

**Amphipoda from the IceAGE-project
(Icelandic marine Animals:
Genetics and Ecology)**

Edited by

Saskia Brix, Anne-Nina Lörz,
Bente Stransky & Jörundur Svavarsson

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AMPHIPODA FROM THE ICEAGE-PROJECT (ICELANDIC MARINE ANIMALS:
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Amphipod family distributions around Iceland

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Abstract

Amphipod crustaceans were collected at all 55 stations sampled with an epibenthic sledge during two IceAGE expeditions (Icelandic marine Animals: Genetics and Ecology) in 2011 and 2013. In total, 34 amphipod families and three superfamilies were recorded in the samples. Distribution maps are presented for each taxon along with a summary of the regional taxonomy for the group. Statistical analyses based on presence/absence data revealed a pattern of family distributions that correlated with sampling depth. Clustering according to the geographic location of the stations (northernmost North Atlantic Sea and Arctic Ocean) can also be observed. IceAGE data for the Amphilochidae and Oedicerotidae were analysed on species level; in case of the Amphilochidae they were compared to the findings from a previous Icelandic benthic survey, BIOICE (Benthic Invertebrates of Icelandic waters), which also identified a high abundance of amphipod fauna.

Keywords

Amphipoda, benthos, deep sea, distribution, Greenland-Iceland-Faroe Ridge, subarctic, taxonomy

Introduction

The international IceAGE project (Icelandic marine Animals: Genetics and Ecology) focuses on the climatic sensitive region at the northernmost part of the North Atlantic and the Nordic Seas (Greenland, Iceland and Nordic Seas reaching to the North Sea). The study area is characterised by a steep temperature gradient (< -0.9 °C to 14 °C) as well as several shallow (< 800 m) submarine ridges which define distinct deep marine basins and host cold-water coral reefs along their slopes (Buhl-Mortensen et al. 2015a, b). Previous studies of benthic invertebrates in the North Atlantic and Nordic Seas including the BIOICE (Benthic Invertebrates of Icelandic waters: 1991–2004) and IceAGE (since 2011: see Brix et al. 2014a) projects have shown that within the abundant peracarid crustacean fauna, more than 50% of the species are new to science (Błażewicz-Paszkowycz et al. 2014). These projects have identified both broadly and narrowly distributed species in the region (e.g., Weissshappel 2000, 2001, Dauvin et al. 2012), where geographically restricted species are distributed to either north or south of Iceland (Svavarsson 1997, Brix and Svavarsson 2010). With cryptic species and species complexes a reoccurring theme for peracarid crustaceans, and particularly for amphipods (Havermans et al. 2013), there can be a significant underestimation of regional biodiversity (Just and Wilson 2004). Previous studies have indicated that integrative taxonomic approaches better allow for robust and transparent species delineation (Sites and Marshall 2004, Dayrat 2005, Leaché et al. 2009, Padial et al. 2010). In order to best capture the diversity, distribution range and dynamic assemblage of the amphipod crustaceans, the first two IceAGE expeditions in 2011 (M85-3) and 2013 (POS456) expanded upon the traditional sampling and preservation methods from previous studies to incorporate molecular approaches.

Despite amphipods being the most common peracarid crustacean order within the IceAGE samples, prior to this study, amphipod crustaceans were underrepresented in project research outputs. The lack of scientific focus on this group was largely due to the large amounts of time and specialised expertise required to process the volume of material. At the beginning of the project, more than 66,000 amphipod specimens had been collected and were available for further identification (DZMB database, unpublished data).

Identifying amphipods is a complex task and owing to the “taxonomic impediment” the number of amphipod experts worldwide is in decline (Coleman 2015). Taxonomy is the fundamental science for understanding and assessment of biodiversity. All ecological and modelling analyses rely on accurate taxonomic information. Considering the known threats to biodiversity, new knowledge of existing species and the discovery of undescribed species from extant collections are urgently required. To overcome this impediment, the IceAGE team initiated several identification workshops. These workshops, run by senior experts, aimed to train early career researchers and to improve taxonomic knowledge of the amphipods around Iceland.

Here the results from two such workshops are presented. These results show the distribution patterns for amphipod families identified from IceAGE samples. For two abundant families, Amphilochidae and Oedicerotidae, species level identification is also presented.

Materials and methods

The IceAGE project and the expeditions were initiated and coordinated by Senckenberg am Meer (<http://www.iceage-project.org>), part of the Senckenberg Forschungsinstitut und Naturmuseum that serves to link scientists to samples collected by German research vessels and to make this material available. All sorting was handled according to Riehl et al. (2014) using an undisturbed cooling chain protocol. Following the field-work process and rough sorting of material to coarse identification levels, material from the IceAGE expeditions were housed in the Senckenberg “Meteor archives” (<http://www.material-archiv.de/en/home.html>). The IceAGE sampling protocol minimises mechanical and physiological stress to specimens during the on-board rough sorting process. This protocol assists in preserving the integrity of the specimens for both morphological and molecular analyses (Riehl et al. 2014). In terms of expedition protocol, the sampling included six depth transects (1: Norwegian Channel, 2: Iceland-Faroe Ridge, 3: Iceland Basin, 4: Irminger Basin, 5: Denmark Strait, 6: Norwegian Sea) between 150 and 2850 m (Figure 1), where samples were collected using epibenthic sleds.

During both identification workshops, sample processing concentrated on amphipods collected with the epibenthic sledge (EBS). It should be noted that three types of gear were used during the IceAGE expeditions: RP sled (Rothlisberg and Pearcy 1977), Brenke sled (Brenke 2005) and C-EBS (Brandt et al 2013). Within these samples, identification was concentrated on those samples which were preserved in 96% ethanol to enable genetic work (see Jazdzewska et al. 2018). Only samples that would provide representatives of the most transects from the IceAGE station grid (Figure 1, red dots). As a result of this strategic sorting approach, a total of 21,658 specimens were identified to family level or lower.

For the families Amphilochidae and Oedicerotidae, all identified specimens have been registered in the permanent zoological collection at either Senckenberg (Frankfurt), the Naturkundemuseum Berlin or the Zoological Museum Hamburg (ZMH), Centrum für Naturkunde (CeNak). All specimens selected as molecular vouchers (Jazdzewska et al. 2018) will be registered in the ZMH. At the time of manuscript

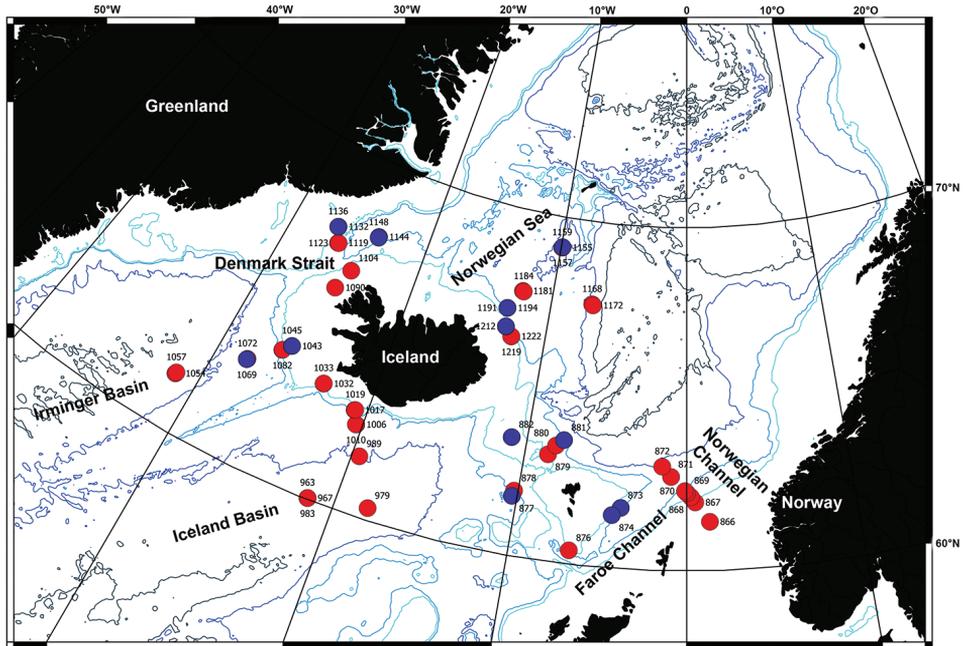


Figure 1. Map of all IceAGE EBS stations where amphipods have been found. Red: stations with amphipods determined; Blue: stations where amphipods were not further determined (873, 874, 877, 881, 882, 1043, 1045, 1069, 1136, 1144, 1148, 1191, 1209, 1212, 1157).

preparation, the higher classification of the Amphipoda was in a state of reassessment (Lowry and Myers 2017). Our paper follows a conservative classification to allow preparation of the material in line with the World Amphipoda Database as of May 2017 (Horton et al. 2017).

Due to the “expert-bias” of participants at our two workshops and the incomplete sorting at family level, small families often received a more detailed treatment, while some larger taxa such as the Lysianassoidea or Phoxocephalidae were dealt with quite cursorily. Families that are known to be very abundant in Icelandic waters, including e.g., the Ampeliscidae (Dauvin et al. 2012) were underrepresented in our samples as we focused on ethanol-fixed samples collected by an epibenthic sledge, which does not adequately sample the Ampeliscidae. The approach to processing this extensive amphipod collection did not allow enumerating the species in every family. Despite these shortcomings, our results can provide a preliminary insight into the Amphipoda collected during the IceAGE expeditions.

