

Taxonomy and distribution of the genus *Amphicteis* (Polychaeta: Ampharetidae) collected by the BIOICE project in Icelandic waters

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Journal of Natural History Vol. 45, Nos. 23–24, June 2011, 1477–1499

Received 28 Jun 2010, Accepted 24 Jan 2011, Published online: 09 May 2011

To cite this article:

Julio Parapar , Gudmundur V. Helgason , Igor Jirkov & Juan Moreira (2011) Taxonomy and distribution of the genus *Amphicteis* (Polychaeta: Ampharetidae) collected by the BIOICE project in Icelandic waters, *Journal of Natural History*, 45:23-24, 1477-1499, DOI: 10.1080/00222933.2011.558640

This is an Accepted Manuscript of an article published by Taylor & Francis in *Journal of Natural History* on 2011, available online: <http://dx.doi.org/10.1080/00222933.2011.558640>

Abstract

Based on material collected during the BIOICE project off Iceland, four species of polychaetous annelids belonging to the genus *Amphicteis* Grube, 1850 (Polychaeta: Ampharetidae) were found: *Amphicteis gunneri*, *Amphicteis ninonae*, *Amphicteis vestis* and *Amphicteis wesenbergae* sp. nov. The differences between *A. gunneri* and *A. ninonae*, two species usually confused in the literature, are reviewed. *Amphicteis vestis* is described from newly collected material and its taxonomy in relation to other ampharetid taxa with modified notopodia is discussed. *Amphicteis wesenbergae* sp. nov. is described; the new species is characterized by the presence of long, slender and evenly tapered paleae, and long dorsal cirri on thoracic and abdominal neuropodia. Several body characters with high value in *Amphicteis* taxonomy, particularly the dorsolateral protrusions of abdominal chaetigers called rudimentary notopodia, are reviewed using scanning electron microscopy. A key to species of the genus *Amphicteis* described or reported in European Boreo-Arctic waters is provided.

Keywords: Polychaeta, Ampharetidae, *Amphicteis*, Iceland, BIOICE

Introduction

The genus *Amphicteis* Grube, 1850 is one of the most widely distributed and species-rich genera within the diverse family Ampharetidae Malmgren, 1866. Day (1964), Fauchald (1977) and Holthe (1986a) characterize the genus *Amphicteis* by the presence of four pairs of branchiae, paleae, smooth buccal tentacles, 17 thoracic chaetigers with notopodia (14 with uncinigerous tori) and 13–19 abdominal segments with uncinigerous pinnules and notopodial rudiments.

Since Holthe (1986b), who reported 18 genera of ampharetids in northeast Atlantic waters, there had been no review of this family in the northern waters of Europe until the study by Jirkov (2001) Jirkov, IA. 2001. *Polychaeta of the Arctic Ocean*, Moscow: Yanus-K. (in Russian)) on Arctic Polychaeta. Recently, significant efforts have been underway to improve and standardize the general knowledge of this family through partial, but valuable, revisions (Jirkov 2008; Reuscher et al. 2009). Four species of *Amphicteis* were hitherto described or reported in European Boreo-Arctic waters (Hansson 1998); Bellan 2001; Jirkov 2001): *Amphicteis gunneri* (Sars, 1835), *Amphicteis midas* (Gosse, 1855), *Amphicteis sundevalli* Malmgren, 1866 and *Amphicteis ninonae* Jirkov, 1985.

The BIOICE (Benthic Invertebrates of Icelandic Waters) expeditions are part of an international, collaborative programme started in 1992, designed to conduct a thorough survey of the marine benthic fauna present in the 200-mile economic zone of Iceland. The BIOICE sampling area covers a depth range from 20 to 3500 m on both sides of the Greenland–Iceland–Faeroe Ridge (GIF Ridge), which is generally less than 500 m deep and constitutes the boundary between the relatively warm North Atlantic Ocean and the much colder Nordic seas of the Arctic Ocean (Weisshappel 2000; Brix and Svavarsson 2010). The polychaete material collected under this project has already been used to describe new taxa (Sanfilippo 2001; Sigvaldadóttir 2002; Chambers and Woodham 2003); papers devoted to the families Glyceridae, Goniadidae and Oweniidae have been published by Kirkegaard (2001) and Parapar (2003, 2006).

Examination of further polychaete material collected during those expeditions revealed the presence of four species of *Amphicteis*, namely *A. gunneri*, *A. ninonae*, *A. vestis* Hartman, 1965 and the new species *A. wesenbergae* sp. nov. *Amphicteis vestis* is reported for the first time in North Atlantic waters since its original description by Hartman (1965) in waters off New England and a new description is provided using scanning electron microscopy (SEM). *Amphicteis wesenbergae* sp. nov. is described. In addition, comments are provided to further elucidate the structure of different body parts with high value in the taxonomy of the genus *Amphicteis*.

Materials and methods

This study is based on material collected during the BIOICE expeditions. In total, 1789 specimens of the genus *Amphicteis* were sorted from 230 samples taken at stations located on both sides of the GIF Ridge, covering a depth range from 17 to 3018 m (Figure 1A).

Specimens were fixed in 10% formalin buffered with borax, and preserved in 70% ethanol. Animals were sorted from samples by the staff at the Sandgerdi Marine Centre (SMC), and then identified at species level by the authors. The material examined is deposited in the collections of the Icelandic Museum of Natural History (IMNH, Reykjavik, Iceland), Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain), Zoologisk Museum (ZMUC, Copenhagen, Denmark). Data on bottom-water temperature, depth and coordinates used herein correspond to the start of each tow. Abiotic data of the samples studied from the BIOICE collection are available from the authors (G.V.H.) upon request. Specimens used for examination with SEM were prepared by critical point drying, covered with gold in

a BAL-TEC SCD 004 evaporator, and examined and photographed under a JEOL JSM-6400 SEM at the SAI (University of A Coruña-UDC, Spain).

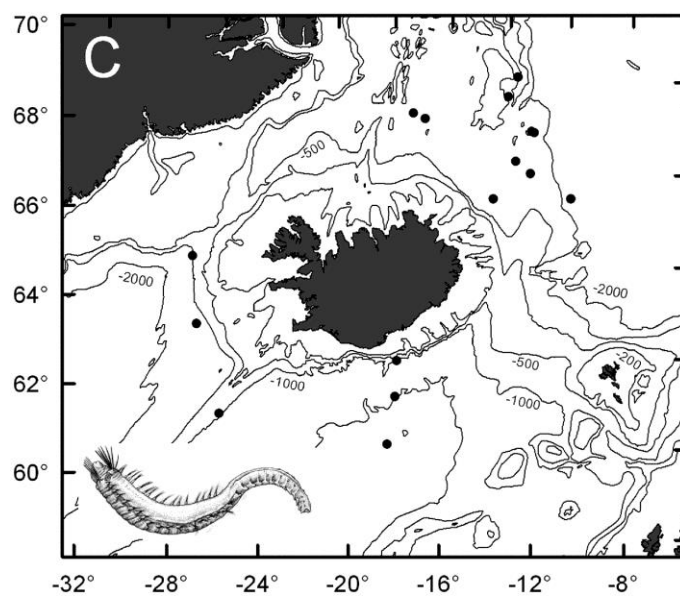
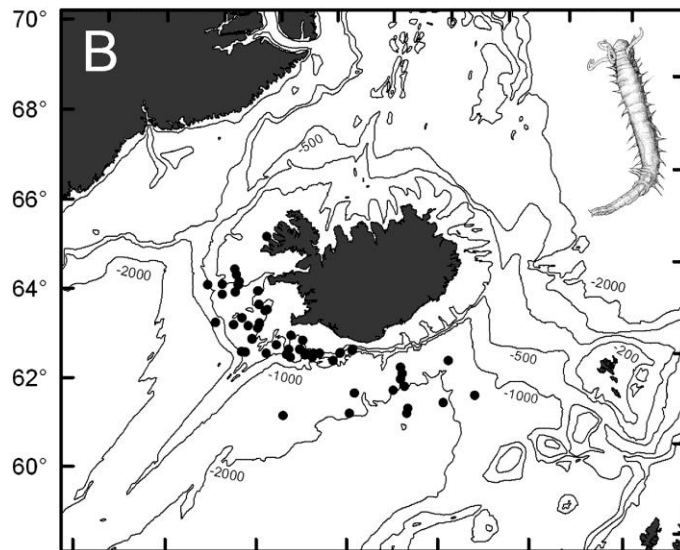
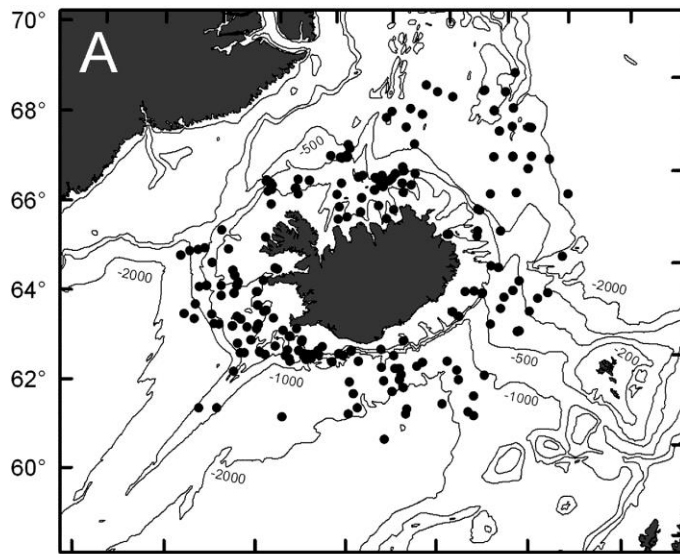


Figure 1. Distribution maps of total *Amphiteis* material examined (A), *Amphiteis vestis* (B) and *Amphiteis wesenbergae* sp. nov. (C).

