataplana mesopharynx* Ax, 1956 which also has many testis follicles and a pharynx with an orientation intermediate between the Otoplaninae- and Parotoplaninae-types. But both species differ in the position of the germaries (lateral of the pharynx in *K. mesopharynx*, frontal in *K. macrobursalia*) and the position of the pharynx (in mid-body in *K. mesopharynx*, further

caudally in *K. macrobursalis*). In addition, all species differ in the size, shape, and number of needles in the genital apparatus.

Adenorhynchus compositus n. sp. (Fig. 7)
Type locality
Lister Ley, medium to fine sand of a sandbank in 4-6 m water depth (around 55.0360° N, 008.4750° E, 11 Mar 2019, 1 individual; 1 Apr 2019, 3 individuals; 23 May 2019, 2 individuals). Abundant companions
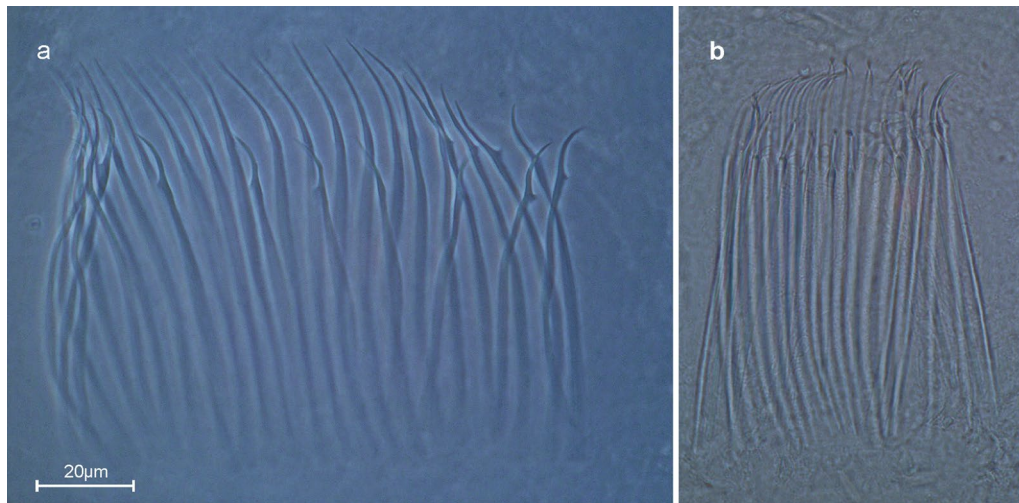
Fig. 6 *Kataplana macrobursalia*, needles of the copulatory organ; **a** strong, **b** slightly squeezed

were *Archimonocelis oostendensis*, *Subulagera rubra*, *Promesostoma convolutum*, *Neoschizorhynchus parvorostro*, and *Pseudoschizorhynchoides ruber*.

Material

Life observations including drawings and photographs. Two whole mounts, one designated holotype (AWI Sylt P2019-201), and one paratype (AWI Sylt P2019-202).

Etymology

The species name refers to the shape of the stylet which is composed of three sections.

Diagnosis

Adenorhynchus with a stylet composed of (1) a slightly tapering tube with its proximal end surrounded by a girdle of curved spines. The distal end of the tube passed into (2) a narrow ring with an irregularly folded structure that is (3) distally followed by a circle of triangular pins.

Description

Slender whitish specimens without eye pigmentations, slowly swimming, some 2 mm long. Front end rather straight with the openings of the voluminous rhabdite glands; rear end conical. Pharynx rather small (diameter 90 μm), in the beginning of the second body half. Vitellaria paired, arranged as lateral tubes that are well separated from the germaries which are positioned in the end of the body; with a small ovoid seminal receptacle between the germaries. Testes roundish, positioned ventrally of the vitellaria and directly in front of the pharynx. Male copulatory organ with small seminal vesicles caudal of the pharynx. The copulatory organ is shaped like a flattened sphere of 70 μm diameter and 50 μm height. It has a weak outer musculature and a central ejaculatory duct. The latter is surrounded by granular secretions that form aggregations in the proximal part of the bulb while most of the bulb is filled by a colourless parenchyma.

The weakly sclerotic stylet has a total length of 41 μm and can be subdivided into three sections. The proximal section is a slightly conical tube of 30 μm length with a proximal diameter of 25 μm and a distal diameter of 20 μm; the surface of the tube bears 8 fine vertical stripes. At its proximal end the tube is surrounded by a girdle of about 20 curved spines some 20 μm in length. In resting stage these spines lie parallel against the tube. The distal end of the tube passes over into the second section which is a narrow (5 μm high) ring with a crenulated (irregularly folded) structure. The distal section is a circle of triangular pins. In resting state these pins bow towards the centre of the tube opening thus closing the ejaculatory duct at its distal end.

Discussion

The general organisation of *A. compositus* fully agrees with *A. balticus* and the generic diagnosis of *Adenorhynchus*. In both species the stylet is composed of a tube-shaped part with some spines near the proximal end and smaller pins near the distal end. Possibly the fine striping seen in the squeezed condition of the *A. balticus* stylet (Fig. 6E in Ax & Heller 1970 [23]) is an equivalent of the middle crenulated section in the stylet of *A. compositus*.