Certain findings of singletons or rarer taxa are important for particular families, i.e., the Sicafodiidae (Campean and Coleman 2017) which is the first record of the family in the northern hemisphere. Here, singletons were excluded from the analyses to reduce “noise”. Distribution maps are provided for the families (or superfamilies) recovered (excluding singletons) with a brief description indicating its significance in the region.

Data analysis

Distribution maps were created for the amphipod families, one superfamily (Lysianassoidea) and one infraorder (Corophiida) occurring at more than two stations using the freeware QGIS, and were assembled using Photoshop CS6. Multivariate analyses were performed on samples where more than 40% of the individuals were identified to family level (76–100%: 14 samples, 51–75%: 5 samples, 41–50%: 14 samples). As a result of this processing methodology we readily acknowledge possible underestimations and restrictions within the dataset. Data were presence/absence transformed before the analysis. Hierarchical agglomerative clustering was based on Bray-Curtis similarity formula (Bray and Curtis 1957) using a group average method. SIMPROF test with 1% significance level was performed in order to confirm multivariate structure within the group (Clarke and Gorley 2015). Multivariate statistical analysis was performed using the Primer 7 package. Differences in the number of families per sample between the groups obtained in the Cluster Analysis were tested with use of Mann-Whitney U test in the STATISTICA 6 package.

Additional multivariate analyses (Bray-Curtis formula, group average grouping method, SIMPROF test with 1% significance level) were also carried out for the two families whose specimens were identified to species level (Amphilochidae – 32 samples and Oedicerotidae – 25 samples). Here, abundance data (number of individuals per station) were standardised and square root transformed prior to analysis (Clarke and Gorley 2015). Additionally, a set of 39 epibenthic sled (RP sled) samples collected during the BIOICE project was analysed (Amphilochidae to species level, see Suppl. material 2). Similarity analyses were performed following the same statistical methods outlined for the IceAGE Amphilochidae.

Results and discussion

Amphipod crustaceans were collected at all 55 stations analysed; however, identification to the family level was only possible for 40 of them (see Figure 1). The number of individuals per station ranged from a few specimens to more than 16,000 individuals (Figure 2). The Norwegian Sea stations were characterised by low amphipod abundances with higher numbers of individuals found at both the shallowest and the deepest stations. Conversely, in the Norwegian Channel, very high abundances were observed at upper bathyal stations, while the highest numbers of Amphipoda in the Iceland Basin were observed at mid-bathyal stations. In other studied areas, no clear pattern associated with depth was noticed. Amphipoda are known to be an abundant group at all depths. Generally, amphipod abundance is high in the shelf zone and at upper bathyal depths (500–1000 m), while they are generally replaced by the Isopoda at greater depths (Brandt 1997a, Brandt et al. 2005, 2015). In this study, a decrease in amphipod abundance at lower bathyal stations is also observed; however, at shallower stations, the number of individuals seems to depend more on local environmental conditions than on depth.

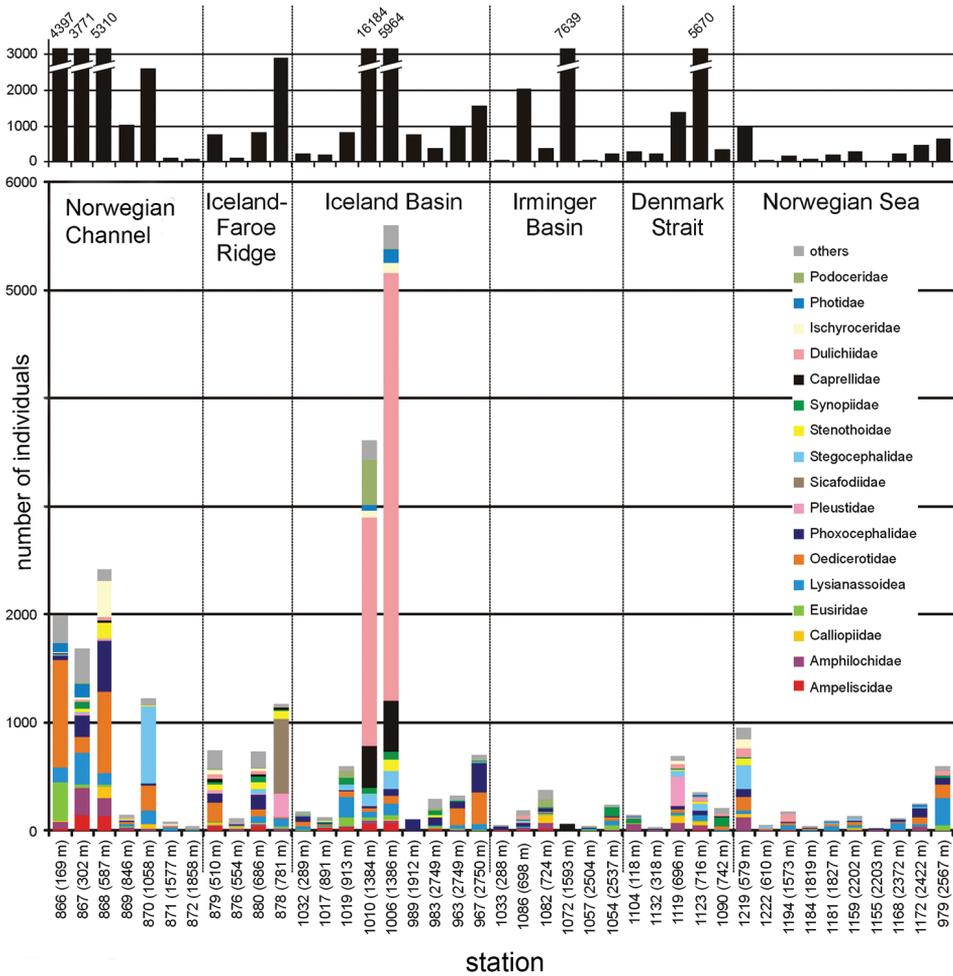


Figure 2. Family distribution at all IceAGE stations ordered by transect. Within each transect (1: Norwegian Channel, 2: Iceland-Faroe Ridge, 3: Iceland Basin, 4: Irminger Basin, 5: Denmark Strait, 6: Norwegian Sea), stations are ordered by depth. The upper graph (black bars) indicates the absolute number of amphipod individuals per station. The lower graph indicates the amphipods sorted to families per station (legend by colours shown on the right side).

In numerical order, the most abundant taxa were the Dulichiidae, Oedicerotidae, Phoxocephalidae, and Lysianassoidea followed by the Amphilochidae (Figure 2). All together, these taxa accounted for more than 50% of the individuals studied. It is worth noting that the dominance of dulichiids resulted from their very high abundance at just two mid-bathyal stations in the Iceland Basin (stations 1006, 1010). The overall frequency of occurrence of this family was 60% and, at most other stations, it was represented by a low number of individuals. A large proportion of these same stations also included representatives of the families Caprellidae, Ischyroceridae, Photidae, and Podoceridae. All of these taxa are moderately mobile, and are known to be associated with sessile organisms,

often being suspension-feeders (e.g., Lincoln 1979, Caine 1989, Brandt 1993, 1997b). Brix et al. (in press) have reported that at the same stations, high numbers of the isopod family Arcturidae are recorded and these are also regarded as having a sedentary lifestyle, associated with other sessile invertebrates. A study of benthic habitats around Iceland revealed very homogenous sediments in the Iceland Basin, dominated by sandy muds occasionally accompanied by a small proportion of gravel (Meißner et al. 2014). However, the region is known to have very productive surface waters and high total organic carbon content in the sediments was observed, which may explain the high abundances of suspension feeding peracarids in our study. The other families that dominated the studied material were more evenly distributed and more frequent (frequency of occurrence often >80%). The numerical dominance of oedicerotids, phoxocephalids, and lysianassoids in the benthic realm is a common feature of both shallow and deep-sea ecosystems in all regions of the World (e.g. Buhl-Jensen 1986, Brandt 1993; Buhl-Mortensen 1996, Weisshappel and Svavarsson 1998, Golovan et al. 2013).

Acanthonotozomatidae Stebbing, 1906

Figure 3a

In the present study, the family was recorded at two of the 40 stations from ca. 600 m north of Faroe Islands, with a total of ten specimens. In a revision of the Iphimediidae and related families, Coleman and Barnard (1991) limited the family Acanthonotozomatidae to the species of the genus *Acanthonotozoma*. Just (1978) published a taxonomic monograph on this genus including data on biogeography and biology. The World Amphipoda Database (Horton et al. 2017) today lists ten species of Acanthonotozomatidae, of which *Acanthonotozoma cristatum* (Ross, 1835) and *Acanthonotozoma serratum* (Fabricius, 1780) occur around Iceland and *Acanthonotozoma magnum* Just, 1978 and *Acanthonotozoma dunbari* Just, 1978 are known from along the east coast of Greenland and Spitsbergen and South Greenland respectively (Just, 1978). *Acanthonotozoma serratum* seems to be confined to depths less than 200 m, whereas *A. cristatum* has been recorded to 700 m (Just 1978). The colour patterns of species of *Acanthonotozoma* can be vivid, ranging from yellow with red stripes (*A. serratum*) to bright red or even purple (*A. inflatum*). Although Just (1978) provided details on the life history of acanthonotozomatids, further details of the biology, such as feeding preferences are not known.

