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Discovery of swimming males of Paratanaoidea (Tanaidacea)

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Abstract: In Tanaidacea morphological identification of male individuals to the species level is complicated by two factors: the presence of multiple male stages/instars confuse the assessment of sexual stage while strong sexual dimorphism within several families obscures the morphological affinities of undescribed males to described females. Males of Paratanaoidea are often morphologically quite different from females and have not been discovered for most genera so far, which has led to the assumption that some tanaidaceans might have parthenogenetic reproduction or simply have undeveloped secondary sex traits. As a part of the IceAGE project (Icelandic marine Animals: Genetics and Ecology), with the support of molecular methods, the first evidence for the existence of highly dimorphic (swimming) males in four families of the superfamily Paratanaoidea (Agathotanaidae, Cryptocopidae, Akanthophoreidae, and Typhlotanaidae) is presented. This study suggests that these males might be the next instars after juvenile or preparatory males, which are morphologically similar to females. It has been assumed that “juvenile” males with a restricted ability for swimming (*e.g.*, undeveloped pleopods) have matured testes, are capable of reproduction, and mate with females nearby, while swimming males can mate with distant females. Our explanation of the dimorphism in Tanaidomorpha lies in the fact that males of some species (*e.g.*, *Nototanais*) retain the same lifestyle or niche as the females, so secondary traits improve their ability to guard females and successfully mate. Males of other species that have moved into a regime (niche) different than that of the female have acquired complex morphological changes (*e.g.*, *Typhlotanais*).

Key words: Icelandic waters, IceAGE, Crustacea, sexual dimorphism, biodiversity, barcoding.

Introduction

Sexual dimorphism is a widespread phenomenon to be observed in various groups of animals as a consequence of sexual selection that stays in balance with natural selection (Andersson 1994). It may involve a wide variety of traits that allow the sexes to be distinguished morphologically. Some of the traits, especially those concerning gonads or copulatory organs, might be hardly seen, although their role in preventing misidentification of potential mating partners is unquestionable (Andersson 1994). Easier to observe, and often more spectacular, are the morphological differences that are classified as secondary sexual characteristics. They might involve prominent morphological changes such as variety in pigmentation and ornamentation, as well as proliferation of particular organs as weapons appearing in both sexes or in only one sex. Finally, dimorphism might involve changes in physiology and behaviour changes (Smith 1906; Bückle-Ramirez 1965; Johnson and Attramadal 1982; Conlan 1991; Andersson 1994; Parker 1997).

Tanaidaceans are small marine crustaceans that belong to the less recognized benthic invertebrates (Appeltans *et al.* 2012). Studies of various oceanic ecosystems triggered by the Census of Marine Life (CoML, www.coml.org) have improved the knowledge of tanaidaceans in various areas (see Błażewicz-Paszkowycz *et al.* 2012). As such, some aspects of tanaidacean taxonomy, evolution and biology have been elucidated, but many questions remain unanswered. One such question is the nature and underlying causes of sexual dimorphism of some Tanaidacea.

Sexually dimorphic traits of Tanaidacea are variously developed (Sieg 1982; Larsen 2005). Males of two suborders, Apseudomorpha and Neotanaidomorpha, are relatively well known, and reported for numerous species (*e.g.*, Hansen 1913; Gardiner 1975), although it was emphasized that many representatives of both suborders are simultaneous hermaphrodites (*e.g.*, Lang 1953; Gardiner 1975; Drumm and Heard 2007) with possible self-fertilization (Kakui and Hiruta 2013). Nevertheless, mature males of those suborders are often reported and, usually without hesitation, identified to species level. Those males often have better developed eyes (*Pakistanapseudes* Bacescu, 1978), stronger and more intensively ornamented chelipeds (*Spinosapseudes* Gutu, 1996), or better developed antennules (*Whiteleggia* Lang, 1970) or pleopods (*Leviapseudes* Sieg, 1983); the pleon is more strongly ornamented and the first pereopods are strongly enlarged (*Pseudosphyrapus* Gutu, 1980). Still, both sexes share species-specific characters that reside in mouth parts, pereopods or uropods.

The secondary traits in males of the deep-sea Neotanaidomorpha are powerfully developed, involving growth of the chelae to enormous size and reduction of the mouthparts (Gardiner 1975). Taxonomic identification of such males is often difficult, but still possible, as both sexes occasionally share species-specific characters (Larsen and Błażewicz-Paszkowycz 2003).

Tanaidomorpha, which presumably represent the most apomorphic suborder of Tanaidacea, exhibit at least four types of males. The first type observed in Tanaidae Dana, 1849, are similar to Apseudomorpha in retaining males that share species-specific character with females, but usually have bigger chelae, numerous aesthetascs on antennules, better developed pleopods and occasionally a more attenuated cephalothorax (*e.g.*, Bird 2008; Edgar 2008). Males of the second type have non-functional mouthparts and, since they are not able to feed, probably live only a very short time and are called "terminal" (Larsen 2001). Those males are recorded for shallow-water families such as *e.g.* Tanaissuidae Bird and Larsen, 2009, Nototanaidae Sieg, 1976, and Leptocheliidae Lang, 1973. In addition to the often reduced mouthparts, those males have highly enlarged or elongated chelipeds and numerous aesthetascs on multiarticulated antennules, but they still share species-specific characters with the females, therefore morphological identification is usually possible (*e.g.*, Jażdżewski 1969; Bird and Bamber 2000; Bamber 2013).

Males of the second type, occasionally called preparatory, morphologically resemble non-ovigerous females (Błażewicz-Paszkowycz 2001; Larsen 2005) although they have thicker antennules (sometimes with an additional article) and better developed pleopods; in species in which females lack pleopods (*Collettea*), they are present in males. This type of male has been reported for Agathotanaidae Lang, 1971, Anarthruridae Lang, 1971, Colletteidae Larsen *et* Wilson, 2002, as well as for Tanaellidae Larsen *et* Wilson, 2002. Because morphologically they resemble the females or juvenile stages, they are occasionally called "juvenile males", although they are presumably sexually mature (Bird and Holdich 1988).

The third type of male (swimming or natatory) is morphologically most different from females and is often indeterminable to species even by qualified specialists, although they may be seen as a more extreme version of the first type. The bodies of those males have a "hydrodynamic appearance" that includes strong pleopods supported with long plumose setae and antennular flagellae with numerous aesthetascs. These males have also uropods and pereopods morphologically different than those in female and have non-functional mouth-parts, which suggest that they are short-living and solely devoted to finding females (Larsen 2001). Swimming males of Leptocheliidae and Paratanaidae, although they have a very different appearance from the females, occasionally share species-specific characters (uropods in *Bassoleptochelia verro* Błażewicz-Paszkowycz *et* Bamber, 2012).

The most intriguing males are those of the Typhlotanaidae Sieg 1984, which appear to share no species-specific characters with females. Sieg (1986) and Błażewicz-Paszkowycz (2004, 2005) have matched females and males of *Typhlotanais adipatus* Tzareva, 1982, *Typhlotanais grahami* Błażewicz-Paszkowycz, 2004, and *Peraeospinosus subtigaleatus* Błażewicz-Paszkowycz, 2004, by the fact that the same "pairs" were found in a series of samples or occurred in high abundance (Siciński *et al.* 2012).

Table 1

Literature records of swimming males of Paratanaoidea except records of some shallow water families: Heterotanoididae Bird, 2012; Leptocheliidae Lang, 1973; Paratanaidae Lang, 1949; Pseudozeuxidae Sieg, 1982; Tanaissuidae Bird *et* Larsen, 2009; Teleotanaidae Bamber, 2008).

Family	Species	References
Agathotanaidae	*Agathotanais ingolfi*	this paper
	male 6A	this paper
Akanthophoreidae	*Akanthophoreus gracilis*	Kudinova-Pasternak 1970; Hansen 1913 (as *L. hanseni*)
	Akanthophoreus longiremis?	G.O. Sars 1896
	male 2	this paper
	leptognathiid?	Larsen 2003
Anarthruridae	*Siphonolabrum fastigatum*	Sieg 1986
Colletteidae	*Tumidochelia uncinata*	Hansen 1913
Cryptocopidae	*Cryptocope* sp.?	Kudinova-Pasternak 1970
	Cryptocopoides aff. *arcticus*	this paper
Leptognathiidae	*Leptognathia breviremis*?	Kudinova-Pasternak 1970
	Leptognathia?	Kudinova-Pasternak 1970
Pseudotanaidae	*Pseudotanais forcipatus*	Hansen 1913
	Pseudotanais falcifer	Błażewicz-Paszkowycz and Bamber 2011
Typhlotanaidae	*Pulcherella pulcher*	this paper
	Torquella	this paper
	Typhlotanais sp. A	this paper
	Dimorphognathia heroae	Sieg 1986
	Typhlotanais finmarchicus	G.O. Sars 1900
	Typhlotanais grahami	Błażewicz-Paszkowycz 2004
	Typhlotanais adipatus	Sieg 1986
	Peraeospinosus subtigaleatus	Błażewicz-Paszkowycz 2005
incertae sedis	*Paranarthrurella voeringi*	Jóźwiak *et al.* 2009
	Andrognathia plumosa	Sieg 1983

Some authors have recorded the swimming males as unidentified taxa (Bird and Holdich 1989), while others tried to pair males and females, but those decisions were purely intuitional (see Table 1 and references therein). Even so, in many species or genera of Tanaidacea males have never been discovered or proven to exist. The failure to find males that could be confidently paired with a female has led to the assumption that tanaidaceans might have parthenogenetic reproduction (Sieg 1978) or simply have totally undeveloped secondary sex traits (Larsen 2005).

In samples taken during the recent IceAGE expeditions (Icelandic marine Animals: Genetics and Ecology) we found seven highly dimorphic swimming males. Our aim was to test species allocation based on DNA barcoding using COI as a marker. Supported by molecular methods, we document highly dimorphic males in four paratanaoid families: Agathotanaidae Lang, 1971, Cryptocopidae Sieg, 1977, Akanthophoreidae Sieg, 1986, and Typhlotanaidae Sieg, 1986. We describe for the first time swimming males of *Agathotanais ingolfi* (Hansen, 1913) and *Crypto-*

copoides aff. *arcticus*, as well as five males identified only to family: one male from the family Agathotanaidae Lang, 1971, three from the family Typhlotanaidae Sieg, 1984, and one from the family Akanthophoreidae Sieg, 1986.

Materials and methods

Specimens were collected during the IceAGE1 cruise in August/September of 2011 on board of the R/V *Meteor*, using a variety of sampling gear. Most tanaidaceans were collected using RP, Brenke, and camera-Brenke epibenthic sleds (Rothlisberg and Pearcy 1977; Brenke 2005; Brandt *et al.* 2013). Upon retrieval of the epibenthic sled, material still in the nets was washed into the cod ends with ambient seawater, and these contents were processed as quickly as possible. Samples from each net of the 2-net sleds (Brenke 2005; Brandt *et al.* 2013) were preserved separately. Specimens and accompanying sediment were processed in a cold lab (4°C), preserved in chilled (-20°C) 96% ethanol, and stored at -20°C. For the first 24 hours, preserved samples were gently mixed every few hours to ensure thorough preservation, and the ethanol was changed after 24 hours. A subsample of approximately 100 mL of material was sorted on board during the cruise; subsequent sorting was conducted upon return to land (see Riehl *et al.* (2014) for sampling, preservation, and sorting details). For the RP sled (Rothlisberg and Pearcy1977), collected material was gently elutriated through a series of sieves from 1mm to 300 mm, with each fraction preserved separately. From the sorting performed on board, 141 tanaidaceans specimens comprising females from at least 53 species and seven unidentified males were prepared for sequencing, and provisional identifications assigned. These specimens came from 16 stations spanning depths from 209 to 2572 meters.

Genetics. — Extraction of DNA from identified female and unidentified male specimens was performed at the Smithsonian Institution in Washington, D.C. according to the protocols described in Riehl *et al*. (2014). PCRs employed two primer sets: jgLCO (5'-TIT CIA AYC AYA ARG AYA TTG G-3') and jgHCO (5'-TAI ACY TCI GGR TGI CCR AAR AAY CA-3'), or LCO-1498 (Folmer *et al*. 1994) and Nancy (5'-CCC GGT AAA ATT AAA ATA TAA ACT TC-3'). Standard 50 μL PCR mixtures were employed for both primer sets. The reaction protocol for jgLCO/jgHCO consisted of an initial denaturation at 95°C for 3 min., 34 reaction cycles of [95°C for 30 sec, 48°C for 30 sec, 72°C for 45 sec], and a final extension at 72°C for 5 min. The reaction protocol for LCO-1498/Nancy consisted of an initial denaturation at 94°C for 2 min., 40 reaction cycles of [94°C for 30 sec, 42°C for 30 sec, 72°C for 60 sec], and a final extension at 72°C for 10 min. Purified PCR products were sequenced on an ABI 3730xl sequencer.

Forward and reverse sequences for each specimen were aligned in Sequencher 5.0.1 (Gene Codes Corp., Ann Arbor MI USA) and edited to resolve disagreements and remove primer regions. Processed sequences were then queried against the GenBank database using BLAST (Altschul *et al*. 1990) to check for contamination and erroneous sequences. Sequences significantly matching microbial, fungal, or other non-crustacean taxa were removed from further analysis. An additional 29 tanaidacean sequences were obtained from GenBank. Sequences were aligned using the CLUSTAL algorithm (Larkin *et al*. 2007) in BioEdit, and any sequences not translating correctly to amino acids were excluded. Sequences of males and their closest identified female matches were deposited in GenBank under Accessions KJ934599–KJ934621.

The final alignment of vetted, fully identified female tanaidacean sequences was used as a database against which the male sequences were queried so that species (or higher taxonomic) identity could be determined. The pairwise number of differences and percent similarity were calculated in MEGA 5 (Tamura *et al*. 2011) with gaps excluded on a pairwise basis. Ambiguous positions in a sequence were not counted as pairwise differences if one of the potential resolutions was compatible with the other sequence (*e.g.*, R *versus* A or Y *versus* C). For the closest match to each male sequence, the number of synonymous and non-synonymous substitutions was recorded.

