

A tip of the iceberg—Pseudotanaidae (Tanaidacea) diversity in the North Atlantic

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Abstract

During two IceAGE expeditions, a large collection of Tanaidacea was gathered from the shelf down to the slope (213–2750 m) in six areas off Iceland—the Irminger Basin, the Iceland Basin, the Norwegian Sea, the Denmark Strait, the Iceland-Faroe Ridge, and the Norwegian Channel. In this collection, members of the family Pseudotanaidae were most numerous component. We examined 40 samples collected with different gears (e.g., EBS, VVG, GKG), in which 323 pseudotanaid individuals were counted and covered a total depth from 213.9 to 2746.4 m. Morphological identification of the material has revealed the presence of five species: *Akanthinotana* cf. *longipes*, *Mystriocentrus biho* sp. n. *Pseudotana* *misericorde* sp. n., *P. svavarssoni* sp. n., and *P. sigrunis* sp. n. The description of the four new species has been presented in the paper and a rank of the subgenus *Akanthinotana* is elevated to a genus rank. A large group of morphologically almost identical specimens, similar with *P. svavarssoni* sp. n. from a wide depth range and from various areas off Iceland was discriminated to species by applying morphometric methods; one distinct species (*P. svavarssoni* sp. n.) and complex of presumably cryptic species the species was discovered. Based on current data and literature records, similarity among fauna of Pseudotanaidae was assessed with applying Bray–Curtis formula. As results, potential zoogeographic regions in the North Atlantic have been distinguished.

Keywords Tanaidacea · Pseudotanaidae · *Pseudotana* · *Mystriocentrus* · *Akanthinotana* · New species · Zoogeography
IceAGE · Iceland · North Atlantic

Introduction

Iceland is located at the junction of the Mid-Atlantic Ridge and Greenland–Scotland Ridge (Logemann et al. 2013.) The submarine ridges play an essential role in the oceanic circulation and distribution of water masses, and hence, in the distribution of marine fauna (Asthorsson et al. 2007; Brix and Svavarsson 2010; Schnurr et al. 2014). The Greenland–

Scotland Ridge hampers the interaction between two water masses: the warm water originated in the southern part of North Atlantic, and the polar water from the Arctic Ocean (Logemann et al. 2013; Jochumsen et al. 2016). The warm and saline Atlantic water flows northwards in the near-surface layer via the Reykjanes Ridge, to continue northernmost as the North Icelandic Irminger Current north-west of Iceland, and over the Iceland-Faroe Ridge east of Iceland (Asthorsson et al. 2007). The cold Arctic water is transported south, partly in the near-surface layer along the Greenland coast (the East Greenland Current), and in part as a bottom current carrying a very cold and dense water from the Nordic Sea down to the south off Iceland (Perkins et al. 1998; Hansen and Osterhus 2000). Since the water masses below the threshold of the Ridge are separated (Jochumsen et al. 2016), biological processes and species composition of faunas in basins located on both sides of the Ridge are thought to be different (Gislason and Astthorsson 2004; Astthorsson et al. 2007).

The specific oceanography of waters surrounding Iceland renders the region an important field laboratory in which to investigate diversity, distribution, and migration of the marine

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fauna. The Icelandic marine Animals Genetic and Ecology (IceAGE) project aimed to understand how underwater physical structures (e.g., submerged ridges) and non-physical barriers (e.g., currents, temperature, salinity) affect the distribution of benthic organisms (Brix et al. 2014). Traditional taxonomic methods as well as modern approaches to biodiversity research (ecological modeling and molecular species discrimination) have been studied for such groups as Isopoda, Tanaidacea, Ophiuroidea, and Mollusca (Brix, 2011; Błażewicz-Paszkowycz et al. 2014; Khodami et al. 2014; Mikkelsen and Todt 2014; Schnurr and Maljutina 2014; Todt and Kocot 2014). Benthic samples collected from an extensive depth range (117–2750 m), at different localities around Iceland, providing an opportunity to test if, and to what extent, topographic and oceanographic barriers (i.e., ridges, currents) influence the distribution, community structure, and diversity of benthic organisms.

The Tanaidacea (Peracarida, Malacostraca) are small marine crustaceans commonly occurring in diverse benthic habitats. As they are brooders and have no planktonic larvae, their mobility is low, and thus their dispersal ability is considered to be limited (Błażewicz-Paszkowycz et al. 2012, 2014). Tanaids may reach high densities (Larsen 2005); under specific environmental conditions (i.e., depth), they were found to be more abundant than amphipods, isopods, or mysids (Bamber 2005). Although the interest in the tanaidacean fauna has been observed to increase during the last decade (e.g., Bamber 2012; Błażewicz-Paszkowycz et al. 2013; Drumm and Bird 2016), the taxon still remains inadequately known. Over 1300 of the species described so far represent some 2–3% of their estimated diversity (Błażewicz-Paszkowycz et al. 2012).

The IceAGE cruises carried out in 2011 and 2013 (Brix et al. 2013) provided an opportunity to obtain a large collection of tanaidaceans and the family Pseudotanaididae Sieg, 1976 accounted for a substantial part of it (unpublished data of the authors). The family is widespread in the world's ocean, and its members being encountered within a wide depth range: from 0.5 to over 7000 m (Bird and Holdich 1989a; Błażewicz-Paszkowycz et al., 2012; Pabis et al. 2015). Pseudotanaids have been reported from different habitats, e.g., hard bottom, algae, coral reefs, cold seeps, mud volcanos, and hydrothermal vents (Bird 1999; Błażewicz-Paszkowycz and Bamber 2011; Larsen, 2012; Stepień unpublished data).

So far, 51 species have been described and 21 species have been recorded in the North Atlantic (Fig. 2). Lilljeborg (1864) was the first to report on pseudotanaids, although the family would be established in 1976 by Sieg (1976). Lilljeborg described *Pseudotanais forcipatus* (Lilljeborg 1864) as *Tanais forcipatus* from the Swedish coast. Almost 20 years later, Sars (1882) erected the genus *Pseudotanais* and synonymized the species of Lilljeborg. Moreover, the list of North Atlantic pseudotanaids was supplemented by records of *P. macrocheles* Sars, 1882 and *P. lilljeborgi* Sars, 1882 from

the Norwegian coast (Sars 1882) and *P. affinis* Hansen, 1887 from the Kara Sea (Hansen 1887). Hansen (1913) added new records of the previously known species and described three new species (*P. abyssi* Hansen, 1913; *P. oculatus* Hansen, 1913, and *P. longipes* Hansen, 1913) from off Iceland and Greenland. The wide distribution of those species in arctic, subarctic, and boreal regions was subsequently reported by numerous authors (e.g., Sars 1896; Greve 1965a, b, c; along the Norwegian coast; Stephensen 1937: off Greenland, Iceland, and Faroe). The number of pseudotanaid species known in the North Atlantic remained unchanged for the next 60 years until two further species (*P. jonesi* Sieg, 1977, *P. similis* Sieg, 1977) were described by Sieg from the Bay of Biscay (Sieg 1977). Furthermore Sieg (1977) proposed splitting genus *Pseudotanais* to two subgenera: *Akanthinotanais* (A.) and *Pseudotanais* (P.).

In a series of papers describing results of BIOGAS, GASCOR, and EPI VI programmes, Bird and Holdich (1985, 1989a, b) highlighted the high biodiversity of pseudotanaids in the depth range of 1100–4800 m in the North Atlantic, mainly west of Great Britain and in the Bay of Biscay. They erected two new genera—*Mystriocentrus* Bird and Holdich, 1989a and *Parapseudotanais* Bird and Holdich, 1989b, and described eleven species, namely *Mystriocentrus serratus* Bird and Holdich, 1989a; *Parapseudotanais abyssalis* Bird and Holdich, 1989b; *Pseudotanais* (P.) *corollatus* Bird and Holdich, 1989a; *P. (P.) colonus* Bird and Holdich, 1989b; *P. (P.) denticulatus* Bird and Holdich, 1989a; *P. (P.) falcicula* Bird and Holdich, 1989b; *P. (P.) longispinus* Bird and Holdich, 1989a; *P. (P.) scalpellum* Bird and Holdich, 1989b; *P. (P.) spatula* Bird and Holdich, 1989a; *P. (P.) spicatus* Bird and Holdich, 1989b; and *P. (P.) vulsellula* Bird and Holdich, 1989a. Finally, one more species, *P. (P.) falcifer* Błażewicz-Paszkowycz and Bamber, 2011 from a mud volcano off Norway, was added to the list (Błażewicz-Paszkowycz and Bamber 2011).

Our aims in this work were to (1) assess, based on literature data and new records from the IceAGE project, the diversity and distribution of the Pseudotanaididae in the North Atlantic, understood as the area north of 40° N (Dinter 2001); (2) describe new species belonging to the family; and (3) based on current data and literature records to assess the similarity among fauna of Pseudotanaididae in various region of The North Atlantic to pinpoint potential zoogeographic regions.

While working on the IceAGE collection, we found a large group of morphologically almost identical specimens from all the basins off Iceland where the samples were collected (the Iceland and Irminger Basins, Denmark Strait, Norwegian Sea, Iceland-Faroe Ridge and the Faroe-Shetland Channel) from a wide depth range. Considering the low mobility of the Tanaidacea (they are tube-building brooders without planktonic stage) and the presence of geographic barriers around Iceland (i.e., submarine ridges, a complex current system), we hypothesize that those morphologically almost identical

individuals found in different environmental regimes are distinct species. To test the hypothesis, we attempted to discriminate between the species (which are presumably a cryptic species complex) using a morphometric approach.

Study area

Iceland lies at the junction of the Mid-Atlantic Ridge (MAR) and the Greenland–Scotland Ridge (GSR) (Logemann et al. 2013). As a result of the topography, the oceanic area around Iceland is divided into four basins (Fig. 1). The Iceland and Irminger Basins, located south of the island to the east and west, respectively, are separated by the Reykjanes Ridge, an extension of MAR (Malmberg and Valdimarsson 2003). The two basins are bounded by the Greenland–Iceland Sill (Denmark Strait) to the west and by the Iceland–Faroe Ridge to the East (Malmberg and Valdimarsson 2003). The northern and north-eastern basins are the Iceland Sea and the Norwegian Sea, respectively (Malmberg and Valdimarsson 2003), the former being split into two parts by the Kolbeinsey Ridge.

The area south of Iceland is primarily affected by the Atlantic water masses (Fig. 1). The southern and south-eastern shelf is bathed by the South Icelandic Current (SIC) that flows north and north-east and transports the Modified North Atlantic Water

(MNAW). Upon reaching the Faroe–Shetland Ridge, SIC turns to the south-east to flow along the ridge and to open out into the Faroe Current. The south-eastern Icelandic slope (at a depth of 500–1100 m) is bathed by the anticlockwise current, made up by the Norwegian Sea Deep Water (NSDW) (Malmberg and Valdimarsson 2003). This water mass, called here the Iceland–Scotland Overflow Water (ISOW), crosses the Iceland–Faroe Ridge, passes the Iceland Basin, and continues into the Irminger Basin (Meißner et al. 2014).

The deep part (deeper than 1500 m) of the Irminger Basin is affected by ISOW as well as by the Denmark Strait Overflow Water (DSOW), which passes through the Denmark Strait and flows south along the Greenland slope) and the Labrador Sea Water (formed in the Labrador Sea) (Malmberg 2004; Meißner et al. 2014) (Fig. 1). The shallower part of the Basin remains under the influence of the Irminger Current (IC), which transports MNAW along the Reykjanes Ridge. IC flows north along the slope (Logemann et al. 2013). Upon reaching the Denmark Strait, IC turns south to flow along the Greenland slope.

The Denmark Strait is, in part, affected by MNAW transported by an IC branch, the North Icelandic–Irminger Current (NIIC) flowing north along the Icelandic shelf edge (Meißner et al. 2014). A cold-water mass [i.e., the Arctic Polar Water (APW, DSOW)] flows along the East Greenland shelf and slope.

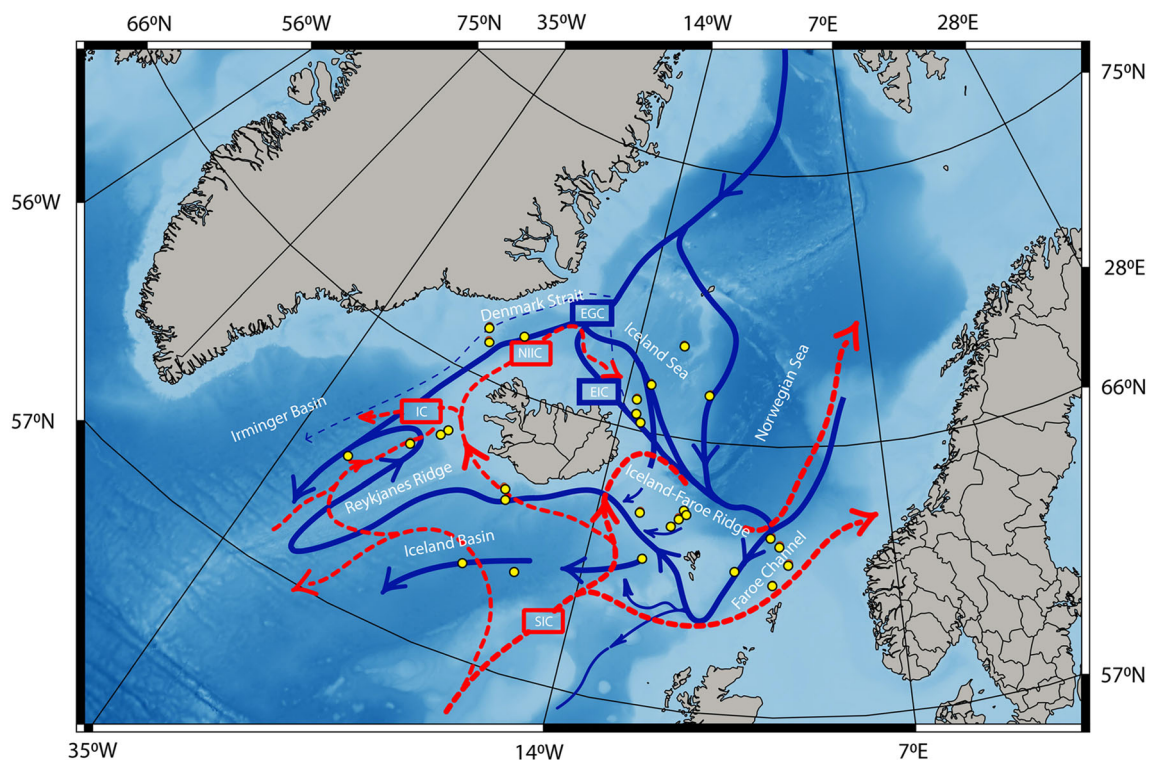


Fig. 1 Study area and location of sampling station (yellow dots) in the N Atlantic during IceAGE expeditions. Red lines: warm currents (branches of North Atlantic Current); blue lines: cold currents of arctic origin; dashed lines: surface currents; not-dashed lines: deep sea current. EGC

East Greenland Current, EIC East Icelandic Current, IC Irminger Current, NIIC North Icelandic–Irminger Current, SIC South Icelandic Current; after Hansen and Osterhus (2000) and Ostmann et al. (2014)

The north and north-eastern areas experience mixing of several water masses (Meißner et al. 2014). NICC transports the Atlantic water which loses heat here. In addition, shallow areas are affected by the Norwegian Sea Arctic Intermediate Water, deeper parts being influenced by NSDW (Fig. 1). East of the Kolbeinsey Ridge, NIIC and the Arctic Water form the East Icelandic Current (EIC) which bathes the north-eastern continental slope to eventually reach the northern flank of the Iceland-Faroe Ridge. EIC is underlain by the North Icelandic Jet, a cold undercurrent which flows west, within the depth range of 200–1000 m, to cross the Kolbeinsey Ridge and reach the northern part of the Denmark Strait.

Material and methods

Samples

This study is based on the pseudotanaid collection obtained during two (2011 and 2013) IceAGE cruises on board the RVs *Meteor* and *Poseidon* (Brix et al. 2014). The samples were collected from the shelf down to the slope (213–2750 m) in six areas off Iceland, henceforth referred to as “basins”: the Irminger Basin, the Iceland Basin, the Norwegian Sea, the Denmark Strait, the Iceland-Faroe Ridge, and the Norwegian Channel (Fig. 1).

The pseudotanaid material was obtained with different sampling devices: a Van Veen grab (VV), a Shipek grab (SG), a box corer (GKG), and an epibenthic sledge (EBS). It was sieved (500 µm mesh size) using chilled seawater, and preserved in 4% formaldehyde for morphological research; some individuals were fixed in pre-cooled 96% undenaturated ethanol for molecular analyses (Riehl et al. 2014). For the purpose of this work, the formaldehyde-treated samples were used only.

A total of 40 samples were examined, which yielded 323 pseudotanaid individuals. Four samples were collected in the Iceland Basin, 6 in the Irminger Basin, 6 in the Denmark Strait, 11 in the Norwegian Sea, 5 in the Norwegian Channel, and 8 off the Iceland-Faroe Ridge (Table 1).

Taxonomic description

Representative females were dissected using chemically sharpened tungsten needles; appendages were mounted in glycerine on slides. Working drawings were prepared using a microscope equipped with a *camera lucida*; the publication-quality illustrations were prepared using a digital tablet and Illustrator software (Coleman 2003). The morphological terminology follows that proposed by Błazewicz-Paszkowycz and Bamber (2011). The spatulate setae mentioned by Bird and Holdich (1989a, b) are referred to as the sensory setae here.

The material has been deposited in the Universität Hamburg Zoological Museum Center of Natural History (CeNak) (Germany) (Table 2).

Measurements

We applied a morphometric analysis to strengthen the identification of the most numerous and widely distributed circum-Icelandic species of the genus *Pseudotanaid* (described as *P. svavarssoni*, sp. n. see below). Ovigerous females and neutri individuals (similar in size to ovigerous females) from each basin, with unbroken appendages and a complete blade-like spine, were selected for the analysis (Table 3).

The measurements were made with a camera connected to the microscope (Nikon Eclipse Ci-L) and NIS-Elements View software (www.nikoninstruments.com). The body width and the length of the carapace, pereonites, pleonites, and pleotelson were measured on whole specimens. The length was measured along the axis of symmetry, whereas the width, perpendicular to the axis of symmetry, at the widest spot. As the pseudotanaid pleotelson is usually curved, it was often impossible to observe on a slide; therefore, instead of measuring the total body length, we took three measurements (i.e., the lengths of the carapace, total pereonites, and five pleonites). Thus, the body length is a sum of lengths of all the body segments without the pleotelson.