Amathillopsidae Pirlot, 1934

Figure 3b

In total, 50 amathillopsid individuals were reported from 12 stations, most from the two upper bathyal stations just South of Iceland. *Cleonardopsis* was found at stations west of

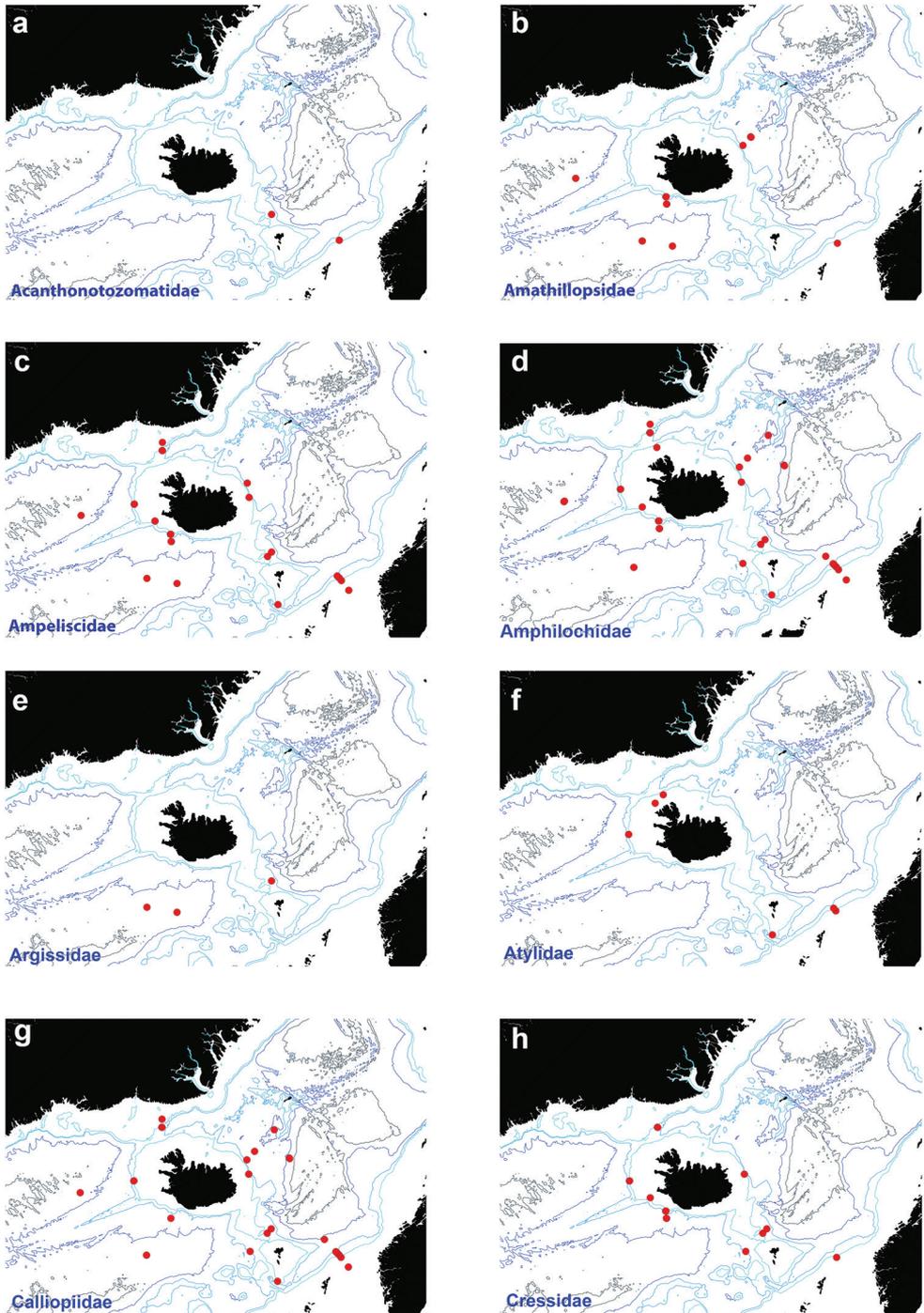


Figure 3. Distribution map for **a** Acanthonotozomatidae **b** Amathillopsidae **c** Ampeliscidae **d** Amphiloichidae **e** Argissidae **f** Atylidae **g** Calliopiidae **h** Cressidae in sorted IceAGE EBS samples.

Iceland whereas *Amathillopsis* is reported from the eastern stations. Forty-six specimens of *Cleonardopsis* were recorded, distributed in the Iceland Basin (eight stations) and the Irminger Basin (one station). The Amathillopsidae consists of a few little known, but morphologically spectacular, large amphipods, which lead a pelagic or benthopelagic life. Amathillopsids are found from the Arctic to the Antarctic. In the North Atlantic, the most commonly reported species is *Amathillopsis spinigera* Heller, 1875, with the lesser cited *A. affinis* Miers, 1881 possibly also present. In the present study, four specimens of this genus were recorded at three deep stations in the Norwegian Sea. The genus *Cleonardopsis* was reassigned to the Amathillopsidae in the new subfamily Cleonardopsinae (Lowry 2006). The species *Cleonardopsis carinata* K.H. Barnard, 1916 shows a cosmopolitan distribution in the deep sea. Described from South Atlantic waters (Cape Peninsula area; Barnard 1916), it has also been reported from eastern Greenland (Stephensen 1944), Bay of Biscay (Elizalde et al. 1993, Dauvin and Sorbe 1995, Frutos and Sorbe 2014a) and eastern Indonesia (off the Moluccas; Pirlot 1934).

Ampeliscidae Krøyer, 1842

Figure 3c

Ampeliscidae were reported from 23 of the 40 stations studied, with a total of 492 specimens. The Ampeliscidae are a benthic, soft sediment, generally tube-dwelling family. This group has strong grain-size and depth constraints (Dauvin et al. 2012). The family is known from intertidal to abyssal depths and often have antenna and pereopod morphology adapted for different feeding strategies at depth (Barnard 1961). The four genera in the family have some delimitation with depth with *Ampelisca*, the most diverse genus with more than 200 species, being a generalist in both depth and habitat requirements. This genus most frequently occurs in shallower waters, and numerous species are recorded from the Atlantic Ocean (Dauvin et al. 2012). A number of papers have recorded and described species from this family from northern Atlantic waters, particularly Scandinavian, Faroe Island and Icelandic waters and consequently there is a wealth of information regarding the depth, sediment, and distributional patterns of the group (Sars 1890–1895, Bellan-Santini and Dauvin 1988, 1997, 2008, Dauvin 1996, Dauvin et al. 2012). Thirteen of the 20 species of Ampeliscidae previously documented from Icelandic waters (Dauvin et al. 2012), were recorded in the IceAGE samples. The majority of ampeliscid species collected are in the genus *Ampelisca*. There were six species from the samples reported as new to Icelandic waters, with three of these new to science (Peart 2018). Relatively low abundances were observed compared to the BIOICE study (Dauvin et al. 2012). The genera *Byblis* (with more than 90 species), *Haploops* (with more than 20 species) and *Byblisoides* (six species) have been more frequently reported from deeper waters (Dauvin et al. 2012). The distribution reported here (Figure 3c) is supported by published data, which reports a wide distribution of Ampeliscidae around Iceland with the majority of the species occurring between 500 and 1500 m.

Amphilochidae Boeck, 1871

Figure 3d

Amphilochids were reported from 33 of the 40 stations studied, with a total of 1110 specimens. The family Amphilochidae is cosmopolitan and interestingly includes one species (*Gitanopsis alvina* Bellan-Santini and Thurston, 1996) from hydrothermal vents at the Mid-Atlantic Ridge (Bellan-Santini and Thurston 1996). The general body shape of amphilochids is small (1–5 mm mostly) and slightly stout, and observations of living specimens from the Norwegian and Barents seas support the impression that they are not fast swimmers (Tandberg, Vader personal observation). Amphilochids occur at all depths and temperatures, and are quite abundant in the North Atlantic, as in other cold seas. A total of 1110 amphilochid specimens were recorded in the the study, distributed across the genera *Amphilochus*, *Amphilochopsis*, *Amphilochoides*, *Gitana*, *Gitanopsis*, and *Paramphilochoides* (for a discussion on the genus *Amphilochopsis* see Tandberg and Vader (2018)). These specimens constituted 13 of the 17 species of Amphilochidae previously reported from the eastern North-Atlantic and Arctic (Vader and Tandberg, personal communication about a manuscript in preparation). Amphilochidae were found at 33 of the 40 stations that have been processed, with three stations (two in the Norwegian Channel and one north east of Iceland) having more than 100 specimens each. The Amphilochidae were found across all depth and temperature ranges in the IceAGE station network. Previous studies of amphilochids around Iceland indicated that the highest abundance and diversity occurs in the north of Iceland (Weisshappel and Svavarsson 1998).

Argissidae Walker, 1904

Figure 3e

Argissids were collected at three of the 40 sampling stations, all located south of Iceland, at 686–2749 m, with a total of six specimens. The family Argissidae comprises the single species *Argissa hamatipes* (Norman, 1869), originally described from shallow water in St. Magnus Bay, Shetland Islands, Scotland. Another species, *A. stebbingi* Bonnier, 1896, described from bathyal muddy bottoms of the southern Bay of Biscay, is currently considered a junior synonym of *A. hamatipes*. However, Lowry and Myers (2017) note that the genus *Argissa* is in need of revision since the distribution, depth range and morphological variation attributed to *A. hamatipes* are implausible when attributed to a single species. In the southern Bay of Biscay, *A. hamatipes* was collected with a suprabenthic sledge on sandy and muddy sand bottoms of the continental shelf (31–179 m), with a decreasing frequency of occurrence with depth (Sorbe 1984) and also at bathyal depths (711–1098 m) on muddy bottoms (Dauvin and Sorbe 1995, Frutos and Sorbe 2014a, Sorbe and Elizalde 2014). *Argissa hamatipes* is known to oc-

cur from the northeastern Atlantic Ocean and Norwegian Arctic (Palerud and Vader 1991). According to Wildish and Peer (1981) *A. hamatipes* is a deposit feeder. Given the current monotypic status of the family, this material is assigned to *A. hamatipes* extending the bathymetric distribution of this species to 2749 m, and supporting the need for a revision of the genus *Argissa*.