Taxonomy. — Specimens were examined with Nikon SMZ 1500 dissecting and Nikon Eclipse compound microscopes. Dissected appendages were stained with chlorazol black and mounted on slides. The morphological terminology generally follows that proposed by Błażewicz-Paszkowycz (2005) and Błażewicz-Paszkowycz and Bamber (2011). The material was given voucher numbers according to the database of the German Centre for Marine Biodiversity Research (Access 2010, DZMB HH; see Table 2) and stored at 4°C. All specimens will be deposited at the Zoological Institute and Museum of the University of Hamburg (Germany) as soon as the taxonomic work is completed.

Results

Genetics. — A total of 141 tanaidacean sequences were obtained, comprising 134 females and seven males (Table 3). The final alignment contained 558 positions; details of the full sequence dataset and phylogenetic trees constructed from it will be treated in a forthcoming manuscript. Two of the males had no close match to identified specimens, while the remaining five yielded close matches (Table 4). While it is unwise to draw absolute conclusions from sequence similarity analysis at a single locus, in a group such as Paratanaoidea in which so little is known about sexual dimorphism and it is difficult to identify useful morphological characters for males, even basic sequence comparison can provide taxonomic hypotheses that allow progress to be made.

Table 2

Details of the collection used in the present study.

Expedition and isolate_ID	DZMB HH no. (specimen voucher)	GenBank accession no.	ZMH no.	Sex	Station	Location	Depth [m]	Date
ITan 029	20253	KJ934610	K44197	female	1010	62°33.10'–62°33.22' N, 20°23.71'–20°22.87' W	1385–1389	2 Sep 2011
ITan 053	20275	KJ934609	K44189	male (4)	1072	63°00.46'–63°1.10' N, 28°4.09'–28°03.15' W	1569–1594	08 Sep 2011
ITan 188	20412	KJ934615	K44195	male (6A)	963	60°02.73'–60°2.73' N, 21°28.06'–21°29.88'W	2747–2749	28 Aug 2011
ITan 122	20346	KJ934612	K44192	female	1072	63°00.46'–63°01.10' N, 28°04.09'–28°03.15' W	1569–1594	9 Sep 2011
ITan 092	20316	KJ934611	K44191	male (5)	1072			
ITan 051	20275	KJ934606	–	male (2)	1072			
ITan003	20227	KJ934617	K44198	female	979	60°21.48'–60°20.72' N, 18°8.24'–18°8.60' W	2568–2572	30 Aug 2011
ITan004	20228	KJ934618	K44199	female	979			
ITan005	20229	KJ934619	K44200	female	979			
ITan008	20232	KJ934620	K44201	female	967	60°02.77'–60°02.78'N, 21°28.54'–21°30.07'W	2750–2747	29 Aug 2011
ITan187	20411	KJ934621	K44202	female	963	60°02.73'–60°2.73' N, 21°28.06'–21°29.88'W	2747–2750	28 Aug 2011
ITan112	20336	KJ934616	–	male (7)	1054	61°36.19'–61°36.97'N, 31°22.60'–31°22.18'W	2537–2538	07 Sep 2011
ITan062	20286	KJ934614	K44193	female	1072	63°00.46'–63°01.10' N, 28°04.09'–28°03.15' W	1569–1594	9 Sep 2011
ITan091	20315	KJ934613	–	male (6)	1072			
ITan069	20293	KJ934600	K44194	female	1072			
ITan099	20323	KJ934601	K44196	female	1072			
ITan050	20274	KJ934599	K44190	male (1)	1072			

Male 2 was only 75% similar to its nearest matches, but because they were two congeneric females of the family Akanthophoreidae, it is likely that male 2 also belongs to this family. Further sampling and sequencing will be required to completely determine its identity.

Male 6A was just 62.8% and 62.2% similar to male 4 and *A. ingolfi* Hansen, 1913, respectively, including 32 non-synonymous changes. The next-closest matches were to *Paranarthrura* aff. *lusitanus* Bird *et* Holdich, 1988, and *Paranarthrura* sp. A, indicating that male 6A might belong to the Agathotanaidae, but this designation must remain tenuous pending further sequencing.

Male 1. The COI sequence from this specimen was 100% identical to two of the six *Typhlotanais* sp. A females, and somewhat similar to the remaining four (75–77% similar). These four *Typhlotanais* sp. A sequences were all 100% identical to each other, and could potentially represent a separate species.

Male 4. This sequence was virtually identical to the *Agathotanais ingolfi* female sequence; not counting positions in one or the other sequence that were ambiguous due to sequencing difficulties, just one sequencing ambiguity in the se-

Table 3

New tanaid sequences generated in this study, according to major taxonomic groups. "At least" reflects incomplete species identification and possible undescribed species.

	Family	No. Genera	No. Species	No. Sequences
Tanaidomorpha	Agathotanaidae	3	≥4	7
	Akanthophoreidae	?	?	6
	Cryptocopidae	5	≥8	15
	Leptochelidae/Paratanaidae	≥4	≥5	11
	Neotanaidae	1	1	1
	Pseudotanaidae	2	2	2
	Tanaidae	2	2	2
	Tanaellidae	1	2	4
	Typhlotanaidae	4	≥13	50
	Tanaidomorpha total:	at least 22	at least 37	98
Apseudomorpha	Apseudidae	2	7	9
	Metapseudidae	3	3	3
	Parapseudidae	1	1	1
	Kalliapseudidae	3	3	10
	Sphyrapodidae	2	2	20
	Apseudomorpha total:	11	16	43
Grand total:		at least 33	at least 53	141

Table 4

Results of male sequence comparison to female (*i.e.* identified) sequences. %sim– percent similarity; NSYN – non-synonymous difference; SYN – synonymous difference; CA – compatible ambiguity; IA – incompatible ambiguity.

Male ID	Best match	%sim (# matches)	Nature of differences	ID conclusion
male 1	*Typhlotanais* sp. A, *Typhlotanais* sp. C	100% (554/554)	–	*Typhlotanais* sp. A
male 2	akanthophoreid	75.0% (393/524)	34 NSYN, 97 SYN	Akanthophoreidae
	akanthophoreid	68.5% (359/524)	27 NSYN, 138 SYN	
male 4	*Agathotanais ingolfi*	99.8% (500/501)	14 CA, 1 IA	*Agathotanais ingolfi*
male 5	*Cryptocopoides* aff. *arcticus*	99.8% (491/492)	1 SYN, 1 CA	*Cryptocopoides* aff. *arcticus*
male 6	*Torquella* sp. A	99.8% (533/534)	1 SYN	*Torquella* sp. A
male 6A	male 4	62.8% (211/336)	32 NSYN, 92 SYN, 6 CA, 1 IA	Agathotanaidae
	Agathotanais ingolfi	62.2% (209/336)	32 NSYN, 93 SYN, 9 CA, 1 IA	
male 7	*Pulcherella pulcher*	96.2% (405/421)	14 NSYN, 2 SYN	*Pulcherella* sp.

quence of male 4 was incompatible with the *A. ingolfi* female sequence. It therefore seems highly likely that this is the male of *A. ingolfi*.

Male 5. This sequence was virtually identical to the *Cryptocopoides* aff. *arcticus* female; the two sequences differed only by a single synonymous substitution (TTA/TTG: Leu) and one sequencing ambiguity in the male sequence that was incompatible with the female sequence. These minor differences make it highly likely that this is the male of *Cryptocopoides* aff. *arcticus*.

Male 6. This sequence was virtually identical to the *Torquella* sp. A female; just one synonymous difference (CCA/CCG: Pro) separated them.

Male 7. This sequence was similar to five sequences of *Pulcherella pulcher* (Hansen, 1913). Fourteen amino acids differed between the two, in addition to two synonymous differences. While 96.2% similarity is quite high, our lack of knowledge of inter- *versus* intraspecific COI variability in this family (or tanaidaceans in general) warns against a full species determination. Nevertheless, it seems likely that male 7 belongs to the genus *Pulcherella*.

Taxonomy. — The allocation of males and females with genetic tools has been followed by analysis of their morphology. As such, we present the results of morphological analysis of all seven males and those females that represent species new to science. Morphology of the female of *Agathotanais ingolfi* and *Pulcherella pulcher* are well known as redescribed by Lang (1971) and Błażewicz-Paszkowycz (2007), respectively, so we exclude them from taxonomic analysis. One female examined in this study superficially resembles *Cryptocopoides arcticus*. A few differences in morphology between our specimen and the specimen drawn by Hansen (1913) are obvious, but because collection of *C. arcticus* studied by Hansen might be a complex of cryptic species (see remarks under *C.* aff. *arcticus*; pp. 433–435) we have decided to draw our female (pp. 432 and 434) and postpone description of a new species until the Hansen's collection is morphologically revised.

Three other specimens of females also represented new species: one specimen belongs to the genus *Torquella* Błażewicz-Paszkowycz, 2007, and two others to *Typhlotanais* G.O. Sars, 1882. Although the differences in morphology between all currently known species classified to *Torquella* and *Typhlotanais* are evident, the scarcity of the material hampered describing the new species. Two additional females represent two distinct, apparently congeneric species of family Akanthophoreidae. Male 2 revealed only a 75% similarity with these females but because they have much lower similarity to females of Typhlotanaidae, Colletteidae, Tanaellidae, Cryptocopidae, and Pseudotanaidae (below 60% similarity), we anticipate that the male and both females might represent the same family.

Family Agathotanaidae Lang, 1971

Agathotanais Hansen, 1913

Agathotanais ingolfi Hansen, 1913

(Figs 1–2)

Material. — Female ITan 029; male ITan 053 (Table 2).

Male diagnosis. — Cephalothorax short, reaching half length of pereonite-3; pereon as long as pleon and pleotelson; pleotelson caudal process in shape of terminal spine, that is almost as long as last three pleonites. Antennule of seven arti-

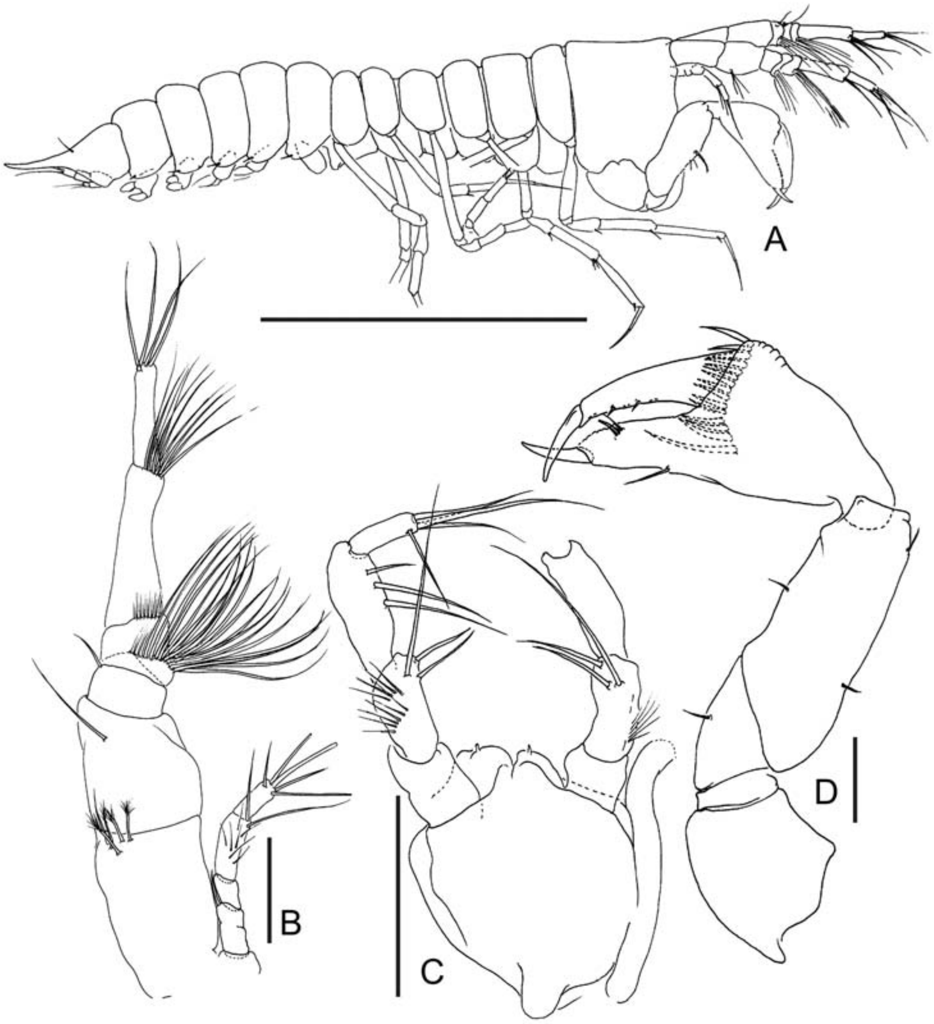

Fig. 1. *Agathotanais ingolfi*, male: lateral view (**A**), antennule and antenna (**B**), maxilliped and maxilla(?) (**C**), cheliped (**D**). Scale = 1mm for A and 0.1 mm for B–D.

cles; articles 1–2 of subequal length, but only a little wider than article-3; article-5 1.4 times as long as article-6. Antenna of five articles, not reaching distal margin of antennule article-2. Maxilliped palp articles all longer than wide, article-2 with long seta; endites poorly developed, short, not reaching distal margin of palp article-1. Cheliped basis very short, without posterior lobe; carpus 2.5 as long as wide; chela wider and longer than carpus, with fine single seta on ventral margin; inner surface with a row of 15 robust setae; pereopods 4–6 dactylus and unguis longer than propodus. Uropod biramous; endopod with one article 2.5 times as long as wide; exopod distinct but minute, 0.25 length of endopod.