Appendages were measured (length and width) by measuring their articles on dissected specimens. A total of 173 characters and 29 specimens from four different “populations” (with respect to regions and depth: “*population 1*” (P1) from the deep (~2000 m) part of the Norwegian Sea; “*population 2*” (P2) from the deep (~1300–1500 m) part of the southern basins: the Iceland and Irminger; “*population 3*” (P3) from the shallow (~200 m) part of the southern Irminger Basin; and “*population 4*” (P4) from the shallow (~400–600 m) part of the Iceland–Scotland Ridge (the Iceland–Faroe Ridge and the Norwegian Channel) was measured. For the statistical analysis, the following 42 characters/ratios were used:

- (1) The combined carapace, pereonite, and pleonite length (CPP)
- (2) The CPP to carapace length ratio
- (3) The CPP to pereonite-1 length ratio
- (4) The CPP to pereonite-2 length ratio
- (5) The CPP to pereonite-3 length ratio
- (6) Length of CPP to pereonite-4 length
- (7) Length of CPP to pereonite-5 length
- (8) The CPP to pereonite-6 length ratio
- (9) The combined pleonite length to pleon width ratio
- (10) The antennule to carapace length ratio
- (11) The antennule to antennule article-1 length ratio
- (12) The antennule article-3 to article-2 length ratio
- (13) The antenna article-2 to article-2 distal spine length ratio

Table 1 Main characteristics of the sampling stations where Pseudotanaidæ species were collected during IceAge cruises (according to Brix et al. 2012); (EBS epibenthic sledge, GKG box corer, SG Shippek grab, VV Van Veen grab)

Cruise	Area	Station	Gear	Date	Latitude [N]	Longitude [W]	Depth [m]	Temperature [°C]	Salinity	Oxygen [$\mu\text{mol/kg}$]
IceAge I	Iceland Basin	963-1	EBS	28.08.2011	60° 02.73'	21° 29.86'	2746.4	2.65	34.99	258.38
IceAge I	Iceland Basin	979-1	EBS	30.08.2011	60° 21.48'	18° 08.24'	2567.6	2.65	34.99	258.38
IceAge I	Iceland Basin	1010-1	EBS	02.09.2011	62° 33.10'	20° 23.71'	1384.8	3.88	35.02	254.57
IceAge I	Iceland Basin	1019-1	EBS	03.09.2011	62° 56.32'	20° 44.61'	913.6	5.29	35.08	242.79
IceAge I	Irminger Basin	1043-1	EBS	05.09.2011	63° 55.46'	25° 57.66'	213.9	7.42	35.19	246.74
IceAge I	Irminger Basin	1051-1	GKG	07.09.2011	61° 37.41'	31° 22.11'	2538.9	3.16	34.94	254.17
IceAge I	Irminger Basin	1054-1	EBS	07.09.2011	61° 36.19'	31° 22.60'	2537.3	3.16	34.94	254.17
IceAge I	Irminger Basin	1066	GKG	08.09.2011	62° 59.97'	28° 04.78'	1621.8	4.28	34.99	245.53
IceAge I	Irminger Basin	1072-1	EBS	08.09.2011	63° 00.46'	28° 04.09'	1593.8	4.28	34.99	245.53
IceAge I	Irminger Basin	1086-1	EBS	09.09.2011	63° 42.53'	26° 23.05'	698.1	6.19	35.09	231.52
IceAge I	Denmark Strait	1116-1	GKG	14.09.2011	67° 12.82'	26° 16.31'	683.1	0.07	34.90	292.96
IceAge I	Denmark Strait	1129-1	GKG	14.09.2011	67° 38.77'	26° 44.78'	320.6	0.70	34.62	290.90
IceAge I	Denmark Strait	1132-1	EBS	14.09.2011	67° 38.48'	26° 45.28'	318.1	0.70	34.62	290.90
IceAge I	Denmark Strait	1136-1	EBS	14.09.2011	67° 38.15'	26° 45.99'	315.9	0.70	34.62	290.90
IceAge I	Denmark Strait	1141-1	GKG	15.09.2011	67° 50.22'	23° 42.11'	1241.6	-0.66	34.91	278.77
IceAge I	Denmark Strait	1148-1	EBS	15.09.2011	67° 50.79'	23° 41.76'	1248.8	-0.66	34.91	278.77
IceAge I	Norwegian Sea	1178-1	GKG	20.09.2011	67° 38.71'	12° 10.10'	1818.8	-0.85	34.91	1818.80
IceAge I	Norwegian Sea	1184-1	EBS	15.09.2011	69° 05.60'	09° 56.01'	2172.6	-0.75	34.91	266.74
IceAge I	Norwegian Sea	1152-1	GKG	17.09.2011	69° 06.89'	09° 54.72'	2203.8	-0.75	34.91	266.74
IceAge I	Norwegian Sea	1155-1	EBS	17.09.2011	69° 06.66'	09° 55.02'	2202.8	-0.75	34.91	266.74
IceAge I	Norwegian Sea	1159-1	EBS	17.09.2011	67° 35.28'	06° 57.47'	2401.8	-0.82	34.91	271.26
IceAge I	Norwegian Sea	1166-1	GKG	19.09.2011	67° 35.28'	06° 57.47'	2401.8	-0.82	34.91	271.26
IceAge I	Norwegian Sea	1168-1	EBS	19.09.2011	67° 36.38'	07° 00.08'	2372.6	-0.82	34.91	271.26
IceAge I	Norwegian Sea	1184-1	EBS	20.09.2011	67° 38.63'	12° 09.72'	1819.3	-0.85	34.91	1819.30
IceAge I	Norwegian Sea	1188-1	GKG	21.09.2011	67° 04.32'	13° 00.89'	1580.6	-0.74	34.90	269.25
IceAge I	Norwegian Sea	1212-1	EBS	22.09.2011	66° 32.63'	12° 52.48'	317.2	1.36	34.84	291.81
IceAge I	Norwegian Sea	1216-1	GKG	22.09.2011	66° 18.06'	12° 22.38'	730.8	-0.40	34.90	283.58
IceAge I	Norwegian Sea	1219-1	EBS	22.09.2011	66° 17.34'	12° 20.82'	579.1	-0.40	34.90	283.58
IceAge I	Norwegian Sea	871-4	GKG	26.07.2013	62° 45.31'	00° 54.09'	1562.7	-0.78	34.91	298.34
IceAge II	Norwegian Channel	872-4	EBS	27.07.2013	63° 01.88'	01° 29.91'	1858.3	-0.79	34.91	295.35
IceAge II	Norwegian Channel	872-5	GKG	27.07.2013	63° 01.80'	01° 27.05'	1842	-0.79	34.91	295.35
IceAge II	Norwegian Channel	873-2	GKG	28.07.2013	61° 46.63'	03° 52.38'	835.1	-0.70	34.91	303.51
IceAge II	Norwegian Channel	873-6	EBS	28.07.2013	61° 46.52'	03° 52.38'	833.7	-0.70	34.91	303.51
IceAge II	Iceland-Faroe Ridge	879-2	SG	31.07.2013	63° 06.02'	08° 35.14'	505.9	1.33	34.95	305.41
IceAge II	Iceland-Faroe Ridge	879-5	EBS	31.07.2013	63° 06.10'	08° 34.32'	510.9	1.33	34.95	305.41
IceAge II	Iceland-Faroe Ridge	880-2	EBS	31.07.2013	63° 23.36'	08° 09.42'	686.0	-0.43	34.91	306.23
IceAge II	Iceland-Faroe Ridge	880-3	GKG	31.07.2013	63° 24.79'	08° 09.42'	688.1	-0.43	34.91	306.23
IceAge II	Iceland-Faroe Ridge	881-4	EBS	01.08.2013	63° 34.66'	07° 42.69'	1043.6	-0.57	34.91	303.94
IceAge II	Iceland-Faroe Ridge	881-6	VV	01.08.2013	63° 38.50'	07° 47.03'	1073.4	-0.57	34.91	303.94
IceAge II	Iceland-Faroe Ridge	882-2	VV	02.08.2013	63° 25.01'	10° 58.80'	441.4	0.27	34.90	311.93
IceAge II	Iceland-Faroe Ridge	882-5	EBS	02.08.2013	63° 25.04'	10° 58.20'	440.5	0.27	34.90	311.93

Table 2 Distribution of species described during this study

Area	Station	Depth [m]	<i>Akanthinotanaia</i> cf. <i>longipes</i>	<i>Mystriocentrus biho</i> n.sp	<i>Pseudotanaia misericonde</i> n.sp	<i>Pseudotanaia sigrunis</i> n.sp	<i>Pseudotanaia svavarssoni</i> n.sp	<i>Pseudotanaia svavarssoni</i> complex	Pseudotanaidae indet	Total of individuals
Iceland Basin	963-1	2746.4	–	–	–	1	–	1	–	2
Iceland Basin	979-1	2567.6	–	–	–	–	–	1	–	1
Iceland Basin	1010-1	1384.8	1	–	1	–	–	3	–	5
Iceland Basin	1019-1	913.6	–	1	–	–	–	1	–	2
Irminger Basin	1043-1	213.9	–	–	–	–	–	18	–	18
Irminger Basin	1051-1	2538.9	–	–	–	–	–	1	–	1
Irminger Basin	1054-1	2537.3	–	3	4	–	–	2	–	9
Irminger Basin	1066	1621.8	–	–	1	–	–	–	–	1
Irminger Basin	1072-1	1593.8	–	–	–	–	–	2	–	2
Irminger Basin	1086-1	698.1	–	–	–	–	–	1	–	1
Denmark Strait	1116-1	684.1	–	–	–	1	–	–	–	1
Denmark Strait	1129-1	683.1	–	–	–	–	–	1	–	1
Denmark Strait	1132-1	320.6	–	–	–	–	–	3	–	3
Denmark Strait	1136-1	318.1	–	–	–	–	–	2	–	2
Denmark Strait	1141-1	1241.6	–	–	–	–	–	1	–	1
Denmark Strait	1148-1	1248.8	–	–	–	–	–	5	–	5
Norwegian Sea	1178-1	1818.8	–	–	–	–	–	2	–	2
Norwegian Sea	1152-1	2172.6	–	–	–	–	6	–	5	11
Norwegian Sea	1155-1	2203.8	–	–	–	–	1	–	–	1
Norwegian Sea	1159-1	2202.8	–	–	–	–	127	–	–	127
Norwegian Sea	1166-1	2401.8	–	–	–	–	2	–	–	2
Norwegian Sea	1168-1	2372.6	–	–	–	–	49	–	–	49
Norwegian Sea	1184-1	1819.3	–	–	–	–	–	8	–	8
Norwegian Sea	1188-1	1580.6	–	–	–	–	–	6	–	6
Norwegian Sea	1212-1	317.2	–	–	–	4	–	9	–	13
Norwegian Sea	1216-1	730.8	–	–	–	4	–	6	–	10
Norwegian Sea	1219-1	579.1	–	–	–	2	–	5	–	7
Norwegian Channel	871-4	1562.7	–	–	–	–	–	2	–	2
Norwegian Channel	872-4	1858.3	–	–	–	–	–	3	–	3
Norwegian Channel	872-5	1842	–	–	–	–	–	1	–	1
Norwegian Channel	873-2	835.1	–	–	–	–	–	2	–	2
Norwegian Channel	873-6	833.7	–	–	–	–	–	1	–	1
Iceland-Faroe Ridge	879-2	505.9	–	–	–	–	–	2	–	2
Iceland-Faroe Ridge	879-5	510.9	–	–	–	–	–	3	–	3

Table 2 (continued)

Area	Station	Depth [m]	<i>Akanthinotanais cf. longipes</i>	<i>Mystricentrus biho</i> n.sp	<i>Pseudotanais misericonde</i> n.sp	<i>Pseudotanais sigruntis</i> n.sp	<i>Pseudotanais svavarssoni</i> n.sp	<i>Pseudotanais svavarssoni</i> complex	Pseudotanais indet	Total of individuals
Iceland-Faroe Ridge	880-2	686.0	-	-	-	-	-	1	-	1
Iceland-Faroe Ridge	880-3	688.1	-	-	-	1	-	-	-	1
Iceland-Faroe Ridge	881-4	1043.6	-	-	-	-	1	1	-	1
Iceland-Faroe Ridge	881-6	1073.4	-	-	-	-	1	1	-	1
Iceland-Faroe Ridge	882-2	441.4	-	-	-	2	1	1	-	3
Iceland-Faroe Ridge	882-5	440.5	-	-	-	2	-	-	-	11
	Total		1	4	6	18	185	105	5	323
	sum %		0.3	1.2	1.8	5.5	57	32.4	1.5	

- (14) The antenna article-3 to article-3 distal spine length ratio
- (15) The cheliped carpus length to width ratio
- (16) The cheliped basis to carpus length ratio
- (17) The cheliped propodus length to width ratio
- (18) The cheliped fixed finger length to propodus length ratio
- (19) The pereopod-1 basis length to width ratio
- (20) The pereopod-1 propodus to carpus length ratio
- (21) The pereopod-1 propodus to dactylus + unguis length ratio
- (22) The pereopod-1 unguis to dactylus length ratio
- (23) The pereopod-2 propodus to carpus length ratio
- (24) The pereopod-2 propodus to dactylus + unguis length ratio
- (25) The pereopod-2 propodus to blade-like spine length ratio
- (26) The pereopod-3 propodus to carpus length ratio
- (27) The pereopod-3 propodus to dactylus + unguis length ratio
- (28) The pereopod-3 propodus to blade-like spine length ratio
- (29) The pereopod-4 propodus to carpus length ratio
- (30) The pereopod-4 propodus to dactylus + unguis length ratio
- (31) The pereopod-4 propodus to blade-like spine length ratio
- (32) The pereopod-4 propodus to carpus distal seta length ratio
- (33) The pereopod-5 propodus to carpus length ratio
- (34) The pereopod-5 propodus to blade-like spine length ratio
- (35) The pereopod-4 propodus to carpus distal seta length ratio
- (36) The pereopod-6 propodus to carpus length ratio
- (37) The pereopod-6 propodus to dactylus + unguis length ratio
- (38) The pereopod-6 propodus to blade-like spine length ratio
- (39) The pereopod-6 propodus to carpus distal seta length ratio
- (40) The pleonite combined length to uropod basis and endopod combined length ratio
- (41) The uropod basis length to width ratio
- (42) The uropod exopod to endopod length ratio

Statistical analysis

The Kruskal–Wallis test with multiple post-hoc comparison (Statistica 10 software) was used to find out which of the ratios or characters determined significantly differentiate between the four “populations” studied. The characters and ratios identified by the test were used further to perform the principal component analysis (PCA) and analysis of similarity (ANOSIM). PCA is an ordination method in which samples (specimens here) regarded as points in a multi-dimensional space are projected onto a best fit plane (Clarke and Gorley 2006). Prior to the analysis, the data were normalized.

ANOSIM (Clarke and Gorley 2006) was conducted to test for the degree and significance of differences between a priori determined groups (“populations”) of specimens: ANOSIM calculates a test statistic (*Global R*) which equals 1 if all individuals within a population are more similar to each other than to any individual in another population, and 0 if there is no difference between populations (Clarke and Gorley 2006). The relevant dissimilarity matrix was constructed using the normalized Euclidean distance.

Table 3 Morphological characters and proportion found in *Pseudotanaeis svarvarssoni* sp. n. individuals to be differentiated: P1—group of individuals from deep Norwegian Sea, P2—deep Southern Basins, P3—shallow Irminger Basin, P4—shallow Iceland-Faroe Ridge. H—value of Kruskal–Wallis test (df = 3; N = 29); probabilities; Z—multiple comparison value

Group	Variable	(V1) combined length of carapace, pereonites and pleonites	(V2) length of pereopod-1 propodus to carpus length	(V3) length of pereopod-1 propodus to dactylus + unguis length	(V4) length of pereopod-3 propodus to blade-like spine length	(V5) length of pereopod-6 propodus to distal seta on carpus length	(V6) length of cheliped carpus to width	(V7) length of cheliped propodus to width
P1	Measurements	1.21–1.74	2.28–2.53	1.15–1.29	1.41–1.75	2.62–6.42	1.78–2.15	1.47–1.63
	Range	0.98–1.98	2.35–2.51	1.2–1.38	1.46–1.66	2.98–6.46	1.86–2.08	1.49–1.59
	SD	0.5	0.08	0.09	0.1	1.24	0.11	0.05
P2	Measurements	1.45–1.57	2.48–2.58	0.99–1.28	1.4–1.58	1.48–4.79	1.33–1.73	1.38–1.51
	Range	1.47–1.59	2.46–2.56	1.01–1.29	1.41–1.59	1.6–4.94	1.36–1.76	1.36–1.5
	SD	0.06	0.05	0.14	0.09	1.67	0.20	0.07
P3	Measurements	1.38–1.59	1.78–2.19	0.86–1.06	1.21–1.45	2.98–4.4	1.53–2.01	1.36–1.98
	Range	1.34–1.54	1.56–2.36	0.88–1	1.25–1.41	3.18–4.88	1.56–1.9	1.55–1.93
	SD	0.1	0.11	0.06	0.08	0.85	0.17	0.19
P4	Measurements	0.76–1.75	1.77–2.61	0.78–0.95	1.12–1.62	1.66–3.88	1.55–1.97	1.45–2.01
	Range	0.84–1.44	1.94–2.62	0.82–1.02	1.14–1.46	1.96–3.44	1.57–1.91	1.53–1.89
	SD	0.3	0.34	0.10	0.16	0.74	0.17	0.18
Kruskal-Wallis	H	13.33	13.52	20.01	15.52	9.25	13.92	10.36
	p	0.004	0.003	0.0002	0.001	0.01	0.002	0.01
Multiple comparison	Groups	G1 & G4	G1 & G3	G1 & G3	G1 & G3	G1 & G4	G1 & G2	G1 & G3
	Z	3.48	3.18	3.56	3.25	2.83	2.89	2.72
p		0.002	0.008	0.002	0.006	0.02	0.02	0.03

Fig. 2 Distribution of the Pseudotanaididae species in the North Atlantic based on literature (present study not included): Bird and Holdich (1989a, b); Błażewicz-Paszkowycz and Bamber (2011); Bruce et al. (1963); [Dahl] in Sieg (1977); [Deboutteville (1960), Deboutteville et al. (1954)] in Sieg (1983); [Fee, Hatch] in Sieg (1977); Greve (1965a, b, c); Hansen (1887, 1913); Holdich and Bird (1986); Holdich and Jones (1983); Just (1970); Kruuse, Ryder, Wandel in Hansen (1913); Liljeborg (1864); Sars (1882, 1896); Stephensen (1937); Sieg (1977); [Vanhöffen, Kruuse, Ryder, Herring, Sars] in Hansen (1913); [Vanhöffen, R. Herring, H.J. Hansen, Sars, A.M. Norman, Stappers, Th. Scott] in Hansen (1913); see Table 4

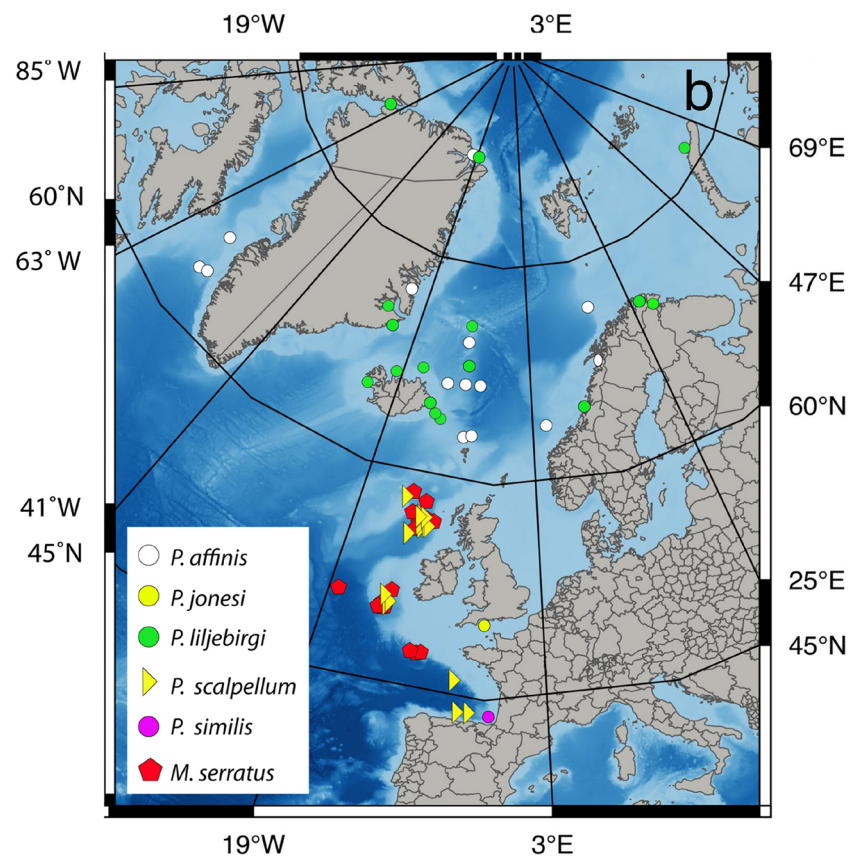
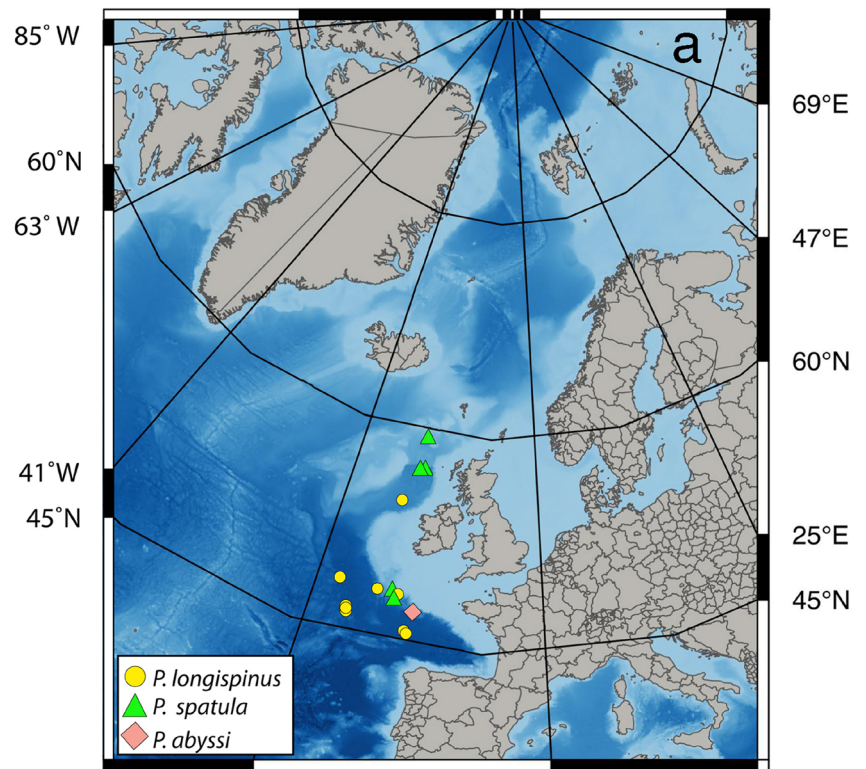


Fig. 2 (continued)