Atylidae Lilljeborg, 1865

Figure 3f

Atylidae occurred in samples from the Denmark Strait and the Faroe Channel at stations associated with strong bottom currents, in six of the 40 stations studied, with a total of 20 specimens. Palerud and Vader (1991) reported seven species of North-Atlantic Atylidae, currently ascribed to the genera *Atylus* and *Nototropis* (see Bousfield and Kendall 1994). Atylids are sometimes larger than 10 mm (Hendrycks, personal communication) and show particularly strong lateral compression along the dorsal pereonites with some species with middorsal carinae. Characteristic for this taxon is a notch in the dorsal keel of urosomite 1. The cuticle of atylids in most cases is thin and yellowish or unpigmented. Little is known of the ecology of atylids, though they appear to occur more commonly in soft bottom shallow-water habitats.

Calliopiidae Sars, 1893

Figure 3g

The family was present at 24 of the 40 stations studied, with a total of 470 specimens indicating its relative importance in this cold-water area. The relatively speciose family Calliopiidae is represented in the north east Atlantic by 39 species from 12 genera (Vader and Tandberg, unpublished data) which accounts for almost 50% of the known Calliopiidae in the world (Horton et al. 2017). Calliopiidae appear to favour colder waters, although many species are known from more temperate waters, few (if any) are found in warm waters (Bousfield and Hendrycks 1997). Several calliopiid species are known to be associates of molluscs, crustaceans (Vader and Tandberg 2013, 2015) and sponges (Vader 1984, Amsler et al. 2009). Non-associate calliopiid species are found on sandy or muddy seafloors and in macroalgae from littoral to bathyal depths (d'Udekem d'Acoz 2012). One species, *Apherusa glacialis* (Hansen, 1888) is associated exclusively with sea-ice habitat. Most species are carnivorous or detritivorous (Bousfield and Hendrycks 1997). Weisshappel (2001) showed a distinct difference in the species composition of the Calliopiidae on different sides of the Greenland-Iceland-Faroe ridge, with 72% of the species being restricted to one side of the ridge.

Cressidae Stebbing, 1899

Figure 3h

The family Cressidae was reported from 14 of the 40 stations studied, with a total of 190 specimens. Cressids have a compact body, specialised mandible and an extremely lengthened mandibular palp (Krapp-Schickel 2005). The family Cressidae is found mainly in the northern regions of the Atlantic and is comprised of ten species in two genera, *Cressa* Boeck, 1871 and *Cressina* Stephensen, 1931 (Horton et al. 2017). Three species have been identified so far as part of the IceAGE program, the same species as were indicated by Stephensen (1931) namely: *Cressa carinata* Stephensen, 1931, *Cressa minuta* Boeck, 1871 and *Cressina monocuspis* Stephensen, 1931.

Cyproideidae Barnard, 1974

Figure 4a

Cyproideidae was reported from three of the 40 stations studied. Twenty-four cyproideid specimens were recorded in the IceAGE material, mainly on the upper slope in both Irminger and Iceland basins (13 and ten individuals, respectively). A single specimen was also recorded from a northern Faroe station (station 879). The Cyproideidae are characterised by immensely broadened coxae 3/4 with contiguous abutting margins and overlapping coxae 1/2. The Cyproideidae includes 20 genera with 46 species (Horton et al. 2017). Cyproideids are found in association with marine algae, intertidal rocks or coral debris (Barnard 1972b, Lowry and Stoddart 2003, Azman 2009). They are also known to have associations with live corals (Myers 1985, Thomas 1999), sponges (Ortiz et al. 2000) and crinoids (Lowry and Azman 2008). Cyproideids are most diverse in the littoral shallow marine waters of the Indo-West Pacific (Barnard and Karaman 1991, Lowry and Azman 2008, Ariyama 2016), with just two genera recorded in the north east Atlantic: *Peltocoxa* and *Stegoplax*. *Peltocoxa* comprises five species, two of which (*P. brevirostris* (Scott and Scott, 1893) and *P. damnoniensis* (Stebbing, 1885)) occur in the Atlantic (Lincoln 1979, Palerud and Vader 1991). *Stegoplax* comprises a single deep-sea species, *Stegoplax longirostris* Sars, 1882 with a boreal distribution (Sars 1883, 1890–1895, Stephensen 1925, 1938, Buhl-Jensen 1986, Palerud and Vader 1991).

Dexaminidae Leach, 1814

Figure 4b

Dexaminids were found at four of the 40 stations studied in shallow areas east of Faroe Islands, Iceland Basin and Denmark Strait and at one deep station (2749 m) in the

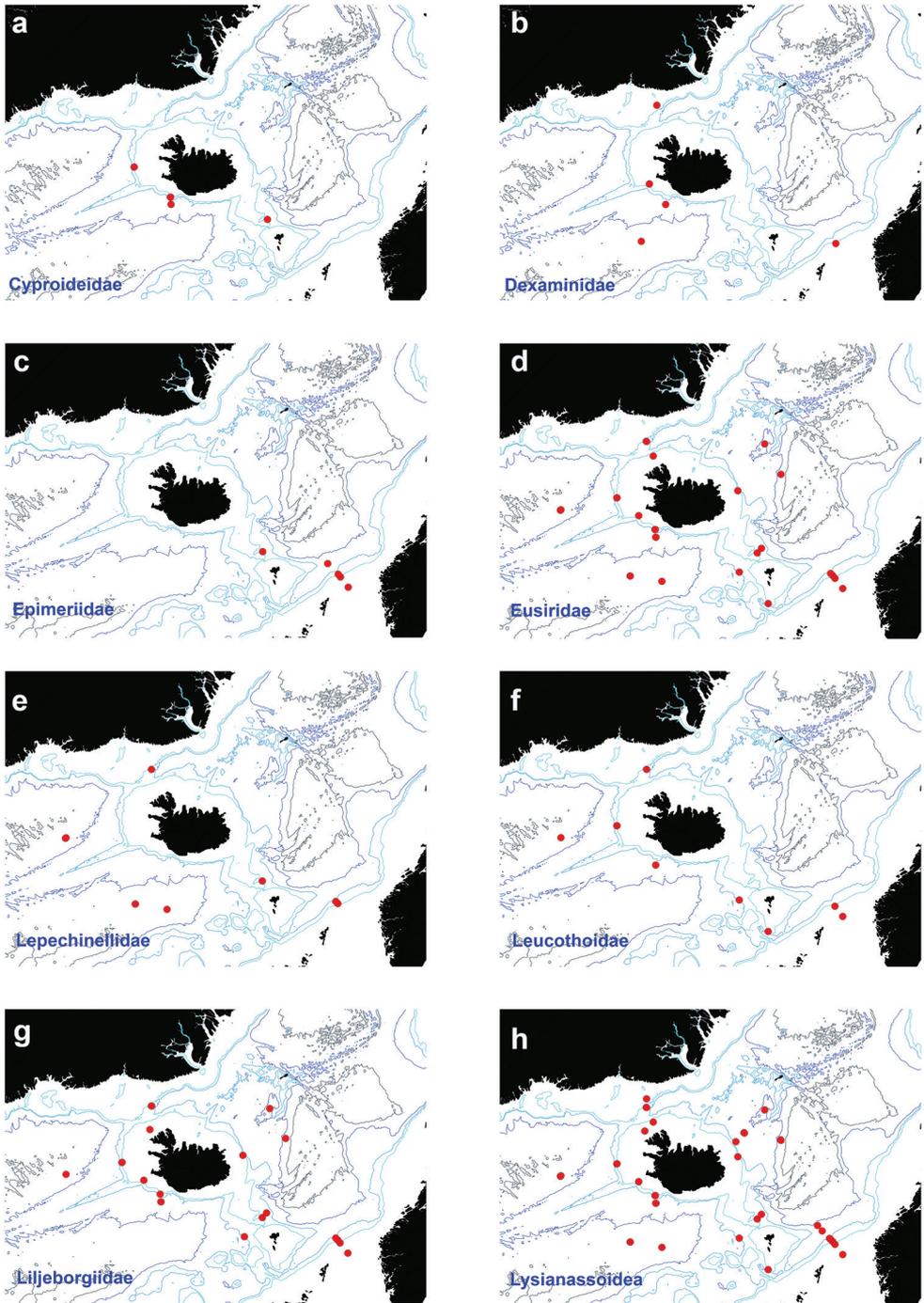


Figure 4. Distribution map for **a** Cyproideidae **b** Dexaminidae **c** Epimeriidae **d** Eusiridae **e** Lepechinellidae **f** Leucothoidae **g** Liljeborgiidae **h** Lysianassoidea, in sorted IceAGE EBS samples.

Iceland Basin, with a total of 14 specimens. Four species of the family Dexaminidae have been reported in the North-Atlantic (Palerud and Vader 1991). Dexaminids usually have carinate pleon segments, except for the genus *Guernea*, and their urosome segments 2 and 3 are fused. *Dexamine spinosa* (Montagu, 1813) and *Dexamine thea* Boeck, 1861 occur in shallow-water to 60 m (Lincoln 1979). *Tritaeta gibbosa* (Spence Bate, 1862) is associated with various invertebrates, living in sponges and ascidians (Lincoln 1979), and has also been shown to live in pouches in the integument of holothurians (Laetz et al. 2013). The Greenlandic *Guernea nordenskioldi* (Hansen, 1888), recently found both in Russia and in Svalbard waters, may well occur in the IceAGE samples. The short bodied *Guernea coalita* (Norman, 1868), a more southern species, is fossorial and occurs in fine sediments (Kim et al. 2011).