Male description. — Body 2.0 mm long (Fig. 1A). Cephalothorax short, reaching half length of pereonite-3; pereonites shorter than pleonites, pereon as long as pleon and pleotelson; pleon as long as pereonites 2–6; pleotelson caudal process with distinct terminal spine, that is as long as last three pleonites.

Antennule (Fig. 1B) with seven articles; articles 1–2 subequal, relatively robust, but only a little wider than articles 3–4; article-1 with a group of two simple and three broom setae distally; article-2 with simple seta distally; article-3 short; article-4 similar length to article-3 but longer ventrally than dorsally; article-5 1.4 times as long as article-6; articles 4–6 ventral margins with dense row of aesthetascs; article-6 with four setae distally.

Antenna (Fig. 1B) short, not reaching distal margin of antennule article-2, with five articles; article-1 fused to body; article-2 twice as long as article-3, with simple seta; article-3 unarmed; article-4 twice as long as article-3, with two distal setae; article-5 a little shorter than article-4, with five simple distal and subdistal setae.

Maxilliped (Fig. 1C) basis fused, forming almost round plate; endites poorly developed, short, not reaching distal edge of palp article-1, each with minute distal spine; palp articles 1–4 longer than wide; palp article-1 unarmed, article-2 with one long seta and two short setae on inner margin and rows of long setules on outer margin; article-3 twice as long as wide, with three setae on inner margin; article-4 relatively slender, with four distal or subdistal setae.

Cheliped (Fig. 1 D) basis unarmed, almost as long as wide, without posterior lobe; ischium narrow; merus wedge-shaped, with minute simple seta on ventral margin; carpus 2.5 as long as wide, with one seta on ventral margin and two, distal and subproximal setae on dorsal margin; propodus larger than carpus with a row of 15 robust setae on inner surface near insertion of dactylus; fixed finger with robust distal spine, with one simple seta on ventral margin and three minute on cutting edge; dactylus curved and tipped with robust spine, with two small spines on lower margin.

Pereopod-1 (Fig. 2A) coxa with minute seta; basis as long as carpus and propodus combined, naked; ischium short, with one seta; merus half as long as carpus, with two small setae on ventral margin; carpus with one small spine and two small setae distally; propodus 1.2 as long as carpus, with short, distoventral spine; dactylus as long as unguis, together 0.7 times as long as propodus.

Pereopod-2 (Fig. 2B) basis as long as carpus and propodus combined, naked; ischium with one seta; merus half as long as carpus, with two small setae distoventrally; carpus as long as propodus, with three short setae distally; propodus with short, distoventral spine; dactylus as long as unguis, together 0.8 times as long as propodus.

Pereopod-3 (Fig. 2C) similar to pereopod-2, but merus 0.7 as long as propodus.

Pereopod-4 (Fig. 2D) basis a little longer than merus, carpus and propodus combined with one dorsal broom seta; ischium with two setae; merus 0.8 as long as carpus, with two small distoventral setae; carpus as long as propodus, with two

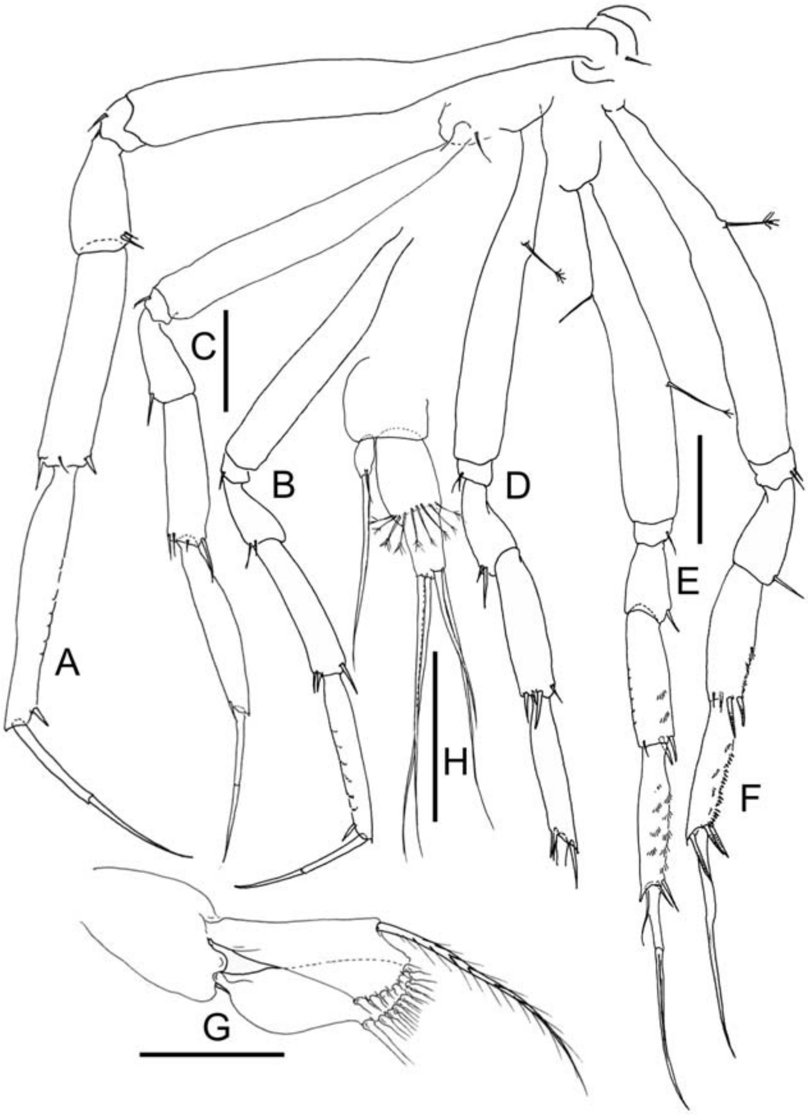

Fig. 2. *Agathotanais ingolfi*, male: pereopods 1–6 (**A**–**F**, respectively), pleopod (**G**), uropod (**H**). Scale = 0.1 mm.

short, robust, distoventral spines and one fine distal seta; propodus with three short, distal spines; dactylus broken.

Pereopod-5 (Fig. 2E) similar to pereopod-4, but only one seta observable on merus and ischium; unguis 2.5 as long as dactylus, together as long as propodus and half of carpus combined.

Pereopod-6 (Fig. 2F) similar to pereopod-5, but basis with two broom setae and ischium with two setae.

Pleopod (Fig. 2G) endopod with eight setae on distal margin; exopod with six setae on distal margin and one subdistal seta that is only 0.25 as long as all other setae.

Uropod (Fig. 2H) endopod with two completely fused articles; the "fused" line supported with at least eight broom setae; distal article much narrower than proximal, with four long setae distally; exopod small with long and short distal setae.

Remarks. — Male of *Agathotanais ingolfi* is distinguished by shorter antennae that barely reach the distal margin of antennule second article. This character is well supported by morphology of the female of *Agathotanais* in which that appendage is reduced to the two-articled bud. Other noticeable characters of the male, which might be characteristic to the genus, are slim chelipeds attached to the body *via* sclerite, and reduced maxilliped endites. Beyond that, the male has a distinct spine on the pleotelson. A similar spine has been observed in *Pulcherella pulcher* and male 6A, classified to Typhlotanaidae and Agathotanaidae, respectively (this paper) and also in *Paranarthrurella voeringi* Jóźwiak, Stępień *et* Błażewicz-Paszkowycz, 2009, although it is not as distinct as in the two former. An elongated pleotelson was observed also in *Typhlotanais adipatus* Tzareva, 1982 (Sieg 1986) and *Typhlotanais grahami* Błażewicz-Paszkowycz, 2004, although not as sharply pointed as in *A. ingolfi*, *P. pulcher* or, mentioned above, male 6A. Consistent with this idea, the next-nearest matches to *A. ingolfi* and male 6A are indeed *Paragathotanais* and *Paranarthrura*.

Bird and Holdich (1988) studied an extensive series of males of *Agathotanais ingolfi* collected in the Rockall Trough and Bay of Biscay and distinguished two stages, *e.g.* subadult (preparatory) with rudimentary pleopods and adult (mature) with pleopods supported with simple setae. Failing to find a swimming male and observing well developed genital cones in the males with setiferous pleopods, they have concluded that the species might have shortened life-cycle and lack swimming males.

The only specimen of the "swimming" male of *Agathotanais ingolfi* examined here was smaller (2 mm long) than the female (2.9–3.6 mm, see Bird and Holdich, 1988). The difference in size between adult female and swimming male has been already observed (Sieg 1986; Błażewicz-Paszkowycz 2004; 2005; Jóźwiak *et al*. 2009).

Agathotanaidae, male 6A

(Figs 3–4)

Material. — male ITan 188 (Table 2).

Male diagnosis. — Cephalothorax long, a little longer than three first pereonites; almost as long as pleon; pleotelson caudal process in shape of terminal spine, that is shorter than two last pleonites. Antennule of seven articles; article-1 is 1.5 as long as article-2, only a little wider than article-3; articles 3–5 short; article-6 twice as long as article-5; article-7 twice as long as article-6. Antenna of seven articles.

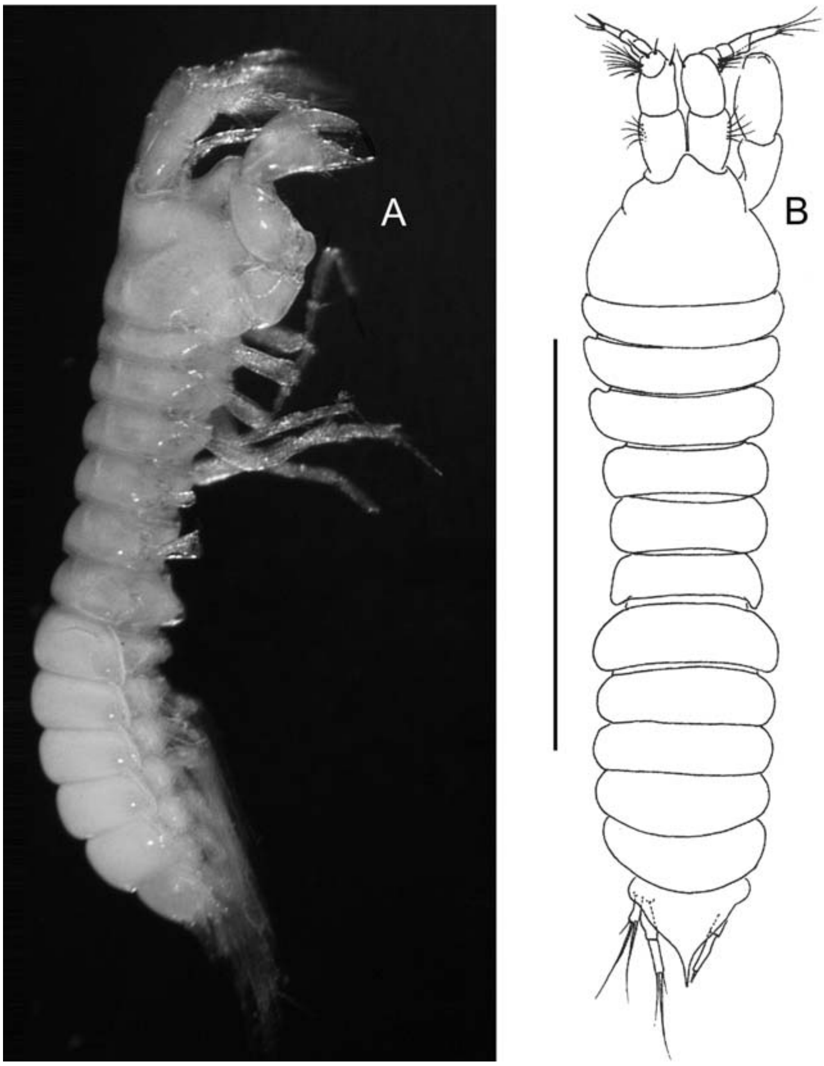

Fig. 3. Agathotanaidae 6A, male: dorsal (**A**), lateral (**B**). Scale = 1 mm.

Maxilliped palp articles all short, article-2 with long inner seta; endites well developed. Cheliped basis very well developed, with posterior lobe; carpus almost twice as long as wide; chela wider and longer than carpus, with two setae on ventral margin; inner surface with a row of 14 robust setae; in pereopods 4–6 dactylus and unguis longer than propodus. Uropod biramous; endopod with two articles; exopod with one article almost as long as endopod proximal article.

Male description. — Body 1.8 mm long (Fig. 3A). Cephalothorax as long as pereonites 1–3; pereon subequal to the length of pleon; pleotelson caudal process with distinct terminal spine (Fig. 4G).