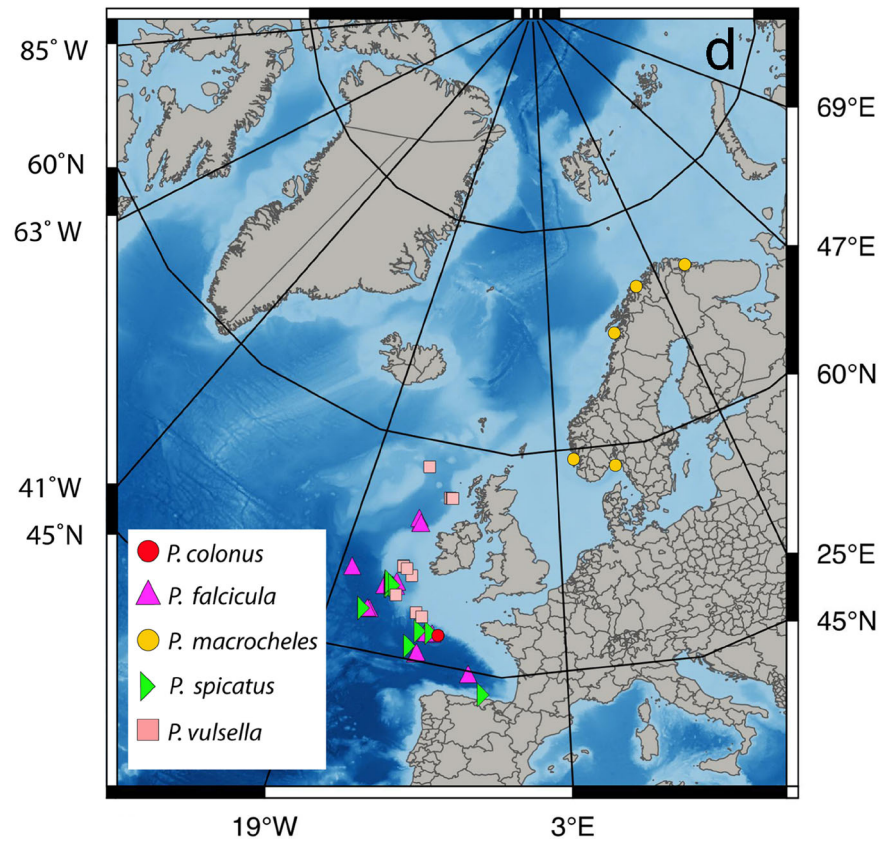
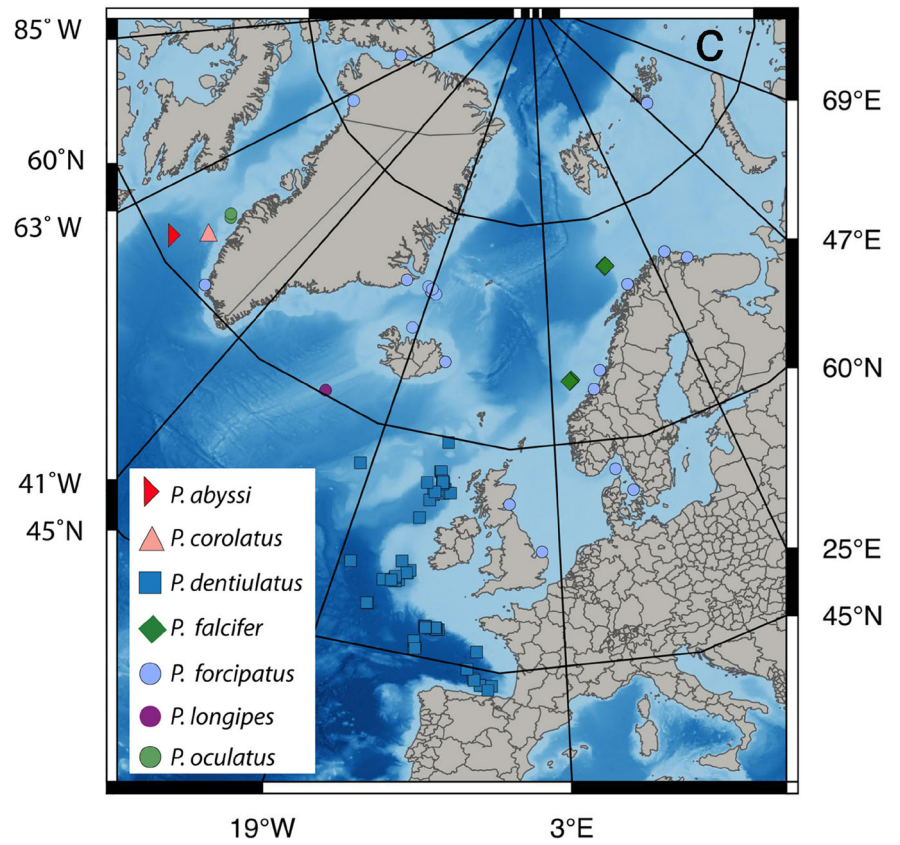
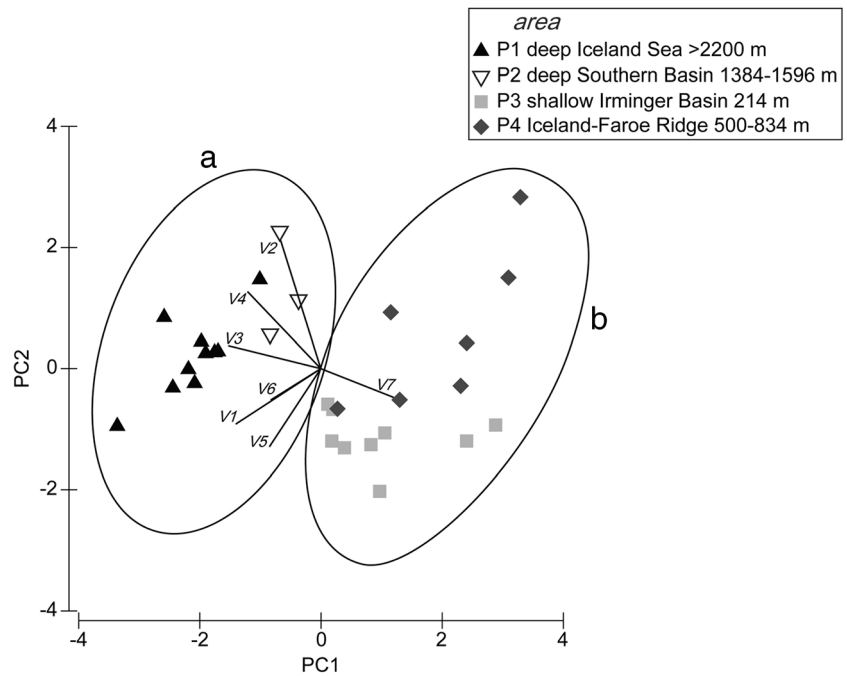


Fig. 3 Plot of principal component analysis based on seven morphometric characters (V1–7) of *P. svavarssoni* sp. n. and *P. svavarssoni* complex. List of character in Table 3



Similarities between the North Atlantic sites of pseudotanaids were determined in multivariate analysis using the group-average cluster and derived from the presence/absence-based Bray-Curtis similarity coefficient. In case of the species with particularly wide distribution (e.g., *P. affinis*, *P. lilljeborgi*, *P. forcipatus*), the records from a type locality and/or vicinity of the type localities only were included to analysis. In this approach, all potentially erroneous records and the records of possible cryptic species were excluded. PCA, ANOSIM, and group-average clustering were run using the PRIMER v. 6 package (Clarke and Gorley 2006).

Results

Species composition

The morphological approach adopted in this study allowed to identify five pseudotanaid species representing three genera: *Akanthinotanaid* Sieg, 1977, *Mystriocentrus* Bird and Holdich, 1989b, and *Pseudotanaid* Sars, 1882. The third genus yielded three species (including two new for science), *Akanthinotanaid* and *Mystriocentrus* being represented by one species each.

Species discrimination

PCA run with the seven morphometric characters initially identified as significantly discriminating (Table 3) was applied to the most numerous pseudotanaid species (*Pseudotanaid svavarssoni* sp. n.) and resulted in the first five PCs accounting for 90% of the total variation. Most of the variability in the seven characters is captured in the 2D projection plotted in

Fig. 3. The first and the second PC axes (PC1 and PC2) explain 44 and 16% of the total variance, respectively. PC1 axis

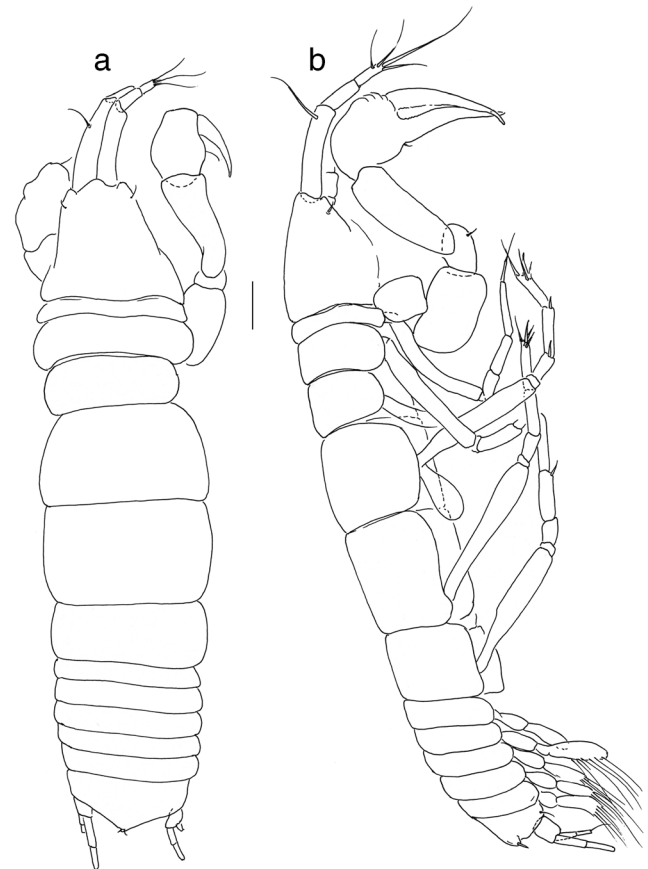
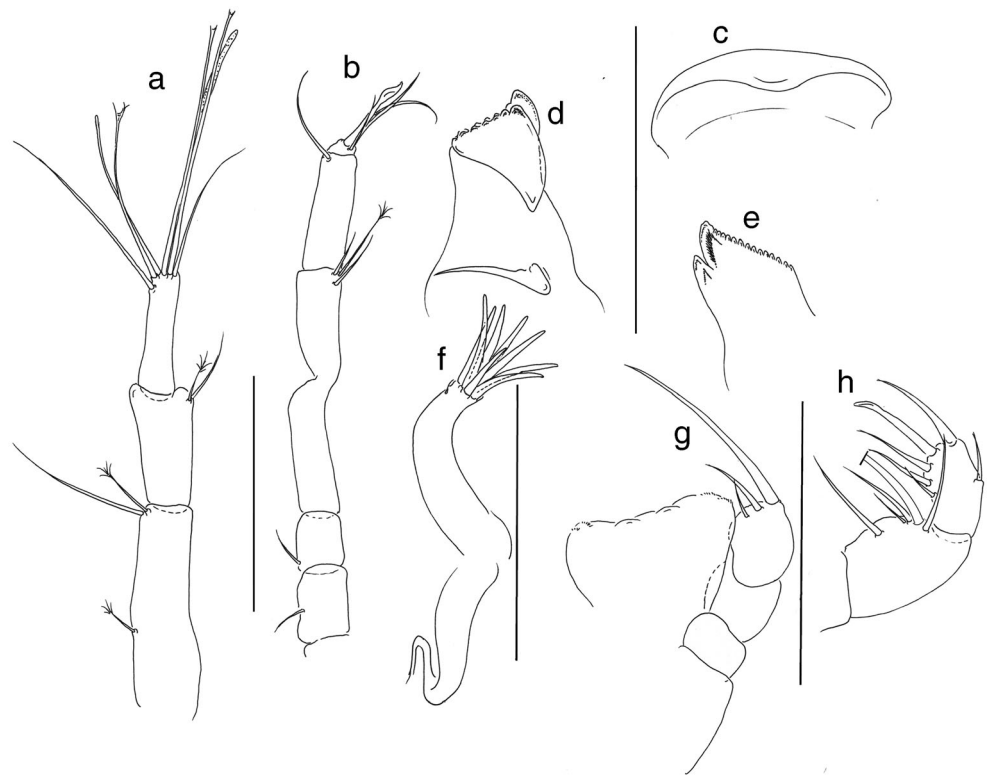


Fig. 4 *Mystriocentrus biho* sp. n., female with oostegites (cat no...). **a** Dorsal view. **b** Lateral view. Scale: 0.1 mm

Fig. 5 *Mystriocentrus biho* sp. n., preparatory female, paratype (cat no. ...). **a** Antennule. **b** Antenna. **c** Labrum. **d** Left mandible. **e** Right mandible. **f** Maxillule. **g** Maxilliped. **h** Details of maxilliped palp. Scale: 0.1 mm for **a–b** and 0.01 mm for **c–h**



separated the specimens examined into two groups (A, B) (Fig. 3). The group A consists of those individuals collected from deeper stations (> 1300 m) in the Irminger and Iceland Basins as well as the Norwegian Sea, the group B includes specimens found in shallow-water (< 800 m) samples from the Iceland–Scotland Ridge and the Irminger Basin.

Most variables decreased along the PC1 axis (from left to right), the highest values being attained by characters V4, V1, and V2 (Fig. 3, Table 3). An opposite trend (values increasing along PC1) was shown by the V7 (chela propodus length to width ratio only).

ANOSIM showed significant morphometric differences ($Global R = 0.68$, $p = 0.1\%$) between populations from the regions examined. The highest differences were found between the specimens representing “population 1” (deeper stations in the Norwegian Sea) and “population 3” (shallow stations in the Irminger Basin) ($Global R = 0.88$, $p = 0.1\%$) as well as between specimens from “population 1” and “population 4” (shallow stations in ISR) ($Global R = 0.83$; $p = 0.1\%$). Significant, relatively high differences were also detected between specimens from “population 2” (deeper stations in the Irminger and Iceland Basins) and “population 3” ($Global R = 0.74$; $p = 0.5\%$) and between specimens from “population 1” and “population 2” ($Global R = 0.63$, $p = 1\%$). Differences in morphometry between specimens from “population 3” and “population 4” were weaker ($Global R = 0.33$), but still significant ($p = 0.7\%$).

The morphometric analysis confirmed morphological differences between groups of individuals collected from different regions and depths. The differences, although present, are detectable only with careful measurement of the seven characters identified; therefore, the results indicated the presence of at least two (but possibly four) cryptic species. Moreover, as the strongest differences were observed between specimens from deep stations in the Norwegian Sea and all the other individuals (Table 3), we decided to choose a holotype for the newly described species (*P. svavarssoni* sp. n., see below) from those stations. As the differences between the other three sets of specimens (shallow stations in ISR, and Irminger Basin, deeper stations in the Irminger and Iceland Basins) were less pronounced, we decided to retain them as the “*svavarssoni*” complex until genetic data would lend reasonable support to the presence of distinct species.

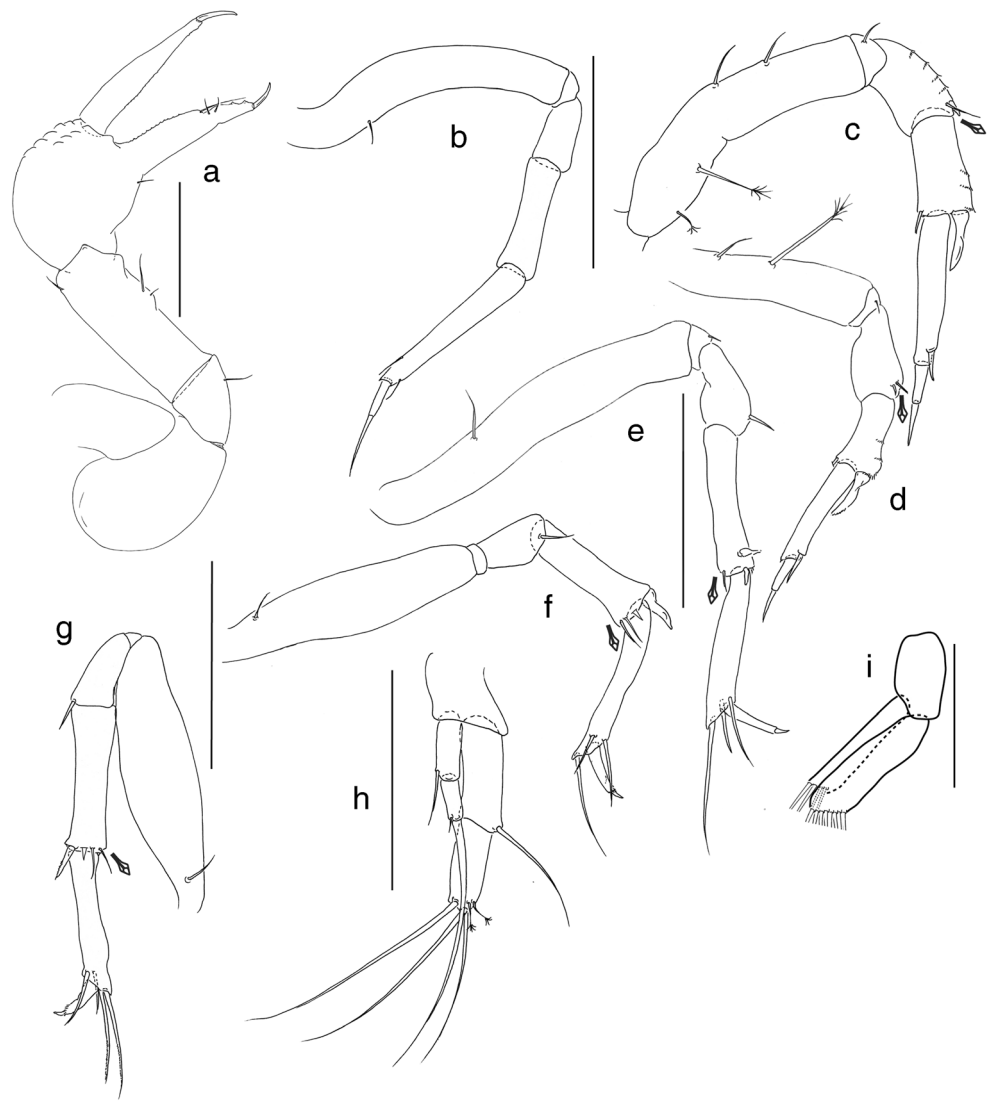
Taxonomic descriptions

Family Pseudotanaidae Sieg 1976

Genus: *Mystriocentrus* Bird and Holdich, 1989a

Diagnosis (amended after Bird and Holdich, 1989b): pereonite-2 similar in length or longer than pereonites 1 and 3; antenna articles 1 and 2 with simple setae, and with thickened seta on article-6 (terminal); molar process acuminate and simple; maxilliped endites fused, palp article-4 with thickened

Fig. 6 *Mystriocentrus biho* sp. n., preparatory female. **a** Cheliped. **b** Pereopod-1. **c** Pereopod-2. **d** Pereopod-3. **e** Pereopod-4. **f** Pereopod-5. **g** Pereopod-6. **h** Uropod. **i** Pleopod. Scale: 0.1 mm



seta; cheliped propodus almost as long as wide (1–1.2 times as long as wide), and small folds in distodorsal corner; chela forcipate, with serrate inner margin; pereopods 2–6 with blade-like spine on carpus.

Type species: *M. serratus* Bird and Holdich, 1989a

Species included: *M. serratus* Bird and Holdich, 1989b; *M. biho*, sp. n.

Remarks: Until examination of the Pseudotanaids from IceAGE collection (present studies), the *Mystriocentrus* was monotypic genus. Most of the diagnostic character for genus given as by Bird and Holdich 1989a, b (e.g., relatively long pereonite-2, thickened seta on antennule article-6 and maxilliped palp article-4, forcipate seta with serrate incisive margins and folds in distodorsal corner, and blade like spines on carpus of pereopods 2–6 well define this genus so far. Observed in type species “spatulate

setae” on merus and carpus (through which the genus received its name Bird and Holdich 1989a: 277) might not be so robust generic character, although still valid for species identification (see Remarks page 14).

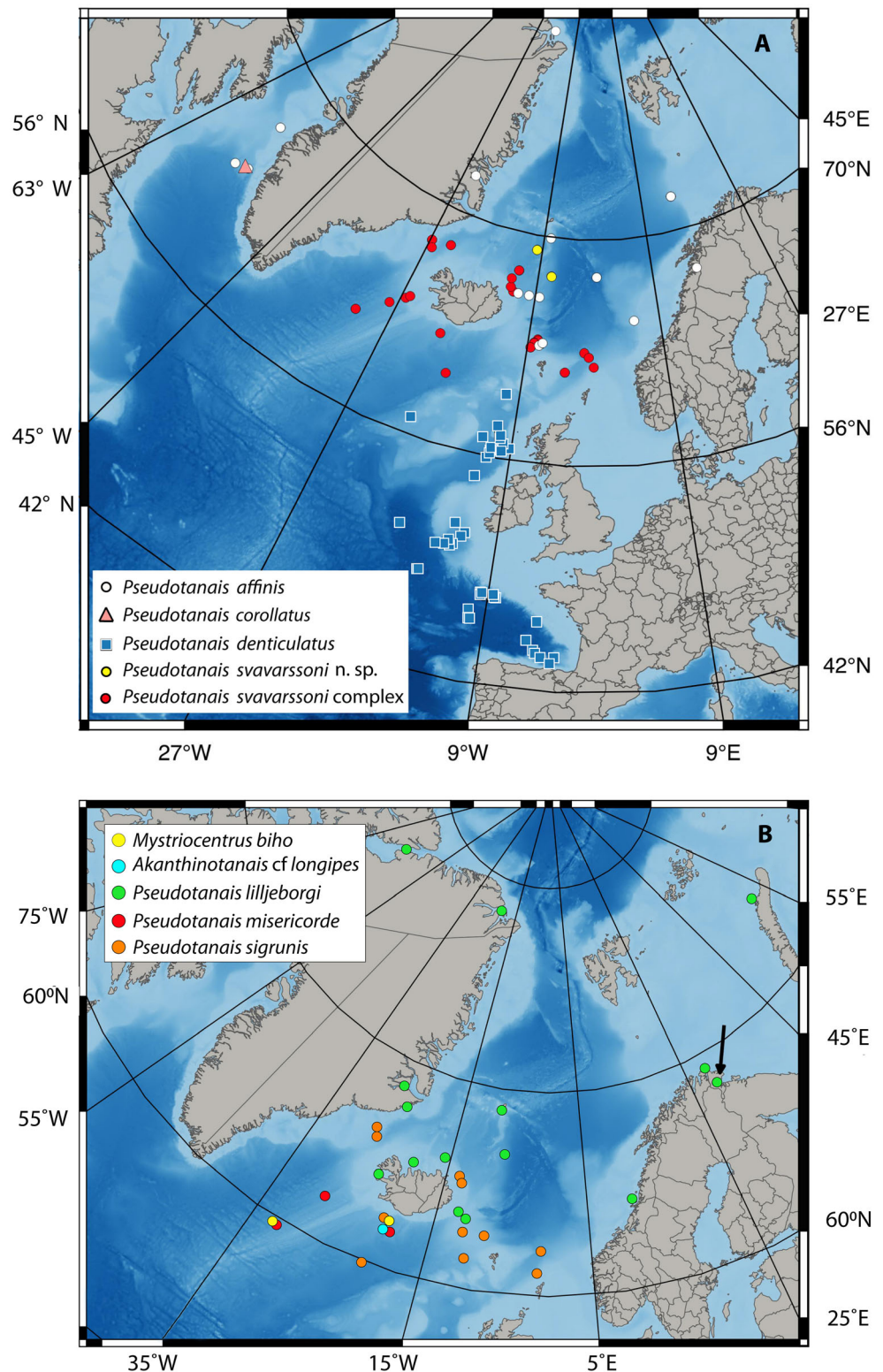
Mystriocentrus biho sp. n. Registered in ZooBank under: urn:lsid:zoobank.org:act:0AED0F58-63D5-4524-A857-FE6EC2883162 Figs. 4, 5, and 6

Material examined: Holotype: Ovigerous female, ZMH K-54850, St 1054-1, 61° 36.82' N 31° 22.26' W–61° 36.98' N 31° 22.18' W, depth 2545.7–2536.8 m, EBS, 07 Sep 2011.