Fig. 7 *Adenorhynchus compositus*. **a** Organisation, **b** copulatory organ, **c** stylet. *st* stylet, *sv* seminal vesicle, *cop* copulatory organ, *ge* germany, *go* genital opening, *pg* prostatic glands, *ph* pharynx, *sr* seminal receptacle
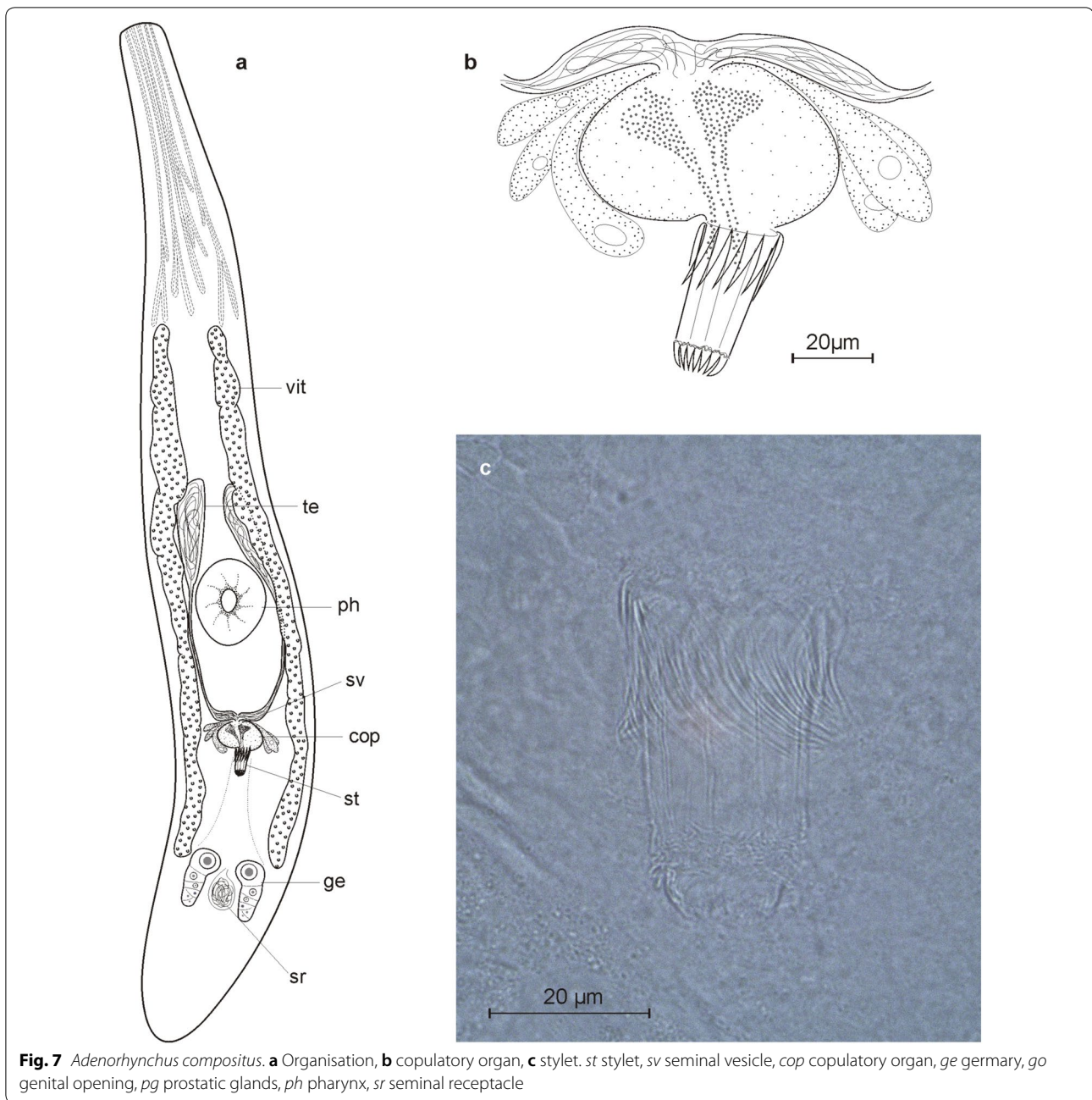
Though composed of the same elements, both species grossly differ in the shape of the stylet and thus can easily be distinguished.
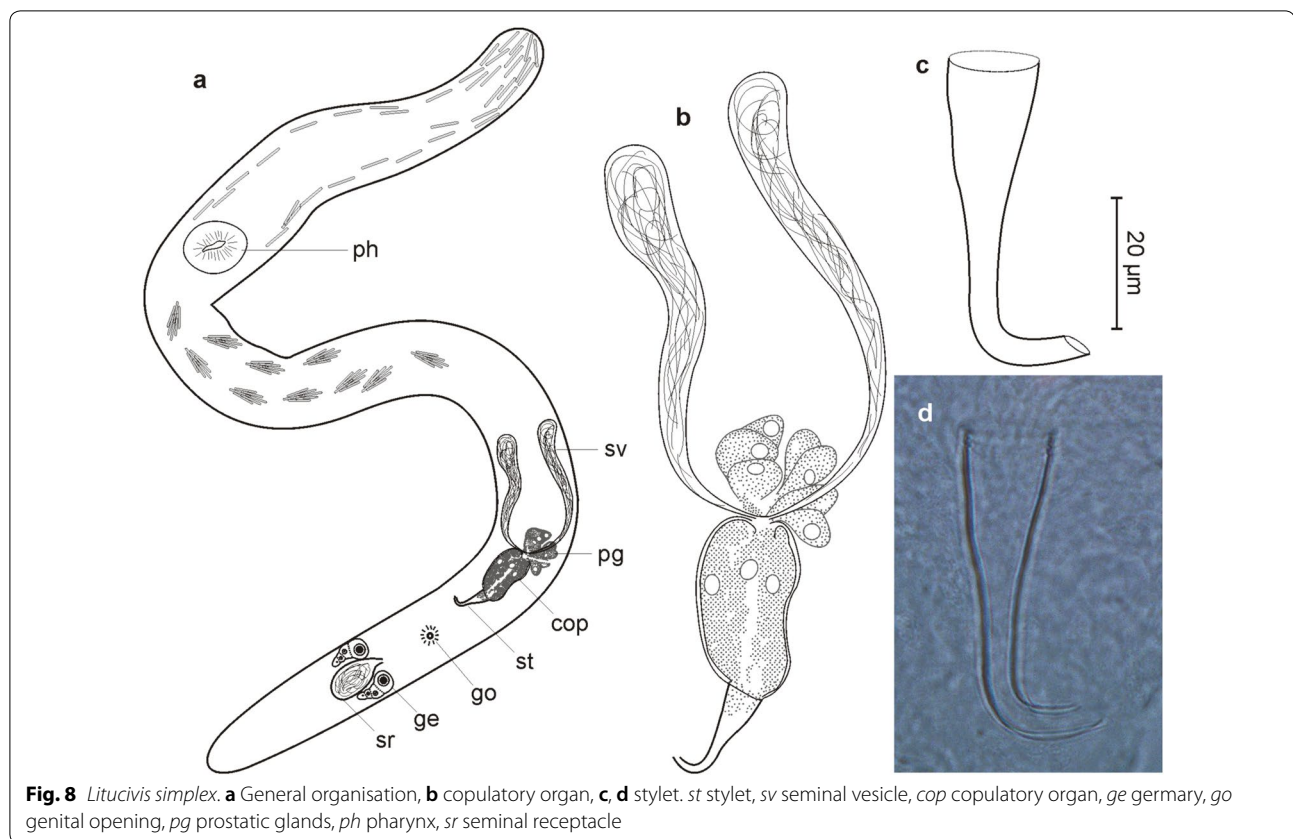
Litucivis simplex n. sp. (Fig. 8)
Localities
North Sea, fine sand 4 km north-west of the Island of Sylt, 6 m water depth (type locality; 55.0865° N, 008.3280° E, 6 Dec 2018, 4 individuals). Further localities: Lister Ley, sand bank in 5 m water depth, medium to fine sand (55.0349° N, 008.4720° E, 25 Feb 2019, 1 individual). The species occurred together with *Proxenetes cimbricus* and *Gnathorhynchus conocaudatus*.