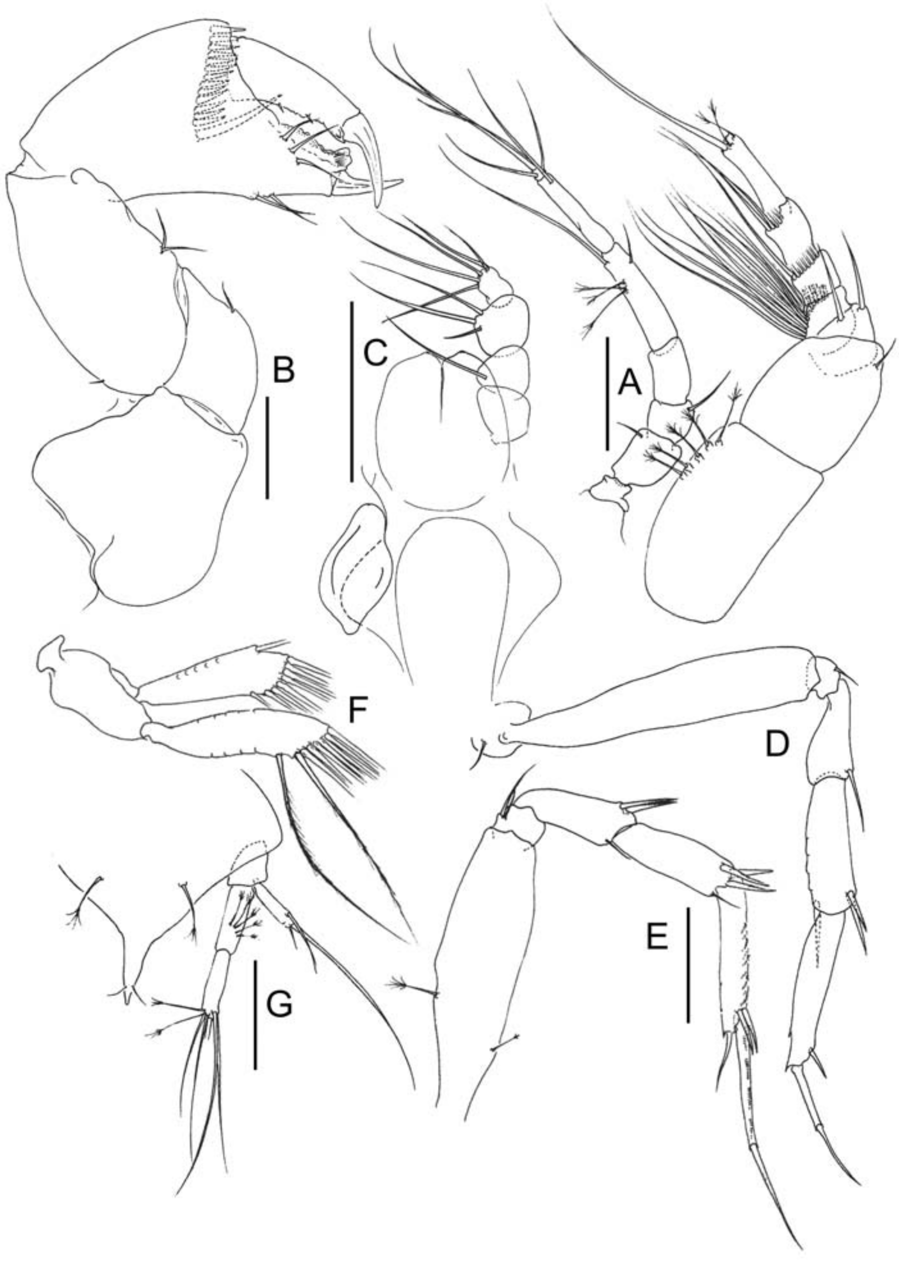

Fig. 4. Agathotanaidae 6A, male: antennule and antenna (**A**), cheliped (**B**), maxilliped and maxilla (**C**), pereopod-2 (**D**), pereopod-5 (**E**), pleopod (**F**), pleotelson and uropod (**G**). Scale = 0.1 mm.

Antennule (Fig. 4A) with seven articles; article-1 is 1.5 as long as article-2, but only a little wider than article-3; article-1 with five broom setae on outer margin; article-2 with minute inner seta distally; articles 3–5 of similar length; article-3 with two distal, simple setae; articles 4–5 with numerous aesthetascs; article-6 1.5 times as long as article-5, but 0.7 times as long as article-7, with some aesthetascs distally.

Antenna (Fig. 4A) article-1 small; article-2 a little longer than article-3, each with simple seta distally; article-4 as long as article-2, naked; article-5 twice as long as article-4, with three broom setae subdistally and one long simple seta distally; article-6 a little longer than article-5, with one distal seta; article-7 minute with five simple setae.

Maxilliped (Fig. 4C) basis fused, forming almost round plate; endites relatively well-developed, reaching distal edge of palp article-2, each with minute distal tubercle; palp articles 1–4 wide and short; palp article-1 unarmed, article-2 with one long seta on inner margin; article-3 with three setae on inner margin; article-4 relatively slender, with five distal setae.

Cheliped (Fig. 4B) basis unarmed, almost as long as wide, distoventral corner rounded; merus wedge-shaped, with minute simple seta on ventral margin; carpus 1.8 as long as wide with one minute proximodorsal seta and two ventral setae; propodus larger than carpus with a row of 14 robust setae on inner surface near insertion of dactylus; fixed finger with robust distal spine, with two simple setae on ventral margin and three setae on cutting edge; cutting edge well calcified with prominent process in its distal part; dactylus curved, tipped with robust spine, with two small spines on lower margin.

Pereopod-2 (Fig. 4D) coxa with minute seta; basis as long as carpus and propodus combined; ischium short, with one seta; merus with simple, distal seta; carpus 1.5 as long as merus with three long spines distally; propodus 1.2 as long as carpus, with short, distoventral spine; dactylus as long as unguis, together 0.7 times as long as propodus.

Pereopod-4 (Fig. 4E) basis a little longer than merus and carpus, with two broom setae; ischium with two setae; merus as long as carpus, with two distoventral spines and one seta; carpus as long as propodus, with three distoventral spines and one fine distal seta; propodus with two distoventral spines and one distodorsal seta; dactylus as long as unguis, together almost twice as long as propodus.

Pleopod (Fig. 4F) endopod with eight setae on distal margin; exopod also with eight setae on distal margin and one subdistal seta.

Uropod (Fig. 4G) endopod with two subequal articles; proximal article with five broom setae; distal article with five simple setae and two broom setae. Exopod with one article that is almost as long as endopod proximal article, with two distal and one subdistal seta.

Remarks. — Chelipeds attached to body *via* basal lobe question the placement of male 6A in the family Agathotanaidae; however morphological features (*e.g.*, well developed antenna, relatively robust cheliped and long maxilliped endites), and genetic evidence (62% similarity to *Agathotanais ingolfi*) make Agathotanaidae a likely family. With the current data it can be only concluded that this male does not represent *Agathotanais* itself.

Family Cryptocopidae Sieg, 1977
Subfamily Cryptocopinae Sieg, 1977
Cryptocopoides Sieg, 1976
Cryptocopoides aff. *arcticus* (Hansen, 1913)
(Figs 5–8)

Material. — Female ITan 122; male ITan 092 (Table 2).

Female diagnosis. — Pleonite-4 with one lateral seta; pleonite-5 with long and short lateral setae. Antennule article-4 1.2 times as long as article-3. Mandible *pars incisiva* with three spines on lower margin. Pereopods 2–3 merus with two fine, short and longer, ventrodistal setae. Pereopod-6 propodus twice as long as merus. Pereopods 4–5 ischium with two setae. Pleopod with four and seven setae on exopod and endopod, respectively.

Description of female. — Body (Fig. 5A) compact, 2.1 mm long. Cephalothorax about as long as pereonites 1–3 together, naked, eyes absent. Pereonite-1 the shortest, one-fourth as long as cephalothorax; pereonite-2, a little longer than pereonite-3; pereonites 4–5 longest, twice as long as cephalothorax; pereonite-6 just longer than pereonite-1. Pleon of five free subequal pleonites bearing pleopods; pleonite-4 with one lateral seta; pleonite-5 with short and long lateral setae. Pleotelson as long as last four pleonites.

Antennule (Fig. 6A) article-1 stout, 1.6 times as long as wide, 0.8 times as long as distal three articles together, tapering, with distal tuft of four broom setae and one outer distal simple seta reaching half of article-4; article-2 a little longer than wide, 0.6 times as long as article-1, with one broom, one long and one short inner distal setae and one simple outer distal seta; article-3 just longer than wide, 0.7 times as long as article-2, with single inner and outer simple distal setae and two broom setae distally; article-4 slender, 1.2 times as long as article-3, with five distal setae and one aesthetasc.

Antenna (Fig. 6C) of six articles, proximal article destroyed during dissection; articles 2–3 with simple setae; article-3 one-third as long as article-4; article-4 with two simple and four broom setae distally; article-5 0.4 times as long as article-4 with one distal seta; article-6 minute, with four distal setae.

Labrum (Fig. 5B) hood-shaped, distally densely setose. Left mandible (Fig. 5C) with at least eight rounded teeth on *pars incisiva*; wide, crenulate *lacinia mobilis* with extended outer margin; *pars molaris* stout with blunt, distal “teeth” and three spines on lower margin. Right mandible (Fig. 5D) without *lacinia mobilis*; *pars incisiva* with three wide teeth; *pars molaris* (Fig. 5D’) as in mandible left. Maxillule (Fig. 5E) endite with nine slender distal spines and two fine setae on distal margin, palp not observed. Maxilla (Fig. 5F) semi-rounded with distinct protrusion proximally. Labium (Fig. 5G) distally simple; reduced outer lobes finely setose.

Maxilliped (Fig. 5H) basis with long seta reaching distal margin of endites; endites unfused (Fig. 5H’), with two small oval tubercles on distal margin; palp ar-

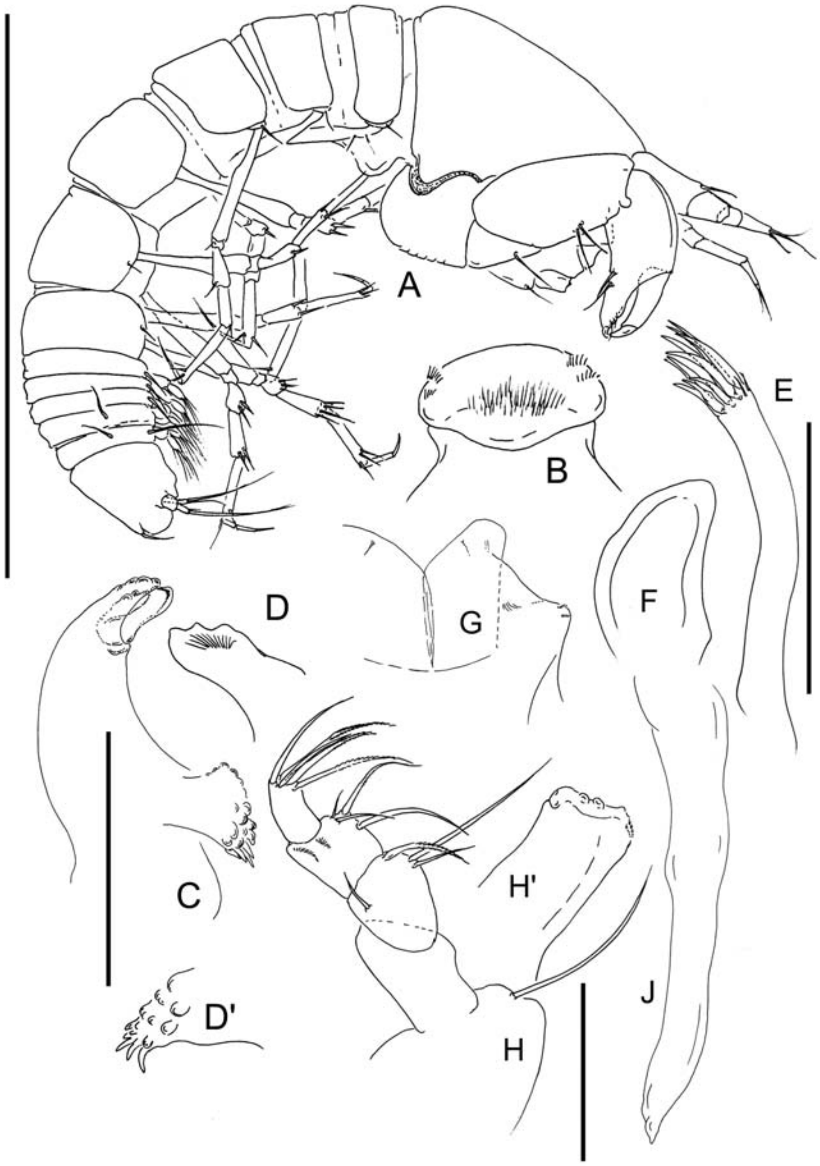

Fig. 5. *Cryptocopoides* aff. *arcticus*, female: lateral view (**A**), labrum (**B**), left mandible (**C**), mandible right *pars incisiva* (**D**), mandible *pars molaris* (**D'**), maxillule (**E**), maxilla (**F**), labium (**G**), maxilliped palp (**H**), maxilliped endite (**H'**), epignath (**J**). Scale = 1 mm for A and 0.1 mm for B–H.

ticle-1 naked; article-2 with one fine outer distal seta, inner margin with one long and two short simple setae; article-3 distally with two longer and two fine inner setae, with some microtrichia on outer margin; article-4 with five setae; epignath (Fig. 5J) pointed distally.

Cheliped (Fig. 6D) sclerite small, partly under carapace; basis distally rounded, with scale-like ornamentation on ventral margin; merus subtriangular with single, long ventral seta; carpus with rounded dorsoproximal extension, 1.7 times as long as wide, with two relatively long mid-ventral setae, one fine mid-dorsal seta (distal seta not seen); propodus slender, a little longer than carpus, palm 1.2 times as long as wide, with a row of three setae on inner surface near dactylus insertion; fixed finger 0.6 times as long as palm, with two ventral setae, three fine setae on cutting edge, which bears rounded crenulations in distal half; dactylus with fine proximal seta.

Pereopod-1 (Fig. 6E) coxa with seta; basis slender, ten times as long as wide, with dorso-proximal penicillate and simple setae; ischium with one ventral seta; merus one-third as long as basis, with two fine (longer and shorter) ventrodistal setae; carpus 1.6 times as long as merus with five fine distal setae; propodus subequal to carpus, with one ventrodistal and dorsodistal seta; dactylus and unguis 0.9 times as long as propodus, with subproximal seta.

Pereopod-2 (Fig. 6F) similar to pereopod-1, but propodus with long and short distodorsal setae.

Pereopod-3 similar to pereopod-2.