Systematics

Family **AMPHARETIDAE** Malmgren, 1866

Genus *Amphicteis* Grube, 1850

Type species

Amphicteis gunneri (Sars, 1835) as *Amphitrite*

Diagnosis

Prostomium with a pair of dorsal longitudinal ridges and a pair of transverse nuchal grooves. Four pairs of branchiae of variable shape (usually cirriform and sometimes foliaceous or pennate). Branchial ridge usually present and with a pair of nephridial pores. Paleae usually present and well developed; absent in some species. Buccal tentacles smooth. Seventeen thoracic chaetigers and 14 thoracic uncinigers. Thoracic notopodia with distal ventral cirrus. Fifteen to twenty abdominal chaetigers with uncinigerous pinnules and rudimentary notopodia. All thoracic neuropodia of thoracic type; all abdominal neuropodia of abdominal type. Thoracic and abdominal uncini with a single vertical row of teeth of similar size, pygidium with a pair of anal cirri.

Remarks

According to Hartman (1959) and Fauchald (1977), the genus *Crossostoma* Gosse, 1855 was traditionally considered invalid and a synonym of *Amphicteis*. However, Hartley (1985:309), when re-establishing the validity of *A. midas* (Gosse, 1855), the type species of the genus *Crossostoma*, recognized the interbranchial region as markedly different to that of the group of species close to the genotype *Amphicteis gunneri* (compare fig. 1 with fig. 3 in Hartley 1985) and therefore suggested that it was necessary to reconsider the status of *Crossostoma*. This suggestion has not been adopted in later works (Hartmann-Schröder, 1996), probably because Hartley's article was not included in Holthe's papers (1986a:88; 1986b:56), the latter constituting the reference works on the taxonomy of European Terebellomorpha. Only a revision of the genus in European waters could confirm or deny this possibility.

Jirkov (2001:439) considered characters such as the presence or absence of paleal chaetae, number of pairs of gills and number of thoracic uncinigers as of low taxonomic value in generic discrimination in the family Ampharetidae (see also Jirkov 2008:111). Therefore, Jirkov (2001:407) proposed *Phyllamphicteis* Augener, 1918 (two of four pairs of branchiae lamellate and originally described with 18 thoracic chaetigers, although re-examination of the holotype revealed only 17), *Paramphicteis* Caullery, 1944 (no paleae) and *Pseudoamphicteis* Hutchings, 1977 (papillose buccal tentacles and originally described with two pairs of branchiae but actually possessing four as revealed during re-examination of the paratype in London) as junior synonyms of *Amphicteis*.

Amphicteis gunneri (Sars, 1835)

(Figures 2, 3, 4A–C, 5)

Amphitrite gunneri: Sars : 50–51, pl. 11, fig. 30a–d.

Amphicteis gunneri: Malmgren 1866:365–366, fig. 46; Fauvel 1927:231; Augener 1928:779 (partim?); Annenkova 1929:497, fig. 47 (partim); Holthe 1986a:89; Holthe 1986b:56–57, fig. 21, map 20; Hartmann-Schröder 1996:495; Jirkov 2001:471–472 (textfigure).

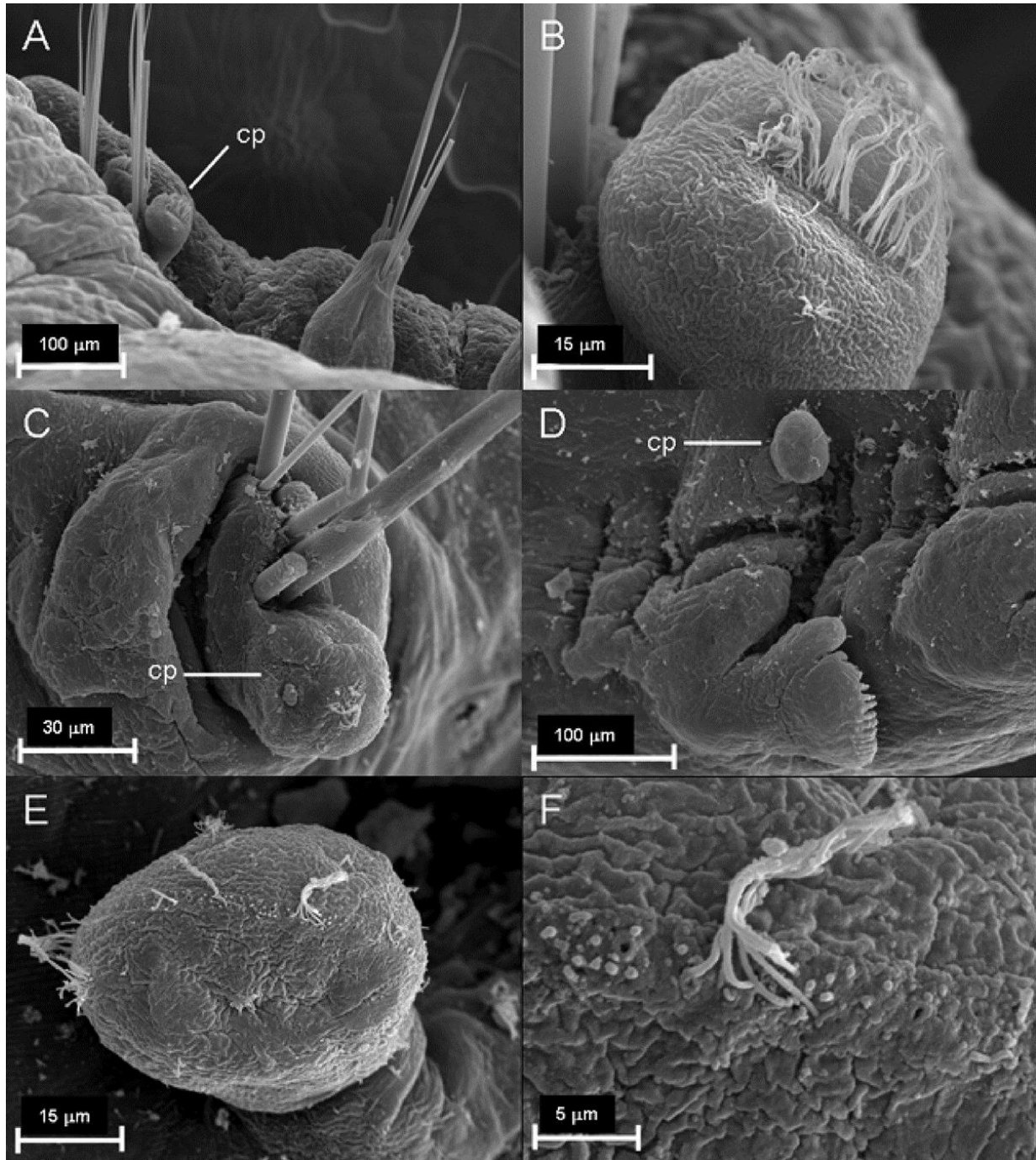


Figure 2. *Amphicteis gunneri* (Sars, 1835). Scanning electron micrographs from IMNH 24079. (A) Thoracic chaetigers 1–3, right side, dorsal view; (B) chaetiger 2, ventral clavate papilla; (C) chaetiger 17, notopodium; (D) mid-abdominal chaetiger; (E) mid-abdominal notopodial clavate papilla; (F) detail of ciliature of abdominal notopodial clavate papilla. Abbreviations: cp, clavate papilla.