Material
Life observations and photographs. Four whole mounts, one designated holotype (AWI Sylt P2019-203), and 3 paratypes (AWI Sylt 2019-204 to 206).

Fig. 8 *Litucivis simplex*. **a** General organisation, **b** copulatory organ, **c**, **d** stylet. *st* stylet, *sv* seminal vesicle, *cop* copulatory organ, *ge* germany, *go* genital opening, *pg* prostatic glands, *ph* pharynx, *sr* seminal receptacle

Etymology

The species name refers to the simple structure of the stylet as compared to *Litucivis serpens* which is currently the only other species in the genus.

Diagnosis

Promesostomidae with a pharynx in the frontal third of the body and a stylet shaped like a narrowing funnel with a right-angled end bending.

Description

Long (1.5 to 2.0 mm) very slender specimens with a body diameter of 60 to 80 μm in free creeping animals; body whitish without eye pigmentations. Pharynx dorsoventrally oriented, in the end of the first third of the body. Frontal end rounded, with pronounced rows of rhabdites reaching back to the pharynx and drop-shaped packages of rhabdites reaching back to mid-body. Individual rhabdites are some 40 μm long with a pattern of longitudinal stripes. Genital opening positioned in the beginning of the last quarter of the body; caudal end rounded, with voluminous (adhesive?) glands.

Male organs

The paired testes are positioned laterally in front of the pharynx and are rather small and inconspicuous. The deferent ducts could not be observed until they enlarge to a noticeable pair of external seminal vesicles, starting shortly behind the mid of the body and reaching a length of 250 to 300 μm. The copulatory organ is a weakly muscular tube of 80 μm length and 40 μm diameter with the ejaculatory duct in its centre and surrounded by granular secretions. Four nuclei positioned among the secretions indicate that prostatic glands occur inside the copulatory bulb. Other secretions enter the copulatory bulb together with the ejaculatory duct, with the secreting prostatic cells clearly outside the bulb. The stylet is a funnel-shaped narrowing pipe of some 55 μm total length with a bent distal end. The proximal opening of the stylet has a diameter of 13 μm that narrows to 5 μm along the proximal half. Then the stylet continues with a rather constant diameter. At some 42 μm from the proximal opening the stylet turns at about a right angle. The distal bent part has a length of 10 to 15 μm and ends with a slightly oblique opening 5 μm in diameter.

Female organs

The studied specimens were not yet in full female maturity; therefore the extension of the vitellaries is not clear. The paired germaries are positioned laterally in the body some 100 μm caudally of the genital opening. They are separated by a voluminous seminal receptacle. A sphincter was seen separating the seminal receptacle from the efferent duct, with a few sperm in the apparently rather wide duct. Whether or not the latter duct is already the female part of the genital atrium could not be decided from the studied developmental stages.

Discussion

The family *Promesostomidae* Hartog, 1964 unites species with a single genital pore, paired male and female gonads, and a single connection between the female gonads and the exterior. In most genera, the pharynx is positioned in the middle or caudal third of the body; a pharynx in the frontal third only occurs in *Litucivis* Ax & Heller, 1970. *L. simplex* differs from *L. serpens* in the shape of the stylet, the more frontal position of the testes, and the presence of external prostatic glands.