Pereopod-4 similar to pereopod-5. Pereopod-5 (Fig. 6G) basis 6.5 as long as wide with two broom setae on both ventral and dorsal margin; ischium with two simple, ventral setae; merus 0.3 times as long as basis, with two distinct ventrodistal spines; carpus 1.5 times as long as merus, with two ventrodistal spines, and two dorsodistal spines and one dorsodistal seta; propodus 1.3 times as long as carpus, with two ventrodistal setae and one dorsodistal seta; dactylus and shorter unguis not fused, together 0.8 times as long as propodus.

Pereopod-6 (Fig. 6H) as pereopod-5, but propodus with two dorsodistal setae.

Pleopods (Fig. 6I) all alike, with naked basis; endopod shorter than exopod; endopod with one distolateral seta and three terminal setae, exopod with seven distal setae.

Uropod (Fig. 6J) biramous; stout basis naked; exopod of two articles, just longer than proximal endopod article, proximal article with single, long distal seta, distal article with one longer and one shorter distal seta; endopod longer than exopod, of two articles, proximal article with two broom setae distally, distal article with two simple and two broom setae distally.

Remarks. — According to the records by Hansen (1913), *Cryptocopoides arcticus* is a species widely distributed in Icelandic waters *e.g.* Denmark Strait, Iceland Plateau, and Irminger, Norwegian, and Iceland Basins. It was also recorded near Jan Mayen, the western part of Greenland (Davis Strait), the coasts of Norway, Spitsbergen, the Kara Sea (type locality), and Novaya Zemlya in a wide bathymetric range from 18 to 2583 m (Stebbing 1900; G.O. Sars 1909; Hansen 1913). Beyond that, Hansen (1913) has emphasized a presence of *C. arcticus* in both “warm” and “cold” areas of *Ingolf* Station, *e.g.* in waters of temperatures from 0.5 to 6.1°C. Those observations were called by him “very interesting” and, together with records

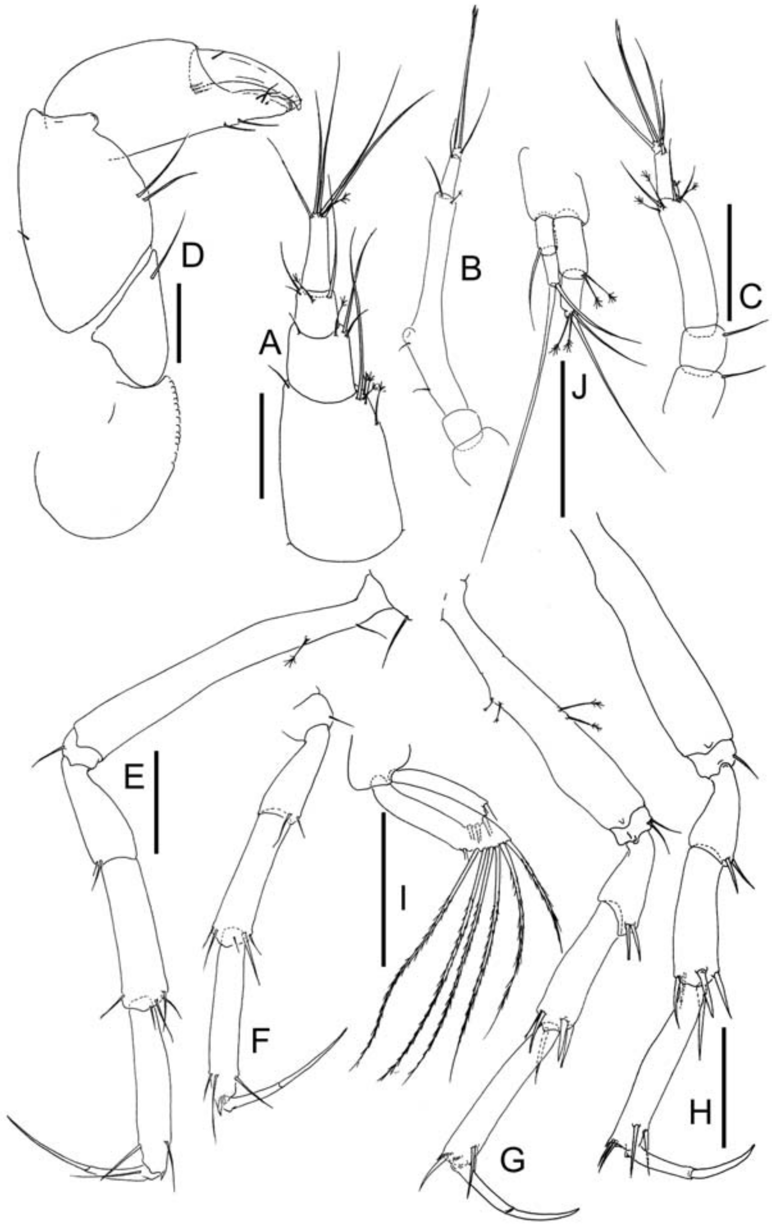

Fig. 6. *Cryptocopoides* aff. *arcticus*, female: antennule (**A**), antennae right and left of the same specimen (**B**–**C**), cheliped (**D**), pereopod-1 (**E**), pereopod-2 distal articles (**F**), pereopod-5 (**G**), pereopod-6 (**H**), pleopod (**I**), uropod (**J**). Scale = 0.1 mm.

on a wide geographical and a wide bathymetrical distribution, suggest that *C. arcticus* might represent a group of cryptic species. Figures made by Hansen (1913) do not show enough morphological details to say without doubt if the specimen found by us is conspecific with *C. arcticus s. str.* The presence of several haplotypes of *C. arcticus* in just the IceAGE collection raises the possibility of cryptic species and that even *C. arcticus* studied by Hansen might be a species complex. For these reasons we refer to our specimens as *Cryptocopoides* aff. *arcticus*.

Undoubtedly, the morphology of *C. arcticus* of all historical collections (*e.g.*, Stebbing 1900; G.O. Sars 1909; Hansen 1913) and Sieg (1977) should be carefully re-examined, as important morphological characters (*e.g.* number and length of the setation on the pleotelson, pleopods and pereopods 2–3) might have been overlooked. Another taxonomic problem with this species has been caused by a revision by (Sieg 1977), who synonimized *C. arcticus* with *C. antarcticus* Vanhöffen, 1914 (Błażewicz-Paszkowycz and Bamber 2011), although his figures were based on Hansen's specimens from the North Atlantic instead of the Southern Ocean (G.J. Bird personal communication).

The specimens of *C.* aff. *arcticus* found by us in the Irminger Basin can be distinguished from Hansen's specimen by the lateral setation of pleonites. The specimen studied by us has a short seta on the fourth pleonite, and long and short setae on the sixth pleonite, while Hansen's (1913) specimen has s short seta on pleonites 3–5.

Another species present in the North Atlantic is *C. nobilis* Błażewicz-Paszkowycz *et* Bamber, 2011, but it can be distinguished by the presence of a distoventral spine on the carpus of pereopods 2–3 and has a relatively long antennule article-4, that is at least four times as long as wide.

Diagnosis male. — Cephalothorax long, reaching half the length of pereonite-5; pereon as long as pleon, but apparently narrower than pleon; pleotelson, as long as two last pereonites, caudal process curved dorsally (rump-shape), without distinct terminal spine. Antennule of seven articles; article-1 longer than article-2; article-2 clearly wider than article-3; article-6 1.8 times as long as article-7. Antenna of seven articles, reaching above distal margin of antennule article-2. Maxillule and maxilla present. Maxilliped palp articles 2 and 4 longer than wide; article 3 with one long and two minute setae distally. Cheliped carpus 1.5 as long as wide; chela only a little longer than carpus; propodus with two setae on ventral margin; inner surface with a row of eleven robust setae near dactylus insertion; pereopods 4–6 dactylus and unguis together shorter than propodus. Uropod biramous; endopod of three articles; exopod of two articles reaching almost half the length of endopod.

Male description. — Body 1.8 mm long (Fig. 7A). Cephalothorax long, reaching half the length of pereonite-5; pereon as long as pleon, although apparently more weakly developed; pleotelson as long as two last pleonites, caudal process curved dorsally (rump-shaped) without distinct terminal spine, tipped with two setae (Fig. 8M).

Antennule (Fig. 8A) with seven fully developed articles and one terminal, rudimental article; articles 1–2 robust, and apparently wider than article-3, both naked; article-1 1.5 as long as article-2; article-3 short, with one seta dorsally; arti-

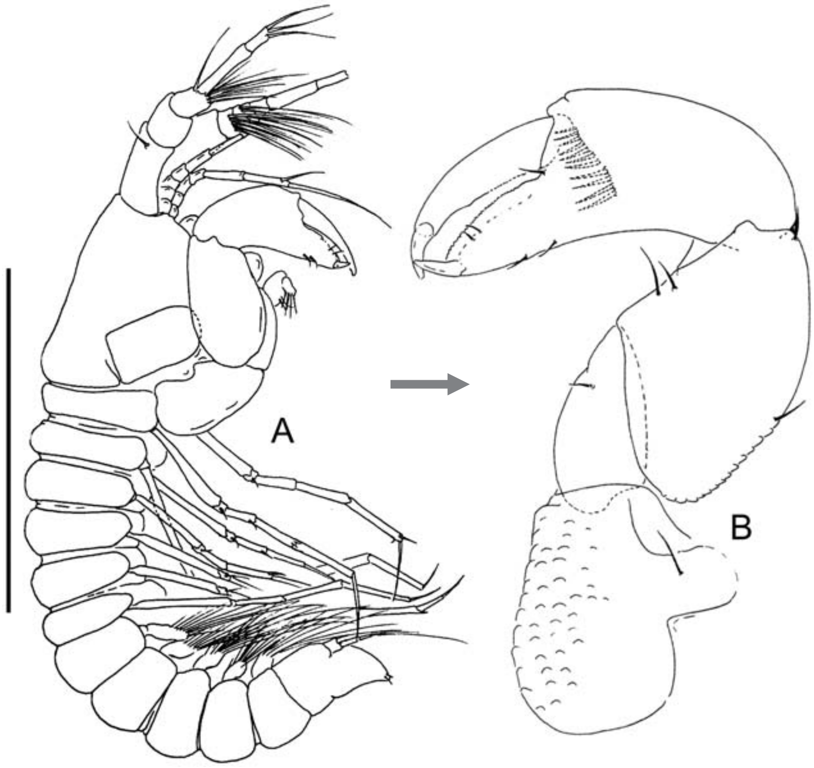

Fig. 7. *Cryptocopoides* aff. *arcticus*, male: lateral view (**A**), cheliped (**B**). Scale = 1 mm.

cle-4 similar to article-5, but longer dorsally than ventrally; article-6 1.8 times as long as article-7; articles 4–6 ventral margins with dense row of aesthetascs; article-7 with one aesthetasc and three distal and subdistal setae.

Antenna (Fig. 8B) with seven articles; article-1 fused to body; article-2 twice as long as article-3 with simple seta; article-3 with one seta; article-4 little longer than article-3, naked; article-5 a little longer than article-6, with one long and two short ventrodistal setae; article-6 with two distal setae; article-7 minute, with four distal setae.

Maxillula (Fig. 8C) palp tapering distally, without distal setation. Maxilla (Fig. 8D) almost oval, unarmed.

Maxilliped (Fig. 8E–F) basis fused, forming almost elongated plate; endites narrow, each with two fine setae on distal margin; palp article-1 longer than wide, unarmed, article-2 with one long seta and two fine short setae on inner margin; article-3 as long as wide, with two long and two fine setae on inner margin; article-4 with four long and one short distal setae.

Epignath (Fig. 8G) with pointed distal tip.

Cheliped (Fig. 7B) basis unarmed, almost as long as wide, posterior lobe large, with scale-like ornamentation ventrally; merus wedge-shaped, with minute simple

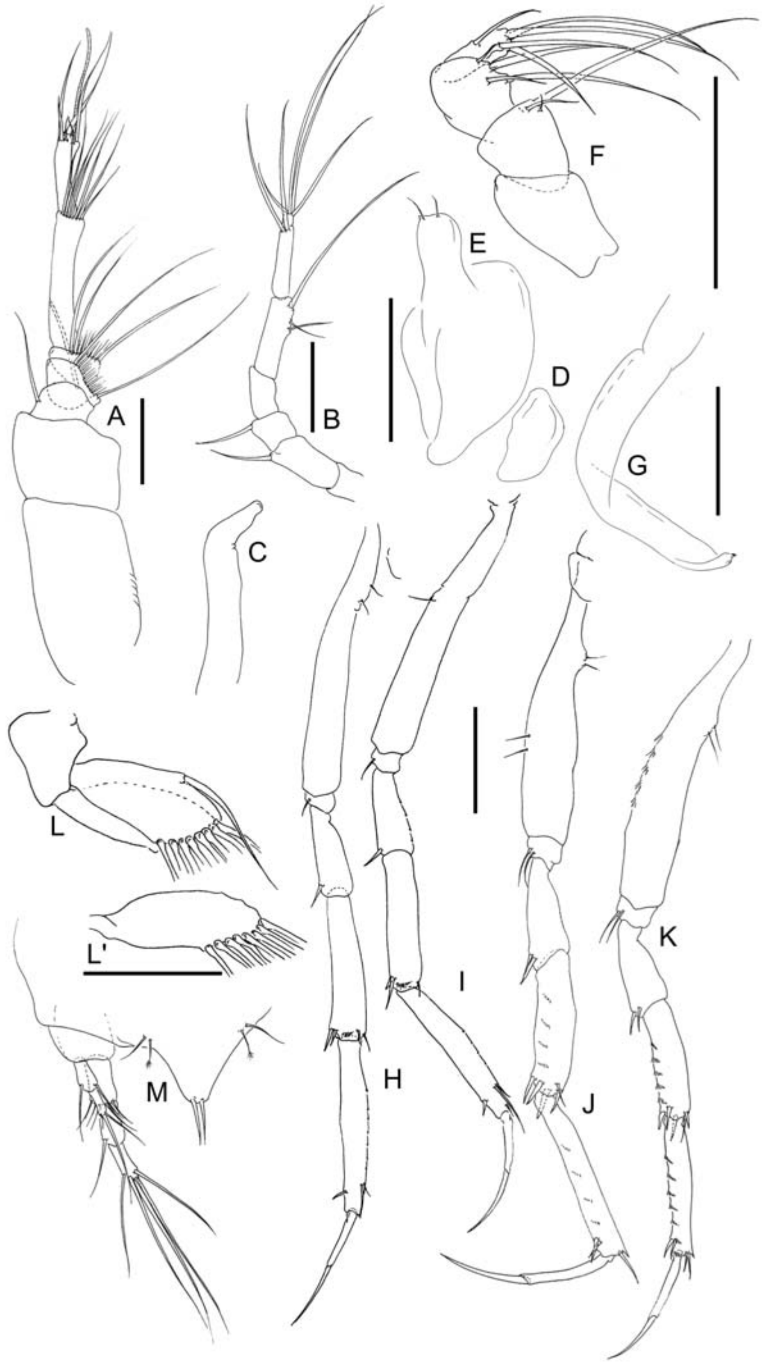

Fig. 8. *Cryptocopoides* aff. *arcticus*, male: antennule (**A**), antenna (**B**), maxillule palp (**C**), maxilla (**D**), maxilliped basis and palp (**E**–**F**, respectively), epignath (**G**), pereopods 1, 2, 5 and 6 (**H**–**K**, respectively), pleopod (**L**), pleopod exopod (**L'**), uropod (**M**). Scale = 0.1 mm.

setae on ventral margin; carpus 1.7 times as long as wide, with two setae on ventral margin and two, distal and subproximal, on dorsal margin; propodus larger than carpus and 1.5 times as long as wide, with a row of eleven robust setae on inner surface near insertion of dactylus; fixed finger with robust distal spine, with two fine setae on ventral margin and two minute on inner margin; dactylus slightly curved, tipped with robust spine.