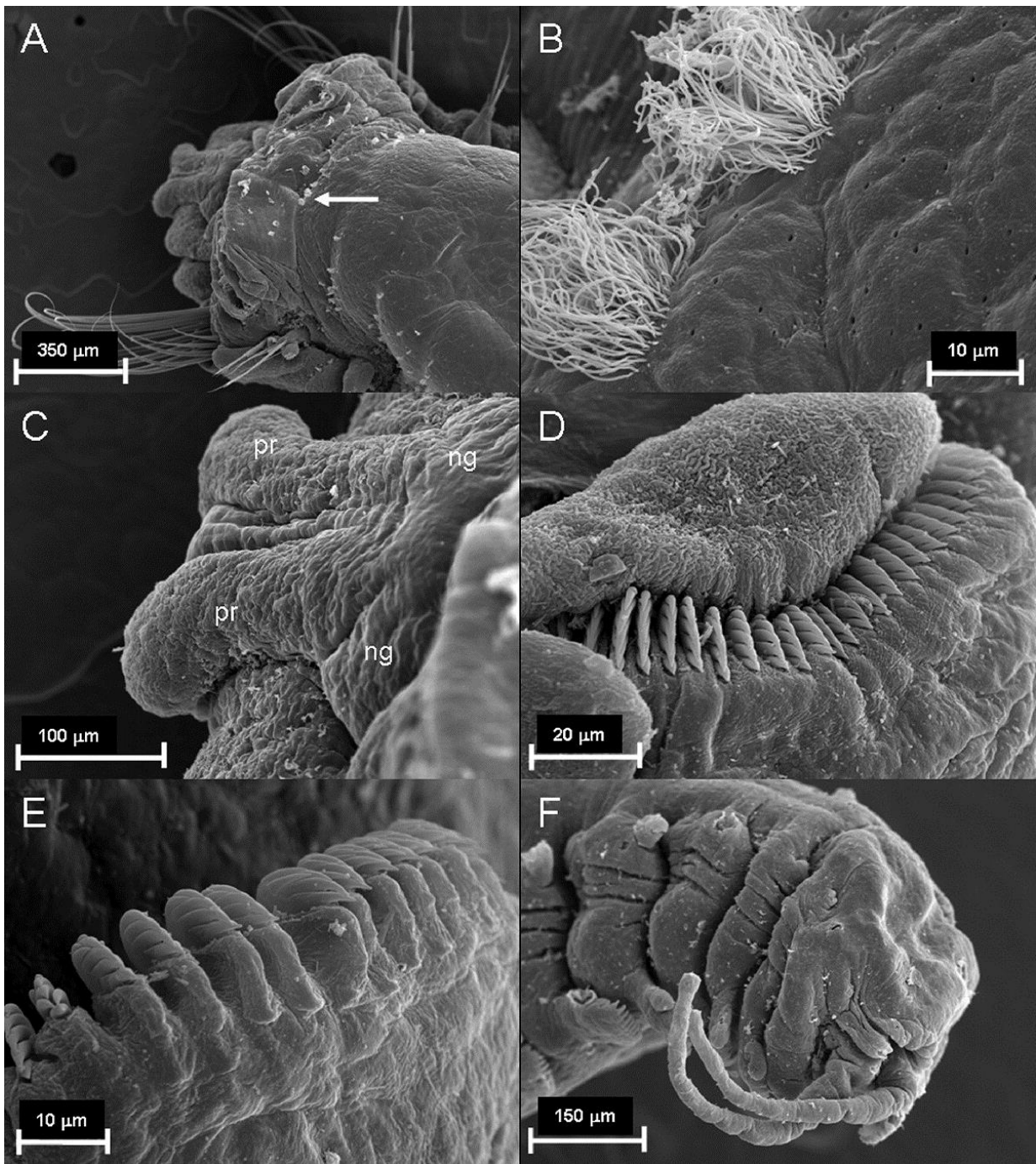


Figure 3. *Amphicteis gunneri* (Sars, 1835). Scanning electron micrographs from IMNH 24079. (A) Anterior end, dorsal view; (B) detail of dorsal ciliated tufts behind branchiae (arrow in A); (C) prostomium; (D) thoracic neuropodium and uncini; (E) abdominal uncini; (F) posterior region, lateral view. Abbreviations: pr, prostomial ridge, ng; nuchal groove.

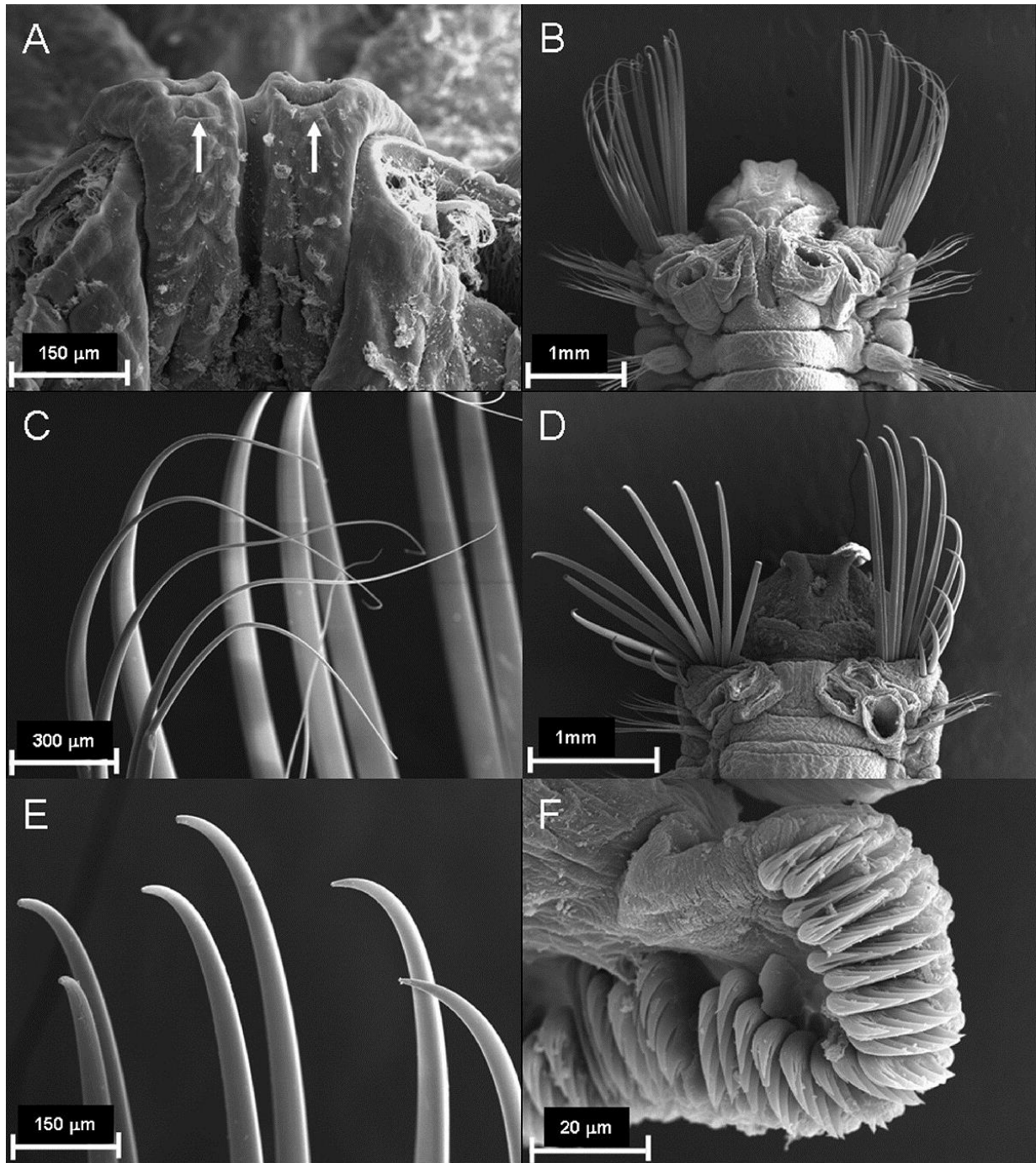


Figure 4. *Amphichteis gunneri* (Sars, 1835 Sars, M. 1835. *Beskrivelser og Iagttagelser over nogle mærkelige eller nye i Havet ved den Bergenske Kyst Levende Dyr af Polypernes, Acephalernes, Radiaternes, Annelidernes og Moluskernes Classer med en kort Oversigt over de hidtil af Forfatten sammesteds fundne Arter og deres Forekomsten Bergen*). Scanning electron micrographs from IMNH 24080. (A) Pair of nephridial pora (arrows) located on the ridge connecting the two groups of branchiae; (B) anterior end, dorsal view; (C) paleae, distal end. *Amphichteis ninonae* Jirkov, 1985, scanning electron micrographs, (IMNH 24081). (D) Anterior end, dorsal view; (E) paleae, distal end; (F) abdominal neuropodia with uncini.

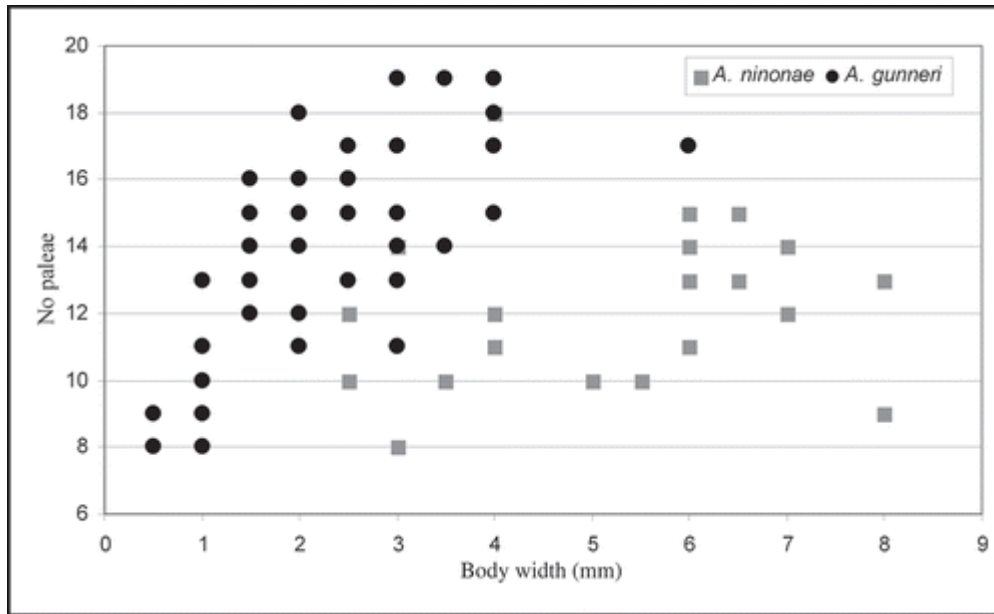


Figure 5. Number of paleae versus body width in BIOICE specimens of *Amphicteis gunneri* (Sars, 1835) and *Amphicteis ninonae* Jirkov, 1985.