Epimeriidae Boeck, 1871

Figure 4c

Epimeriidae were reported from five of the 40 stations studied, with a total of 55 specimens, in the area of Iceland-Faroe Ridge, at depths less than 1600 m. This family usually feature prominent teeth carinae (d'Udekem d'Acoz 2010, Krapp-Schickel 2011) and/or robustly elongated coxal plates (Moore 1981, Barnard and Karaman 1991). Members of the Epimeriidae are bottom-dwelling, epibenthic amphipods represented by two genera in the northern Atlantic, *Epimeria* and *Paramphithoe* (Palerud and Vader 1991, Horton et al. 2017). Although the species are not abundant, this readily recognisable family are frequently recorded from shallow to deep waters of northern Atlantic and Arctic waters as well as around Iceland. Epimeriids contain members of several feeding types, such as filter feeders and micro-predators (Dauby et al 2001).

Eusiridae Stebbing, 1888

Figure 4d

Eusiridae were reported from 27 of the 40 stations studied with representatives in all sampling areas and depth zones. A total of 775 specimens of Eusiridae have so far been identified from the IceAGE samples. Eusirids are abundant members of the deep-sea fauna off Iceland (Weisshappel 2000), known to be predators (Enequist 1949) with good swimming capabilities (Bousfield and Hendrycks 1995). *Rhachotropis* Smith, 1883 was the dominant genus (see Lörz et al. 2018), with three other genera represented; namely *Eusirus*, *Cleonardo*, and *Eusirella*. About half of the specimens collected, 355 individuals, were from a single station at 169 m, which was also the shallowest sampled (station 866). This easternmost station is at the edge of the North Sea in contrast

to other stations containing eusirids, which are in the Arctic waters of the Norwegian Greenland Seas. This shallow station was dominated by a small *Rhachotropis* species with large eyes, *Rhachotropis northriana* d'Udekem d'Acoz, Vader & Legezynska, 2007.

Lepechinellidae Schellenberg, 1926

Figure 4e

Lepechinellids were reported from ten of the 40 stations studied, with a total of 103 specimens. The lepechinellids are well adapted to a demersal or epibenthic lifestyle on soft substrates in deeper waters (Barnard 1973). The family Lepechinellidae comprises five genera, three of which (*Lepechinella*; *Lepechinelloides*; *Lepesubchela*) have been reported in our study area (Thurston 1980, Palerud and Vader 1991, Johansen and Vader 2015). The genus *Lepechinella* was the most speciose and abundant taxon in the IceAGE samples. More than half of the lepechinellids collected, 60 individuals, were sampled from a single station at 500 m depth at the Iceland-Faroe Ridge (station 879). Owing to the fragility of the slender spines and thin elongate pereopods characteristic of the taxon, intact lepechinellids are difficult to obtain; however, the majority of specimens collected were considered to be in good condition. Morphological characters are known to vary strongly with growth and gender amongst lepechinellids (Barnard 1973, Thurston 1980). The present samples obtained a range of sizes of both genders of *Lepechinella arctica* Schellenberg, 1926, providing a promising opportunity for further studies on this species.

Leucothoidae Dana, 1852

Figure 4f

Leucothoids were reported from nine of the 40 stations studied, with a total of 35 specimens. The Leucothoidae are well represented within the Atlantic Ocean, though mainly in warmer regions. The documented Atlantic Ocean leucothoids have broad shared distributions with eight species also known from South and West Africa, 13 from the Caribbean and Gulf of Mexico, five from Brazil, three species from the Azores, Biscay, and Mid-Atlantic Ridge near Santa Cruz das Flores, and seven species from United Kingdom waters to the central and northern Atlantic. A new species of leucothoid is described based on specimens collected during the IceAGE expedition (Krapp-Schickel 2018). Leucothoids are usually found near, with, or in sponges or tunicates, and thus specimens are often overlooked inquilines (White 2011). During processing of IceAGE material, only juvenile and male individuals attributable to three species were identified, namely to the *Leucothoe spinicarpa* complex, *L. lilljeborgi* Boeck, 1861 and *L. vaderotti* Krapp-Schickel, 2018 (Krapp-Schickel 2018).

Liljeborgiidae Stebbing, 1899

Figure 4g

Three hundred eleven liljeborgiid specimens were collected from 20 of the 40 stations studied and covering a range of depths and distinct hydrological features. The Liljeborgiidae are micropredators, with some being known associates of other invertebrates, including hermit crabs (Vader 1995). Thirteen species of Liljeborgiidae have been reported from the North Atlantic (Vader and Tandberg, unpublished data). Liljeborgiids are primarily benthic species and can occasionally be quite abundant in benthic samples. A single station at 303 m depth in the Norwegian Trench (station 867) was characterised by an extremely high abundance of Liljeborgiidae (113 individuals).

Lysianassoidea Dana, 1849

Figure 4h

A total of 2008 specimens of lysianassoids and allied taxa was reported from 38 of the 40 stations studied occurring at depths from 169 to 2743 m. This superfamily is an incredibly large, diverse group of amphipods, which includes scavengers, predators, ectoparasites, obligate associates, and inquilines (e.g., Lowry and Stoddart 1983). The recent revision of Lowry and Myers (2017) has greatly restricted the concept of the Lysianassoidea to 130 genera in 12 families, where formerly the superfamily was composed of 22 families, 173 genera, and 1042 species. Lysianassoids range from a few millimetres in body length to the largest known amphipod, the 34 cm plus *Alicella gigantea* (Chevreux, 1899) which occurs in the deep North Atlantic and Pacific. Lysianassoidea are distributed globally and are particularly abundant at depth, where they form a specialist necrophagous guild, feeding on large and small food-falls (Horton and Thurston 2013). Many lysianassoids are highly mobile, fast swimmers, detecting food-falls from long range through chemoreception (e.g., Premke et al. 2003). Vader and Tandberg (unpublished) list almost 200 species of lysianassoid and allied taxa (including the Alicellidae, Scopelocheiridae, Valettiopsidae, and Eurytheneidae) from the eastern North-Atlantic and Arctic. The great diversity and abundance of lysianassoid taxa identified in the IceAGE material precluded anything more than a cursorial observation during the workshops and a sample set of this size is certainly worthy of a more in-depth study.

Melphidippidae Stebbing, 1899

Figure 5a

In total, 254 melphidippid specimens were recorded from 16 of the 40 stations. Melphidippids have elaborate spination and elongate slender legs and are, at least partially,

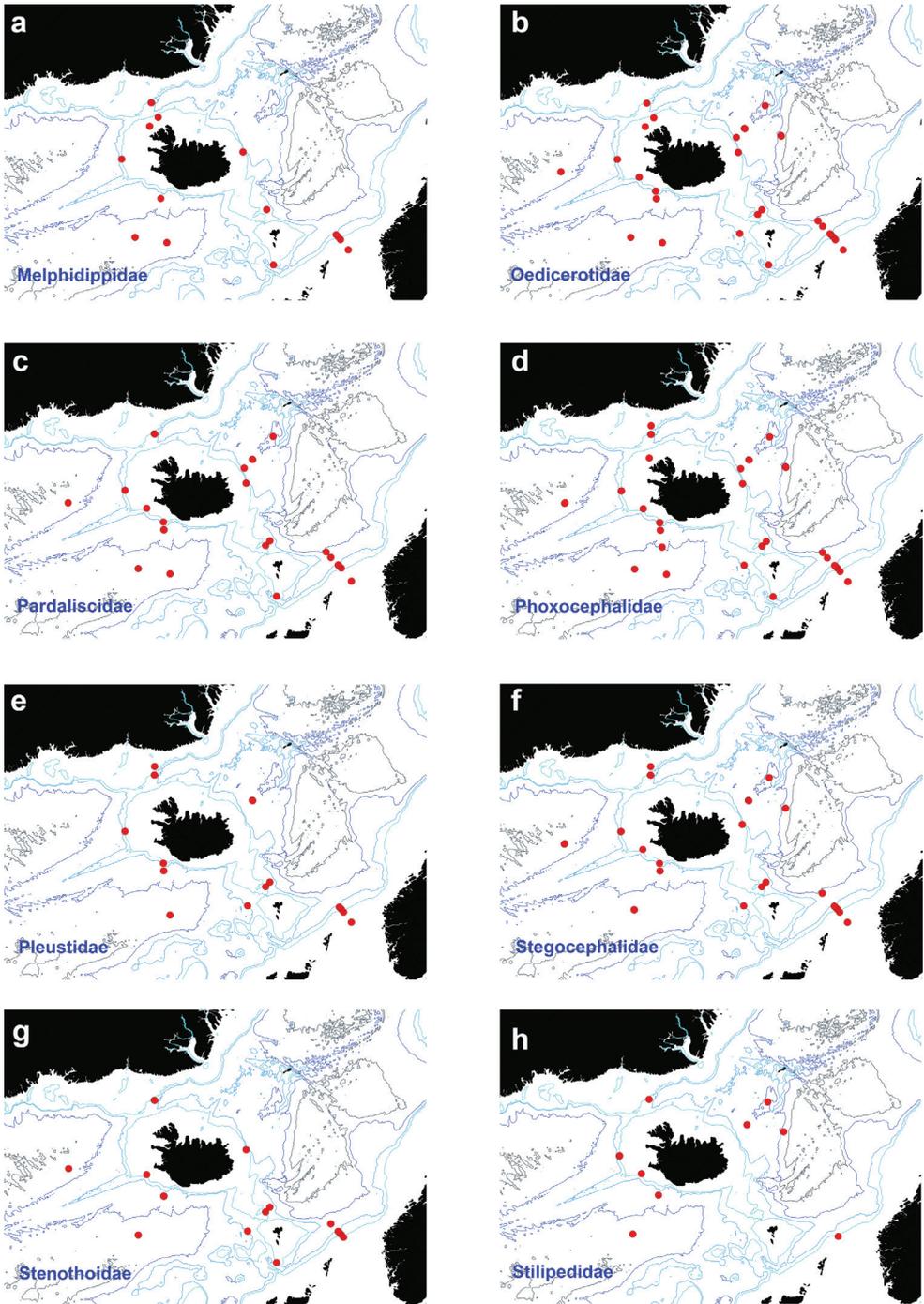


Figure 5. Distribution map for **a** Melphidippidae **b** Oedicerotidae **c** Pardaliscidae **d** Phoxocephalidae **e** Pleustidae **f** Stegocephalidae **g** Stenothoidae **h** Stilipedidae, in sorted IceAGE EBS samples.