Pereopod-1 (Fig. 8H) basis 1.2 as long as merus and carpus combined, with two minute setae proximally; ischium short, with one seta; merus 0.6 times as long as carpus, with one small distoventral spine; carpus as long as propodus, with two small, distoventral spines and two fine distodorsal setae; propodus with short, distoventral spine and two distodorsal fine setae (longer and short); dactylus as long as unguis, together 1.4 times as long as propodus.

Pereopod-2 (Fig. 8I) similar to pereopod-1. Pereopod-3 similar to pereopod-2.

Pereopod-4 similar to pereopod-5.

Pereopod-5 (Fig. 8J) basis slightly longer than merus and carpus combined, with two fine setae on dorsal and two on ventral margin; ischium with two setae; merus 0.8 as long as carpus, with two small distoventral spines; carpus 0.8 times as long as propodus, with four small spines distally and one fine distodorsal seta; propodus with two small distoventral spines and one distal seta; dactylus subequal to unguis, together slightly shorter than propodus.

Pereopod-6 (Fig. 8K) similar to pereopod-5, but propodus with two fine setae distodorsally.

Pleopod (Fig. 8L–L') endopod with eight setae on ventral margin and one seta on dorsal margin; exopod with eight setae on ventral margin.

Uropod (Fig. 8M) endopod with three subequal articles; article-1 with a few broom setae distally; article-2 with one distal seta; article-3 with five long distal setae; exopod with two subequal articles; proximal article with two simple distal setae; distal article with two distal setae.

Remarks. — The male of *Cryptocopoides* aff. *arcticus* can be distinguished from other known males by a complex of the characters: antennules with short articles 3–5 and long articles 6–7; antennae with long seta on articles 2–3; maxilliped endites narrow and supported with two setae, palp articles with long seta; ischium of pereopods 4–6 with two setae; pereopod-6 propodus with two distodorsal setae; both uropod rami biarticulated, proximal article of endopod twice as long as distal one. From the known swimming males (Table 1), the male of *C.* aff. *arcticus* most resembles the male of *Andrognathia plumosa* Sieg, 1983 known from a single record in the Ross Sea, Southern Ocean (Sieg 1983); no female has been satisfactory matched with this species. However, during the studies of tanaidaceans collected along Victoria Land (Błażewicz-Paszkowycz and Siciński 2014) one species of *Cryptocopoides* was recorded. Without molecular support it is not possible to confirm that the male of *Andrognathia plumosa* represents the same genus, but, because that of *C.* aff.

arcticus described by us and that of *A. plumosa* described by Sieg (1983) share many morphological characters, it is quite possible that these two taxa are congeneric.

Family Akanthophoreidae Sieg, 1986
Male 2
(Fig. 9)

Material. — Male ITan 051.

Male diagnosis. — Cephalothorax as long as first four pereonites; pereon as long as first four pleonites, but apparently narrower; pleon well developed, as long as cephalothorax and pereon together, caudally pointed, but without terminal spine. Antennule distal article longer than preceding article. Cheliped carpus 1.8 as long as wide; chela only a little longer than cheeped carpus. Pereopods 4–6 dactylus and unguis together shorter than propodus. Uropod biramous; endopod of three articles; exopod not longer than one-third of endopod.

Remarks. — The specimen was destroyed during the dissection for DNA extraction, so its morphology could not be studied in detail. Nevertheless the species can be distinguished from the other males collected during the IceAGE Project by elongated distal articles of antennule and the cheliped carpus that is twice as long as wide. Beyond that, this male, has a long, biarticulated endopod of the uropod and a short biarticulated exopod.

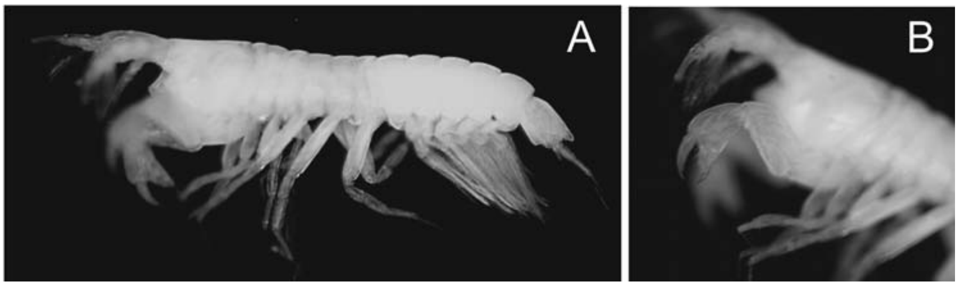

Fig. 9. Male 2: lateral view (**A**), body front magnified (**B**). No scale available.

Typhlotanaidae Sieg, 1986
Pulcherella Błażewicz-Paszkowycz, 2007
Pulcherella pulcher (Hansen, 1913)
(Fig. 10)

Material. — Females: ITan 003–005; ITan 008; ITan 187; male: ITan 112 (Table 2).

Male diagnosis. — Cephalothorax as long as first three pereonites; pereon as long as first four pleonites, but apparently narrower; pleon well developed, as long as cephalothorax and pereonites together, caudal process with robust terminal spine. Antennule distal article as long as preceding article. Cheliped carpus three

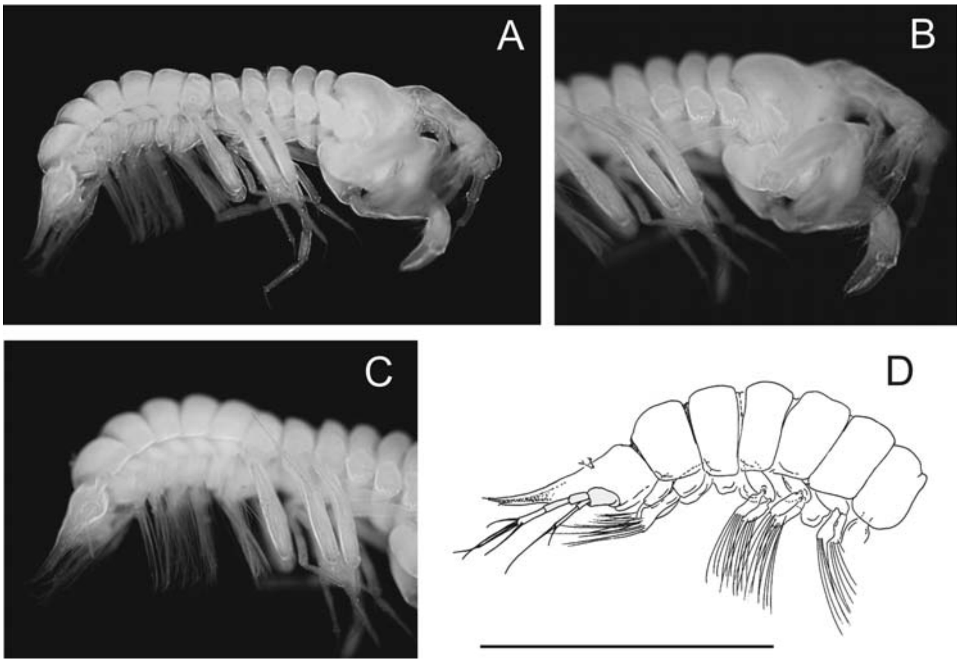

Fig. 10. *Pulcherella pulcher*, male: lateral view (**A**), body front magnified (**B**), pleon (**C**–**D**). No scale available.

times as long as wide; chela only a little longer than cheliped carpus. Pereopods 4–6 dactylus and unguis together longer than propodus. Uropod biramous; endopod of three articles; exopod as long as two-third of endopod.

Remarks. — This male was destroyed during the dissection for DNA extraction, so no detailed morphological analysis is possible at the moment. The male, similar to the female, has a slender cheliped and long uropod, with an apparently slim and long exopod.

Torquella Błażewicz-Paszkowycz, 2007

Torquella sp. A

(Figs 11–13)

Material. — Female: ITan062; male: ITan091 (Table 2).

Female diagnosis. — Pereonite-2 twice as long as pereonite-1. Pereonite-3 longer than wide. Chela 2.4 times as long as wide. Antennule article-3 about twice as long as article-2. Pereopod-1 merus and carpus 0.6 as long as basis, merus with distoventral spine; carpus with two setae and one short distodorsal spine; propodus with short and long distodorsal spines and one ventral seta. Pereopod-2 merus with robust spine and distoventral seta. Pereopods 4–5 distal seta of propodus reaches end of unguis. Uropod exopod as long as endopod proximal article.

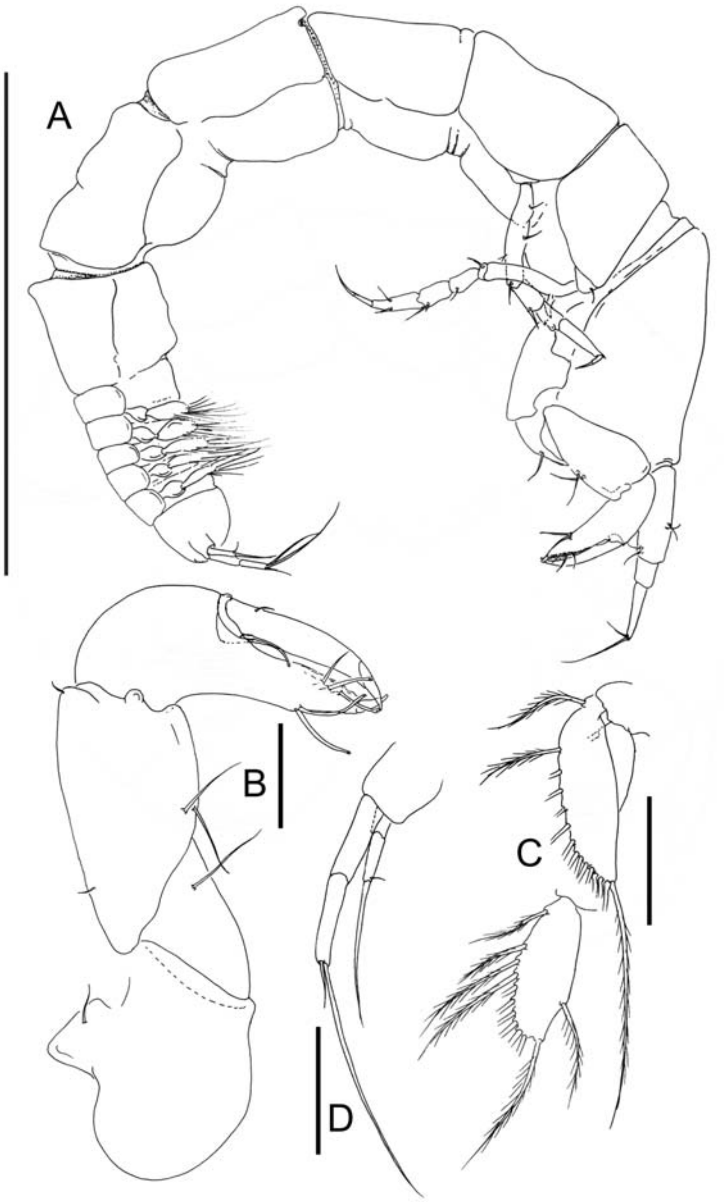

Fig. 11. *Torquella* sp. A, female: lateral view (**A**), cheliped (**B**), pleopod (**C**), uropod (**D**). Scale = 1 mm for A and 0.1 mm for B–D.