Material examined

BIOICE sample 2049 (five specimens); 2075 (three); 2089 (six); 2090 (one); 2091 (two); 2094 (six); 2100 (12); 2102 (one); 2110 (one); 2111 (one); 2119 (five); 2129 (two); 2131 (one); 2154 (ten); 2161 (three); 2172 (one); 2209 (four); 2212 (eight); 2215 (one); 2216 (two); 2230 (two); 2236 (four); 2239 (one); 2241 (two); 2267 (two); 2277 (three); 2279 (one); 2282 (two); 2299 (one); 2310 (three); 2311 (one); 2314 (fourteen); 2324 (one); 2327 (three); 2328 (two); 2337 (twelve); 2348 (one); 2356 (one); 2358 (one); 2359 (one); 2363 (three); 2372 (two); 2374 (three); 2377 (seven); 2379 (one); 2380 (three); 2385 (one); 2387 (one); 2390 (four); 2397 (one); 2400 (one); 2403 (four); 2417 (two); 2418 (eight); 2423 (two); 2424 (one); 2430 (one); 2434 (two); 2435 (four); 2450 (one); 2466 (one); 2475 (one); 2522 (three); 2524 (two); 2526 (one); 2569 (one); 2572 (one); 2573 (one); 2592 (one); 2594 (two); 2595 (three); 2597 (one); 2603 (two); 2606 (nine); 2610 (four); 2612 (two); 2613 (one); 2615 (two); 2618 (two); 2619 (three); 2629 (one); 2642 (one); 2660 (one); 2666 (five); 2668 (one); 2673 (eight); 2697 (four); 2707 (four); 2710 (five); 2712 (14); 2713 (nine); 2717 (two); 2720 (four); 2743 (two); 2754 (two); 2769 (one); 2772 (ten); 2779 (one); 2791 (one); 2792 (six); 2813 (one); 2830 (one); 2849 (four); 2867 (seven); 2868 (one); 2872 (one); 2873 (four); 2877 (two); 2883 (three); 2884 (one); 2897 (three); 2909 (five); 2937 (eight); 2939 (one); 2965 (one); 2967 (two); 2970 (one); 2976 (three); 2978 (one); 2979 (three); 2983 (one); 3032 (one); 3050 (two); 3061 (one); 3062 (six); 3099 (two); 3114 (four); 3115 (one); 3127 (one); 3204 (three); 3216 (eleven); 3219 (four); 3238 (two); 3259 (two); 3260 (three); 3263 (one); 3280 (twelve); 3281 (three); 3501 (one); 3507 (two); 3518 (one); 3524 (one); 3527 (fourteen); 3528 (two); 3535 (six); 3538 (four); 3543 (eleven); 3544 (two); 3549 (two); 3550 (nine); 3558 (three); 3562 (one); 3591 (one); 3600 (one); 3608 (one); 3609 (one); 3610 (fourteen); 3621 (four); 3624 (fourteen); 3625 (twenty-five); 3627 (four); 3632 (fourteen); 3633 (seventeen); 3634 (four); 3635 (one); 3636 (seven); 3637 (six); 3638 (two); 3639 (one); 3643 (three); 3645 (five); 3648 (one); 3649 (fourteen); 3650 (one); 3652 (four); 3661 (one).

Occurrence

In all, 628 specimens of *A. gunneri* (35.10% of the total specimens examined) were collected in 176 BIOICE samples. According to its geographical distribution around Iceland, *A. gunneri* is present in high numbers at all depth and water temperature ranges; it seems to be absent only in shallower localities (less than 100 m depth). Depth range: 100–2613 m; temperature range: – 0.86 to 8.04°C.

Reported distribution

Arctic and Boreal Atlantic, northeastern South America, Indian Ocean, Japan (Imajima 2001). Wesenberg-Lund (1951) reported this species from Iceland but regards it as rare, particularly on the northern coast.

Historically, most records of *A. gunneri* in the literature were not accompanied by descriptions and, when diagnoses were provided, these were usually short and uninformative because generic characters are commonly used to characterize the species. As previously stated by Hartley (1985:313) the confusing definition of the taxon makes it impossible to assess the distribution of *A. gunneri* from literature. Because of this, we agree with Hartley (1985:314) that a close re-examination of material attributed to the nominal species from different localities around the world will reveal a number of different species. Consequently, the true distribution of the species may be restricted to Arctic and North Atlantic European waters (see map in Jirkov 2001:471) with a southern boundary of distribution probably located in the English Channel. Therefore, until a global revision of *Amphicteis* is completed, the specific name *A. gunneri* should be used with caution.

Remarks

The transition from thorax to abdomen in Ampharetidae is marked by the loss of notochaetae and either the complete loss, or a reduction, of notopodia (Hutchings, 2000:206). The genus *Amphicteis*, along with other ampharetid genera such as *Amage* Malmgren, 1866, *Amagopsis* Chlebovitch, 1964, *Amphisamytha* Hessle, 1917, *Anobothrus* Levinsen, 1884, *Asabellides* Annenkova, 1929, *Hobsonia* Banse, 1979, *Mexamage* Fauchald, 1972, *Paramage* Caullery, 1944, *Phyllampharete* Hartman and Fauchald, 1971, and *Samytha* Malmgren, 1866, is characterized by the presence of so-called “rudimentary notopodia” in abdominal chaetigers (see Fauchald 1977:125; Holthe 1986b:56; Reuscher et al. 2009:5). The study of several BIOICE specimens of *A. gunneri* using SEM revealed that the abdominal notopodia are reduced entirely except for a clavate ciliated papilla, which is already present in the ventral part of thoracic notochaetal bundles in anterior chaetigers (Figure 2A–C), remaining as a solitary papilla in abdominal chaetigers (Figure 2D). Both in thorax and abdomen, those papillae are provided with an apical ciliated band (Figure 2B, E, F). This particular feature was previously suggested by Hartley (1985:310) for *A. gunneri* and for *A. midas* by Holthe (1986a:21). The location of these papillae at the base of the notopodium and the presence of apical ciliature might suggest some kind of sensory function linked to the role of the thoracic notochaetae in the movement of the animal inside the tube or in its irrigation (Holthe, 1986a:21). Hence, these structures would have remained in the abdominal region for that purpose, after evolutionary reduction of notopodial bundles in the genus. Perhaps linked to some kind of sensory perception, a high number of cuticle pori and a dense cover of ciliated tufts (Figure 3A, B) has been observed by SEM on the dorsal surface behind the branchiae.

The clavate papillae are referred to as rudimentary abdominal notopodia by many authors. Similar abdominal structures in other genera, such as *Amage*, may correspond to a formation of different origin from that proposed here for *Amphicteis*. The study of some BIOICE specimens of *Amage auricula* Malmgren, 1866 Malmgren, AJ. 1866/1865. Nordiska Hafs-Annulater. Oefversigt af K

Vetenskaps-Akademiens Förhandlingar., 22: 355–410., the type species of the genus, did not reveal the presence of such papillae in the thoracic notopodia whereas rudimentary abdominal notopodia were much more noticeable. Both presence and nature of this character across ampharetid genera seem far from being definitively clarified, and the real value of this character in the taxonomy of this family can only be assessed after a thorough revision of the taxa endowed with this apparently diverse configuration.

The study of some specimens of *A. gunneri* under SEM also provided information on other diagnostic characters of the genus *Amphicteis*, namely the shape of the prostomium, thoracic and abdominal uncini and nephridial pori. The prostomium of *A. gunneri* (Figures 3C, 4B), *A. ninonae* (Figure 4D) and *A. wesenbergae* sp. nov. (Figure 10A) correspond well with Jirkov's *Amphicteis*-type, bearing a pair of longitudinal ridges and a pair of transverse nuchal grooves (Jirkov 2001). We agree with Reuscher et al. (2009:4) on the desirability of not using terms like “glandular” when describing these prostomial structures, because no histological studies support their use. Jirkov (2008:112) denies that these are of glandular nature, as many authors since Hessle (1917) have claimed. According to Mackie (1994) and Jirkov (2008:115), thoracic and abdominal neuropodia in *Amphicteis* differ in shape and uncini disposition, in that all thoracic uncini are of a thoracic type and all abdominal uncini are of abdominal type. Uncini are located in deep grooves in the thoracic uncinigers and on the edge of erect pinnules in the abdominal uncinigers; this feature (Figure 3D, E) is not exclusive to *Amphicteis*, but is shared with other genera of Ampharetidae. Thoracic and abdominal uncini in *Amphicteis* are characteristically provided with one vertical row of teeth of similar size (Figure 3D, E) and two anal cirri are inserted in the pygidium (Figure 3F). The nephridial papillae, always present in Terebellomorpha but often hardly visible (Jirkov 2008), open in a pair of nephridial pores located on the branchial ridge between both groups of branchiae (Figure 4A). The shape of the paleae, slender and evenly tapered (Figure 4B, C), distinguish *A. gunneri* from *A. ninonae*. Their number, which seems to be related to the body size in both species (Figure 5) was counted in some specimens revealing a similar range in *A. gunneri* (8–18) and *A. ninonae* (8–19).

Hartley (1985), after studying British and North Sea material, provided a redescription of *A. gunneri* and re-established *A. midas* (Gosse, 1855) as a valid species. He found that both species could be readily distinguished by morphological and ecological features. While *A. midas* is a shallow-water species (< 30 m) in the studied area, *A. gunneri* is restricted to deeper waters. *Amphicteis midas* was not found among the BIOICE material, which was mostly collected from deep waters. The presence of *A. midas* in shallow coastal waters of Iceland cannot, however, be ruled out because it is likely that it might have previously been confused with *A. gunneri* in previous works in the same area, such as those by Saemundsson (1918), Ditlevsen (1929, 1937), Spärck (1937), Einarsson (1941) Einarsson, H. 1941. Survey of benthonic animal communities of Faxa Bay (Iceland). *Meddel Komm Danmarks Fisk Havundersøgelser, Fisk.*, 11: 1–46.) and Wesenberg-Lund (1950, 1951).

Material examined

BIOICE sample 2014 (four specimens); 2045 (one); 2046 (two); 2057 (one); 2070 (eight); 2085 (six); 2089 (one); 2094 (one); 2110 (one); 2113 (one); 2129 (three); 2145 (three); 2167 (one); 2174 (two); 2315 (one); 2319 (one); 2328 (eleven); 2359 (one); 2372 (one); 2572 (one); 2575 (three); 2576 (three); 2592 (one); 2594 (three); 2603 (two); 2604 (one); 2606 (four); 2610 (one); 2613 (one); 2619 (three); 2626 (one); 2627 (six); 2666 (four); 2673 (two); 2683 (one); 2792 (two); 2901 (one); 3099 (one); 3115 (one); 3252 (four); 3638 (five).