Scoliopharyngea magnaspina n. sp. (Figs. 9, 10)
Localities

Type locality: North Sea, fine sand 3 km north-west of the Island of Sylt, 6 m water depth (55.0755° N, 008.3102° E, 27 Nov 2018, 10 individuals). Further localities: (1) Lister Ley, well-sorted fine sand from a sandbank, 5 m water depth (55.0365° N, 008.4750° E, 18 Sep 2017, 1 individual). (2) North Sea, fine sand 5 km north-west of the Island of Sylt, 6 m water depth (55.0865° N, 008.3280° E, 6 Dec 2018, 2 individuals). (3) North Sea, fine sand 4 km north-west of the Island of Sylt, 6 m water depth (55.0831° N, 008.3203° E, 6 Dec 2018, 1 individual). All localities were also populated by *Haplopharynx rostratus*, *Bradynectes sterreri*, *Gnathorhynchus conocaudatus*, and *Diascorhynchus rubrus.*

Material

Life observations and photographs. Four whole mounts, one designated holotype (AWI Sylt P2019-207), and three paratypes (AWI Sylt P2019-208 to 210).

Etymology

The species name refers to the large spines in the cirrus.

Diagnosis

Promesostomidae with frontal testes, paired eye-pigmentations, and a copulatory organ divided into a muscular bulb and a flexible tube, the latter containing a cirrus of medium to large spines.

Description

Very slender specimens with pronounced protandry; in male maturity 1.0 to 1.5 mm long, in female maturity 1.4 to 1.8 mm long with a body diameter of 50 to 60 μm (free-swimming specimens). Frontal end densely packed with prominent rhabdites (8 to 12 μm long), further roundish to ovoid agglomerations of rhabdites (diameter up to 25 μm) behind the brain. With paired reddish-brown eye pigmentations and a pharynx in the end of the second or the beginning of the last third of the body; pharynx orientation oblique with the opening towards the ventro-caudal side. The genital opening is half-way between the pharynx and the rounded caudal end. Around the genital opening, the body diameter was slightly constricted in several specimens. Adhesive glands take the very end of the body.

Male organs were only observed in specimens < 1.5 mm. The paired testes are positioned laterally in the body, starting directly behind the brain and partly concealed by the rhabdite-agglomerations. Paired external seminal vesicles directly behind the pharynx. The copulatory organ is divided into two sections, a proximal cylindrical muscular bulb of 80 μm length and 35 μm diameter, and a distal tube of 40 to 60 μm length and 10 to 15 μm diameter that contains the cirrus. The muscular bulb is covered with weak outer longitudinal and strong inner circular muscles. Parts of the bulb are filled with prostatic secretions, but the secretory cells are outside the bulb. The distal tube is weakly muscular (presumably, only longitudinal fibres) but has an apparently hardened outer surface; it reaches freely into the genital atrium. In some specimens this surface was smooth and the length of the tube was about 40 μm and its diameter 15 μm. In other specimens the diameter was only 10 μm, but the length up to 60 μm with a wrinkled surface. It seems the outer lining of the tube can be stretched to some 60 μm but is not flexible enough to return to its original state. The distal part of the tube contains the cirrus (total length 25 μm). In passive state the spines of the cirrus are all oriented in a longitudinal direction. In the everted state they spread outside; then it can be recognised that the bundle contains spines varying in length between some 3 and 15 μm.