Remarks. — This is undoubtedly an undescribed species of *Torquella* (Figs 11–13), the tenth member of the genus that can be distinguished from the other species by the presence of a robust spine on the merus of pereopod-2. The only member of *Torquella* formally described from Icelandic waters is *T. grandis*

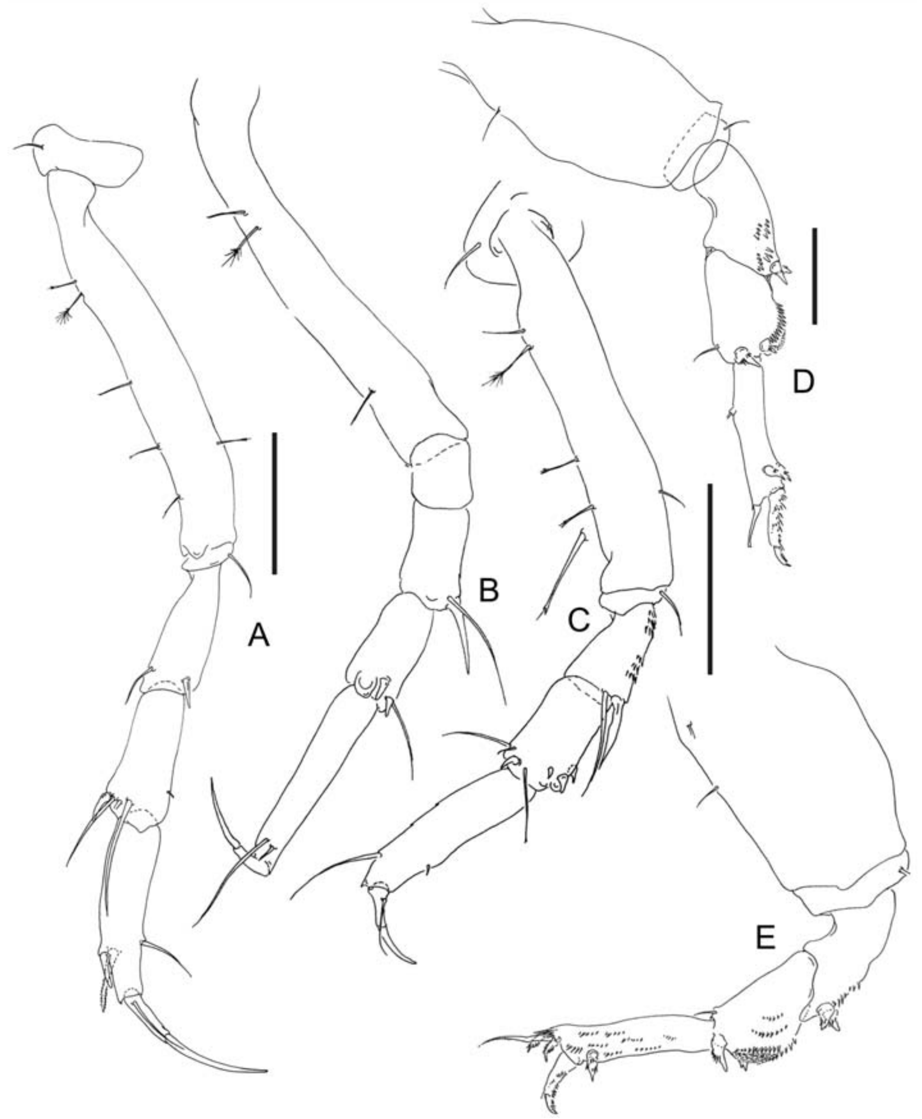

Fig. 12. *Torquella* sp. A, female: pereopods 1–4 and 6 (**A**–**E**, respectively). Scale bar = 0.1 mm.

(Hansen, 1913), although the diversity of this genus in the North Atlantic is much higher (Bird 2001). *T. grandis* can be distinguished from *Torquella* sp. A by slender uropods, whose exopod is apparently longer than proximal article of endopod. Additionally the new species has a distinct tubercle on distal margin of carpus of pereopods 2–3 (Fig. 12B–C). So far, a similar structure has been published for *T. iberica* Błażewicz-Paszkowycz, Bamber *et* Cunha, 2011 although three other undescribed species from the NE Atlantic share this character and the long meral spine on pereopod-2 (G.J. Bird unpublished data).

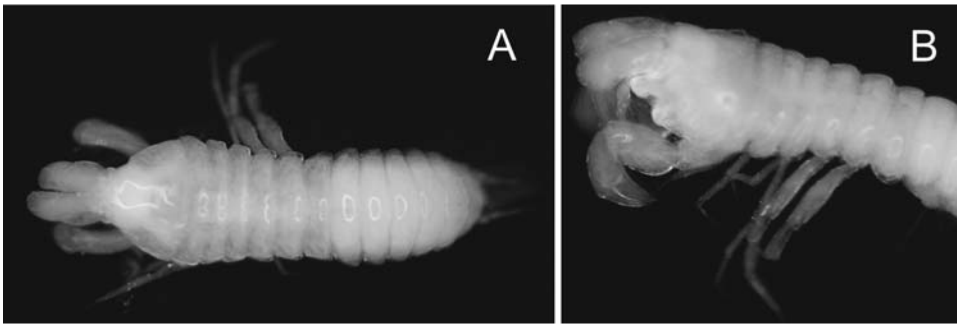

Fig. 13. *Torquella* sp. A, male: dorsal view (**A**), magnified (**B**). No scale available.

Male diagnosis. — Cephalothorax a little longer than pereonites 1–3 combined; pereonites 1–3 narrower than pereonites 4–6; pereon as long as pleon; pleon well developed, as long as cephalothorax and pereon together, caudally pointed, but without terminal apophysis. Antennule articles 1–2 robust; distal article longer than preceding article. Cheliped carpus 1.9 times as long as wide. Uropod endopod of three articles; exopod not longer than one third of endopod.

Typhlotanais G.O. Sars, 1882
Typhlotanais sp. A
(Figs 14–17)

Material. — Females: ITan069, ITan099; male ITan050 (Table 2).

Female diagnosis. — Pereonites 1–3 without corrugation. Pereopods 4–6 propodus distal setae not longer than unguis. Uropod short, a little longer than pleotelson, endopod four times as long as wide, 1.3 times as long as exopod.

Remarks. — *Typhlotanais* sp. A is apparently a new species, however because of insufficient material we refrain from presenting an official description of the species.

Female of *Typhlotanais* sp. A (Figs 14–15) shows some similarity with *Typhlotanais angusticheles* (Kudinova-Pasternak, 1989) having slim and attenuated antennules, with four setae along an article-3 that is relatively long in comparison to aricle-1 (see Kudinova-Pasternak 1989, p. 33). Beyond that *T. angusticheles* and *Typhlotanais* sp. A have slim chelipeds (Fig. 15) with long ventral setae on merus and carpus. Similarly long antennule and slim chelae with long setae are characteristic for *Typhlamia* Błażewicz-Paszkowycz, 2007, but that genus has long uropods with an uniarticulated endopod. *T. angusticheles* and *Typhlotanais* sp. A. have short uropods with biarticulared exopod.

Because of poor description of *T. angusticheles* and the lack of the access to that material, detailed comparison with *Typhlotanais* sp. A is not possible, but it cannot be excluded that both are congeneric and represent a new genus.

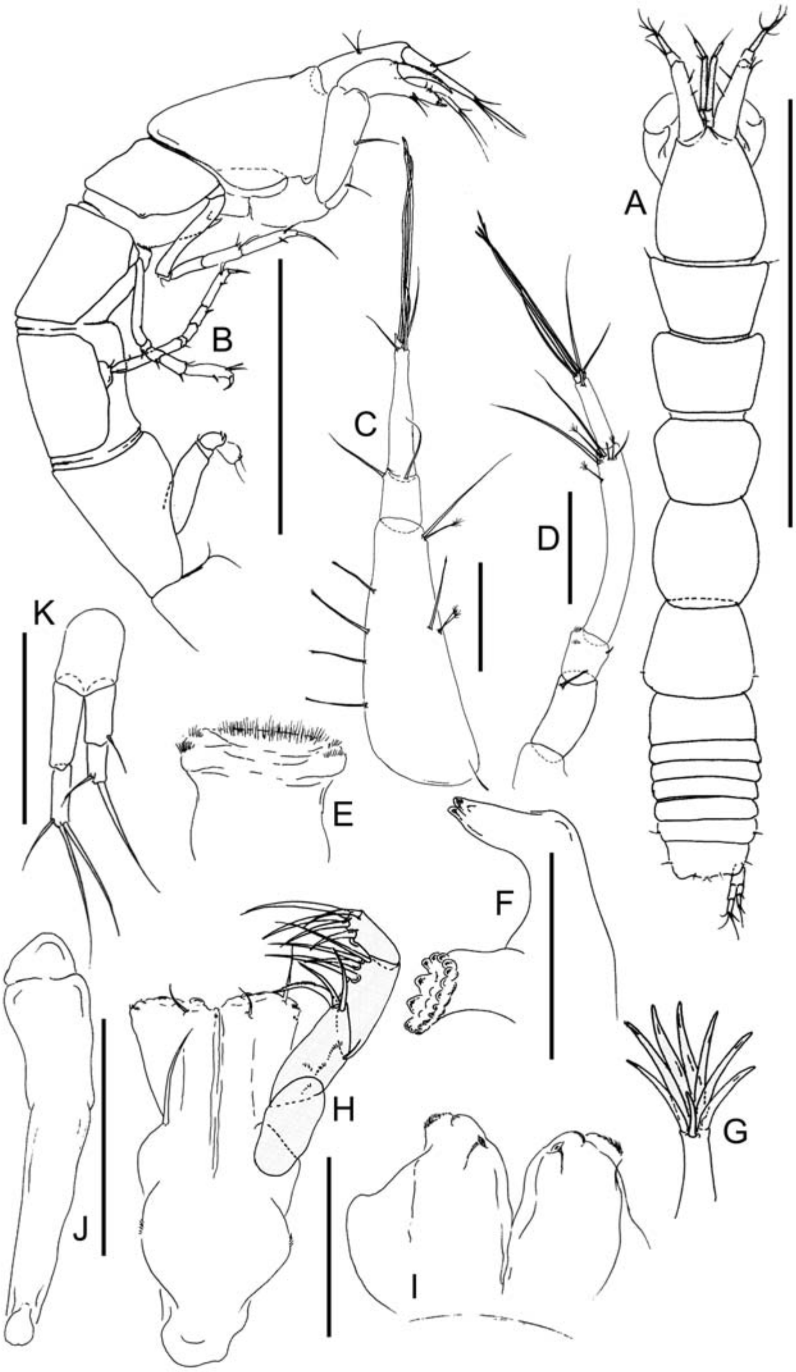

Fig. 14. *Typhlotanais* sp. A, female: dorsal view (**A**), lateral view (**B**), antennule (**C**), antenna (**D**), labrum (**E**), right mandible (**F**), maxillule endite tip (**G**), maxilliped (**H**), labium (**I**), epignath (**J**), uropod (**K**). Scale = 0.1 mm for A–B and 0.1 mm for C–K.

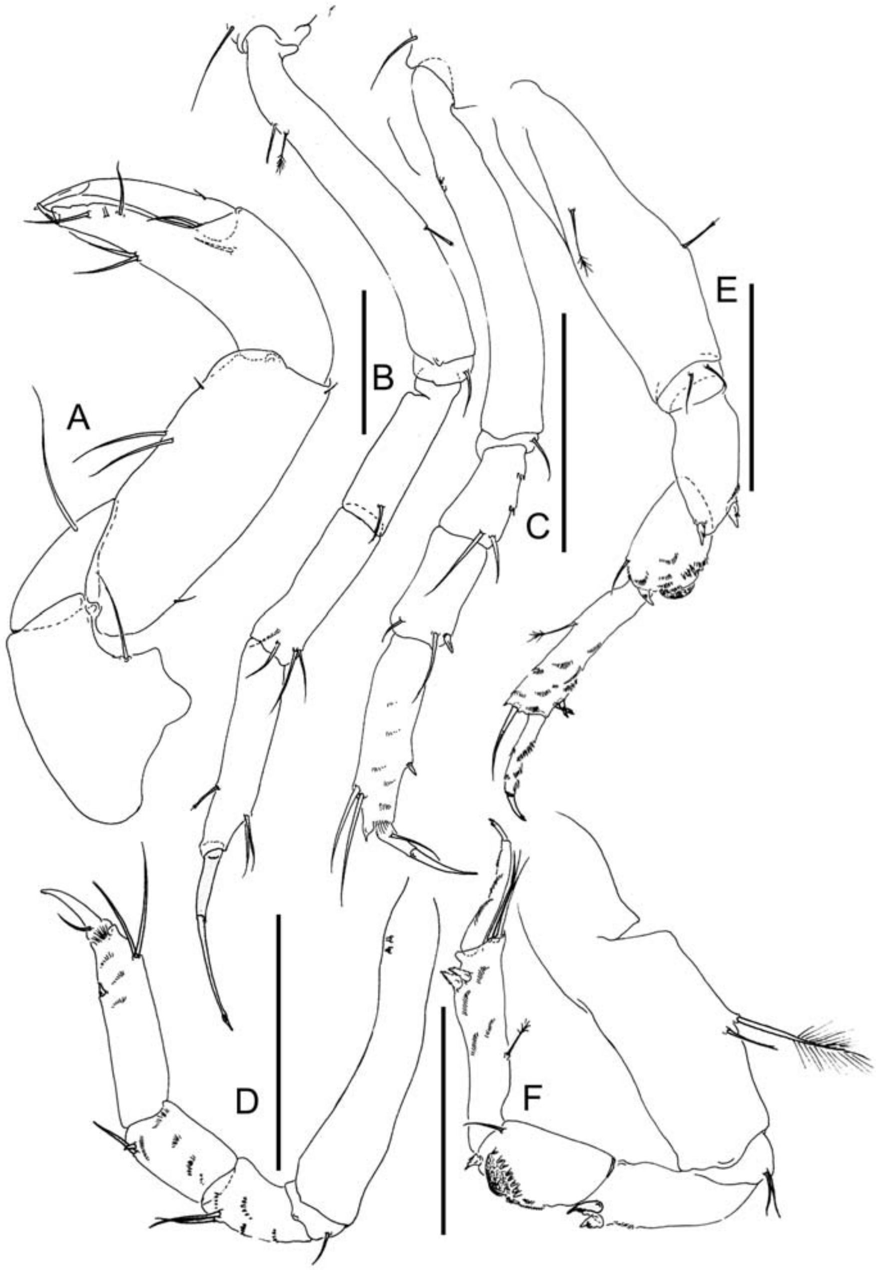

Fig. 15. *Typhlotanais* sp. A, female: cheliped (**A**), pereopods 1–4 and 6 (**B**–**F**, respectively). Scale = 0.1 mm.