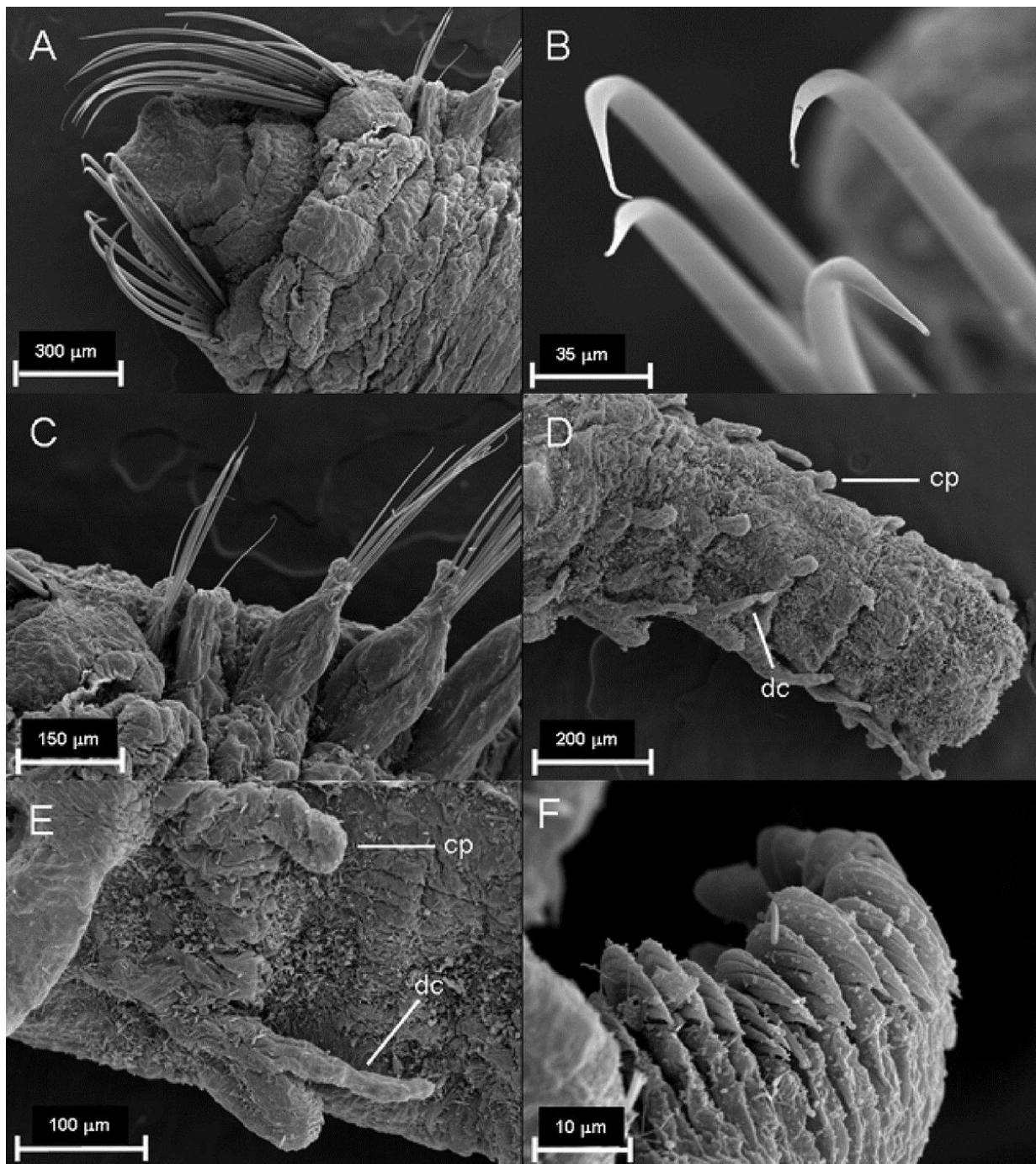


Figure 10. *Amphicteis wesenbergae* sp. nov. Scanning electron micrograph from paratype (ZMUC-POL-2148). (A) Anterior end, dorsal view; (B) paleae, distal end; (C) thoracic chaetigers 1–4, dorsal view; (D) posterior end, dorsal view; (E) abdominal mid-body chaetiger; (F) abdominal uncini. Abbreviations: cp, clavate papilla; dc, dorsal cirrus.

Amphicteis ninonae Jirkov, 1985

(Figures 4D–F, 5)

Amphicteis ninonae: Jirkov, 1985: 1894–1897 (textfigure); Jirkov, 2001: 472–473 (textfigure).

Amphicteis gunneri: Augener, 1928: 779 (partim?); Annenkova, 1929: 497, fig. 47 (partim); Ditlevsen, 1937: 39–40 (partim?) - *non* Sars, 1935.

Occurrence

In all, 101 specimens of *A. ninonae* (5.65% of the total) were collected in 40 BIOICE samples. In contrast to *A. gunneri*, this species seems to be restricted to the north and east coasts of Iceland. Depth range: 134–2067 m; temperature range: –0.8 to 7.57°C.

Reported distribution

Norwegian Sea, Arctic Seas (Hansson 1998; Deubel 2000). Our findings confirm the presence of this species in Icelandic waters, which was previously reported by Jirkov (2001).

Remarks

Amphicteis ninonae has often been confused with *A. gunneri* and to some extent perhaps also with *A. midas*. Nevertheless the low boreal distribution proposed for *A. midas* (see Hartley, 1985:311) against the high-latitude distribution of *A. ninonae* (see above), makes it difficult to believe that both species occur in sympatry. Following Jirkov (1985:1896; 2001:472), *Amphicteis ninonae* is primarily characterized by the colour (dark brown), and number (8–16) and shape (blunt tips) of paleae (Figure 4D, E and key below). We agree with Jirkov (1989:111) that *A. ninonae* has abdominal rudimentary notopodia. The BIOICE specimens are usually larger than those of *A. gunneri* and the number of paleae seems to have a weaker correlation with body size (Figure 5).

Amphicteis vestis Hartman, 1965

(Figures 1, 6–8)

Amphicteis vestis: Hartman, 1965 215–216, fig. 46.

Material examined

BIOICE sample 2213 (two specimens); 2215 (181); 2216 (two); 2221 (23); 2222 (five); 2226 (one); 2229 (one); 2230 (three); 2233 (one); 2236 (one); 2237 (twenty-nine); 2268 (one); 2273 (six); 2282 (twelve); 2285 (one); 2303 (eight); 2308 (twenty-five); 2311 (one); 2390 (one); 2391 (four), 2392 (three); 2393 (twelve); 2398 (one); 2400 (one); 2401 (thirty-six); 2417 (two); 2418 (six); 2423 (one); 2424 (fifteen); 2434 (five); 2435 (thirty-one); 2469 (one); 2475 (five); 2484 (one); 2712 (one); 2713 (one); 2716 (one); 2717 (sixteen); 2719 (one); 2856 (one); 2859 (three); 2860 (five); 2867 (one hundred and eleven); 2868 (fifty-eight); 2869 (five); 2873 (one); 2976 (three); 2979 (eight); 2983 (43); 3067 (eleven); 3072 (one); 3164 (one); 3500 (one); 3501 (four); 3505 (one); 3510 (three); 3519 (one); 3522 (one); 3524 (one); 3528 (one); 3539 (one); 3550 (sixteen); 3565 (one); 3608 (nineteen); 3617 (sixteen).

Description

Body between 1.4 mm and 10 mm long, and 0.2 to 0.5 mm wide. Thorax and abdomen well defined; thorax about twice width and three times length of abdomen (Figure 6); barely tapering towards posterior part. Prostomium pointed anteriorly with a pair of ciliated pits (nuchal organs?) located at both sides of anterior part (Figure 7A, B). No eyes seen. Buccal tentacles few and fairly large, with distal end expanded and ciliated on one side, but not papillated (Figure 7C–E). Four pairs of long and deciduous branchiae arranged in one outer row of three pairs and a fourth one in an inner position (Figure 7F). All branchiae of similar size; the inner one being thickest and the posteriormost of the outer row thinnest. Between 13 and 15 long and slender paleae with tapering ends. Seventeen thoracic chaetigers with notopodia with notochaetae; the posterior fourteen also with neuropodia with uncini located in a furrow

distinctly off the neuropodial margin (Figure 8A). First abdominal segment with notopodia transformed in a double-winged expansion stretching across dorsum but with a large median notch (Figures 6, 8B–D); inner margins of fans with ciliature (Figure 8D, E); no rows of papillae or ciliature seen in outer margins of fans. Thirteen abdominal segments; anterior ones longer than posterior ones, only with neuropodia with uncini at the very margin of the torus (Figure 8F). Pygidium with a pair of short lateral cirri. Notochaetae slightly flattened distally before tapering into slender tips. Thoracic and abdominal uncini slightly different in shape; thoracic uncini with three or four horizontal rows of three or four teeth above rostrum (Figure 8A); abdominal uncini with two horizontal rows of seven or eight teeth above rostrum (Figure 8F).

Colour in alcohol pale yellow. No tubes observed. Oocytes present in some specimens in the body cavity, visible through body wall.