Paratypes: neutrum (dissected), ZMH K-54852, St. 1019-1, 62° 56.46' N 20° 44.06' W–62° 56.52' N 20° 43.77' W, depth 916.1–909.4 m, EBS, 03 Sep 2011.

Two neutri, ZMH K-54851, St 1054-1, 61° 36.82' N 31° 22.26' W–61° 36.98' N 31° 22.18' W, depth 2545.7–2536.8 m, EBS, 07 Sep 2011.

Fig. 7 Distribution of the Pseudotanaidae species collected during IceAGE cruises. Distribution of *Pseudotanaïs affinis*, *P. corollatus*, *P. denticulatus*, and *P. lilljeborgi* as in the Fig. 2



Diagnosis: Pereonite-2 similar in length to pereonite-3; pereonite-3 clearly narrower, 0.8 times as wide as pereonite-4; maxilliped endites with small tubercles; pereopods 2–3 carpal blade-like spines long, 0.4 times as long as propodus.

Etymology: The name is composed of the first letters from the last names of Graham J. Bird and David M. Holdich, who erected the genus *Mystriocentrus*.

Description of ovigerous female: *Body* (Fig. 4) 1.9 mm length, 3.8 times as long as wide. Carapace 18% of total

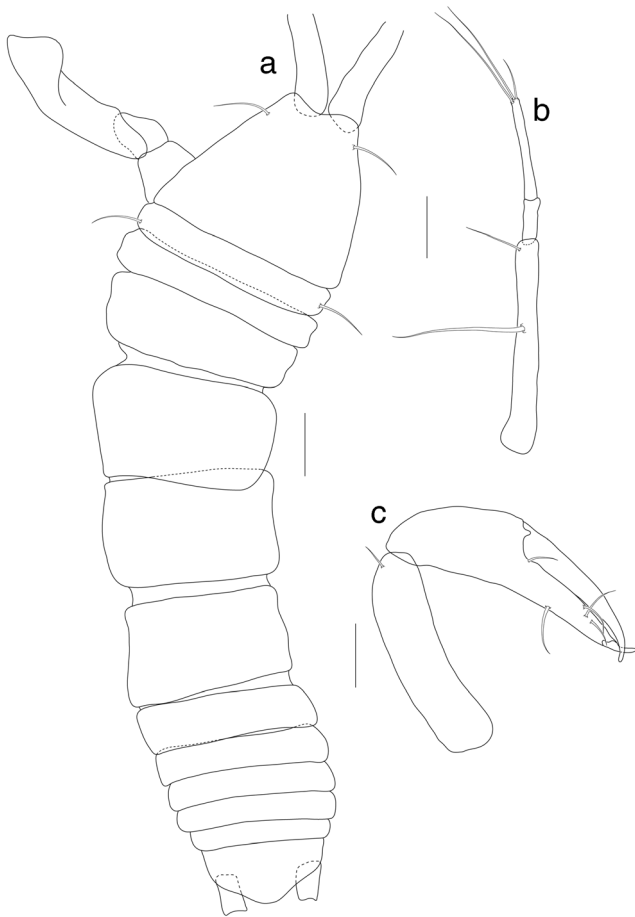


Fig. 8 *Akanthinotanaïs* cf. *longipes*, preparatory female. **a** Dorsal view. **b** Antennule. **c** Cheliped. Scale: 0.1 mm

body length, subtriangular, 0.8 times as long as wide, with simple setae on each antero-lateral margin. *Pereon* 55% of total body length, pereonite-1, half times as long as pereonite-2; pereonite-2 0.9 times as long as pereonite-3; pereonite-3, 0.8 times as wide as pereonite-4; pereonite-4 1.2 times as long as pereonite-3; pereonite-5 similar in length and width to pereonite-4; pereonite-6 half times as long as pereonite-5; pereonites 0.1, 0.2, 0.3, 1.2, 1.2, and 0.3 times as long as broad, respectively. *Pleon* 17% of total body length, with five similar in length pleonites, each 0.1 times as long as wide. *Pleotelson* 10% of body length; pleonites together with pleotelson as long as pereonites 4–6 combined length.

Antennule (Fig. 5a) article-1 3.7 times as long as wide, with penicillate middle seta, one penicillate and one simple distal setae on outer margin; article-2 2.1 times as long as wide, half times as long as article-1, with simple and penicillate distal setae on inner margin; article-3 3.5 times as long as wide, as long as article-2, with one subdistal seta, tipped with one aesthetasc, one simple, one distally rounded, three distally furcate setae.

Antenna (Fig. 5b) article-1 fused, broken during dissection; article-2 1.5 times as long as wide, with seta on middle outer margin; article-3 1.3 times as long as wide, 0.8 times as long as article-2, with seta on proximal outer margin; article-4 four times as long as article-3, 6.3 times as long as wide, with two simple and one penicillate distal setae; article-5 3.4 times as long as wide, half times as long as article-4, with distal simple seta; article-6 vestigial, with one thickened, sensory seta and three simple setae distally.

Mouthparts. *Labrum* (Fig. 5c) rounded, hood-shape, naked. *Left mandible* (Fig. 5d) incisor distal margin blunt and serrated, *lacinia mobilis* large and distally serrated; molar acuminate and simple. *Right mandible* (Fig. 5e) with incisor distal margin serrated; *lacinia mobilis* fused to a small process. *Maxillule* (Fig. 5f) distally bent, with eight slender distal spines. *Maxilliped* (Fig. 5g, h) endites completely fused, distal edges with small tubercles and lateral margins finely setose. *Palp* article-1 and article-2 naked; article-3 with three and one short setae on inner margin; article-4 with one thickened seta (Fig. 5h) and four simple inner and distal setae and one outer seta.

Cheliped (Fig. 6a) basis 1.6 times as long as wide; merus subtriangular, with simple midventral seta; carpus three times as long as wide, with two midventral setae, and with simple distodorsal seta; propodus (palm) as long as wide, small folds in distodorsal corner and small ventral seta; fixed finger 5.1 times as long as wide, 1.2 times as long as propodus, with serrated inner margin and three small inner setae; dactylus simple with slightly serrated inner margin.

Pereopod-1 (Fig. 6) basis 5.7 times as long as wide, with simple dorsoproximal seta; ischium 0.4 times as long as wide, naked; merus 1.8 times as long as wide, 0.6 times as long as carpus, naked; carpus 2.7 times as long as wide, 0.6 times as long as propodus, naked; propodus 6.6 times as long as wide, with dorsoproximal and distodorsal seta; dactylus 0.1 times as long as propodus, unguis 1.5 times as long as dactylus, together 0.5 times as long as propodus.

Pereopod-2 (Fig. 6c) basis 5.5 times as long as wide, with two simple ventral setae and with two penicillate dorsoproximal setae; ischium half times as long as wide, with simple seta; merus 1.5 times as long as wide, 0.9 times as long as carpus, with microtrichiae ventrally, spine and sensory seta distoventrally; carpus twice as long as wide, 0.6 times as long as propodus, with simple distodorsal seta and blade-like distoventral spine (0.4 times as long as propodus); propodus six times as long as wide, with distoventral spine; dactylus 0.2 times as long as propodus, unguis subequal propodus together almost as long as half of propodus.

Pereopod-3 (Fig. 6d) basis 3.5 times as long as wide, with one simple and one penicillate seta on ventral margin; ischium 0.3 times as long as wide, with simple ventral seta; merus 1.6 times as long as wide, and 1.1 times as long as carpus, with sensory seta and spine distoventrally; carpus half as long as

wide, and 0.6 times as long as propodus, with microtrichiae ventrally, small distodorsal seta and blade-like spine distoventral spine (0.4 times as long as propodus); propodus six times as long as wide, with one distoventral spine; dactylus 0.3 times as long as propodus, unguis 0.6 times as long as dactylus, together 0.6 as long as propodus.

Pereopod-4 (Fig. 6e) basis six times as long as wide, with ventroproximal simple seta; ischium 0.6 times as long as wide, with simple seta; merus 1.8 times as long as wide, 0.6 times as long as carpus with simple distoventral seta; carpus five times as long as wide, subequal propodus, with blade-like spine (broken) and spine distoventrally, and with sensory seta distodorsally; propodus six times as long as wide, with two distoventral setae and long distodorsal seta; dactylus with unguis half as long as propodus; unguis 0.2 as long as dactylus.

Pereopod-5 (Fig. 6f) as pereopods-4, but carpus with one sensory seta and one simple seta, on dorsal margin distally, with one spine and with one blade-like spine ventral margin.

Pereopod-6 (Fig. 6g) similar to pereopod-4 but basis 3.7 times as long as wide, carpus with one sensory seta, one simple seta, one spine and one blade-like spine; propodus with four setae terminally.

Pleopoda (Fig. 6i) basal article 3.6 as long as wide, endopod 5.3 as long as wide, with four distal setae; exopod 3.3 as long as wide, with eight distal setae.

Uropod (Fig. 6h) basal article as long as wide, naked; exopod 1.7 times as long as basis, and as long as endopod article-1, with two articles, article-1 1.3 times as long as article-2, with distal seta, article-2 with one small subdistal and one strong distal setae; endopod 1.8 times as long as exopod, with two articles; article-1 1.2 times as long as article-2, with long simple seta distally on outer margin; article-2 with three long simple and two short penicillate setae distally.

Distribution: *M. biho* sp. n. was recorded in Irminger and Iceland Basins at the depth range 913–2540 m (Fig. 7b). The new species is the second member of the genus *Mystricentrus*, that is so far known only from the North Atlantic (Fig. 2b).

Remarks: The *Mystricentrus biho* sp. n. can be recognized from the congener *M. serratus* Bird and Holdich, 1989a, b by the proportion of pereonites 2–3. In the new species, the pereonite-2 is similar in length to pereonite-3, but twice as long as pereonite-3 in *M. serratus*. Beside that, pereonite-3 is visibly narrower than rest of the pereonites (0.8 times as wide as pereonite-4) in the new species, but similar size in *M. serratus*. Additionally, *M. biho* sp. n. has one sensory (spatulate) setae on merus and carpus of the pereopods 2–6, while in *M. serratus* one to three such setae present; blade-like spine on pereopods 2–3 carpus are clearly longer (0.4 times as long as propodus) in *M. biho* than in *M. serratus* (0.1–0.2 times as long as propodus). Finally, the new species can be distinguished by appearance of maxilliped endite that has small tubercles on the distal margin; the distal margin of maxilliped endites in *M. serratus* is smooth.

Genus *Akanthinotanis* Sieg, 1977

Diagnosis (after Sieg 1977): Pereopods without blade-like spines.

Remarks: The Pseudotanaidae is a morphologically consistent family with few autapomorphic characters (Bird and Holdich, 1989a). Distinguished by Sieg (1977), two subgenera—*Akanthinotanis* (Sieg, 1977) and *Pseudotanais* (Sieg, 1977)—were seen by McLelland (2008) distinct enough to erect them as genera or even subfamily. Although the research by McLelland unfortunately were never published, Bird and Larsen (2009) treated the two taxa as valid genera in their phylogenetic analyses adding in its result two other genera *Mystricentrus* Bird and Holdich, 1989b and *Parapseudotanais* Bird and Holdich, 1989a.

The phylogenetic analysis is beyond the purpose of this paper, but it is essential to mention that molecular markers approach ascertain *Pseudotanais* itself as not monophyletic and highly diverse taxon (Jakiel and Błażewicz, in preparation), that can be straightforwardly split into at least few new genera. Furthermore, the same approach apparently demonstrated that *Akanthinotanis* is not monophyletic with *Pseudotanais* supporting McLelland proposition to treat them both as valid genera.

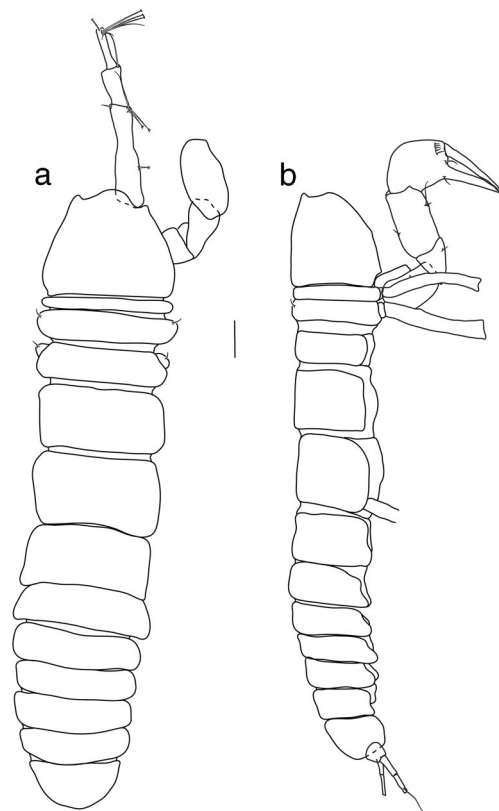
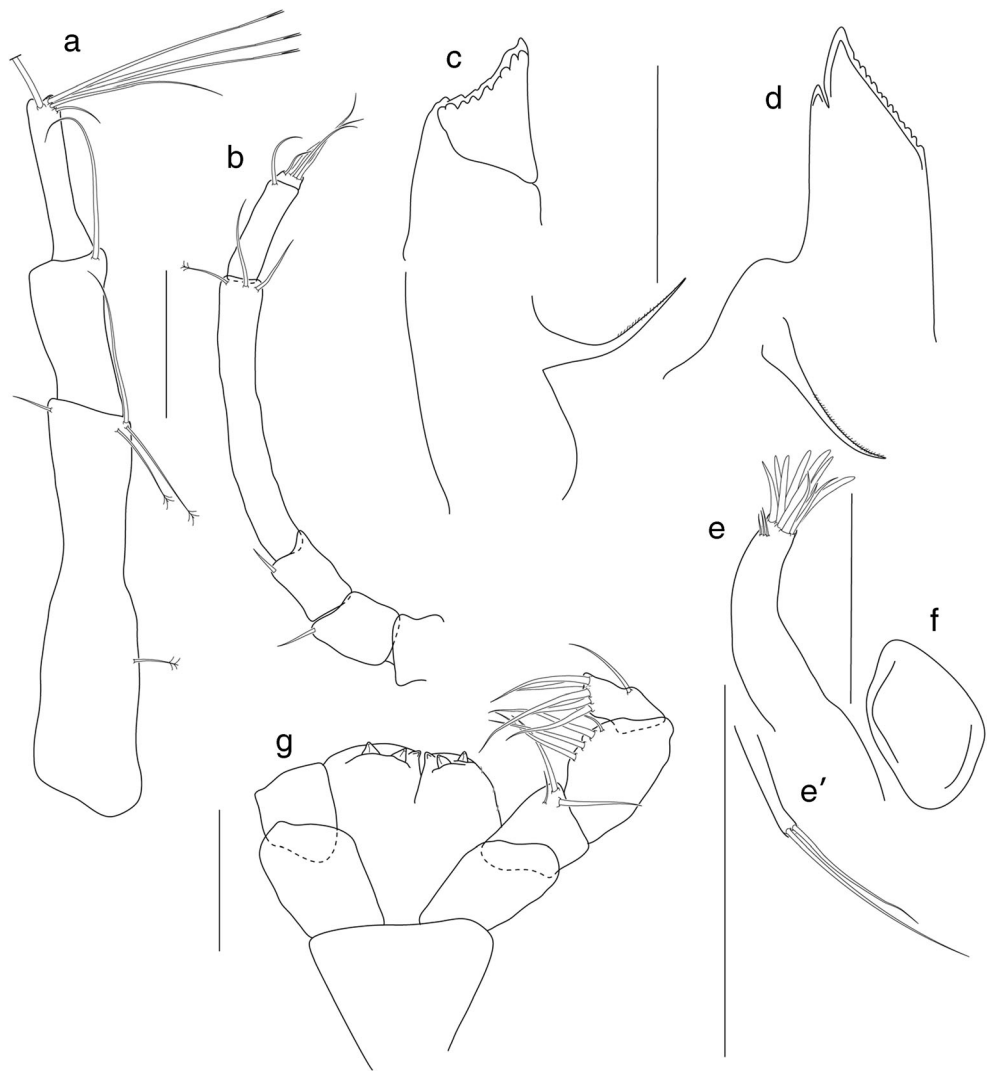


Fig. 9 *Pseudotanais miserlicorde* sp. n., preparatory female. a Dorsal view. b Lateral view. Scale: 0.1 mm

Fig. 10 *Pseudotanaïs misericoꝛde* sp. n., preparatory female. A antennule, B antenna, C left mandible, D right mandible, E maxillule endite, E' maxillule palp, F maxilla, and G maxilliped. Scale: 0.1 mm for A–B and 0.01 mm for C–G



Akanthinotanaïs cf. *longipes*

Fig. 8

Material examined: one neutrum, ZMH K-54853, St. 1010-1, 62° 33.17' N 20° 23.18' W–62° 33.22' N 20° 22.88' W, depth 1383.3–1387.8 m, EBS, 02 Sep 2011.

Distribution: *Akanthinotanaïs longipes* was described by Hansen (1913) from *Ingolf* Expedition (st. 78; 60° 37' N 27° 52' W, depth 364 m, temp. 4.5 °C) in the Iceland Basin and so far it is the only known location of the species (Fig. 2c).

In the IceAGE collection, the only specimen presumably conspecific with *A. longipes* was found in Iceland Basin at the depth 1387 m (Fig. 7b).

Remarks: As the only individual collected during the IceAGE cruises was preserved in poor condition, its full identification and comparison of details with those of *Akanthinotanaïs longipes* (Hansen, 1913) was not possible. However, the absence of eyes, the presence of slender antennule and cheliped, and the absence of a blade-like seta on pereopod-1 allowed us to regard it as

conspecific with *A. longipes*. Only three akanthinotanaïds known at present are blind, but only *A. longipes* is elongated (3.0 times as long as it is wide) and has a not-forcipated cheliped. Two other blind akanthinotanaïds *Akanthinotanaïs gaussi* (Vanhöffen, 1914) and *Akanthinotanaïs similis* (Sieg, 1977) have rather robust chela which is 2.0 and 2.5 times, respectively, as long as it is wide.

Genus *Pseudotanaïs* G.O. Sars, 1882

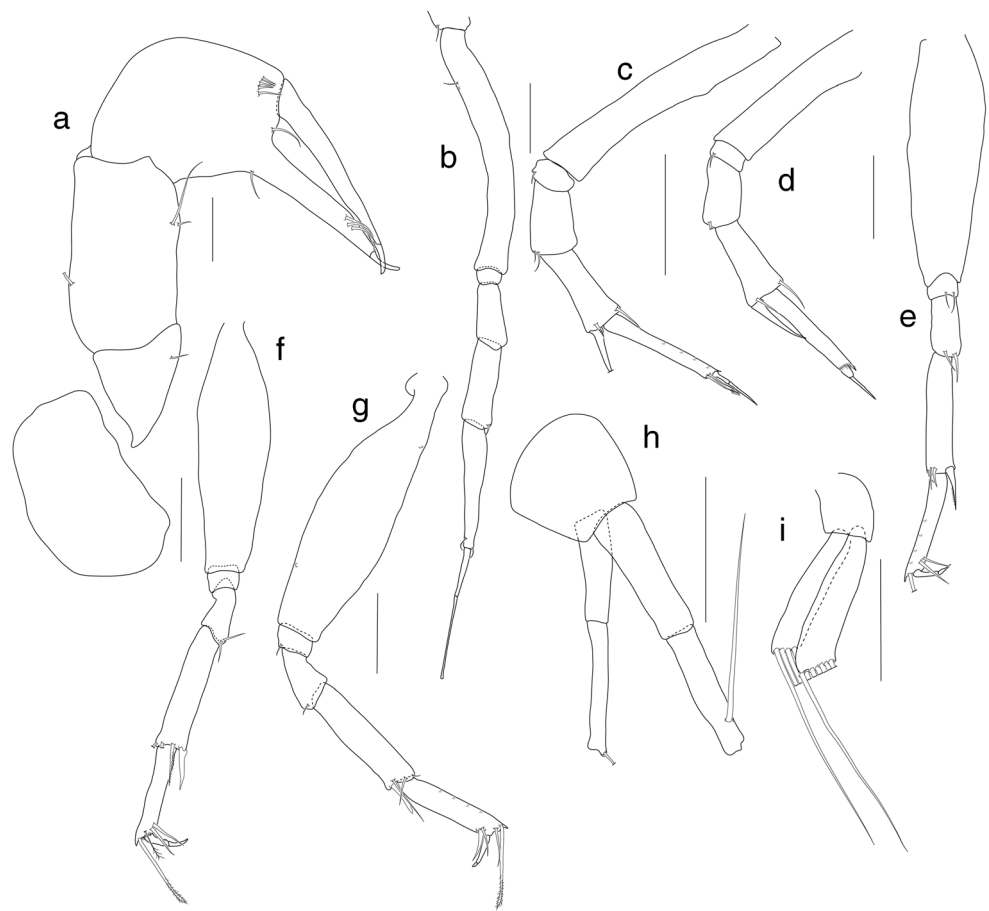
Pseudotanaïs misericoꝛde sp. n.