Male diagnosis. — Cephalothorax as long as pereonites 1–4 and half of pereonite-5 combined; pereon as long as first four pleonites, but apparently narrower; pleon a little shorter than cephalothorax and pereon combined, caudal process pointed, without terminal spine. Antennule distal article 0.6 times as long as preceding article. Labrum large and naked. Cheliped carpus twice as long as wide; chela almost as long as carpus, pereopods 4–6 dactylus and unguis together shorter than propodus. Uropod biramous; endopod of two articles, proximal article 1.8 times as long as distal article; exopod as long as endopod proximal article.

Male description. — Body 2.0 mm long (Fig. 16A–B). Cephalothorax long reaching half length of pereonite-5; pereon as long as four pleonites, although apparently weaker developed; pleonites 1–5 as long as combined length of carapace and pereonites 1–4; pleotelson pointed without terminal spine (caudal process).

Antennule (Fig. 17A) with six articles; articles 1–2 robust, apparently wider than article 3 and 4; article-1 1.8 times as long as article-2; article-1 with a group of broom setae distally; article-2 with three broom and one simple distoventral setae and one short distodorsal seta; article-3 short with two long simple setae; article-4 as long as article-3; article-5 1.8 times as long as article-6; articles 4–6 ventral margins with dense row of aesthetascs; article-6 tipped with two long and two short setae, one aesthetasc and one broom seta.

Antenna (Fig. 17B) of eight articles; article-2 twice as long as article-3, with simple seta; article-3, with one seta; article-4 as long as article-2, naked; article-5 almost as long as combined length of articles 6–8, with two distal simple seta and four broom setae; articles 6–8 subequal; article-6 with one simple seta; article-7 unarmed; article-8 tipped with more two simple setae.

Labrum (Fig. 17C) distinct, naked. Maxilliped (Fig. 17D) basis fused; endites rounded, unarmed; palp article-1 short, unarmed, article-2 with one short seta on inner margin; article-3 a little longer than wide, with three long and one fine seta on inner margin, article-4 relatively slender, with four long and two fine distal setae.

Cheliped destroyed during dissection.

Pereopod-1 (Fig. 17E) basis with fine dorsal seta, a little longer than merus and carpus combined; ischium short, with one seta; merus 0.6 times as long as carpus, with small distoventral seta; carpus 0.9 as long as propodus, with one minute spine and four distal setae; propodus with short, distoventral spine and two fine distodorsal setae; dactylus broken.

Pereopod-2 (Fig. 17F) coxa with one seta; basis a little longer than merus and carpus combined, with fine seta on ventral margin; ischium with one seta; merus 0.7 times as long as propodus, with minute spine and distoventral fine seta; carpus 0.8 times as long as propodus, with minute spine and four fine distal setae; propodus with short, distoventral spine and two fine distodorsal setae; dactylus one-fourth as long as propodus; unguis broken.

Pereopod-3 broken.

Pereopod-4 (Fig. 17G) basis almost as long as carpus and propodus combined, with fine, dorsal seta; ischium with two setae; merus as long as carpus, with two small distoventral spines; carpus 0.7 as long as propodus, with three short distal spines and fine distodorsal seta; propodus with two distoventral and one disto-

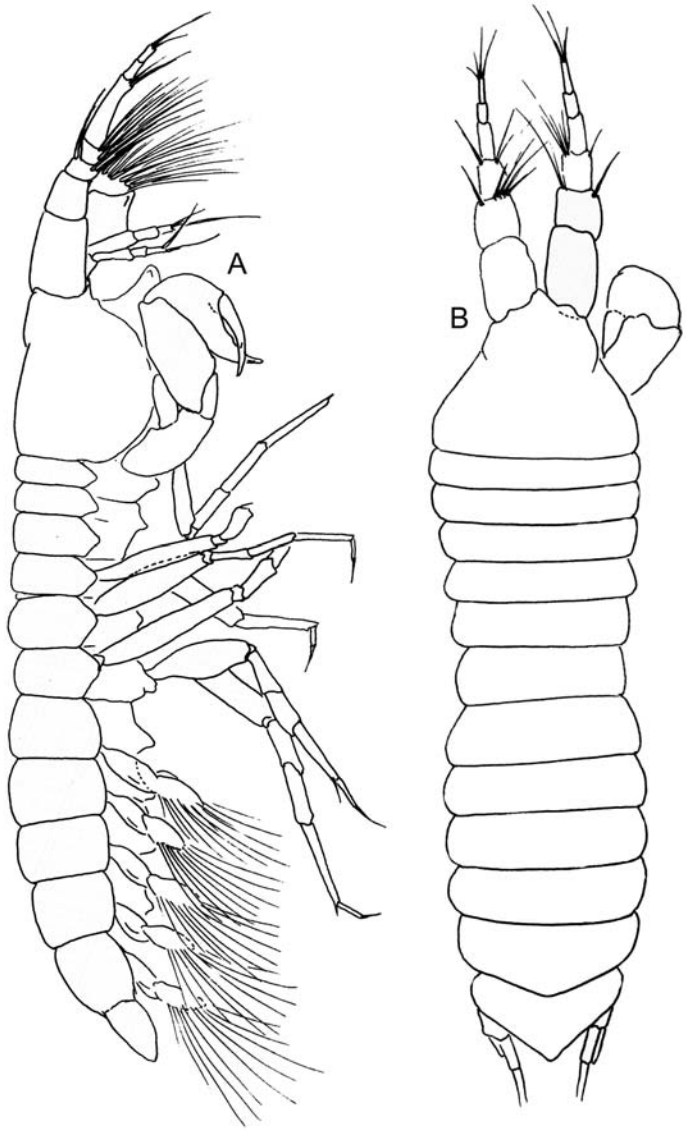

Fig. 16. *Typhlotanais* sp. A, male: dorsal view (**A**), lateral view (**B**). No scale available.

dorsal spines; dactylus two-third as long as propodus and twice as long as unguis; propodus and unguis a little shorter than propodus.

Pereopod-5 similar to pereopod-4.

Pereopod-6 (Fig. 17H) similar to pereopod-5, but propodus with three disto-dorsal setae.

Pleopod (Fig. 17I) endopod with 14 setae on distal margin, most proximal setae very short; exopod with 12 setae on distal margin and one subdistal seta.

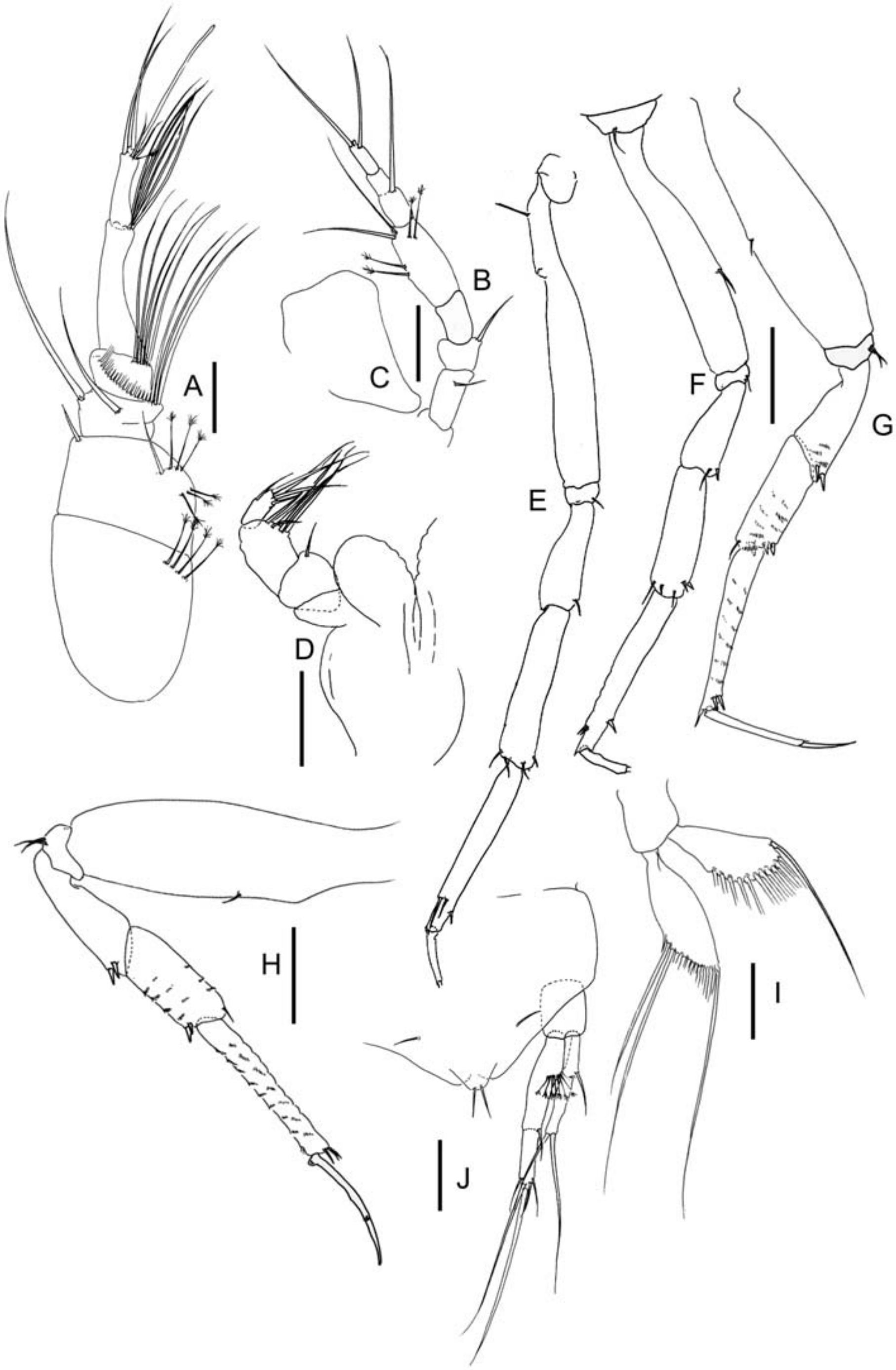

Fig. 17. *Typhlotanais* sp. A, male: antennule (**A**), antenna (**B**), labrum (**C**), pereopods 1–2 and 5–6, (**E**–**H**, respectively), pleopod (**I**), fragment of pleotelson and uropod (**J**). Scale = 0.1 mm.

Uropod (Fig. 17J) endopod with two partly fused articles; the "fused" line supported by one simple seta, proximal article twice as long as article-2, with a bunch of broom setae in the middle; distal article with two long distal and three fine subdistal setae; exopod as long as endopod proximal article, with simple seta on outer margin and two distal setae.

Remarks. — The male of *Typhlotanais* sp. A has a six-articulated antennule. Such an antennule was noted for two other members of Typhlotanaidae – *Typhlotanais finmarchicus* (G.O. Sars, 1882) and *T. grahami* Błażewicz-Paszkowycz, 2004, while *Typhlotanais adipatus* Tzareva, 1982 and *Peraeospinosus subtigaleatus* Błażewicz-Paszkowycz, 2007 have seven-articled antennules. Although *T. finmarchicus* has six-articled antennules, the first article is unusually robust and much wider than following articles compared to other taxa (G.O. Sars 1896). The number of the articles in the antennule was the main character of the system proposed by Sieg (1976) and it is still a feature starting each family diagnosis. Variability in the number of that articles in four males of Typhlotanaidae call this character into question for distinguishing males of at least in the family Typhlotanaidae.

Discussion

The weak development of secondary sexual traits of the juvenile or preparatory males such as in some paratanaoids, is explained as delayed maturation and described as a mating tactics ("female mimicry hypothesis" or "status-signal hypothesis") where a subadult male that is harder to distinguish from females is less likely to be attacked by mature males, or is more likely to be tolerated by adults in the breeding area (Andersson 1994). Both of these hypotheses could be applied to tri-morphic males of the sphaeromatid isopod *Paracerceis sculpta* (Holmes, 1904), in which large, ornamented males defend and reproduce with groups of mature females, while smaller males with undeveloped secondary sexual traits are taken for females by mature males (Shuster 1992).

Our study demonstrates that the families from which only juvenile-type males were known, such as Agathotanaidae, Anarthruridae, Colletteidae, Tanaellidae (*e.g.,* Larsen 2002), have also "swimming" males in some instances. The presence of "swimming" males does not necessary preclude preparatory or juvenile males being sexually mature (Bird and Holdich 1988), although their ability to reproduce needs to be supported by histological studies. If "juvenile-males" with a restricted ability for swimming (*e.g.* undeveloped pleopods) have matured testes and are capable of reproduction, they could mate with females nearby, while swimming males could mate with distant females. Moreover in food deprived deep-sea habitats, where population densities might be near the threshold of what is reproductively sustainable (Rex and Etter 2010), investing energy in terminal (swimming) males might be too great an expenditure. From this perspective, the presence in the population of numerous non-swimming males as observed by Bird and Holdich (1988) might be a strategy for living in low density. More studies implementing population genetics are undeniably needed, but it could be assumed that those swimming males maintain or increase the genetic diversity of the population through increased gene flow, which might be crucial to survival in an environment as unpredictable as the deep-sea.

It is widely thought that sexual dimorphism evolves primarily in response to sexual selection and/or natural selection arising from sex differences in reproductive roles (Darwin 1871; Andersson 1994). The evolutionary benefits of mobility and dispersal (*e.g.*, Dieckmann *et al*. 1999; Hellberg 2009) could select for swimming adaptations in males to increase local reproductive success, and potentially inter-population connectivity. Indeed, in the deep sea, where population densities tend to be low (Gage and Tyler 1991; Rex and Etter 2010), life history strategies that increase male-female encounter rates and/or "encounter radii" should be especially advantageous.

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