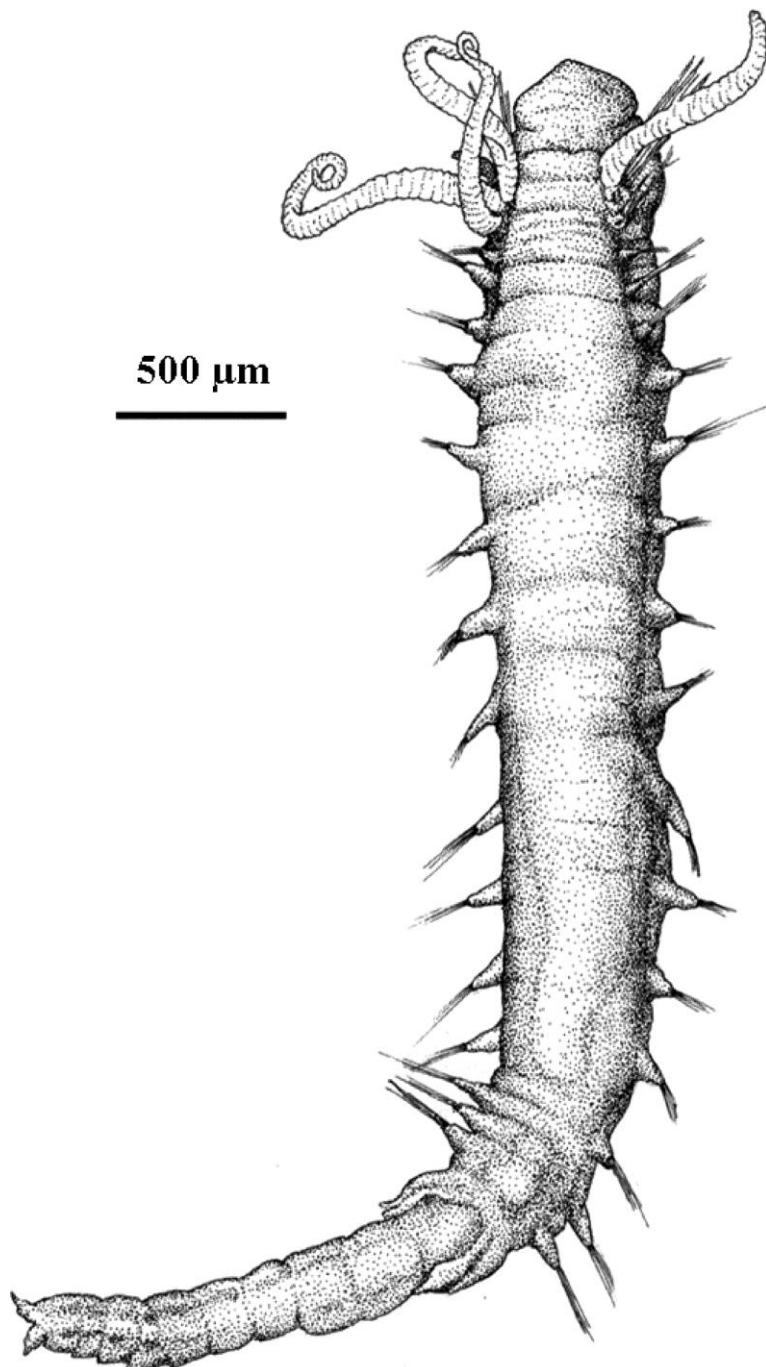


Figure 6. Dorsal view of *Amphicteis vestis* Hartman, 1965 (IMNH 24082).

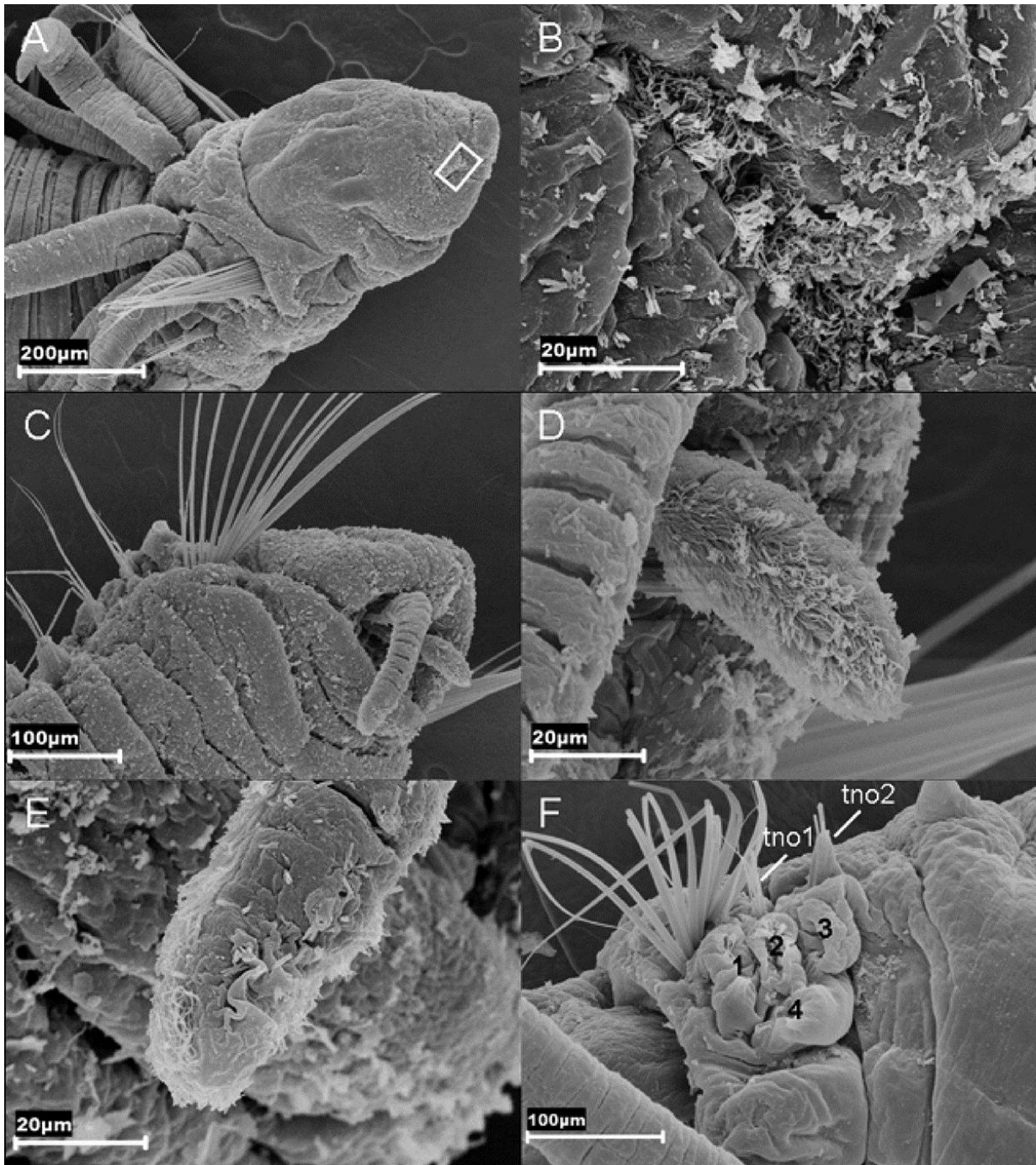


Figure 7. *Amphiteis vestis* Hartman, 1965. Scanning electron micrographs from IMNH 24083. (A) Anterior end in dorsal view; (B) ciliated nuchal pit; (C) ventral view of anterior end; (D) detail of ciliated side of buccal tentacle; (E) detail of non-ciliated side of buccal tentacle; (F) basal scars of right branchiae (numbered). Abbreviations: tno, thoracic notopod.

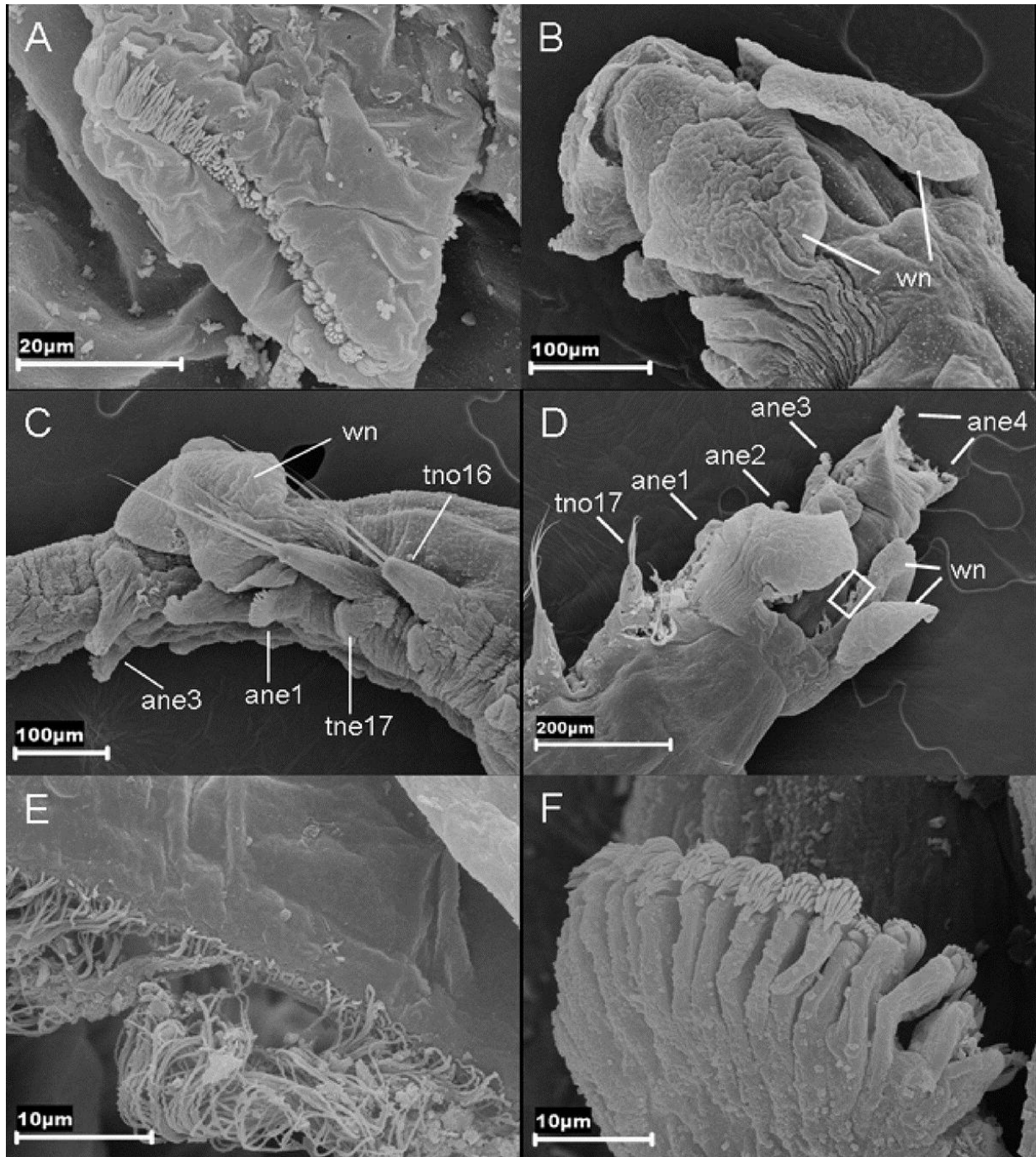


Figure 8. *Amphicteis vestis* Hartman, 1965. Scanning electron micrographs from IMNH 24084. (A) Tenth thoracic neuropodia and uncini; (B) first abdominal chaetiger, dorsal view of winged expansion of notopod; (C, D) lateral and dorsal views of transitional zone between thorax and abdomen; (E) detail of ciliature present on inner edge of winged notopodia; (F) first abdominal neuropodia and uncini. Abbreviations: wn, winged notopodia of first abdominal chaetiger; tno, thoracic notopod; tne, thoracic neuropod; ane, abdominal neuropod.