Figs. 9, 10, and 11

Material examined: Holotype: neutrum, ZMH K-54854, St. 1054-1, 61° 36.82' N 31° 22.26' W–61° 36.98' N 31° 22.18' W, depth 2545.7–2536.8 m, EBS, 07 Sep 2011.

Paratypes: neutrum (dissected), ZMH K-54855, St. 1010-1, 62° 33.17' N 20° 23.18' W–62° 33.22' N 20° 22.88' W, depth 1383.3–1387.8 m, EBS, 02 Sep 2011; three neutri (two dissected), ZMH K-54856, St. 1054-1, 61° 36.82' N 31° 22.26' W–61° 36.98' N 31° 22.18' W, depth 2545.7–2536.8 m, EBS, 07 Sep 2011; neutrum ZMH K-54857, St.

Fig. 11 *Pseudotanaeis misericorde* sp. n., preparatory female. **a** Cheliped. **b** Pereopod-1. **c** Pereopod-2. **d** Pereopod-3. **e** Pereopod-4. **f** Pereopod-5. **g** Pereopod-6. **h** Uropod. **i** Pleopod. Scale: 0.1 mm



1066, 62° 59.97' N 028° 04.78' W, depth 1621.8 m, GKG, 08 Sep 2011.

Diagnosis: Eyes absent. Pereonites 2–3 the same length. Antennule article-1 six times as long as wide. Antenna articles 2–3 with simple setae. Maxilliped molar pointed with upper margin serrated. Maxilliped endites with conical tubercles. Cheliped carpus 1.6 times as long as wide. Chela forcipate, unguis, and dactylus distal spines inside bent. Pereopods 2–6 blade-like spine slender and pointed. Uropod exopod two articulated, 0.8 times as long as endopod.

Etymology: From Latin *misericorde* was called the long and narrow knife used in medieval for delivering a mercy stroke. The name refers to the unusual shape of the blade-like spine on pereopods 2–6, that is long and pointed.

Description of neutrum: *Body* (Fig. 9a, b) 1.8 mm; 5.0 times as long as broad. Carapace almost as long as pereonites 1–3 and half of pereonite-4 combined, naked, lateral margin gently rounded. Pereon 39% of total body length, pereonite-1 half as long as pereonite-2; pereonites 2 the same length and pereonites 3, wilt lateral setae; pereonite-3 half as long as pereonite-4; pereonite-4 as long as pereonites-5; pereonite-5 1.2 times as long as pereonites-6, pereonites 0.1, 0.2, 0.2, 0.5, 0.5, and 0.4 times as long as broad, respectively (data for the holotype). *Pleon* 22.7% of total body length, pleonite-1

slightly wider than all other pleonites. *Pleotelson* 13% of total body length pleonites together with pleotelson almost as long as pereonites 2–6 combined length.

Antennule (Fig. 10a) article-1 six times as long as wide, with middle penicillate seta, one simple and two penicillate distal setae on inner margin and simple distal seta on outer margin; article-2 2.1 times as long as wide, with distal seta longer than article-3 on inner margin; article-3 just longer than article-2, with six distal setae: two simple and three distally trifurcate seta, one seta broken.

Antenna (Fig. 10b) shorter than antennule; article-1 fused with body; article-2 1.1 times as long as wide, with one seta on outer margin; article-3 1.5 times as long as wide, subequal to article-2 with one seta on outer margin; article-4 3.5 times as long as article 3, 7.4 times longer than broad, with two simple and one penicillate setae distally; article-5 0.3 times as long as article-4, with one simple seta distally; article 6 vestigial, with four simple setae distally.

Mouthparts. Labium not observed. Left mandible (Fig. 10c) incisor distal margin blunt and serrated, *lacinia mobilis* large, and distally serrated; molar acuminate; right mandible (Fig. 10d) with incisor distal margin serrated; *lacinia mobilis* fused to a small process. *Maxillule* (Fig. 10e) distally bent, with eight spines and two setae

distally, three fine setae subdistally on outer margin; endite (Fig. 10e') with two distal setae. *Maxilla* (Fig. 10f) ovoid, naked. *Maxilliped* (Fig. 10g) endites completely fused except the most distal fragment, where they stay well separated; distal margin with two conical tubercles, each with visible distal hole, and finely setose lateral margins. Palp article-1 naked, article-2 with three inner setae (two long one short), article-3 with four inner setae (three long and one short), article-4 with and five simple inner and distal setae and one middle outer seta.

Cheliped (Fig. 11a) basis 1.6 times as long as wide; merus subtriangular with single midventral seta; carpus 1.7 times as long as broad, with two midventral (long and short) setae; dorsal margin with simple submiddle distal seta not seen; chela forcipate, propodus (palm) 1.3 times as long as wide and 0.9 times as long as fixed finger, with ventral seta and one seta near dactylus insertion; row of five small setae on inner surface; fixed finger with three seta, distal spine bent upward; dactylus simple as long as fixed finger, distal spine bent downward.

Pereopod-1 (Fig. 11b) slender, basis 7.9 times as long as wide with two dorsoproximal setae (one broken); ischium naked; merus 2.3 times as long as wide, 0.2 times as long as basis, naked; carpus 3 times as long as wide 0.6 times as long as propodus, with fine distodorsal seta; propodus 7 times as long as wide, with two fine distal seta; dactylus 0.3 as long as propodus, dactylus 0.6 times as long as unguis; dactylus and unguis combined as long as propodus.

Pereopod-2 (Fig. 11c) basis 6.5 times as long as wide; ischium with simple seta; merus 1.5 times as long as wide, 0.7 times as long as carpus, with two setae distally; carpus 2.7 times as long as wide, 0.7 times as long as propodus with two setae and one blade-like spine, very slender spine (distally broken) distally; propodus 8.3 times as long as wide with plumose seta distally, ventral margin with microtrichiae; unguis twice as long as dactylus, combined half as long as propodus.

Pereopod-3 (Fig. 11d) similar to pereopod-2, but carpus 2.6 times as long as propodus and propodus 5 times as long as wide, without microtrichiae; blade-like spine on carpus 0.6 times as long as propodus.

Pereopod-4 (Fig. 11e) basis 3.3 times as long as wide, naked; ischium with two setae; merus 0.2 times as long as wide; 0.4 times as long as carpus, with two distal setae; carpus 4.5 times as long as wide, 1.2 times as long as propodus, with blade-like spine (0.4 times as long as propodus) and with three setae distally; propodus 6.2 times as long as wide, with two ventrodorsal simple setae and dorsodistal seta broken; dactylus twice as long as unguis.

Pereopod-5 (Fig. 11f) basis 3.4 times as long as wide; ischium naked (setae probably broken off); merus 2.6 times as long as wide, 0.5 times as long as carpus, with two distal setae; carpus 4.3 times as long as wide, 1.2 times as long as

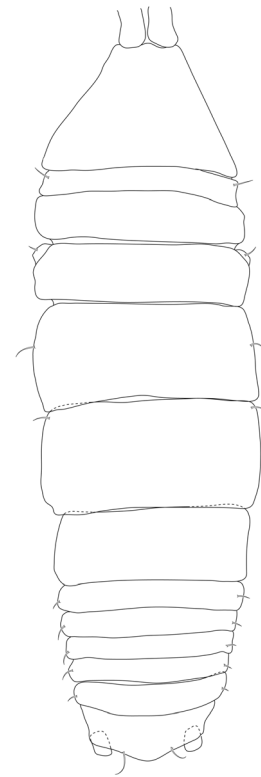


Fig. 12 *Pseudotanais svavarssoni* sp. n., neutrum, holotype (cat no...), dorsal view. Scale: 0.1 mm

propodus, with blade-like spine (0.4 times as long as propodus) and three setae distally (one serrate, two broken); propodus 5.2 times as long as wide, with two distoventral simple setae, one subdistal penicillate seta and one dorsodistal serrated, distally flatten seta; dactylus 1.4 times as long as unguis.

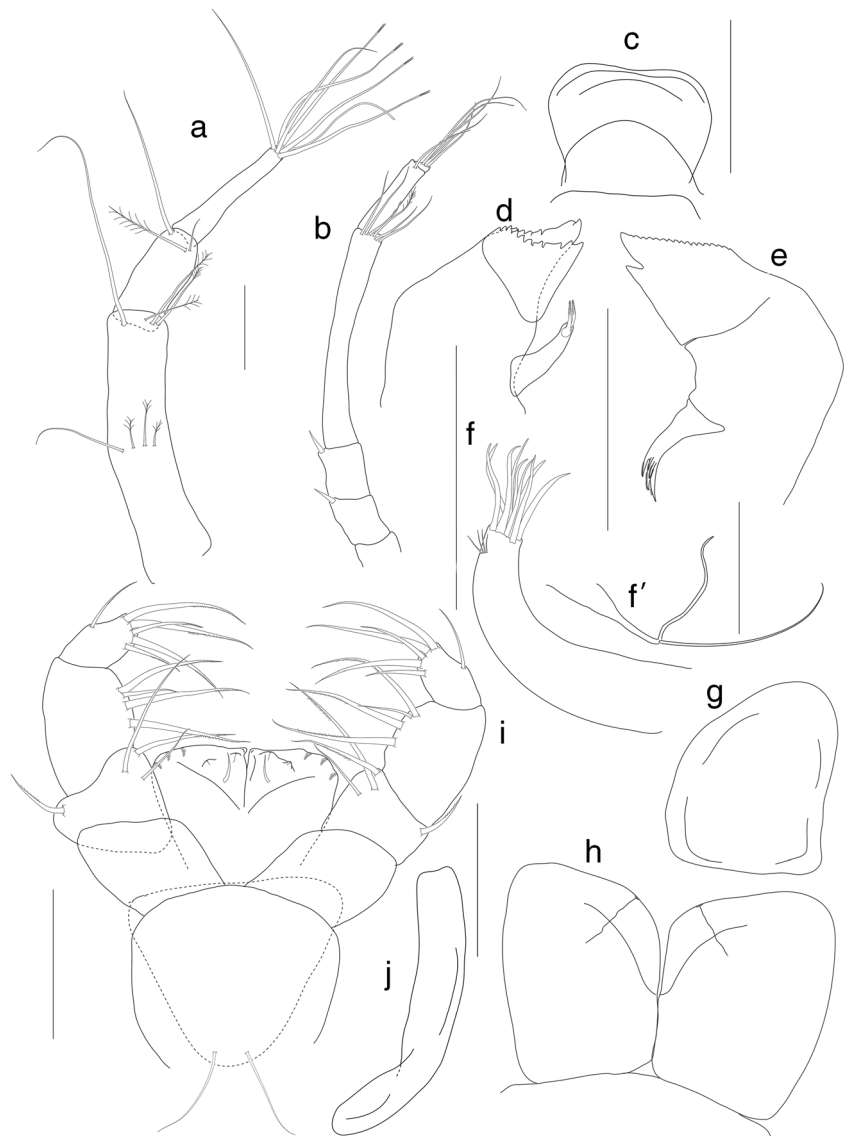
Pereopod-6 (Fig. 11g) basis 3.8 times as long as wide with dorsoproximal seta (broken off); ischium with one seta (second seta probably broken off); merus 2.1 times as long as carpus with one distal seta (second seta probably broken off); carpus 3.8 times as long as wide and 1.1 times as long as propodus, with three simple setae and one blade-like spine (0.3 times as long as propodus), distally; propodus 4.8 times as long as wide with two simple distoventral setae, one simple and one distally serrated, dorsodistal flatten setae; dactylus 5 times as long as unguis.

Pleopod (Fig. 11i) endopod 4.5 times as long as wide, with four distal setae; exopod four times as long as wide with seven distal setae.

Uropod (Fig. 11h) basis naked; exopod 0.8 times as long as endopod, with two articles, article-1 0.8 times as long as article-2, article-2 with at least one distal seta (broken); endopod with two, subequal articles, article-2 with at least one subdistal seta.

Distribution: *P. misericorde* was recorded in the Iceland and Irminger Basins (Fig. 7) at the depth range: from 1383 to 2545 m.

Fig. 13 *Pseudotanaïs svavarssoni* sp. n., preparatory female. A antennule, B antenna, C labrum, D left mandible, E right mandible, F maxillule endite, F' maxillule palp, G maxilla, H labium, I maxilliped, J epignath. Scale: 0.1 mm for A–B and 0.01 for C–J



Remarks: *Pseudotanaïs misericoorde* sp. n. represents the group of blind pseudotanaids with a forcipate chela and exopod of the uropod almost as long as the endopod. These two characters delineate also *Pseudotanaïs vulsella* Bird and Holdich, 1989b and *P. falcicula* Bird and Holdich, 1989a, both recorded in Porcupine Bank and Rockall Trough.

P. misericoorde, as *P. vulsella*, has the same conical tubercles on distal margin of maxilliped endites but the new species can be distinguished from *P. vulsella* by slender blade-like carpal spines (“blade” part is much narrower than in all other species). In *P. falcicula* tubercles in edge of the maxilliped endites are very small (Bird and Holdich, 1989b, Fig. 19g) besides straight distal spines in chela dactylus and fixed finger, what allow to comfortably distinguish it *P. falcicula* from the new species.

Pseudotanaïs svavarssoni sp. n.

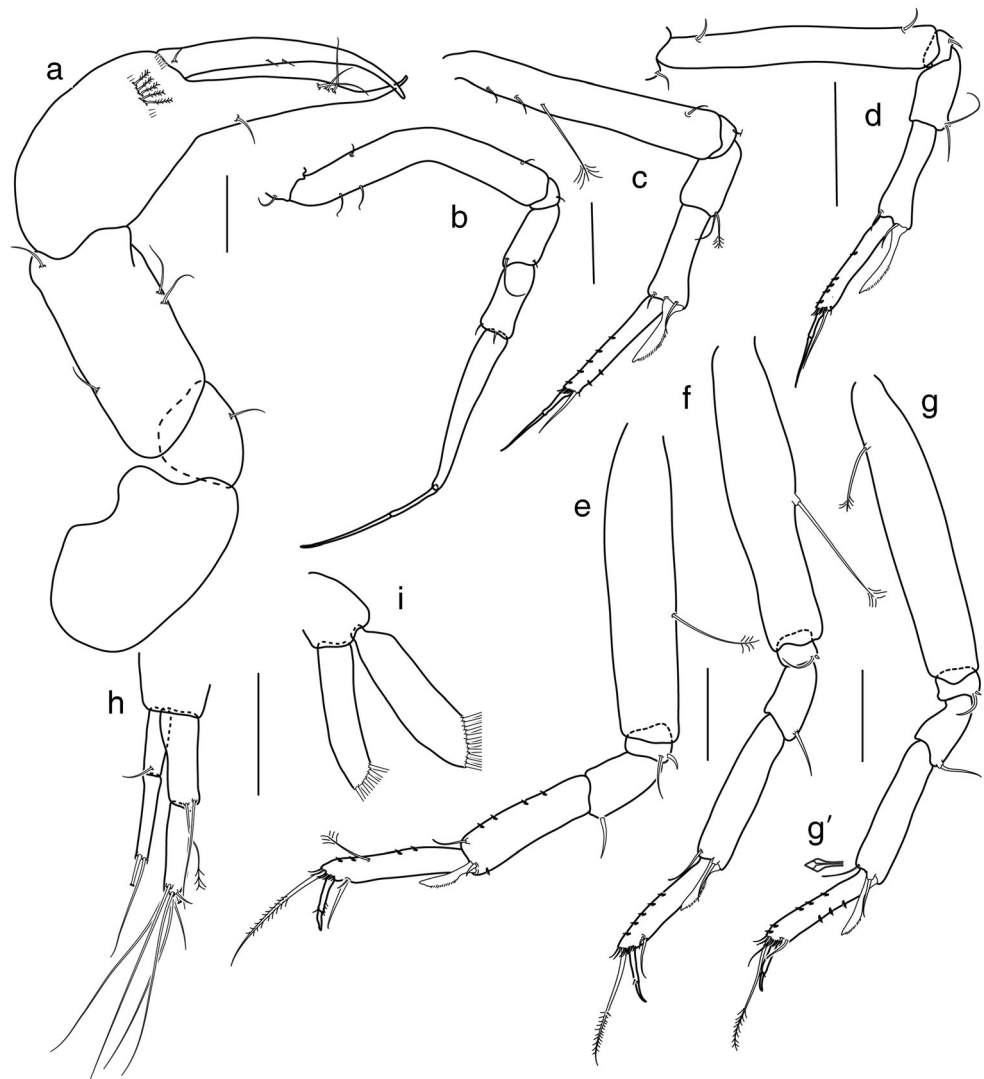
Figs. 12, 13, and 14

Material examined: Holotype: neutrum ZMH K-54858, 1168-1, 67° 36.38' N 007° 00.08' W, depth 2372.6 m, EBS, 19 Sep 2011.

Paratypes: five neutri, one manca, ZMH K-54859, St. 1152-1, 69° 5.60' N 9° 56.01' W, depth 2172.6 m, GKG, 17 Sep 2011; neutrum, ZMH K-54860, St. 1155-1, 69° 06.89' N 009° 54.72' W, depth 2203.8 m, EBS, 17 Sep 2011; 92 neutri, 35 juvenile males, ZMH K-54861, St. 1159-1, 69° 06.66' N 009° 55.02' W, depth 2202.8 m, EBS, 17 Sep 2011; one neutrum, one juvenile male, ZMH K-54862, St. 1166-1, 67° 35.28' N 6° 57.47' W, depth 2401.8 m, GKG, 19 Sep 2011; 43 neutri, (one dissected), five juvenile males ZMH K-54863, 1168-1, 67° 36.38' N 007° 00.08' W, depth 2372.6 m, EBS, 19 Sep 2011.

Diagnosis: Eyes absent. Carapace, pereonites, and pleonites combined length range between 1.2 and 1.7 mm. Pereonite-1 the shortest. Antennule article-1 four times as long

Fig. 14 *Pseudotanaïs svavarssonii* sp. n., preparatory female. A cheliped, B pereopod-1, C pereopod-2, D pereopod-3, E pereopod-4, F pereopod-5, G pereopod-6, H uropod, and I pleopod. Scale: 0.1 mm



as wide. Antenna articles 2–3 with distal simple setae. Left mandible with two teeth. Maxilliped endites with small tubercles. Cheliped elongated, carpus 1.7–2.1 times as long as wide, propodus 1.4–1.6 times as long as wide. Pereopod-1 propodus 2.2–2.5 times as long as carpus, propodus 1.1–1.3 times as long as combined length of dactylus and unguis. Pereopods 2–6 carpal blade-like spine well developed. Pereopod-3 propodus 1.4–1.7 times as long as blade-like spine. Pereopod-6 propodus 2.6–6.4 times as long as distal carpal seta ratio. Females with pleopods. Uropod exopod two articulated, 0.8 times as long as endopod.

Etymology: The species named after Jörundur Svavarsson, a professor in marine biology at the University of Iceland, the great enthusiast of Icelandic nature and wonderful fellow on the land as well as on the sea.

Description of neutrum: *Body* (Fig. 12) 1.7 mm long, over three times as long as wide. Carapace 18% of total body length, subtriangular, naked. *Pereon* 58% of total body length,

pereonite-1, 0.4 times as long as pereonite-2; pereonite-2 0.9 times as long as pereonite-3; pereonite-3 0.6 times as long as wide as pereonite-4; pereonite-4 0.8 times as long as pereonite-5; pereonite-5 1.5 times as long as pereonite-6; pereonites 1–6: 0.1, 0.3, 0.3, 0.4, 0.5, and 0.4 times as long as wide, respectively; pereonites 1, 4, and 5 with one lateral seta on each margin. *Pleon* 18.8% of total body length, with five similar in length pleonites, each 6.4 times as long as wide, with one seta on lateral margin. *Pleotelson* 6% of total body length; pleonites together with pleotelson almost as long as pereonite-2, two setae on pleotelson distal margin.

Antennule (Fig. 13a) article-1 4.0 times as long as wide, with long simple, and three midlength penicillate setae, and three penicillate and long simple seta distally; article-2 2.2 times as long as wide, and 0.4 times as long as article-1, with one outer distal seta longer than article-3, one penicillate and one simple seta distally; article-3 1.2 times as long as article-2, with two simple and four distally trifurcate and one aesthetasc, distally.