epifaunal. Several studies have indicated that the normal orientation is upside down in a sling created by the elongate pereopods V to VII (Enequist 1949). Four species of the family Melphidippidae are known from the Nordic Seas, *Melphidippa borealis* Boeck, 1871, *M. goesi* Stebbing, 1899, *M. macrura* Sars, 1894 and *Melphidippella macra* Norman, 1869. The most common species is *Melphidippa borealis*, which has a wide depth distribution, from 50 to 2300 m. *Melphidippa goesi* is a more northerly species and is rarer on the Norwegian shelf, yet is frequently found off Iceland at 68 to 688 m. The closely aligned *Melphidippella macra* and *Melphidippa macrura* have more southerly distributions. *Melphidippella macra* has not been recorded from Iceland, is rarely recorded from Norwegian waters but is common in the Skagerrak (Miskov-Nodland et al. 1999). *Melphidippa macrura* is known only from Icelandic waters where water temperatures exceed 3 °C. Distribution of individuals appeared to indicate aggregations with numerous specimens at some stations, up to 83 individuals. Similar high-density records are also reported for *M. willemiana* d’Udekem d’Acoz, 2006, off Svalbard.

Oedicerotidae Lilljeborg, 1865

Figure 5b

Oedicerotids were present and often the most abundant family at 35 of the 40 stations and occurred alongside other fossorial amphipod families including the Phoxocephalidae and Urothoidae. A total of 3569 specimens was reported; nine genera and 21 species were identified from the material. Among amphipods, the Oedicerotidae are a dominant part of the North Atlantic benthic fauna. Oedicerotids live within the surface sediment of the seafloor and are deposit feeders (Enequist 1949) or can be carnivorous (Oliver and Slattery 1985). Shallow-water species are known to migrate into the water column for reproduction around lunar cycles and with tidal rhythms (Alldredge and King 1977, Forward 1986).

Pardaliscidae Boeck, 1871

Figure 5c

Pardaliscids occurred at 26 of the 40 stations studied, with a total of 327 specimens, suggesting that the family is well represented in the North Atlantic. Pardaliscids contain approximately 80 species worldwide (Horton et al. 2017). The family Pardaliscidae have good swimming ability and are mostly found living in deep-sea habitats (Birstein and Vinogradov 1962, Karaman 1974). A few genera are considered benthic, e.g., *Eperopus*; however the majority are thought to range between demersal and epibenthic with the ability to move far up in the water column. Assessment of gnathopod and mouthpart morphology implies that pardaliscids are a predatory family (Hendrycks and Conlan 2003). Weissshappel and Svavarsson (1998) reported pardaliscids from both north and south of Iceland, but the diversity was greater in the southern sites.

Phoxocephalidae Sars, 1891

Figure 5d

Phoxocephalidae were reported from 39 of the 40 stations studied, with a total of 2134 specimens. The family Phoxocephalidae contains 375 species (Horton et al. 2017) recorded in all oceans from tropical to polar zones with very high diversity in Australian waters (Barnard and Karaman 1991). Phoxocephalids are fossorial and burrow within soft sediments (De Broyer et al. 2003) constituting an abundant part of the infaunal amphipod assemblages from the shallow sublittoral to the deep sea (Cumings et al. 1998, Lörz and Bamber 2010, Jazdzewska 2015). They are predators (Oliver et al. 1982, Oliver and Slattery 1985). In the North Atlantic, Pallerud and Vader (1991) reported 21 phoxocephalid species ascribed to seven genera. Phoxocephalids are particularly abundant around Iceland (Brandt 1993, Brandt and Piepenburg 1994, Weisshappel and Svavarsson 1998) and the Norwegian Sea (Buhl-Jensen 1986, Buhl-Mortensen 1996).

Pleustidae Buchholz, 1874

Figure 5e

Pleustidae were reported from 16 of the 40 stations studied, with a total of 594 specimens. The family Pleustidae currently contains 241 species worldwide (Horton et al. 2017). Pleustid species are mostly small to medium-sized (range from 4–20 mm, but most are approx. 10 mm or less), benthic detritivores and carnivores (Bousfield and Hendrycks 1994). Many of the pleustid subfamilies have members which are closely associated with other invertebrates. Globally the distribution of pleustids is mainly Holarctic, North Atlantic and Arctic with only a small group recorded in southern hemisphere waters. The diversity of pleustids is most likely related to the abundance of other benthic invertebrates at the sites, as well as availability of algae for substrate. This potential inquiline association is supported by a patchy distribution, where two of the 15 IceAGE stations contained more than 200 individuals.

Stegocephalidae Dana, 1852

Figure 5f

In total, 1552 stegocephalids were found at 29 of 40 stations studied. Four of these stations reported more than 100 specimens, including one with 704 individuals (station 870). Stegocephalidae have been found at all depths and temperature ranges in the IceAGE material which aligns with the findings of the BIOICE expedition (Berge and Vader 1997). The family Stegocephalidae is common in the North Atlantic and

contains 26 genera and more than 100 species (Horton et al. 2017). Stegocephalids are quite variable in size, with the largest species found in the coldest waters. Most species are benthopelagic, while a few species (*Parandania* spp.) are truly pelagic. These latter are caught only irregularly, while some of the benthopelagic species such as *Andaniexis* and *Andaniopsis* may occur in large numbers over deep soft bottoms (Sars 1895, Vader pers. comm). Stegocephalids feed mainly as micro-predators on large invertebrates, quite often coelenterates, but some species are also predators, and a few live in loose associations with other invertebrates (Vader 1984). In the lower latitudes of the North Atlantic, 24 species have been reported (Vader, unpublished data).

Stenothoidae Boeck, 1871

Figure 5g

A total of 500 stenothoid specimens were recorded from 39 of the 40 stations. Stenothoids are well known associates of molluscs, sponges, or coelenterates (Krapp-Schickel and Vader 2015). While some probably profit from the water current created by the host, enabling them to filter-feed or graze their epiphytes, others are known to feed directly on tissues of the host's body or entire polyps. Thus, some species are found only by examination of the host, and not by sledge or trawl sampling methods. The diversity of Stenothoidae is high in the Atlantic Ocean with many species of *Stenothoe* (more species in shallower waters), *Metopa* (more species in deeper regions), and some *Stenula* species found in the study region. Thirty-five species of *Metopa* and ~ 20 species of *Stenothoe* occur in the Atlantic Ocean and Arctic. Two genera, *Metopa* and *Stenothoe* were found abundantly within the IceAGE collections. A third genus, *Stenula*, is rarely present.

Stilipedidae Holmes, 1908

Figure 5h

A total of 30 stilipedids was sampled from ten of the 40 stations studied. The family Stilipedidae is divided into three subfamilies and comprises six genera (*Alexandrella*, *Astyra*, *Astyroides*, *Bathypanoploea*, *Eclysis* and *Stilipes*) (Horton et al. 2017). The Stilipedidae is a cosmopolitan family, and only the genera *Astyra* and *Stilipes* occur in the NE Atlantic. An undescribed bathyal *Stilipes* species has been recorded in temperate waters of the Bay of Biscay (Lagardère 1977, Sorbe and Weber 1995, Frutos and Sorbe 2014a); whereas two *Astyra* species (*A. abyssi* Boeck, 1871 and *A. longipes* Stephensen, 1933) have been reported in boreal waters of Greenland-Iceland-Faroe and Norwegian seas (Stephensen 1931, 1933, 1940, Palerud and Vader 1991, Brandt 1993, Brandt and Piepenburg 1994, Brandt et al. 1996). The genus *Stilipes* and some *Astyra* species are ap-

parently pelagic (Berge 2003). The sampling carried out with sledges in the near-bottom environment (Sorbe and Weber 1995, Frutos and Sorbe 2014b, present study) shows these species could also exhibit a suprabenthic behaviour. *Astyra abyssi* was the most frequently found species (24 specimens), sampled at five stations in the Irminger and Iceland basins and in the Norwegian Channel; whereas *A. longipes* occurred in deeper water in the Norwegian Sea. A different (possibly new) *Astyra* species, was recorded in the Iceland basin at the deepest station (>2700 m) of the expedition (station 967).