Occurrence

In all, 730 specimens of *A. vestis* (40.80% of the total) were collected in 65 BIOICE samples. *Amphicteis vestis* is present at a wide range of depths and, to a lesser extent, of temperatures, but is more frequent in warm waters of the continental shelf and upper slope of the southwestern coast of Iceland (Figure 1). Depth range: 37–2295 m; temperature range: 2.34–7.41°C. Given the small body

size and fragility of this species coupled with its high quantitative presence in the finest fractions of BIOICE samples (0.5 mm), it is likely that this species has been overlooked in previous benthic studies conducted in its area of distribution (see below).

Reported distribution

Amphicteis vestis has been scarcely reported since its original description by Hartman (1965); it has, however, a wide distributional range. Originally described off New England (West Atlantic Ocean), between 200 and 2469 m depth, it was later reported by Kucheruk (1976) from deeper waters (3240–3350 m) off Alaska Bay (Aleutian Arc, Northeast Pacific) and recently by M. Schüller and B. Ebbe (ANDEEP-SYSTCO, preliminary results on line) from deep Antarctic waters below 2000 m depth. Recently, one of us (I.J.) had the opportunity to examine Antarctic specimens and tried to find Kucheruk's material in the Shirshov Institute collections where it was supposedly deposited but with no success in the latter case.

Remarks

The presence of dorsal body features is not rare among the ampharetids. One type of these dorsal features is the so called “elevated notopodia” (Holthe, 1986a.:28), which are present in a variety of genera such as *Anobothrus* Levinsen, 1884 [*Anobothrella* Hartman, 1967 *syn.* and *Sosanides* Hartmann-Schröder, 1965. *syn.*, *sensu* Jirkov (2001)], *Sosane* Malmgren, 1866. [*Sosanella* Hartman, 1965. *syn.*, *Sosanopsis* Hessle, 1917 *syn.*, *Mugga* Eliason, 1955 *syn.* and *Mugoidea* Hartman, 1965 *syn.*, *sensu* Jirkov (2000)] and *Eclysippe* Eliason, 1955. Other types of body modification are the “dorsal ridges” present in *Melinnampharete* Annenkova, 1937 [*Neosamytha* Hartman, 1967 *syn.* *sensu* Jirkov (2001)] and the “fan-shaped notopodia” present in *Jugamphicteis* Fauchald and Hancock, 1981, *Ymerana* Holthe, 1986 and *Zatsepinia* Jirkov, 1986. Some of these genera have previously been reported from Icelandic waters (see Wesenberg-Lund, 1951) and were also found among the ampharetid material from the BIOICE samples, which is currently being studied by the authors.

According to the key to the Ampharetidae genera provided by Reuscher et al. (2009), the presence of this special body feature in the first abdominal chaetiger in *A. vestis* would locate the species in the genus *Jugamphicteis* created by Fauchald and Hancock (1981) and later emended by Holthe (2000). This genus is, to date, composed of four species, namely *J. sibogae* (Caullery, 1944), *J. sargassoensis* (Hartman and Fauchald, 1971), *J. paleata* Fauchald and Hancock, 1981 and *J. galathea* Holthe, 2000. All *Jugamphicteis* species share two synapomorphies (Holthe, 2000:60): presence of prominent nuchal ridges in the prostomium and notopodial fans in the first abdominal chaetiger. *Amphicteis vestis* shares with the genus *Jugamphicteis* the following features: number and shape of paleae and branchiae, number of thoracic and abdominal chaetigers and presence of modified notopodia in the first abdominal chaetiger. Fauchald and Hancock (1981:40) and Holthe (2000:60) pointed out, however, that this species should not be placed in *Jugamphicteis* because of the presence of ciliated nuchal pits in *A. vestis* instead of nuchal ridges and of bilobed foliose notopodia in the first abdominal chaetiger rather than a valve-like pair. The modified notopodia of *A. vestis* show other relevant differences to those of *Jugamphicteis* species. In *Jugamphicteis* they result from the fusion of most of the notopodial folds of the right and left chaetigers, determining a thin, non-muscular membrane at the inner dorsal sides of both folds, leaving free only the dorsalmost part of each fold which ultimately results in a “valve-like” structure *sensu* Fauchald and Hancock (1981:41). On the contrary, in *A. vestis* the pairs of notopodial fans are well-delimited from each other and from those of the other side, hence constituting a “bilobed” structure *sensu* Fauchald and Hancock (1981). Besides, blunt projections are present on the free margins on the dorsal outer sides of the folds in

all *Jugamphicteis* species; these are simple in *J. paleata* and *J. sibogae*, double in *J. galathea* and probably also double in *J. sargassoensis*. In *A. vestis*, both lappets are completely free from each other and bear no projections on the lateral margins.

The ciliature observed on the inner free margins of the lateral lappets in *A. vestis* has never been reported in any ampharetid species. Its biological role is as yet unknown but it is possible that it helps in ventilating the tube.

The presence of fan-shaped notopodia in the thorax–abdomen transitional zone has also been reported in the ampharetid genus *Ymerana* Holthe, 1986. *Ymerana pteropoda* was described as a new genus and species from the Norwegian and Polar seas by Holthe (1986c), who characterized this taxon by the “last pair of (thoracic) notopodia achaetous and transformed into a flattened fan with dorsal lateral wings and ridge across dorsum”. This wing-like notopodium is similar to that of *A. vestis* although in the latter that structure is present as two pairs instead of one. Furthermore, the genus *Ymerana* has three pairs of branchiae, no paleae and 14 thoracic chaetigers with notopodia, with the last pair transformed in the aforementioned way, whereas *A. vestis* has four pairs of branchiae, long and numerous paleae, 17 thoracic notopodia and the fan-like notopodial structure represents the first abdominal chaetiger instead of the last thoracic chaetiger.

Zatsepinia rittichae Jirkov, 1986, collected from the northern Norwegian coasts and at both sides of the GIF Ridge, also has elevated notopodia but differs from *A. vestis* in having those structures in the 11th thoracic chaetiger (12 thoracic chaetigers in total), in lacking paleae and in having two pairs of branchiae.

Following the comments mentioned above and the diagnosis of the genus *Amphicteis*, we agree with Jirkov (2008) that the affinities of *A. vestis* with the genus *Amphicteis* remain highly uncertain. Hence, the shape of the prostomium, with a pair of ciliated pits (nuchal organs?) instead of the characteristic longitudinal ridges, the buccal tentacles being ciliated instead of smooth, the presence of a unique double dorsal fan in the first abdominal chaetiger and the different shape of both thoracic and abdominal uncini (with one vertical row of teeth in *Amphicteis* as opposed to multiple rows in *A. vestis*) suggest that this species belongs neither to *Amphicteis* nor *Jugamphicteis*. Nevertheless, so as not to create more confusion in a highly diverse family with the erection of a new monotypic genus, we decided to maintain the species in *Amphicteis* pending a much needed revision of the genus.

***Amphicteis wesenbergae* sp. nov.**

(Figures 1, 9, 10)

Type material

Holotype

Zoologisk Museum: ZMUC-POL-1871. “Ingolf” Expedition station 117, east Norwegian Sea (69°13' N; 08°23' W), 1889 m depth. The specimen was formerly identified as *A. gunneri*.

Paratypes

Icelandic Museum of Natural History (Reykjavik): IMNH 24085 (BIOICE sample 2018; 15 paratypes); IMNH 24086 (2704; three paratypes); IMNH 24087 (2776; 15 paratypes); IMNH 24088 (2777; one paratype); IMNH 24089 (2844; three paratypes); IMNH 24090 (2863; one paratype); IMNH 24091 (2903; one paratype); IMNH 24092 (3210; one paratype); IMNH 24093 (3519; one paratype); IMNH

24094 (3595; one paratype); IMNH 24095 (3628; three paratypes); IMNH 24096 (3629; 10 paratypes); IMNH 24097 (3636; one paratype); IMNH 24098 (3657; 28 paratypes).

Additional BIOICE material

Museo Nacional de Ciencias Naturales (Madrid): MNCN 16.01/13264 (BIOICE sample 3222; 235 specimens). Zoologisk Museum (Copenhagen): ZMUC-POL-2147 (BIOICE sample 3624; 10 specimens).