Table 4 Geographical distribution of North Atlantic Pseudotanaididae species. * type localities/ source of type localities; 1: Lillieborg 1864, 2: Sars 1882, 3: Hansen 1887, 4: Sars 1869, 5: Hansen 1913, 6: Hansen H.J. in Hansen 1913, 7: Horring in Hansen 1913, 8: Kruuse in Hansen 1913, 9: Norman in Hansen 1913, 10: Ryder in Hansen 1913, 11: Sars in Hansen 1913, 12: Scott in Hansen 1913, 13: Stappers in Hansen 1913, 14: Vanhoffen in Hansen 1913, 15: Wandel in Hansen 1913, 16: Stephensen 1937, 17: Delamare-Deboutteville 1960, 18: Bruce et al. 1963, 19: Greve 1965a, b, c, 20: Just 1970, 21: Dahl in Sieg 1977, 22: Fee in Sieg 1977, 23: Hatch in Sieg 1977, 24: Sieg 1977, 25: Delamare-Deboutteville et al. 1955 in Sieg 1983, 26: Holdich and Jones 1983, 27: Bird and Holdich, 1989a, 28: Bird and Holdich, 1989b, 29: Błażewicz-Paszkojczyk and Bamber 2011, 30: Vanhoffen in Sieg 1977, 31: Kudinova-Pasternak in Sieg 1977

Area	Species/localities	Latitude [N]	<i>A. longipes</i>	<i>A. similis</i>	<i>Mystricetrus serratus</i>	<i>Parapseudatanais abyssalis</i>	<i>P. abyssi</i>	<i>P. affinis</i>	<i>P. colonus</i>	<i>P. corollatus</i>
Bay of Biscay	South	44	-	-	-	-	-	-	-	-
Biscay Abyssal Plains		46	-	-	-	-	-	-	-	-
Bay of Biscay	North	47	-	-	+	+	-	-	+	-
Roscoff/Bloscon		48	-	+	-	-	-	-	-	-
Porcupine Abyssal Plains		48–50	-	-	+	-	-	-	-	-
British coast	Braden, Plymouth	50	-	-	-	-	-	-	-	-
Porcupine Seabight		50–51	-	-	+	-	-	-	-	-
Celtic and Armorican Slope		50–51	-	-	-	-	-	-	-	-
British coast	Isle of Man	55	-	-	-	-	-	-	-	-
Feni Ridge		54–55	-	-	+	-	-	-	-	-
Rockall Trough		54–57	-	-	+	-	-	-	-	-
Sweden coast	Sund	55	-	-	-	-	-	-	-	-
Sweden coast	Kategatt	56	-	-	-	-	-	-	-	-
British coast		56	-	-	-	-	-	-	-	-
Hebridean Slope		56–58	-	-	-	-	-	-	-	-
Sweden coast	Skagerrak	58	-	-	-	-	-	-	-	-
Sweden coast	Gullmar fiord	58	-	-	-	-	-	-	-	-
Norway coast	south of Bergen	60	-	-	-	-	-	-	-	-
Iceland coast	Iceland Basin	60–63	-	-	-	-	-	+	-	-
Iceland coast	Irminger Basin	60–63	+	-	-	-	-	-	-	-
Norwegian coast		60–72	-	-	-	-	-	-	-	-
Norway coast	Trondheimfiord	63	-	-	-	-	-	-	-	-
Davis Strait		61–66	-	-	-	-	+	+	-	+
Iceland coast	IF Ridge	63–64	-	-	-	-	-	+	-	-
Greenland coast	Ameralik fiord	64	-	-	-	-	-	-	-	-
Greenland coast	Angmasivik	64	-	-	-	-	-	-	-	-
Iceland coast	Denmark Strait	65–67	-	-	-	-	-	-	-	-
Norway coast	vicinity of Nesna	66	-	-	-	-	-	-	-	-
Iceland coast	Norwegian Sea	66–67	-	-	-	-	-	+	-	-
Iceland coast	Iceland Sea	66–67	-	-	-	-	-	+	-	-
Norway coast	Raunefjord	67	-	-	-	-	-	-	-	-
Greenland coast	Kap Dalton	69	-	-	-	-	-	-	-	-
Greenland coast	Turner Sound	69	-	-	-	-	-	-	-	-
Norway coast	Balsfjord	69	-	-	-	-	-	-	-	-
Norway coast	vicinity of Malangen	69	-	-	-	-	-	-	-	-
Norway coast	Ullsfjord	69	-	-	-	-	-	-	-	-
Norway coast	Ramfjord	69	-	-	-	-	-	-	-	-
Finmark coast		69	-	-	-	-	-	-	-	-

Table 4 (continued)

Area	Species/localities	Latitude [N]	<i>A. longipes</i>	<i>A. similis</i>	<i>Mystricocetrus serratus</i>	<i>Parapseudatanais abyssalis</i>	<i>P. abyssi</i>	<i>P. affinis</i>	<i>P. colonus</i>	<i>P. corollatus</i>
	close upon the frontiers of Russia									
Greenland coast	Denmark Island	70	-	-	-	-	-	-	-	-
Greenland coast	Karajak Fiord	70	-	-	-	-	-	-	-	-
Jan Mayen		70	-	-	-	-	+	-	-	-
Norway coast	vicinity of Kvalsund	70	-	-	-	-	-	-	-	-
Norway coast	vicinity of Kvaloy	70	-	-	-	-	-	-	-	-
Norway coast	Varanger Fjord	70	-	-	-	-	+	+	-	-
Greenland coast	Forsblad fiord	72	-	-	-	-	+	+	-	-
Greenland coast	Upemivik	72	-	-	-	-	-	-	-	-
Norway coast	Håkon Mosby	72	-	-	-	-	+	-	-	-
	Mud Volcano									
Barents Sea		76	-	-	-	-	-	-	-	-
Norway coast	Spitsbergen	76–79	-	-	-	-	-	-	-	-
Greenland coast	Jørgen Brønlund Fiord	82	-	-	-	-	+	-	-	-
Source			5	17, 24*, 25	28	28	5	3*, 5, 20, 29	27	27
	Localities other than N Atlantic						Antarktyka	Kra Sea*;		
Source							30	Alaska		
								31		
Area			<i>P. falcata</i>	<i>P. forcipatus</i>	<i>P. jonesi</i>	<i>P. lilieborgie</i>	<i>P. longispinus</i>	<i>P. macrocheles</i>	<i>P. oculatus</i>	<i>P. scalpellum</i>
Bay of Biscay			-	-	-	-	-	-	-	-
Biscay Abyssal Plains		+	-	-	-	-	-	-	-	-
Bay of Biscay		+	-	-	-	-	+	-	-	-
Roscoff/Bloscon		-	-	-	-	-	+	-	-	-
Porcupine Abyssal Plains		+	-	-	+	-	-	-	-	-
British coast		-	-	-	+	-	-	-	-	+
Porcupine Seabight		+	-	-	-	-	-	-	-	-
Celvic and Armorican Slope		-	-	-	-	-	-	-	-	-
British coast		-	-	-	+	-	-	-	-	-
Feni Ridge		+	-	-	-	-	-	-	-	+
Rockall Trough		+	-	-	-	-	+	-	-	+
Sweadan coast		-	+	-	-	-	-	-	-	-
Sweadan coast		-	+	-	-	-	-	-	-	-
British coast		-	+	-	+	-	-	-	-	-
Hebridean Slope		-	+	-	-	-	-	-	-	-
Sweadan coast		-	+	-	-	-	-	-	-	-
Sweadan coast		-	+	-	-	-	-	-	-	-
Norway coast		-	-	-	-	-	-	+	-	-
Iceland coast		-	-	-	-	-	-	-	-	-
Iceland coast		-	-	-	-	-	-	-	-	-

Table 4 (continued)

Area	<i>P. denticulatus</i>	<i>P. facifer</i>	<i>P. falcicola</i>	<i>P. forcipatus</i>	<i>P. jonesi</i>	<i>P. lilieborgie</i>	<i>P. longispinus</i>	<i>P. macrocheles</i>	<i>P. oculatus</i>	<i>P. scalpellum</i>
Norwegian coast	–	–	–	+	–	–	–	–	–	–
Norway coast	–	–	–	+	–	–	–	–	–	–
Davis Strait	–	–	–	–	–	–	–	–	+	–
Iceland coast	–	–	–	+	–	+	–	–	–	–
Greenland coast	–	–	–	+	–	+	–	–	–	–
Greenland coast	–	–	–	–	–	+	–	–	+	–
Iceland coast	–	–	–	–	–	+	–	–	–	–
Norway coast	–	–	–	+	–	–	–	–	–	–
Iceland coast	–	–	–	+	–	–	–	–	–	–
Iceland coast	–	–	–	+	–	+	–	–	–	–
Norway coast	–	–	–	–	–	–	–	–	–	–
Greenland coast	–	–	–	+	–	+	–	–	–	–
Greenland coast	–	–	–	+	–	–	–	–	–	–
Norway coast	–	–	–	+	–	–	–	–	–	–
Norway coast	–	–	–	+	–	–	–	–	–	–
Norway coast	–	–	–	+	–	–	–	–	–	–
Norway coast	–	–	–	+	–	–	–	–	–	–
Finmark coast	–	–	–	+	–	–	–	–	–	–
Greenland coast	–	–	–	+	–	+	–	–	–	–
Greenland coast	–	–	–	+	–	+	–	–	–	–
Jan Mayen	–	–	–	–	–	–	–	–	–	–
Norway coast	–	–	–	–	–	+	–	–	–	–
Norway coast	–	–	–	+	–	–	–	–	–	–
Norway coast	–	–	–	+	–	–	–	–	–	–
Norway coast	–	–	–	–	–	+	–	–	–	–
Greenland coast	–	–	–	–	–	–	–	–	–	–
Greenland coast	–	–	–	–	–	–	–	–	–	–
Norway coast	–	–	–	–	–	–	–	–	–	–
Barents Sea	–	–	–	+	–	+	–	–	–	–
Norway coast	–	–	–	–	–	–	–	–	–	–
Norway coast	–	–	–	–	–	–	–	–	–	–
Greenland coast	–	–	–	–	–	–	–	–	–	–
Source	27*	29	28	1*, 5, 6, 7, 9, 11, 12, 13, 14, 16, 19, 21 Franz Joseph Land	18, 24*, 26, 27	4*, 5, 7, 8, 10, 11, 14, 16, 19, 20, 28	28*	2*, 19	5*, 8, 10, 15, 28*, 22, 23, 24	
Localities other than N Atlantic										
Source				12						

Area	<i>P. spatula</i>	<i>P. spicatus</i>	<i>P. vulsella</i>	<i>A. cf. longipes</i>	<i>Mystriocetrus biho</i> n. sp.	<i>P. misericorde</i> n. sp.	<i>P. signunis</i> n. sp.	<i>P. svavarrrsoni</i> n. sp.	<i>P. svavarrrsoni</i> complex
Bay of Biscay	+	+	–	–	–	–	–	–	–
Biscay Abyssal Plains	–	–	–	–	–	–	–	–	–
Bay of Biscay	–	+	–	–	–	–	–	–	–
Roscoff/Bloscon	–	–	–	–	–	–	–	–	–
Porcupine Abyssal Plains	–	+	–	–	–	–	–	–	–

Table 4 (continued)

Area	<i>P. spatula</i>	<i>P. spicatus</i>	<i>P. vubella</i>	<i>A. cf. longipes</i>	<i>Mystriocetrus biho</i> n. sp.	<i>P. misericorde</i> n. sp.	<i>P. sigrumis</i> n. sp.	<i>P. svavarrroni</i> n. sp.	<i>P. svavarrroni</i> complex
British coast	-	-	-	-	-	-	-	-	-
Porcupine Seabight	+*	+*	+*	-	-	-	-	-	-
Celtic and Armorican Slope	+	-	+	-	-	-	-	-	-
British coast	-	-	-	-	-	-	-	-	-
Feni Ridge	-	-	+	-	-	-	-	-	-
Rockall Trough	-	+	+	-	-	-	-	-	-
Sweaden coast	-	-	-	-	-	-	-	-	-
Sweaden coast	-	-	-	-	-	-	-	-	-
British coast	-	-	-	-	-	-	-	-	-
Hebridean Slope	+	-	+	-	-	-	-	-	-
Sweaden coast	-	-	-	-	-	-	-	-	-
Sweaden coast	-	-	-	-	-	-	-	-	-
Norway coast	-	-	-	-	-	-	-	-	-
Iceland coast	-	-	-	-	-	-	-	+	+
Iceland coast	-	-	-	+	+	+	+	-	-
Norwegian coast	-	-	-	-	-	-	-	-	-
Norway coast	-	-	-	-	-	-	-	-	-
Davis Strait	-	-	-	-	-	-	-	-	-
Iceland coast	-	-	-	-	-	-	+	-	+
Greenland coast	-	-	-	-	-	-	-	-	-
Greenland coast	-	-	-	-	-	-	-	-	-
Iceland coast	-	-	-	-	-	-	+	-	+
Norway coast	-	-	-	-	-	-	-	-	-
Iceland coast	-	-	-	-	-	-	-	-	-
Iceland coast	-	-	-	-	-	-	+	-	-
Norway coast	-	-	-	-	-	-	-	-	-
Greenland coast	-	-	-	-	-	-	-	-	-
Greenland coast	-	-	-	-	-	-	-	-	-
Norway coast	-	-	-	-	-	-	-	-	-
Norway coast	-	-	-	-	-	-	-	-	-
Norway coast	-	-	-	-	-	-	-	-	-
Norway coast	-	-	-	-	-	-	-	-	-
Finmark coast	-	-	-	-	-	-	-	-	-
Greenland coast	-	-	-	-	-	-	-	-	-
Greenland coast	-	-	-	-	-	-	-	-	-

Table 4 (continued)

Area	<i>P. spatula</i>	<i>P. spicatus</i>	<i>P. vubella</i>	<i>A. cf. longipes</i>	<i>Mystriocetrus biho</i> n. sp	<i>P. misericorde</i> n. sp.	<i>P. sigurnis</i> n. sp.	<i>P. svavarrroni</i> n. sp.	<i>P. svavarrroni</i> complex
Jan Mayen									
Norway coast									
Norway coast									
Norway coast									
Greenland coast									
Greenland coast									
Norway coast									
Barents Sea									
Norway coast									
Greenland coast									
Source	28*	28*							
Localities other than N Atlantic									
Source									

Antenna (Fig. 13b) shorter than antennule; article-1 fused with body, broken during dissection; article-2 1.1 times as long as wide, with spine on outer margin; article-3 as article-2; article-4 8.0 times as long as wide, with five simple and one penicillate setae, distally; article-5 2 times as long as wide, 0.3 times as long as article-4, with simple distal seta; article-6 short, with five simple distal setae.

Mouthparts. Labrum (Fig. 13c) rounded, hood-shape, naked. *Left mandible* (Fig. 13d) incisor margin irregularly serrated, *lacinia mobilis* large and irregularly serrated; molar acuminate with two serrated distal spines. *Right mandible* (Fig. 13e) with regularly serrated incisor, *lacinia mobilis* fused to a small process; molar acuminate, with five serrated distal spines. *Maxillule* (Fig. 13f) distally bent, with nine distal setae and four subdistal fine setae on outer margin endite (Fig. 13f') with two distal setae. *Maxilla* (Fig. 13g) suboval distally, proximal margin flattened, naked. *Labium* (Fig. 13h) simple (accessory lobe not seen), naked. *Maxilliped* (Fig. 13i) basis short, almost as long as wide with two simple proximal setae directed posteriorly to main axis of the body; endites partly fused, distally separated, distal edge with one seta and a pair of small tubercles on each side, lateral margins finely setose. Palp article-1 naked; article-2 with three setae on inner margin and one seta on outer margin.; article-3 with three long and one short seta on inner margin; article-4 with five simple setae on inner distal margin and one seta on outer margin. *Epignath* (Fig. 13j) naked, linguiform.

Cheliped (Fig. 14a) basis 1.5 times as long as broad; merus subtriangular, with midventral seta; carpus 2.0 times as long as broad, with two midventral setae, and with one subproximal and one distal setae on dorsal margin; chela not-forcinate, slender; propodus (palm) 1.9 times as long as wide, little shorter than fixed finger, and row of five serrated setae on inner side; fixed finger with three setae on cutting edge and one ventral seta, distal spine bent upward; dactylus as long as fixed finger with two seta on inner margin, with distal spine bent downward.

Pereopod-1 (Fig. 14b) slender, coxa with simple seta; basis 6.7 times as long as wide, with two dorsoproximal and one distoventral setae; ischium with one seta, merus 2 times as long as wide, 0.8 times as long as carpus with short distoventral and long dorsoproximal setae; carpus 2.5 times as long as wide, 0.4 times as long as propodus, with two small distal setae; propodus 6.6 times as long as wide, naked; dactylus 0.3 times as long as propodus; unguis 1.8 times as long as dactylus, combined 0.9 times as long as propodus.

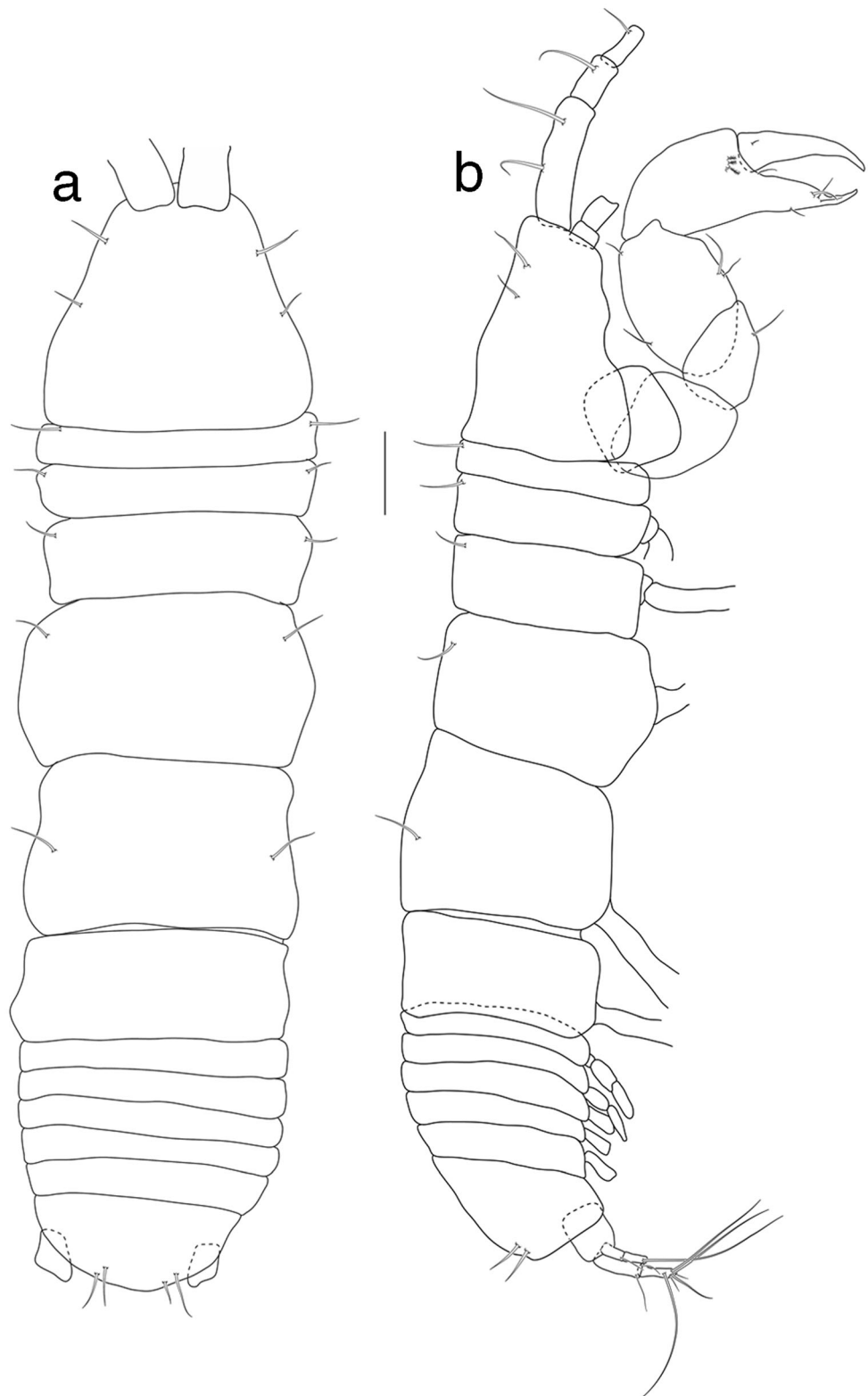
Pereopod-2 (Fig. 14c) basis seven times as long as wide, with two simple and one penicillate seta dorsoproximally, one distoventral seta; ischium with small simple seta; merus 1.8 times as long as wide, 0.7 times as long as carpus, with simple and penicillate setae distoventrally; carpus 3.3 times as long as wide, 0.6 times as long as propodus, with two simple setae and long blade-like spine propodus 7 times as long as wide, with simple distal seta; numerous microtrichiae in distal half;

Table 5 Characters of the “affinis,” “denticulatus,” and “longisetosus” group

	Reference	Antenna article 2–3	Mandibles	Pereopod-1 merus distodorsal seta	Pereopod-1 distodorsal ornamentation	Pereopod-1 carpus merus distoventral ornamentation	Number of the pereonite bearing setae	Number of the pereonite bearing setae
Affinis'								
<i>P. affinis</i>	Hansen 1886/87; Ingolf st 25 (Davis Strait)	Spines	?	Long	Short	Spine	4–6	2,4,5
<i>P. scalpellum</i>	Bird and Holdich 1989	Spines	Acuminate (4 spines)	Long	Short	Spine and seta	1, 4–6	1,2
<i>P. svavarssonii</i> sp. n.	present study	Spines (slender)	Acuminate 2 spines (L); 5 spines (R)	Long	Short	Two long setae (one serrated)	1, 4, 5	1–5
<i>Pseudotanais</i> sp. P	McLelland 2008	Spines	Acuminate (3–5 spines)	Absent	Long	Spine	1, 3–6	1–5
Denticulatus'								
<i>P. corollatus</i>	Hansen 1913, Sieg 1977	Spines	Wide	Short	Short	Two setae	0	0
<i>P. denticulatus</i>	Bird and Holdich 1985	Spines	Wide	Short	Short	Spine and seta	1, 4–6	0
<i>Pseudotanais</i> sp. A	McLelland 2008	Spines	Wide	Absent	Short			
Longisetosus'								
<i>P. longisetosus</i>	Sieg, 1977	Spine and seta	Acuminate (central spine long)	Long	Long	Spine and seta	0	0
<i>P. longispinus</i>	Bird and Holdich 1989a, b	Spines	Acuminate (central spine long)	Long	Long	Spine and seta	0	0
<i>P. nipponicus</i>	McLelland 2007	Spines	Acuminate (central spine long)	Long	Long	Spine and seta	1, 4–6 (dorso lateral), 2–6 (antero-lateral), 4–5 (medio-lateral seta)	5 (2 pairs)
<i>P. spatula</i>	Bird and Holdich 1989a, b	Spines	Acuminate	Long	Long	Spine and seta	1,3	0
<i>Pseudotanais</i> sp. O	McLelland 2008	“Stout spiniform seta”	Acuminate (one spine long)	Long	Long	Spine and seta	3–6	1–5

L left, R right

Fig. 15 *Pseudotanaïs sigrunis* sp. n. preparatory female, holotype (cat no...). **a** Dorsal view. **b** Lateral view. Scale: 0.1 mm



dactylus 0.6 times as long as propodus, unguis 1.7 times as long as dactylus, together 0.9 times as long as propodus.