Synopiidae Dana, 1853

Figure 6a

Synopiidae were sampled at 19 of the 40 stations studied, with a total of 676 specimens. The Synopiidae are a typical deep-sea family distributed worldwide (Barnard 1972a). Synopiids can be easily recognised by the large head and rostrum shape, feebly developed gnathopods, and very large telson. Currently, the Synopiidae comprises 108 species in 18 genera (Horton et al. 2017). Synopiids in NE Atlantic waters are represented by the genera: *Austrosyrrhoe*, *Bruzelia*, *Ileraustrae*, *Jeddo*, *Pseudotiron*, *Stephobruzelia*, *Syrrhoe*, *Syrrhoites*, and *Tiron* (Sars 1890–1895, Stephensen 1931, 1938, 1944, Buhl-Jensen 1986, Palerud and Vader 1991, Brandt et al. 1996, Brandt 1997b, Bachelet et al. 2003, Frutos and Sorbe 2014a). They occur in all the areas studied from the Icelandic shelf and slope to the deeper Norwegian, Irminger and Icelandic basins, the Denmark Strait, and the Faroe Channel. At least 13 species belonging to the genera *Austrosyrrhoe*, *Bruzelia*, *Syrrhoe*, *Syrrhoites*, and *Pseudotiron* have been identified so far. Preliminary identifications show that *Syrrhoites* appears to be the most speciose genus.

Urothoidae Bousfield, 1978

Figure 6b

A total of 138 individuals were present at 12 of the 40 stations examined, all situated south of Iceland (but were not found in the Norwegian Sea). This family comprises amphipods with small body size, 2 mm to 10 mm, which are highly adapted to a fossorial lifestyle (Bousfield 1982). Urothoidae currently comprises 61 species in six genera (Horton et al. 2017). The family has a cosmopolitan distribution and can be found from shallow waters to abyssal depths (Sittrop et al. 2015). Almost all North Atlantic urothoids are shallow water, sandy bottom species; only *Urothoe elegans* (Spence Bate, 1857) and *Carangolia barnardi* Jaume & Sorbe, 2001 occur in deep North Atlantic waters (Lincoln 1979, Jaume and Sorbe 2001). Urothoids are detritus feeders, and their association with soft bottom habitat supports this. The family is commonly encountered in North Atlantic samples where this habitat dominates.

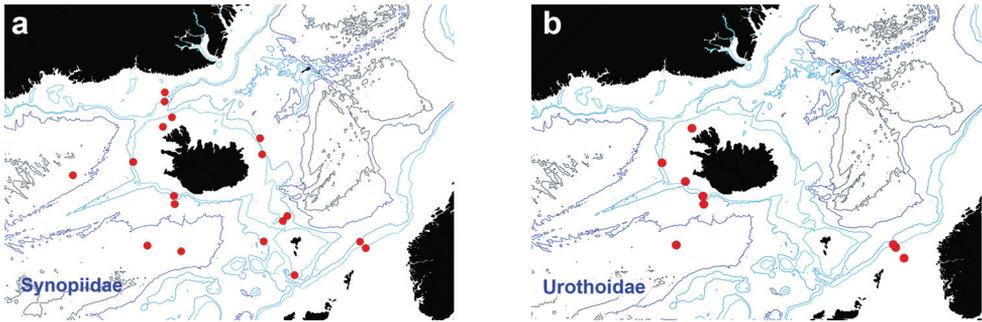


Figure 6. Distribution map for **a** Synopiidae **b** Urothoidae, in sorted IceAGE EBS samples.

Corophiida

Taking into account frequent damage of fragile Amphipoda belonging to the infraorder Corophiida, individuals with uncertain family assignment, are presented in Figure 7.

Aoridae Stebbing, 1899

Figure 7a

Aorids were collected at 12 of the 40 stations, located east, south and west of Iceland (apparently absent at the northern stations), at depths between 168 and 2750 m, with a total of 105 specimens. The family Aoridae contains 250 known species world-wide belonging to 25 genera. According to Palerud and Vader (1991) and Myers (1998), only 15 aorid species belonging to six genera were listed from the North Atlantic and Norwegian Arctic (including Icelandic waters). *Aora*, *Lembos*, and *Microdeutopus* are detritus-feeders and show tube-dwelling habits, whose construction involves secretions produced by glands located on the third and fourth pairs of pereopods (Enequist 1949).

Caprellidae Leach, 1814

Figure 7b

Caprellidae occurred at half of the stations sampled (18 of 40 stations), between 168 and 2747 m, with a total of 1052 specimens. The family Caprellidae is large with 91 genera and more than 400 species. Species are often epibionts, associated with other organisms such as algae, hydrozoans, bryozoans (Caine 1989), or even commensals of some marine invertebrates including echinoderms (Guerra-García 2001, Guerra-García et al. 2008) and decapods (Martin and Pettit 1998). As in most groups, knowledge

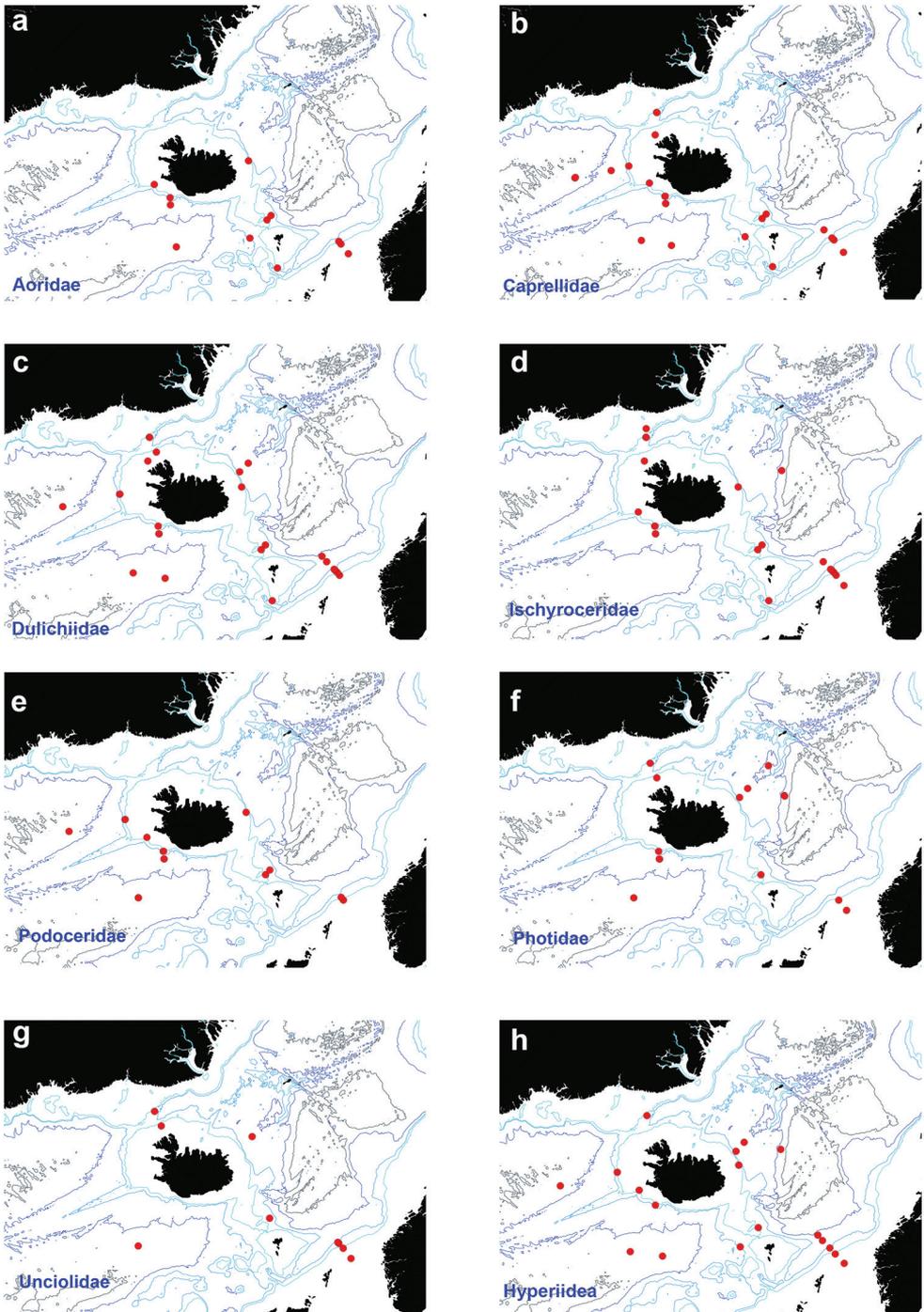


Figure 7. Distribution map for Corophiida **a** Aoridae **b** Caprellidae **c** Dulichiidae **d** Ischyroceridae **e** Podoceridae **f** Photidae **g** Uncioliidae **h** Hyperideae, in sorted IceAGE EBS samples.

of the biology and distribution is more extensive for shallow-water species; but they are also known to have a significant presence in deep-sea ecosystems, with numerous records from Pacific, Atlantic, Arctic, and circum-Antarctic waters (see Guerra-García 2003). In recent years, the number of species reported from the deep-sea has increased, through the revision of collections from different museums (Guerra-García 2003, 2004, Guerra-García and García-Gómez 2003) and new oceanographic expeditions (Laubitz and Sorbe 1996, Guerra-García et al. 2008).