Other material examined

East Greenland: R/V *Sevastopol*, cruise 10, station 1725 (67°32' N; 13°15' W), 1730 m, -0.89°C (one specimen). R/V *Sevastopol*, cruise 15, station 2448 (69°20' N; 12°00' W), 1940 m, -0.9°C (one). R/V *Tunetz*, cruise 105, station 16 (72°50' N; 14°00' W), 960 m, -0.96°C (one). West Norway: R/V *Tunetz*, cruise 105, station 6 (68°00' N; 10°00' W), 260 m, 6.06°C (one).

Description based on holotype

Holotype 9 mm long and 1 mm wide at thorax level. Additional material 7–12 mm long and 0.8–2 mm wide. Thorax and abdomen well defined; thorax about 1.5 times the width and length of abdomen (Figure 9A); barely tapering towards posterior part. Prostomium of *Amphicteis*-type (Figure 10A) with

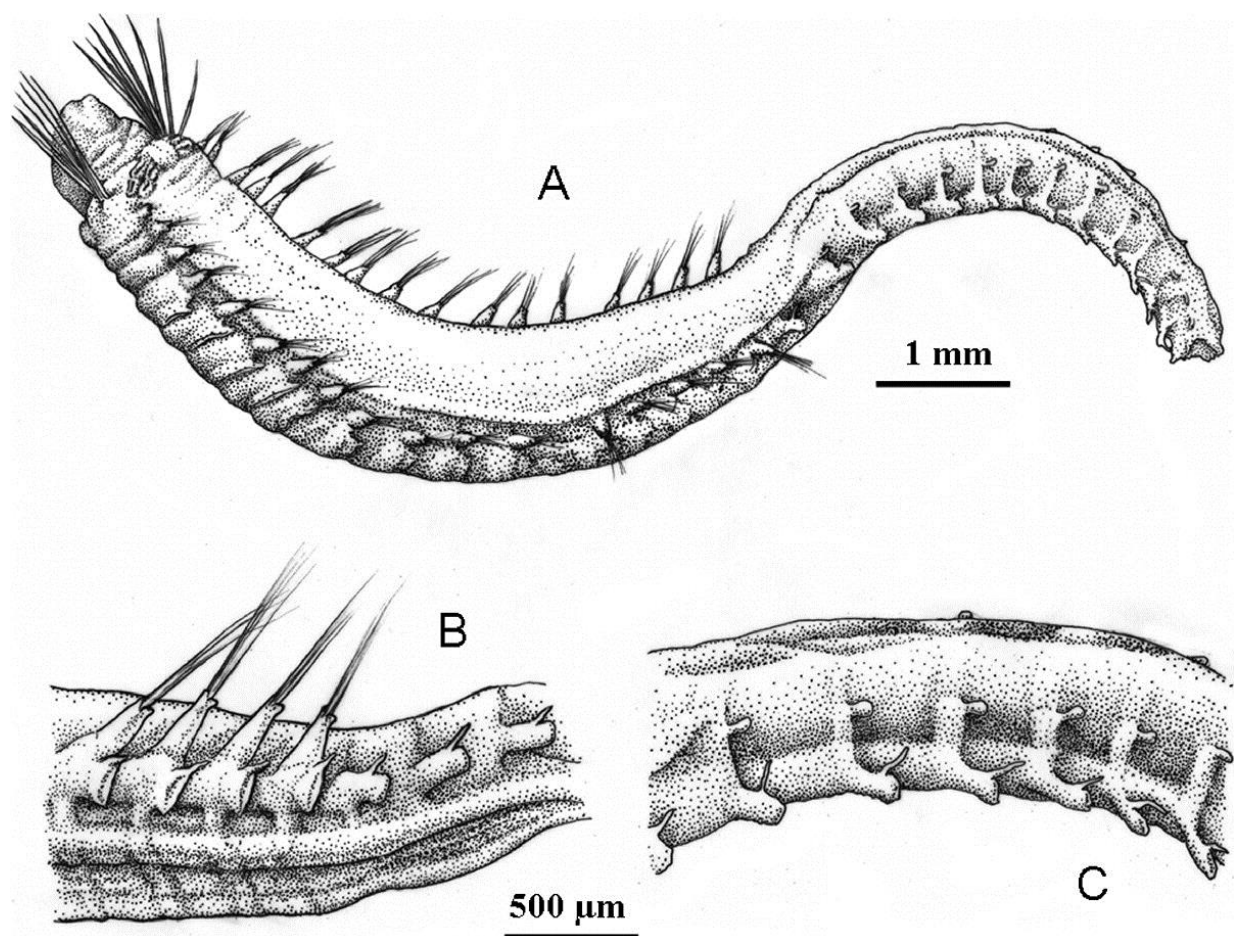


Figure 9. *Amphicteis wesenbergae* sp. nov. Holotype (ZMUC-POL-1871). (A) Dorso-lateral view; (B) thorax–abdomen transition, lateral view; (C) abdominal chaetigers, lateral view.

a pair of dorsal longitudinal ridges, less obvious than in *A. gunneri*, and a pair of well-marked transverse nuchal grooves. No eyes seen. Four pairs of long, tapering and deciduous branchiae (all missing in holotype) separated in left and right groups and arranged in two pairs, the posterior pair slightly displaced mid-dorsally (Figure 10A). Eight to ten long and slender paleae with tapering ends (Figure 10A, B). Seventeen thoracic chaetigers with large notopodia provided with long notochaetae (Figures 9A, 10C); the posterior 14 also with neuropodia provided with dorsal cirri (Figure 9B) and uncini with a single row of teeth. Fifteen abdominal chaetigers provided with large notopodial rudiments, and neuropodia with long dorsal cirri (Figures 9C, 10D, E) and uncini with single row of teeth (Figure 10F). Pygidium with a pair of long lateral cirri. Colour in alcohol pale yellow. Tubes made of mud with some foraminiferans incrustated.

Occurrence

In all, 330 specimens of *A. wesenbergae* sp. nov. (18.45% of the total) were collected in 16 BIOICE samples. *Amphicteis wesenbergae* sp. nov. is present in the warm waters of the deep slope off the southwestern coast of Iceland (Figure 1C). Depth range: 916–2544 m; temperature range: – 0.87 to 5.52°C. The species was also found further north in east Greenland and in the Norwegian Sea (see above).

Remarks

Hartley (1985:314) noted that “... a range of specimens attributed to *A. gunneri* from Greenland, Iceland and the deeper North Atlantic ... found to consist of several closely related species of *Amphicteis*”. In fact, the specimen selected as holotype of *A. wesenbergae* sp. nov., located in the ZMUC polychaete collection, was originally labelled as *A. gunneri*. *Amphicteis wesenbergae* sp. nov. belongs to the group of *Amphicteis* species with narrow, evenly tapered paleae, which also includes *A. gunneri* and *A. sundevalli*. In fact, *A. wesenbergae* sp. nov. and *A. gunneri* have the same number of abdominal chaetigers, and look very similar to each other at first sight. Nevertheless, both species can be easily distinguished by the length of the dorsal cirri on the abdominal neuropodia: long in *A. wesenbergae* sp. nov. and short in *A. gunneri* (compare Figure 2D with Figure 10E).

Etymology

The species is dedicated to the Danish Zoologist Elise Wessenberg-Lund (1896–1969) for her remarkable contributions to the taxonomy of polychaetes of Iceland and Greenland.

Key to Arctic-Boreal species of *Amphicteis*

- 1. Notopodia of first abdominal chaetiger transformed into a double dorsal fan *A. vestis* ¹
 Notopodia of first abdominal chaetiger not transformed.....2
- 2. Tips of paleal chaetae evenly tapering.....3
 Tips of paleal chaetae blunt.....5
- 3. Fifteen abdominal uncinigers.....4
 Between 18 and 20 abdominal uncinigers (upper shelf, high Arctic distribution).....*A. sundevalli* ²

4. Abdominal uncinigers with short dorsal cirrus; longitudinal ridges of prostomium well marked (widely distributed).....*A. gunneri*
- Abdominal uncinigers with long dorsal cirrus; longitudinal ridges of prostomium inconspicuous*A. wesenbergae* sp. nov.
5. Paleal chaetae dark brown; usually more than 10 (8–16) on each side (bathyal, Arctic distribution).....*A. ninonae*
- Paleal chaetae light yellow; usually up to eight (10) on each side (shallow waters, low boreal-lusitanian distribution).....*A. midas*²

Descriptions of *A. midas* and *A. sundevalli* can be found in Hartley (1985:309), Holthe (1986b:58) and Jirkov (2001:473).

Acknowledgements

The senior author (J.P.) wishes to thank Danny Eibye-Jacobsen, Majken Them Tøttrup (ZMUC), Elin Sigvaldadóttir and Karin Sindemark (SMNH) for their help during his stay at both institutions. Igor Jirkov also acknowledges David Hall and Tim Worsfold, Unicomarine Ltd., Letchworth Hertfordshire, UK, for the loan of specimens of *A. midas* for examination. Special thanks to Solrun Bragadóttir and all the women of the SMC involved in sorting of specimens from the BIOICE samples. Ada Castro and Catalina Sueiro (SAIN, UDC) for assisting in the preparation of specimens and use of the SEM, David Romero (UDC) for the line drawings and Noela Sánchez (UDC) for the preparation of maps. Constructive comments by M. Schüller and B. Ebbe are gratefully acknowledged.

This work was partially supported by several grants from the European Union's TMR programme and the UDC and Xunta de Galicia to J.P. to visit the SMC. J.P. also gratefully acknowledges *Synthesis* support made available by the European Community – *Research Infrastructure Action* under the FP6 *Structuring the European Research Area* (Projects DK-TAF-3118 and SE-TAF-4599) to visit the Zoologisk Museum (Copenhagen), and the Swedish Museum of Natural History (Stockholm).

Notes

1. Most probably, this species does not belong to the genus *Amphicteis* (see *Remarks* section for this species).
2. Species not reported in Icelandic waters and not found among BIOICE material.

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