Pereopod-3 (Fig. 14d) similar to pereopod-2, but basis with ventroproximal and ventrodistal simple setae; carpus 0.9 times

as long as propodus, blade-like spine 0.7 times as long as propodus; propodus 7.3 times as long as wide.

Pereopod-4 (Fig. 14e) 4.1 times as long as wide, with penicillate midventral seta; ischium with one short and one long

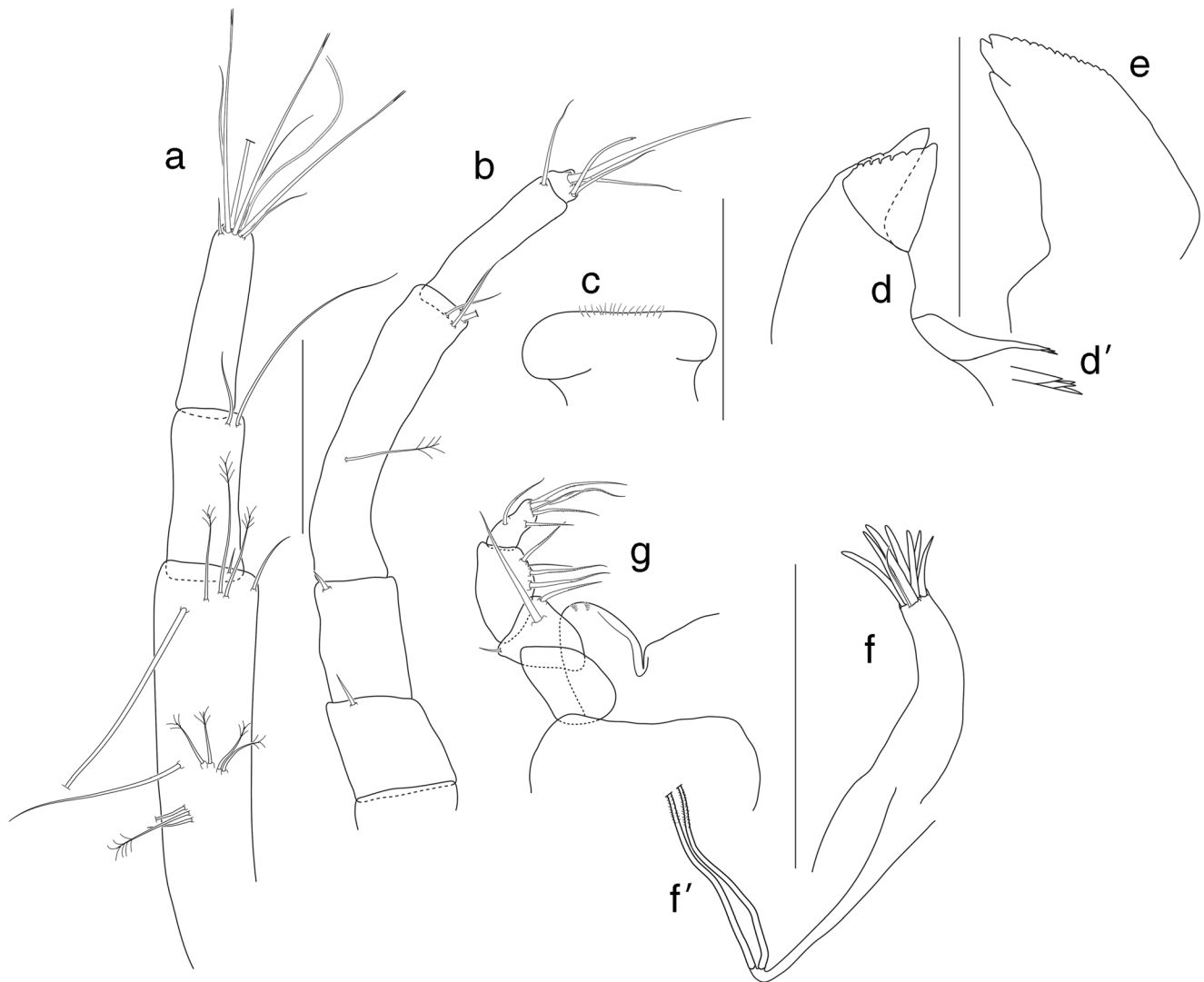


Fig. 16 *Pseudotanais sigrunis* sp. n. preparatory female. A antennule, B antenna, C labrum, D left mandible, D' molar of left mandible, E right mandible, F maxillule endite, F' maxillule palp, G maxilliped. Scale: 0.1 mm for A, B and 0.01 for C–F

simple setae; merus 1.5 times as long as wide, 0.5 times as long as carpus, with one distoventral seta; carpus 3.3 times as long as wide, 0.9 times as long as propodus, dorsal margin with microtrichiae, distodorsal sensory seta and distoventral small spine and blade-like spine (0.4 times as long as propodus); propodus 6 times as long as wide, with distal margin setose and dorsal margin with microtrichiae, short and long ventrodorsal setae and long (as long as propodus) penicillate, distodorsally; dactylus 0.2 times as long as propodus, unguis 0.3 times as long as dactylus, combined 0.3 times as long as propodus.

Pereopod-5 (Fig. 14f) similar to pereopod-4.

Pereopod-6 (Fig. 14g) similar to pereopod-4, but propodus with additional longer seta.

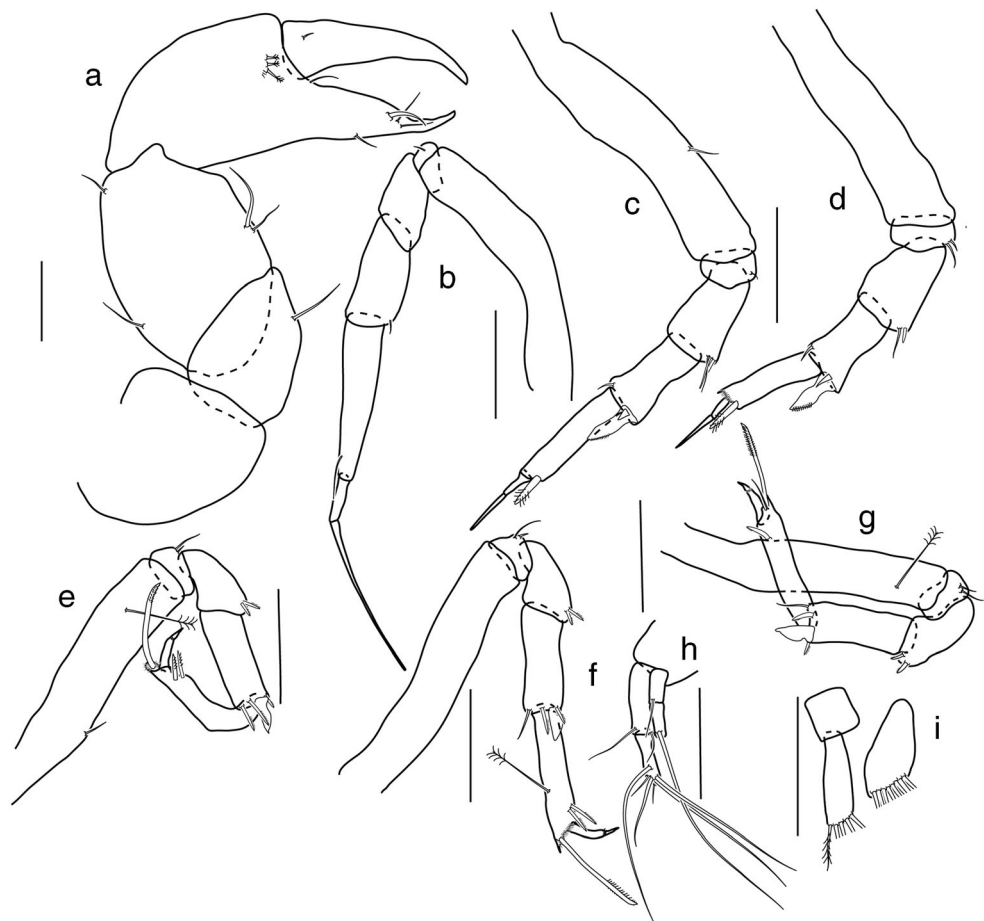
Pleopod (Fig. 14i) endopod 4.6 times as long as wide, with six distal setae; exopod 3.2 times as long as wide, with eleven distal setae.

Uropod (Fig. 14h) basis naked; exopod 0.8 times as long as endopod, with two articles, article-1 0.8 times as long as article-2, with distal seta, article-2 with at two distal setae; endopod with two subequal articles, article-1 with one simple and penicillate distal setae, article-2 with four long, two short simple setae and one plumose seta terminally (Table 4).

Distribution: *Pseudotanais svavarssoni* sp. n. was represented in Norwegian Sea, in the depth range 2172.6–2401.8 m (Fig. 7a).

Remarks: *Pseudotanais svavarssoni* sp. n. with characters such as (1) spines on antenna articles 2–3, (2) acuminate molar, (3) long distodorsal seta on pereopod-1 merus, and (4) elongated uropods, with exopod somewhat shorter than endopod, can be unequivocally regarded as representing the “*affinis*” group. It is distinguished from other members of the group by (1) relatively slender spines on antenna articles 2–3 (the spines are strong in *P. affinis*, *P. scalpellum*, and

Fig. 17 *Pseudotanaïs sigrunis* sp. n., preparatory female. **a** Cheliped. **b** Pereopod-1. **c** Pereopod-2. **d** Pereopod-3. **e** Pereopod-4. **f** Pereopod-5. **g** Pereopod-6. **h** Uropod. **i** Pleopod. Scale: 0.1 mm



Pseudotanaïs sp. P), (2) the presence of two setae on merus of the pereopods 2–3 (the spine in *P. affinis* and *P. scalpellum*, and the spine and seta in *Pseudotanaïs* sp. P are relatively long), as well as a slender dactylus and unguis in the pereopods 4–6 (see Table 5).

The history of the “*affinis*” group is quite convoluted (Bird and Holdich 1985, 1989a). The first species, *Pseudotanaïs affinis* Hansen, 1887, was described from Kara Sea; it was subsequently recognized, based on the Ingolf collection, in numerous locations, e.g., the Davis Strait, around Iceland, south of Jan Mayen, an East Greenland fjord (Hansen 1913; Fig. 2b). Morphological differences between the specimens studied by Hansen (1913) were considered the intraspecific variation, although the eurytopic distribution of the species, reported from both “warm” (2.4–4.5 °C) and “cold” (0.4–0.9 °C) areas over a relatively wide depth range (582–2196 m) suggests a complex of (possibly) cryptic species. Later on, the distribution range of the species was extended to cover an area between off the British coasts down to the Bay of Biscay (Bird and Holdich, 1989b).

The wide distribution and interspecific morphological variability of pseudotanaids was addressed by Bird and Holdich, 1989a). Having conducted comprehensive morphological studies which involved re-examination of

Hansen’s collection, they concluded that the species Sieg (1977) identified and illustrated as *P. affinis* was hardly a member of the “*affinis*” group on account of its wide mandible molar and the setae on antenna articles 2–3. As a result, they erected two new species: *P. corollatus* Bird and Holdich, 1989b to accommodate the former *P. affinis* from the Davis Strait (Hansen 1913), and *P. denticulatus* for the former *P. affinis* from off the west coast of Great Britain and the Bay of Biscay (Bird and Holdich, 1989a).

The presence of the wide mandible led Bird to assume that *P. denticulatus* and *P. corollatus* may come from the same group of species, the “*denticulatus*.” Another species that could be assigned to the group is *Pseudotanaïs* sp. A (McLelland, 2008). Differences between the “*affinis*” and the “*denticulatus*” species-groups are listed in Table 5.

As emphasized by Bird and Holdich (1989b), we are far away from fully recognizing the complexity of the “*affinis*” species-group. Based on the existing knowledge, they provisionally assigned three other species to the group: *P. spatula* Bird and Holdich, 1989a; *P. scalpellum* Bird and Holdich, 1989b; and *P. longispinus* Bird and Holdich, 1989a. Although all those species are, most likely, phylogenetically closely related to the “*affinis*” group (Jakiel unpublished data), they may represent two separate evolutionary lines. The

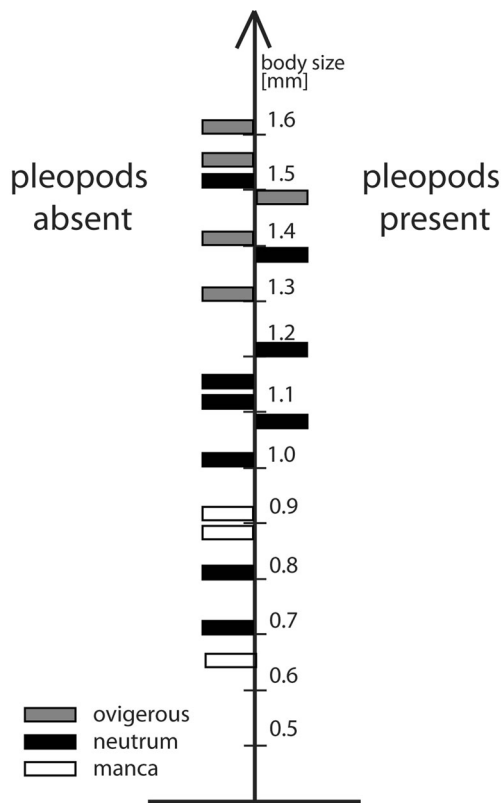


Fig. 18 Morphological variability of the occurrence of the pleopods in different life stages in *Pseudotanaid sigrunis* sp. n.

first (*Pseudotanaid longisetosus* Sieg, 1977; *P. longispinus* Bird and Holdich, 1989a; *P. nipponicus* McLelland, 2007; *P. spatula* Bird and Holdich, 1989b; and *Pseudotanaid* sp. O, McLelland, 2008) is defined by two autapomorphies: the presence of a long seta on the merus and carpus of pereopod-1 and a few setae on the pereopod 1–3 basis. Members of the other line show a long seta only on the merus of pereopod-1 and few (if any) setae on the basis of pereopods 1–3. Further analysis of other *Pseudotanaid* species with an acuminate mandible and the uropod exopod slightly shorter than the endopod support distinguishing still one more species-group, the “*longisetosus*.” Differences between the “*affinis*” and “*longisetosus*” groups are listed in Table 5.

Pseudotanaid svavarssoni species complex

Material examined: two neutri (ZMH K-54810), St. 871-4, 62° 45.31' N 000° 54.09' W, depth 1562.7 m, GKG, 26 Jul 2013; two neutri, one juvenile male (ZMH K-54811), St. 872-4, 63° 01.88' N 001° 29.91' W, EBS, depth 1858.3 m, 27 Jul 2013; manca (ZMH K-54812), St. 872-5, 63° 01.80' N 001° 27.05' W, depth 1842 m, GKG, 27 Jul 2013; two neutri (ZMH K-54813), St. 873-2, 61° 46.63' N 003° 52.38' W, depth 835.1 m, GKG, 28 Jul 2013; juvenile male, St. 873-6, 61° 46.52' N 003° 52.38' W, depth 833.7 m, EBS, 28 Jul 2013; two neutri (ZMH K-54814), St. 879-2, 63° 06.02' N 008° 35.14' W, depth 505.9 m, SG, 31 Jul 2013; two neutri, one

manca (ZMH K-54815), St. 879-5, 63° 06.10' N 008° 34.32' W, EBS, depth 510.9 m, 31 Jul 2013; neutrum (ZMH K-54816), St. 880-2, 63° 23.36' N 008° 09.42' W, depth 686 m, EBS, 31 Jul 2013; juvenile male, (ZMH K-54817), St. 881-4, 63° 34.66' N 007° 42.69' W, depth 1043.6 m, EBS, 01 Aug 2013; neutrum (ZMH K-54818), St. 881-6, 63° 38.50' N 007° 47.03' W, depth 1073.4 m, VV, 01 Aug 2013; ovigerous female, (ZMH K-54819), St. 882-2, 63° 25.01' N 010° 58.80' W, depth 441.4 m, VV, 02 Aug 2013; three neutri, four ovigerous females, two juvenile males, (ZMH K-54820), St. 882-5, 63° 25.04' N 010° 58.20' W, 440.5 m, EBS, 02 Aug 2013; neutrum, (ZMH K-54821), St. 963-1, 60° 2.72' N 21° 29.52' W–60° 2.73' N 21° 29.86' W; depth 2746 m, EBS, 29 Aug 2011; neutrum, (ZMH K-54822), St. 979-1, 60° 20.87' N 18° 8.52' W–60° 20.72' N 18° 8.60' W, 2568.8–2571 m, EBS, 30 Aug 2011; three neutri, (ZMH K-54823), St. 1010-1, 62° 33.17' N 20° 23.18' W–62° 33.22' N 20° 22.88' W, 1383.3–1387.8 m, EBS, 02 Sep 2011; neutrum, (ZMH K-54824), St. 1019-1, (62° 56.46' N 20° 44.06' W–62°

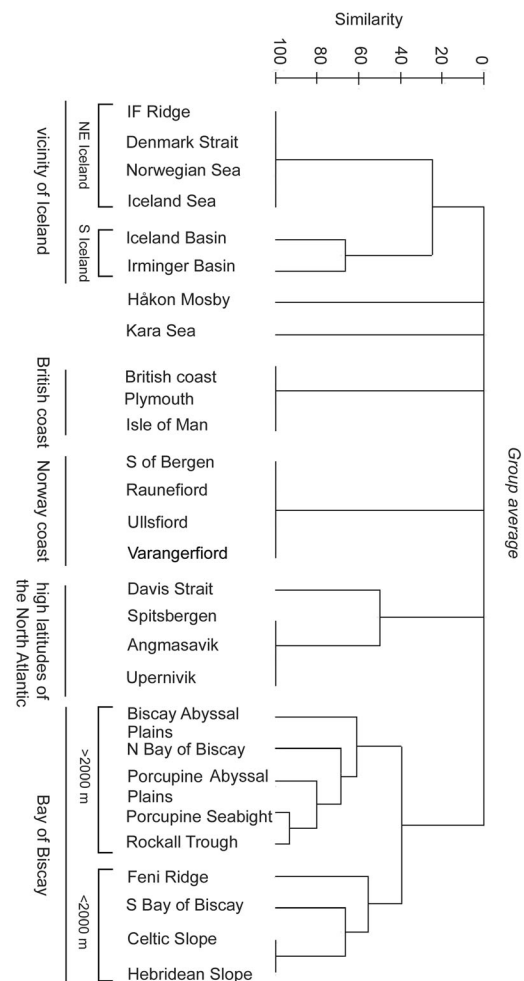


Fig. 19 Dendrogram of similarity (Bray Curtis, average linkage clustering method) of occurrence of *Pseudotanaid* fauna in the North Atlantic based on both present study and literature data (see caption of Table 4)

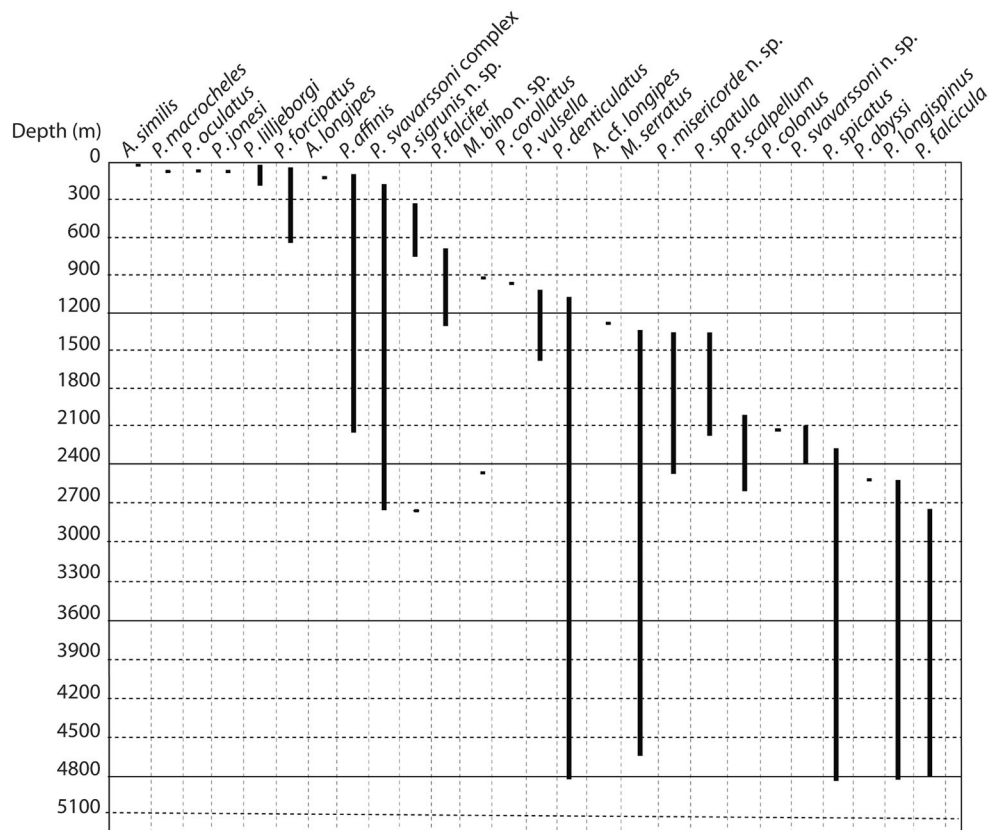


Fig. 20 Bathymetric distribution of the Pseudotanaididae species recorded in the N Atlantic from both the IceAGE collection and literature data. For literature data, see Table 4 caption