Female organs were only observed in specimens > 1.4 mm and none of the individuals studied had mature male and female organs at the same time. The paired vitellaries start shortly behind the brain and stretch caudally back to the genital opening. The paired ovaries take most of the caudal end. The seminal receptacles are a glandular tissue containing aggregations of sperm located between (or, above the junction of) the vitellaries and ovaries. Since this tissue has no distinctly
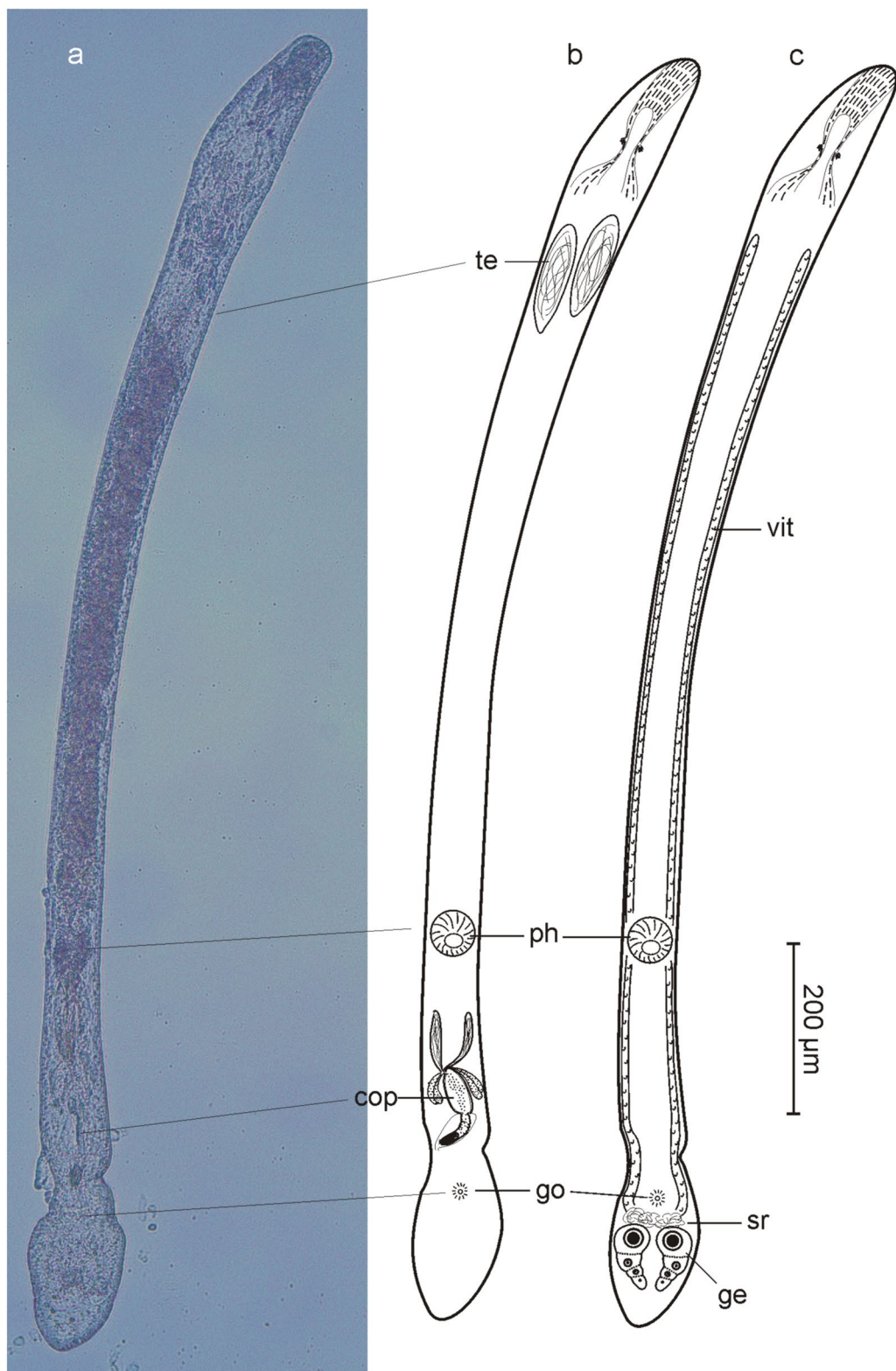
Fig. 9 *Scoliopharyngea magnaspina*, organisation. **a**, **b** Male maturity, **c** in female maturity. *te* testes, *cop* copulatory organ, *ge* germary, *go* genital opening, *ph* pharynx, *vit* vitellary, *sr* seminal receptacle
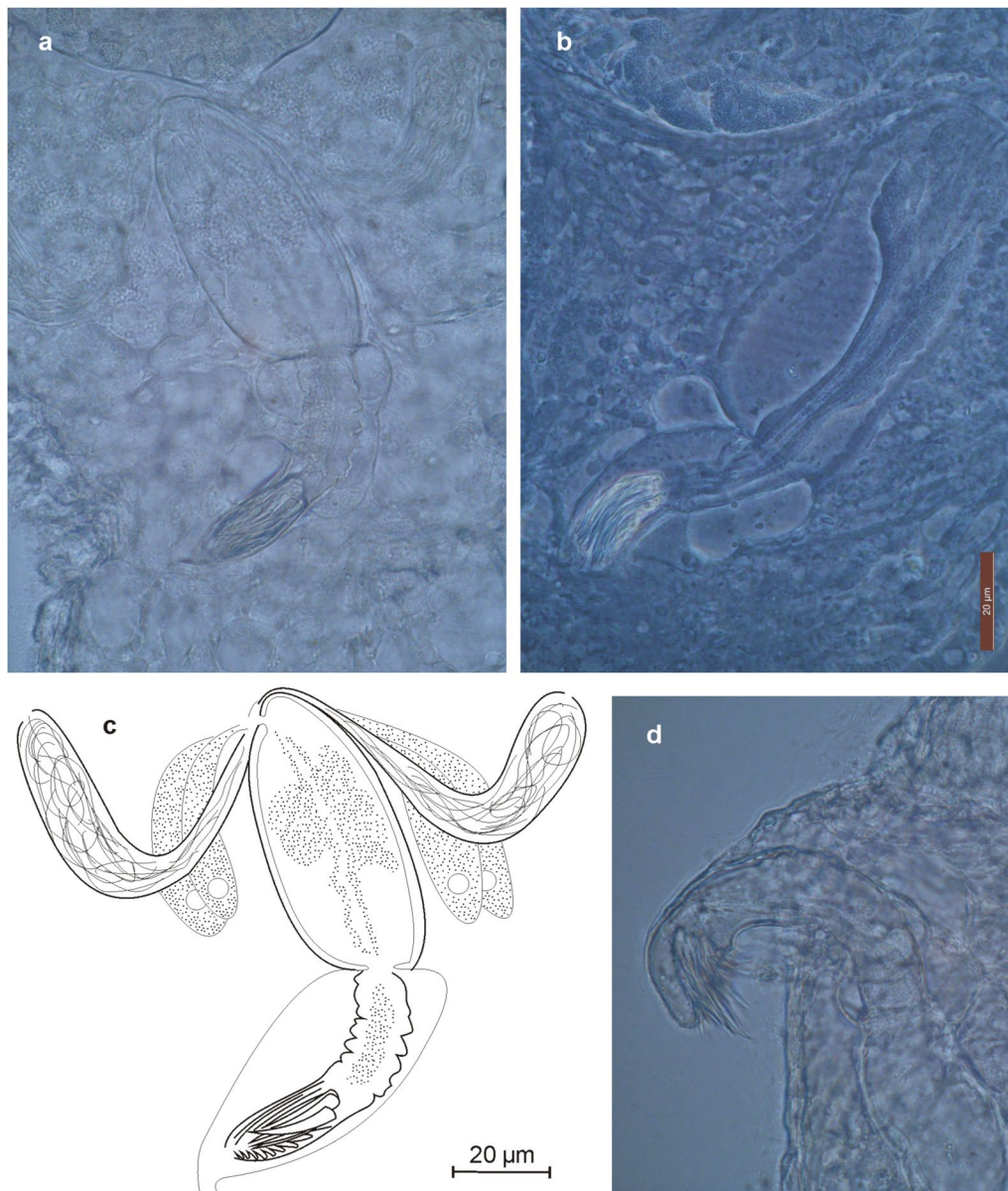
Fig. 10 *Scoliopharyngea magnaspina,* copulatory organs from different individuals

defined outer borderline it is not clear whether the seminal receptacles are separate of fused.

Discussion

The family Promesostomidae Hartog, 1964 unites species with a single genital pore, paired male and female gonads, and a single connection between the female gonads and the exterior. In most species, the copulatory organ is equipped with a stylet; a cirrus only occurs in five genera (*Scoliopharyngia* Ehlers, Müller & Franke, 1994; *Gaziella* De Clerck & Schockaert, 1995; *Cilionema* Karling, Mack-Fira & Dörjes, 1972; *Moevenbergia* Armonies & Hellwig, 1987; and *Protandrella* Ehlers, Müller & Franke, 1994). With respect to the arrangement of sexual organs, in particular the frontal position of the testes, the new species is closest to *Scoliopharyngea*. Differences between the described and the new species are the presence or absence of eye-pigmentations and the size, number, and arrangement of cirrus spines. Since the entire family is in need of revision [24, 25] this classification is preliminary, only.

Promesostoma convolutum n. sp. (Fig. 11)

Type locality

Lister Ley, medium to fine sand of a sandbank, 5 m water depth (55.0350 to 55.0370° N, 008.4720 to 008.4750° E, Feb 2018 and Feb to Mar 2019, > 100 individuals). Steady companions were *Archimonocelis oostendensis*, *Subulagera rubra*, *Cheliplana boadeni*, *Dactyloplana tridigitata*, *Diascorhynchus rubrus*, *Neoschizorhynchus parvorostro*, and *Pseudoschizorhynchoides ruber*.

Material

Life observations including drawings and photographs. Ten whole mounts, one designated holotype (AWI Sylt P2019-211), and 9 paratypes (AWI Sylt P2019-212 to 220).

Etymology

The species name refers to the winding of the stylet, from Latin convolvere = to coil, covolutum = coiled.

Diagnosis

Promesostoma with a sub-proximally coiled stylet of 550-600 μm length ending in a rounded tip with a lateral opening.

Description

Slender unpigmented specimens, free-swimming up to 1.2 mm long. With large paired eyes; rhabdites scattered all over the body with higher densities at the body ends. In medium-sized specimens the pharynx lies in mid-body but it may be shifted to the beginning of the last third in large-sized organisms; the genital opening is always half-way between the pharynx and the rounded caudal end. Arrangement of genital organs as usual in the genus: paired testes laterally in front of the pharynx, paired germaries caudally of the genital opening, and paired vitellaries laterally in the body from the brain to nearly the caudal end. The male copulatory organ (prostatic vesicle sensu Karling 1967 [26]) is situated in front
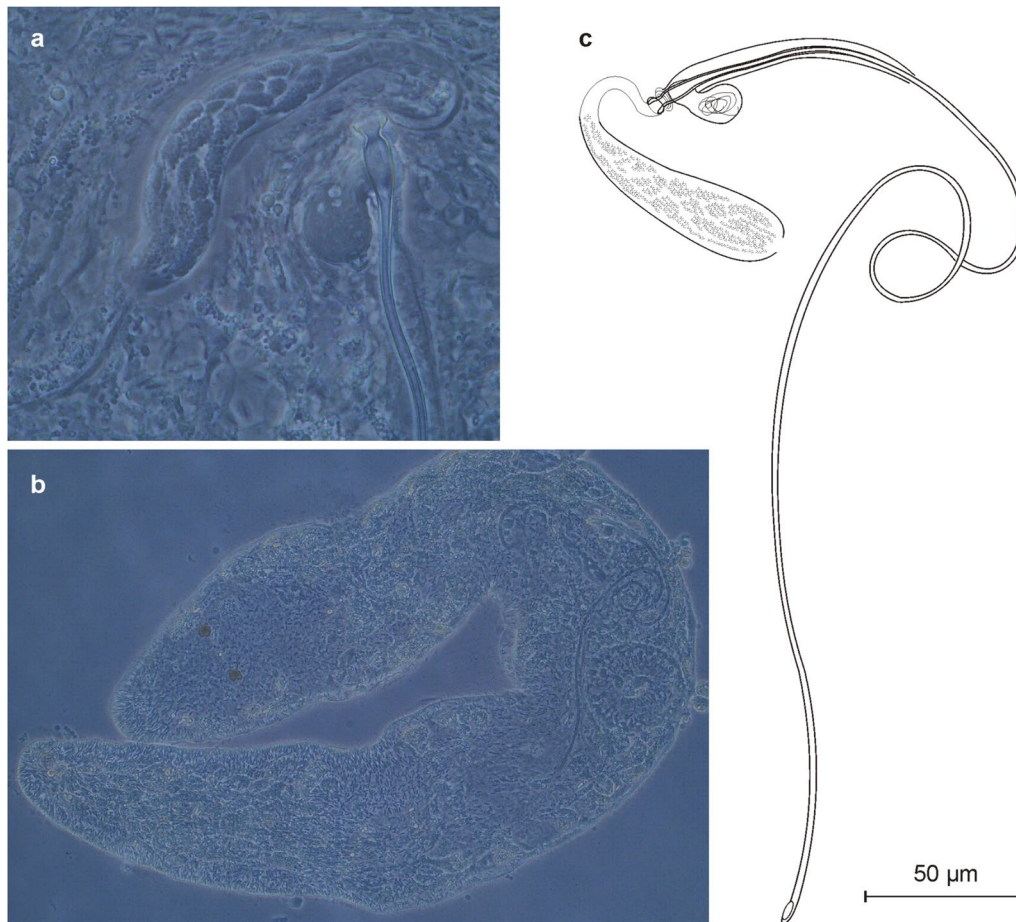
Fig. 11 *Promesostoma convolutum,* copulatory organ (**a**), life specimen (**b**), and copulatory organ with stylet (**c**)

of the pharynx; it is elongate and weakly muscular. External seminal vesicles were not observed.