56.52' N 20° 43.77' W, depth 916.1–909.4 m, EBS, 03 Sep 2011; 15 neutri, three juvenile males, (ZMH K-54825), St. 1043-1, 63° 55.53' N 25° 57.54' W–63° 55.62' N 25° 57.36' W, depth 214.9–216.5 m, EBS, 05 Sep 2011; neutrum, (ZMH K-54826), St. 1051-1, 61° 37.40' N 31° 22.11' W, 2547.5 m, GKG, 07 Sep 2011; two neutri, (ZMH K-54827), St. 1054-1, 61° 36.82' N 31° 22.26' W–61° 36.98' N 31° 22.18' W, 2545.7–2536.8 m, EBS, 07 Sep 2011; two neutri, (ZMH K-54828), St. 1072-1, 63° 0.97' N 28° 3.35' W–63° 1.10' N 28° 3.15' W, depth 1564.2–1567 m, EBS, 09 Sep 2011; neutrum, (ZMH K-54829), St. 1086-1, 63° 42.66' N 26° 22.78' W–63° 42.78' N 26° 22.54' W, depth 688.4–680.3 m, EBS, 09 Sep 2011; neutrum, (ZMH K-54830), St. 1129-1, 67° 38.77' N 26° 44.78' W, depth 320.6 m, GKG, 14 Sep 2011; three neutri, (ZMH K-54831), St. 1132-1, 67° 38.48' N 026° 45.28' W, 318.1 m, EBS, 14 Sep 2011; neutrum, ovigerous female, (ZMH K-54832), St. 1136-1, 67° 38.06' N 26° 46.19' W–67° 37.96' N 26° 46.42' W, depth 315.9 m, EBS, 14 Sep 2011; neutrum, (ZMH K-54833), St. 1141-1, 67° 50.22' N 23° 42.11' W, depth 1241.6 m, GKG, 15 Sep 2011; four neutri, juvenile male, (ZMH K-54834), St. 1148-1, 67° 50.79' N 023° 41.76' W, depth 1248.8 m, EBS, 15 Sep 2011; neutrum male, manca, (ZMH K-54835), St. 1178-1, 67° 38.72' N 12° 10.10' W, depth 1818.9 m, GKG, 20 Sep 2011; six neutri, two

ovigerous females, (ZMH K-54836), St. 1184-1, 67° 38.63' N 012° 09.72' W, depth 1819.3 m, EBS, 20 Sep 2011; three neutri females, two juvenile males, manca, (ZMH K-54837), St. 1188-1, 67° 4.32' N 13° 0.89' W, depth 1580.6 m, GKG, 21 Sep 2011; seven neutri, two juveniles male (ZMH K-54838), St. 1212-1, 66° 32.63' N 012° 52.48' W, depth 317.2 m, EBS, 22 Sep 2011; five neutri, juvenile male, (ZMH K-54839), St. 1216-1, 66° 18.06' N 12° 22.38' W, 730.8 m, GKG, 22 Sep 2011; 5 neutri, (ZMH K-54840), 1219-1, 66° 17.34' N 012° 20.82' W, depth 579.1 m, EBS, 22 Sep 2011.

Diagnosis: carapace, pereonites, and pleonites combined length 0.7–1.7 mm; cheliped carpus 1.3–2.0 times as long as wide, propodus 1.3–2.0 times as long as wide; pereopod-1 propodus 1.7–2.6 times as long as carpus, propodus 0.7–1.2 times as long as combined length of dactylus and unguis; pereopod-3 propodus 1.1–1.6 times as long as blade-like spine; pereopod-6 propodus 1.4–4.7 times as long as distal carpal seta.

Distribution: *P. svavarssonii* species complex is widely represented in the studied area and in the widest depth range (214–2746 m). It occurs in all investigated regions: Iceland-Faroe Ridge, Iceland Basin, Irminger Basin, Denmark Strait Norwegian Channel, and Norwegian Sea (Fig. 7a).

Pseudotanaïs sigrúnis sp. n.

Figs 15, 16, and 17

Material examined: Holotype neutrum (ZMH K-54841); St. 1216-1, 66° 1.06' N 12° 22.38' W, depth 730.8 m, 22 Sep 2011.

Two ovigerous female, (ZMH K-54842), St. 882-2, 63° 25.01' N 010° 58.80' W, depth 441.4 m, 02 Aug 2013; one neutrum, ovigerous female, (ZMH K-54843), St. 882-5, 63° 25.04' N 010° 58.20' W, depth 440.5 m, EBS02 Aug 2013; manca (ZMH K-54844), St. 880-3, 63° 24.79' N 008° 11.63' W, depth 688.1 m, GKG, 31 Jul 2013; neutrum (ZMH K-54845), St. 963-1, 60° 2.72' N 21° 29.52' W–60° 2.73' N 21° 29.86' W, depth 2746.4–2746 m, EBS, 29 Aug 2011; neutrum, (ZMH K-54846), St. 1116-1, 67° 12.82' N 26° 16.31' W, depth 683.1 m, GKG, 14 Sep 2011; three neutri, ovigerous female, manca, (ZMH K-54847), St. 1212-1, 66° 32.63' N 012° 52.48' W, depth 317.2 m, EBS, 22 Sep. 2011; two neutri, manca, (ZMH K-54848), St. 1216-1, 66° 18.06' N 12° 22.38' W, depth 730.8 m, GKG, 22 Sep 11; neutrum, ovigerous female, (ZMH K-54849), St. 1219-1, 66° 17.34' N 012° 20.82' W, depth 579.1 m, EBS, 22 Sep 2011.

Diagnosis: Eyes absent. Antennule article-1 four times as long as wide. Antenna article-2 with seta, article-3 with spine. Mandible molar acuminate with four spines. Maxilliped endites simple. Cheliped robust, chela not forcipate; carpus 1.6 times as long as wide; unguis and dactylus distal spines inside bent. Pereopods 2–6 carpal blade-like spine well developed. Uropod exopod two articulated, as long as endopod article-1.

Etymology: The species named after Sigrún Haraldsdóttir, a great fellow during cruise IceAGE, who tirelessly helped in sorting of the benthic samples onboard.

Description of neutrum: *Body* (Fig. 15) more than three times as long as broad. Cephalothorax 22% of total body length subtriangular, with two pairs of lateral simple seta. Eyes absent. *Pereon* 55% of total body length. Pereonite-1 0.6 times as long as pereonite-2; pereonite-2 0.7 times as long as pereonite-3; pereonite-3 0.6 times as long as pereonite-4; pereonites-4 0.7 times as long as pereonites-5; pereonites-5 twice as long as pereonite-6; pereonites 0.1, 0.2, 0.3, 0.5, 0.6, and 0.4 times as long as broad respectively (measurements for the holotype); pereonites 1–5 each with a pair of simple lateral setae. Pleonites 15% of total length, as long as pereonite-5. Pleotelson 8% of total length, as long as three pleonites combined length, with two pairs of distal seta.

Antennule (Fig. 16a) article-1 3.7 times as long as wide, with outer medial and distal tufts penicillate (3–5) and simple (1–3) setae. Article-2 2.3 times as long as wide and 0.4 times as long as article-1 with short and long outer distal setae; article-3 as long as article-2, with one aestetasc, four simple, three distally trifurcate and one broken seta.

Antenna (Fig. 16b) article-1 fussed with body, article-2 as long as wide with one thin spine, article-3 1.4 times as long as wide, and 1.2 times as long as article-2, with small distal

spine; article-4 four times as long as wide and 2.5 times as long as article-3, with one midlength penicillate seta and three distal setae (one broken); article-5 4.2 times as long as wide and 0.5 times as long as article-4, with one distal seta; article-6 short, with three simple and one bifurcated distal setae.

Mouthparts: *Labrum* hood-shaped, weakly setose (Fig. 16c); *left mandible* (Fig. 16d) incisor margin weakly serrated, *lacinia mobilis* large and irregularly serrated; molar acuminate with four distal spines (Fig. 16d'). *Right mandible* (Fig. 16e) with regularly serrated incisor, *lacinia mobilis* fussed to a small process; molar not seen. *Maxillule* (Fig. 16f) tipped with seven spines and one seta; endite (Fig. 16f') with two distal setae. *Labium* not observed. *Maxilliped* (Fig. 16g) endites distally separated, simple, with microtrichiae in distal corners; palp article-1 naked, article-2 with two inner setae (short and long) and one outer seta; article-3 with four inner setae, article-4 with five simple inner and distal setae and one outer seta. *Epignath* not seen.

Cheliped (Fig. 17a) basis 0.9 times as long as broad; merus triangular with midventral seta; carpus elliptical, 1.5 times as long as wide, with two midventral setae and subproximal and distal setae dorsally; chela not forcipate, propodus (palm) 1.7 times as long as wide, almost as long as fixed finger with two ventral seta and row of three serrated setae on inner side; fixed finger with three setae on cutting edge and one simple seta in near dactylus insertion; dactylus with dorsoproximal seta.

Pereopod-1 (Fig. 17b) basis 6.1 times as long as broad; ischium with simple seta; merus 1.5 times as long as wide, 0.7 times as long as carpus, naked; carpus 2.2 times as long as wide, 0.6 times as long as propodus, with one fine distodorsal seta; propodus 5.8 times as long as wide, with distoventral seta; dactylus 0.3 times as long as propodus, unguis four times as long as dactylus; unguis and dactylus combined 1.3 times as long as propodus.

Pereopod-2 (Fig. 17c) basis 5.4 times as long as wide with middle simple seta; ischium with simple seta; merus 2.1 times as long as wide, 1.1 times as long as carpus, with simple seta and spine distoventrally; carpus 2.4 times as long as wide, 0.7 times as long as propodus with blade-like spine 0.4 times as long as propodus, one distodorsal seta and short distoventral spine; propodus five times as long as wide, with serrated distal spine; dactylus 0.2 times as long as propodus, unguis twice as long as dactylus, dactylus and unguis combined 0.6 times as long as propodus.

Pereopod-3 (Fig. 17d) similar to pereopod-2, but merus with short spine and seta distoventrally; propodus three times as long as wide.

Pereopod-4 (Fig. 17e) basis 5.1 times as long as wide, with one simple seta midlength and one penicillate seta subdistally; ischium with short and long setae; merus 1.6 times as long as wide, 0.6 times as long as carpus, with two serrated distoventral setae; carpus 2.8 times as long as wide and 0.9 times as long as propodus, with blade-like spine 0.3 times as

long as propodus and three serrated spines distally; propodus 5.7 times as long as wide, with two distoventral serrated spines and dorsodistal serrated seta; dactylus 0.3 times as long as propodus, unguis 0.1 times as long as propodus, dactylus and unguis combined 0.3 times as long as propodus.

Pereopod-5 (Fig. 17f) similar to pereopod-4; propodus five times as long as wide, with one distodorsal penicillate seta.

Pereopod-6 (Fig. 17g) similar to pereopod-4; but propodus with one additional simple seta distally.

Pleopoda (Fig. 17i) basal article as long as wide, 3.5 times as long as wide, with five distal setae; exopod 1.9 times as long as wide, with eight distal setae.

Uropod (Fig. 17h) basis naked; exopod 0.6 times as long as endopod, with two articles; article-1 times as long as article-2 with one distal seta; article-2 with two setae (one broken); endopod two articles, article-1 with two distal setae; article-2 with two short and four long distal setae.

Distribution: *P. sigrunis* sp. n. was well represented in IceAGE material. It was recorded at Iceland Faroe Ridge, in Norwegian Channel, Iceland Basin, Denmark Strait, and Norwegian Sea (Fig. 7b) at the depth range from 317 to 731 m and 2746 m.

Morphology variables

Some of the specimens of *P. sigrunis* sp. n. had fully developed pleopods, while the others missed those appendages (4 with and 13 without pleopods). This presence/absence of the pleopods was irrespective to locality, depth, body size, and, in some cases, also to the life stage (Fig. 18), although all studied manca (0.6–0.9 mm) apparently missed the pleopods. *Pseudotanaeis sigrunis* sp. n. was a series of just 17, widely distributed specimens, what hampers further analysis and any reliable conclusion. If the studied individuals are really conspecific, we can hypothesize the presence and the absence of the pleopods can be rationalized by presence in the life-history a dispersal stage.

Remarks: *P. sigrunis* sp. n. with a robust cheliped, acuminate mandible molar, and short, bi-articulated exopod on the uropods is the most similar to *Pseudotanaeis lilljeborgi* Sars, 1882. Two other species with also an acuminate molar and a regular (non-forcipate) chela (*P. colonus* Bird and Holdich, 1989b and *P. falcifer* Błażewicz-Paszkowycz and Bamber, 2011) show a non-articulated exopod on the uropods.

Pseudotanaeis lilljeborgi Sars, 1882 is a *Pseudotanaeis* with a wide geographic distribution (Fig. 2b) and numerous records in the literature (e.g., Sars 1896; Hansen 1913; Greve 1965a, b, c; Stephensen 1937; Just 1970; Bird and Holdich, 1989a), all records being confined to a relatively narrow depth range (139–536 m). The species was described by Sars (1882) based on the type material from Varangerfjord (northern part of Norway) and diagnosed as a non-forcipate member of the genus with eyes and a relatively short exopod on the uropod (not longer than the

proximal article of the endopod), the uropod endopod proximal article being longer than the distal one. Moreover, the species shows long setae on articles 2–3 of the antenna.

Sieg (1977) redescribed *P. lilljeborgi* using the Ingolf material collected off Iceland and Jan Mayen Island by Hansen (1913); he disregarded Hansen's note that the "Icelandic" specimens lacked eyes and their carapace shape differed from that of the "Norwegian" individuals (Hansen 1913, p. 27). In addition, the *P. lilljeborgi* studied by Sieg (1977) showed short setae on the antenna articles 2 and 3, and the exopod uropod somewhat longer than the endopod proximal article, while they were apparently long in the type specimens.

The newly described *Pseudotanaeis sigrunis* sp. n. shows setae on the antenna articles 2–3 to be as short as those in *P. lilljeborgi* studied by Sieg (1977), the exopod uropod being somewhat longer than the endopod proximal article. Therefore, we assume that the part of the Ingolf collection studied by Sieg (1977) is conspecific with *P. sigrunis*.

It is important to emphasize that all except one specimens were found in relatively shallow areas (317–731 m) in nearly all the basins around Iceland, a single individual only being collected at a deeper station (2746 m, the Icelandic Basin). Morphological analyses failed to reveal differences between the "shallow" and the "deep" individuals. Nevertheless, we anticipate that molecular studies involving a larger collection of specimens should show whether (1) the "shallow-water" and the "deep-water" populations of the species are conspecific rather than forming a complex of cryptic species, and (2) other records of *P. lilljeborgi* (e.g., from off the northern part of Norway: vicinity of Kvalsund (Greve 1965a, c), Barents Sea (Strapper unpublished data), and East Greenland (Hansen 1913)) belong to the only one species.

Discussion

The Pseudotanaidae are currently represented by 51 nominal species known worldwide (WoRMS 2018). In the North Atlantic, the number of nominal pseudotanaid species known at present is, together with the new species described in this paper, 25 (Table 4). The IceAGE collection represented by 323 specimens was dominated by *Pseudotanaeis svavarssoni* sp. n. which accounted for 57% of the specimens examined, followed by *Pseudotanaeis sigrunis* sp. n., *Pseudotanaeis misericorde* sp. n., *Mystriocentrus biho* sp. n., and *Akanthinotanaeis* cf. *longipes*, which made up 5.5, 1.8, 1.2, and 0.3% of all the identified specimens, respectively. Because of poor preservation condition, five specimens from the collection we studied could not be identified to the species level (Table 2).

Most of those taxa have a limited zoogeographical range (i.e., one, relatively well-defined basin) and a distinct bathymetric range (Fig. 19). The Bray-Curtis similarity-based

cluster analysis separated the different a priori designated areas into groups based on the pseudotanaid faunas:

- Off the British coast: *P. corollatus* and *P. jonesi*
- Off the Norwegian coast: *P. macrocheles*
- High latitudes of the North Atlantic: *P. oculatus*
- The Bay of Biscay and the Porcupine Abyssal Plain: *P. abyssi*, *P. colonus*, *P. denticulatus*, *P. falcicula*, *P. longispinosus*, *P. scalpellum*, *P. serratus*, *A. similis*, *P. spatula*, *P. spicatus*, and *P. vulsella*
- Off Iceland: north—*P. svavarssoni* sp. n.; south—*A. longipes*, *M. biho* sp. n., *P. misericorde* sp. n., *P. svavarssoni* complex

A separate group in the dendrogram was made up by *P. falcifer* known from mud volcanoes off Norway (Błażewicz-Paszkowycz and Bamber 2011). In addition, the Kara Sea with the original locality of *P. affinis* produced a separate branch in the dendrogram. Three species, namely *P. forcipatus*, *P. affinis*, and *P. lilljeborgi*, are particularly widely distributed, their range extending from the high Arctic (the Barents Sea) to the British coast of the North Sea (e.g., *P. forcipatus*) or from Novaya Zemlya to the coasts of Norway and Iceland to the west coast of Greenland (*P. affinis* and *P. lilljeborgi*) (Table 4).

The bathymetric range of N Atlantic pseudotanaids extends from the upper shelf down to 4800 m (Fig. 20), few of them showing a narrow range (e.g., *A. similis*, *P. macrocheles*, *P. oculatus*, *P. jonesi*, *P. corollatus*, *P. colonus*, *P. abyssi*). Unsurprisingly, all of those species have very narrow zoogeographical distribution and they are often restricted to the type locality (Fig. 2). An exception is *P. macrocheles* that occurs only in Norwegian fjords (Fig. 2d). A few other pseudotanaids recorded in the North Atlantic show a depth range extending from some hundred meters up to 2500 m (e.g., *P. sigrunis* sp.n., 317–731 m; *P. svavarssoni* sp. n., 2172–2401 m; *M. biho* sp. n.; 913–2537 m; *P. scalpellum*, 2081–2634 m; *P. falcifer*, 722–1263 m; *P. spatula*, 1400–2200 m; *P. vulsella*, 1028–1640 m; and *P. misericorde*, 1385, 1621, 2537 m) and have a relatively narrow zoogeographical distribution (Figs. 2 and 7). Five species (*P. longispinus*, *P. spicatus*, *P. falcicula*, *M. serratus*, and *P. denticulatus*) spans their bathymetric range over 3000 m, although the distribution is relatively narrow (Fig. 20). Two of them, *P. denticulatus* and *P. serratus*, show the widest depth range (around 3700 and 3100 m, respectively). Quite a wide depth range has been also found in the *P. svavarssoni* complex (2500 m) and *P. affinis* (1700 m), accompanied by a wide zoogeographical range (Fig. 7), in contrast to *P. lilljeborgi* and *P. forcipatus*, both showing shallower depth ranges (< 500 m), but wide zoogeographical distributions (Fig. 2b).

Conclusion

In the IceAGE collection made in waters surrounding Iceland (Irminger Basin, Iceland Basin, Norwegian Sea, Denmark Strait, Iceland–Faroe Ridge, and Norwegian Channel), five species of pseudotanaids were identified; four of them were new for science (*Mystriocentrus biho* sp. n., *P. misericorde* sp. n., *P. sigrunis* sp. n., and *P. svavarssoni* sp. n.). Apart from species new to the knowledge, *Akanthinotanaid* cf. *longipes* was collected from close place to type locality *A. longipes* Hansen, 1913 that is known only from that original location. One species that is probably complex of closely related species morphologically was very similar with *P. svavarssoni* sp. n. The morphometric approach and analysis highlighted significant differences between specimens collected in northern and southern Icelandic basins; distinct differences were also apparent between specimens collected from shallow and deep waters. Molecular approach is required to confirm our findings. Pseudotanaidae of Iceland are currently represented by seven nominal species.

Distinguished in the analysis, zoogeographical regions are represented by distinct pseudotanaid fauna. Our results stay in contrast to the earlier observation for bivalves (Dijkstra et al. 2009) or munnopsids (Schnurr et al. 2014). The wide distribution of these isopods in the North Atlantic and marine basins are rationalized by their efficient swimming abilities and potentially high ecological plasticity.

Considering a restricted dispersal ability of pseudotanaids, the North Atlantic could be divided into several zones, where distinct species, or discrete group of species, are noted (see Fig. 19). For example, some taxa are known only for the Bay of Biscay while *P. oculatus* were noted in high latitudes in the North Atlantic, but *P. macrocheles* was collected from fjords along Norway coast.

Four of the pseudotanaid species in the North Atlantic are widely distributed. *P. affinis*, *P. macrocheles*, *P. lilljeborgi*, and *P. forcipatus* were noted in various marine basins located around Iceland, Norway, and Greenland. Those records need to be re-examined, and it is highly probable that they represent complex of sister (or cryptic) species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Field study Permits and approval of field or observational studies are not applicable for authors.

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