The stylet is a slender tube of 510–580 µm length (mean 545 µm, n = 9). In un-squeezed specimens the stylet was coiled (two whorls) with the position of the whorls some distance (about 100 µm) caudally of the proximal opening. The proximal opening has an inner diameter of 4.5 µm (outer diameter 6 µm) rapidly narrowing to 2 µm (outer diameter 3.0 µm) at the sphincter. Behind the sphincter it is enlarged again to 4.5/3.5 µm over some 10 µm stylet length, and then reduced again to 2–2.5 µm diameter until the distal end which is rounded with a lateral oval opening. Increasing squeezing-pressure caused the stylet to stretch. The male genital canal bears a strengthened lining in the proximal part (roughly coinciding with the uncoiled section of the stylet) but is faint more distally. Presumably, the strengthened part acts as a copulatory bursa. A small roundish seminal receptacle branches from the most proximal part of the male genital canal. It is connected to the male genital canal by a short and wide duct that seems to be fixed at the proximal enlargement of the stylet. Accessory glands were seen in the genital atrium.

Discussion

Currently the genus *Promesostoma* includes 35 valid species which mainly differ in details of the male genital tract. In most species the stylet is proximally bent or even angled; a straight proximal part is usually limited to short stylets. *P. convolutum* so far is the only species combining a long stylet with a straight proximal part. Long (> 400 µm) stylets are commonly coiled in their most proximal part. In *P. convolutum* the coiling of the stylet tube occurs further distal, similar to *P. maculosum* Ax, 1956 which, however, has a much shorter stylet (250 to 396 µm; Ax 1956 [27], Steenkiste et al. 2011 [28]) and the tips of the stylets differ. The proximal part of the *P. convolutum* stylet resembles *P. serpentistylum* Ax, 1952: in both species the proximal part of the stylet is straight, the diameter enlarged for a short distance behind the sphincter, and with a seminal receptacle connected by a wide duct to the area of this stylet enlargement. These species may be closely related and specimens of *P. convolutum* with a developing stylet may easily be confused with *P. serpentistylum*. Ecologically they occupy 'neighbouring' habitats: *P. serpentistylum* is found in medium sand of the intertidal zone, *P. convolutum* in medium- to fine sand in the shallow subtidal.

Gnathorhynchus rostellatus indivisus n. ssp. (Fig. 12)
Localities
Fine sand of the sandbank separating List Deep from the North Sea (55.0865° N, 008.3280° E, 6 m water depth; 6 Dec 2018, 1 individual). Occurred together with *Litucivis simplex*, *Scoliopharyngea magnaspina*, and *Proxenetes trigonus.*

Material
Live observation and photographs; one whole mount (holotype, AWI Sylt P2019-110).

Etymology
The subspecies name refers to the undivided root of the proboscis hooks, as opposed to the bifurcated root in the nominal species.
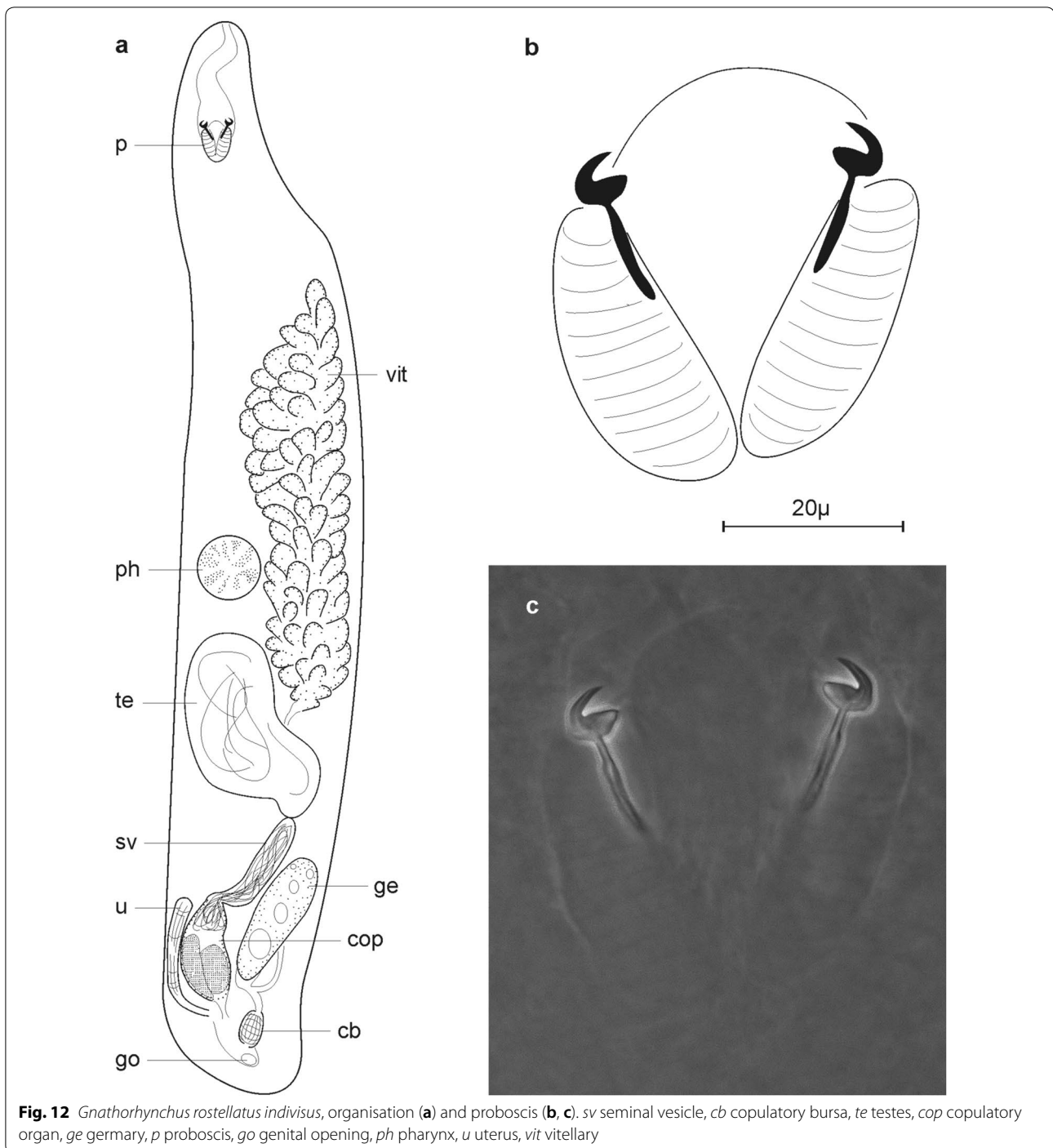
Diagnosis
Gnathorhynchus rostellatus differing from the nominal species in the undivided anchorage of the proboscis hooks.

Description
Unpigmented specimens without eyes, free swimming up to 1 mm long, with a small (diameter 40 µm) pharynx positioned in mid-body. Proboscis small, 40 µ long (including the cone), lateral muscle bundles 32 µ long, maximum width 35 µm. Proboscis hooks sickle-shaped, about 6 µm in diameter, without a basal plate but with a long (12–14 µm) pole-shaped root anchoring the hooks to the inner side of the lateral muscle bundles. A strikingly long (about 100 µm) duct connects the proboscis to its frontal opening.

All gonads are unpaired and there is a single genital opening. The testis lies directly behind the pharynx, directly followed by a wide external seminal vesicle (85 µm long and 25 µm wide) that is separated from the copulatory organ (the internal seminal vesicle) by a slight constriction only. The copulatory organ is ovoid in shape (85 µm long and up to 50 µm wide), with a weak muscular cover, and without sclerotic structures. The proximal third is filled with sperm (internal seminal vesicle); however, since the external and internal seminal vesicles are only separated by a slight constriction, they may be hardly discernible in life organisms. The distal two-thirds of the copulatory organ are entirely filled with large vesicles homogenously filled with very fine (not visibly grained) prostatic secretions. Two of these vesicles could positively be distinguished, but possibly there are more. Distally the copulatory organ is connected to the genital atrium with the subterminal genital opening by a rather short (35 µm) muscular male genital canal. The uterine canal is as long as the male genital canal and enters the common genital atrium next to it. The uterus is a muscular bag some 60 µm long and 6–8 µm wide.

Fig. 12 *Gnathorhynchus rostellatus indivisus*, organisation (**a**) and proboscis (**b**, **c**). *sv* seminal vesicle, *cb* copulatory bursa, *te* testes, *cop* copulatory organ, *ge* germary, *p* proboscis, *go* genital opening, *ph* pharynx, *u* uterus, *vit* vitellary

The vitellary stretches right-sided from the first to the last fifths of the body. The ovary lies to the right of the seminal vesicle; a seminal receptacle could not be positively identified in life material. Both the oviduct and the common duct are short (10–15 μm) and lead to an ovoid copulatory bursa (about 35 μm long and 28 μm wide) than opens into the genital atrium.

Discussion
The most striking feature in Mediterranean representatives of this species is the anchorage of the proboscis hooks in the muscular part of the proboscis by long, bifurcated roots (see Fig. 14 in Brunet 1973 [29]). In the Sylt specimens, the roots are also present but they are not branched (Fig. 11); this is a major difference to *G.*

rostellatus Brunet, 1973. On the other hand, the general organisation of the Sylt specimen conforms well to the original description from the Mediterranean. Therefore, I provisionally treat the specimens with unbranched hook-roots as a sub-species.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s10152-019-0533-y.

Additional file 1: Table S1. 'Baseline data': Position, water depth, sediment type, and species spectrum of Kalyptorhynchia, compiled from Noldt [8, 9]. **Table S2.** 'New data, original': Position, water depth, sediment type, and species spectrum of Platyhelminth species recorded from the subtidal around the island of Sylt, including undescribed species. **Table S3.** 'New data, presence-absence': Subset of Table S2, reduced to presence-absence data of described Kalyptorhynchia species. **Table S4.** 'Site-by-site comparison': Faunal similarity of Kalyptorhynchia based on 15 sites studied both by Noldt and in 2018. **Table S5.** 'Habitat approach 15 sites': Calculation of faunal similarity between 1982-84 and 2016-19 across habitat types, based on the 15 sites studied in both periods. **Table S6.** 'Habitat approach all sites': Calculation of faunal similarity between 1982–1984 and 2016–2019 across habitat types, based on the all sites studied in either period. **Table S7.** 'Species list': List of Platyhelminthes species recorded from the subtidal around Sylt island, including authorities and major references.

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