Dulichiiidae Dana, 1849

Figure 7c

Dulichiiids were moderately abundant at more than half the stations in all areas studied and were found in very large numbers (thousands of individuals) at two stations in the Iceland Basin. They were reported from 24 of the 40 stations studied, with a total of 6547 specimens. In our material, Dulichiidae are represented by the genus *Dulichiosis*, and mainly by the species *Dulichiosis macera* (Sars, 1879). It is one of the most abundant groups, dominating at stations in the Iceland Basin. The Dulichiidae currently comprises six genera (Rauschert 1990, Horton et al. 2017) and a total of 26 known species. The genus *Dulichiosis*, is one of the most speciose, with seven described species that are known mainly from the deep sea (183 to 3229 m) being widely distributed in the North Atlantic, North Pacific and Arctic Oceans as well as in the Indian Ocean (north Madagascar) (Laubitz 1977, 1979, Ledoyer 1986). The presence of glandular pereopods 3–4 and very long, slender pereopods 5–7 suggests that they are filter-feeders and stem-builders. Such behaviour, including self-constructed stems has been described in various coastal species including *Dulichia falcata* (Spence Bate, 1857), *D. rhabdoplastis* McCloskey, 1970, *Dyopedos monacanthus* (Metzger, 1875), *D. porrectus* Spence Bate, 1857 (see McCloskey 1970, Laubitz 1977, 1979, Moore and Earll 1985, Mattson and Cedhagen 1989, Meyer-Rochow et al. 1991, Thiel 1997, 1998), and *Dulichiosis diana*e Corbari & Sorbe, 2017.

Ischyroceridae Stebbing, 1899

Figure 7d

Ischyrocerids were reported from 20 of the 40 stations studied, with a total of 731 specimens. The family Ischyroceridae is a diverse group with 269 described species worldwide (Horton et al. 2017). In the north east Atlantic the family is represented by 28 species (Palerud and Vader 1991, Brandt 1997b). Ischyroceridae are mostly suspension- and deposit-feeders and tube-dwellers occurring mainly on the shelf, although

some species occur also at bathyal and abyssal depths (Lincoln 1979, Brandt 1993, 1997b). Their key feature is the ability to construct tubes with ‘amphipod silk’. Accordingly, hemi-sessile species may occur on soft- and hard-substrata of the northern Atlantic and the Arctic where they can be locally quite abundant (Sars 1893, Barnard and Karaman 1991, Buhl-Mortensen 1996). In the present study, the family was recorded from all areas except the Irminger Basin. Findings from the deeper waters around Iceland, however, were infrequent and restricted to few species (Raitt 1938, Stephensen 1940).

Podoceridae Leach, 1814

Figure 7e

In this study, 638 podocerids were identified from 11 of the 40 stations studied, with clusters in the waters south-west and south-east of Iceland. This diversity is almost certainly underrepresented, as some specimens were most likely identified as corophiids. The Podoceridae have undergone major changes due to the work of Myers and Lowry (2003). The family presently includes eight accepted genera with ~ 100 species and subspecies, the vast majority belonging to the genus *Podocerus* (Horton et al. 2017). Most members of the Podoceridae inhabit temperate and warm waters and are bottom-living genera with depressed and cylindrical bodies; however, both *Xenodice* and *Neoxenodice* are primarily cold-water amphipods. Podocerids are often found as epifauna on macroalgae and large invertebrates such as sponges and ascidians. They are poor swimmers, with the main method of locomotion being crawling and climbing, with the abdomen flexed under the body (Laubitz 1979).

Photidae Boeck, 1871

Figure 7f

Photids were collected at 12 of the 40 stations studied located all around Iceland, excluding the Irminger Basin, at depths between 118 and 2749 m, with a total of 454 specimens. Worldwide, the Photidae contain 163 known species belonging to 17 genera (Horton et al. 2017). According to Stephensen (1933, 1940) and Palerud and Vader (1991), 13 photid species belonging to four genera were listed from the north eastern Atlantic and Norwegian Arctic (including Icelandic waters). With few exceptions, Photidae are known to live in littoral and sublittoral habitats reaching shallow to bathyal depths. In the North Atlantic, *Photis longicaudata* (Spence Bate, 1862) and *Photis reinhardi* Krøyer, 1842 construct short tubes of clay or detritus attached to a firm substratum forming dense aggregations along the seafloor (Enequist 1949).

Unciolidae Myers & Lowry, 2003

Figure 7g

A total of 155 specimens of the family Unciolidae was recovered from ten of the 40 stations studied, in all areas and with a very wide depth range (118–2749 m). Unciolidae are comprised of 18 genera and are distributed worldwide in both cold and warm waters. There are two genera in the subfamily Unciolinae present in Nordic Seas, *Neohela* and *Unciola*. One of the largest and most conspicuous species is *Neohela monstrosa* (Boeck, 1861). It is common in the cold and deep waters of the Norwegian Sea from 300 to 2000 m, and is known to create burrows 10 cm deep and form dense populations on soft deep-sea sediments (Buhl-Mortensen et al. 2016). Another common unciolid, *Unciola planipes* Norman, 1867, is recorded from Skagerrak to north of Lofoten (Vader et al. 1997) and is found below 400 m on the outer parts of the Norwegian shelf (Buhl-Jensen 1986). Other *Unciola* species found in Nordic Seas include *U. crenatipalma* (Spence Bate, 1862) a southerly species not common in Norwegian waters, *U. leucopis* (Krøyer, 1845) and *U. petalocera* (Sars, 1876), which have a northern distribution, found rarely in the Barents Sea (Vader et al. 1997).

Hyperiidæ Milne Edwards, 1830

Figure 7h

Hyperiidæ were reported from 22 of the 40 stations studied, with a total of 134 specimens. The Hyperiidæ is a diverse planktonic suborder of amphipods comprising almost 300 species in 76 genera (Horton et al. 2017). During the IceAGE sampling, specimens of the Hyperiidæ were mostly found in low numbers (1–5 individuals per station). Specimens occurred in remarkably high numbers at two stations situated west of the Norwegian shelf break, in the Norwegian Channel, at around 1000 m. Hyperiidæ are often parasitic or commensal on gelatinous zooplankton (Laval 1980). The IceAGE sampling was carried out by means of an epibenthic sledge and the presence of high numbers of hyperiidæ caught above the seafloor, indicates their hyperbenthic feeding habits. These habits may be frequent and Vinogradov (1999b) has reported swarms of Arctic *Themisto* feeding on particles on the deep-sea floor. Hyperiidæ seem to be commonly occurring throughout the Norwegian Channel and were found in high numbers at around 2700 m depth in the Iceland Basin. All specimens were recovered from depths greater than 600 m.

Statistical Analysis

Within the benthic deep-sea invertebrate assemblages, amphipods are an abundant and diverse group. Worldwide around 10,000 species are described, about 80% of

which are marine (Horton et al. 2017). As the most abundant and diverse crustacean order in the marine benthos, the determination of IceAGE amphipod specimens provided urgently needed baseline data to understand the scale of existing collections and for future studies in the North Atlantic and Nordic seas.

Family level data

Similarity analysis yielded two larger groups of samples, of which one (A) is further divided into two subclusters (Figure 8). The subcluster A1 (65% similarity) contains mostly shallower samples, 169 to 913 m (and one deeper station from 1386 m), from Irminger Basin, Reykjanes Ridge, Iceland Basin and north of the Faroe Islands. These samples are characterised by a high diversity with all 37 amphipod groups recorded. The constant presence (71–100% frequency) of Ampeliscidae, Amphilochidae, Aoridae, Caprellidae, Dulichiidae, Ischyroceridae, Corophiida, Eusiridae, Liljeborgiidae, Lysianassoidea, Oedicerotidae, Pardaliscidae, Phoxocephalidae, Stegocephalidae, and Stenothoidae, is noted here. The shallower group is linked with a small cluster of three deep-water samples (2537–2567 m) collected in the Iceland and Irminger basins having 62% similarity. Compared to the shallower cluster, this group can be defined by the significant absence of two families, the Ischyroceridae and Liljeborgiidae, which were both a constant element in the shallower group.

The second major group, cluster B (Figure 8), contains nine samples at 55% similarity from the Norwegian Sea and east of the Faroe Islands. It is a group of deep-sea samples, 1058 to 2422 m, again aligning with just one shallow sample from 600 m. Twenty-six taxa are found in cluster B, which is characterised by the presence of eight families: Amphilochidae, Calliopiidae, Hyperlopsidae, Lysianassoidea, Oedicerotidae, Pardaliscidae, Phoxocephalidae and Stegocephalidae. Compared to cluster A1, in cluster B, the Ampeliscidae, Dulichiidae, Ischyroceridae, Eusiridae, and Stenothoidae have much lower frequencies (between 11 and 44%).

Differences in family richness are also observed between cluster A1 and B. The mean number of families per sample is significantly higher in cluster A1 ($Z = 3.951$, $p = 0.00007$; 21.4 ± 3.6 , $\text{min} = 17$, $\text{max} = 30$) compared to cluster B (11.2 ± 1.8 , $\text{min} = 9$, $\text{max} = 14$).

The spatial distribution of the clusters (Figure 9) can be associated with the hydrography of the region. The subcluster A1 consists of very widely distributed samples but their common factor is shallow depths (generally less than 1000 m). A similar pattern was observed for the anthuridean isopod *Calathura brachiata* (Stimpson, 1853) (Negoescu and Svavarsson 1997). This distribution can be linked to the warm surface current (North Atlantic Current) that comes from the south, in the Iceland Basin, divides, with one branch flowing around the Faroe islands, and the second branch encircling Iceland along its south and west coast (Ostmann et al. 2014). The subcluster A2 groups deeper stations from the Iceland and Irminger basins, separated by the Reykjanes Ridge. The lack of a barrier effect has already been observed for other peracarids, including Amphipoda (Svavarsson 1997, Negoescu and Svavarsson 1997, Brix et al. 2014b, Jażdżewska et al.

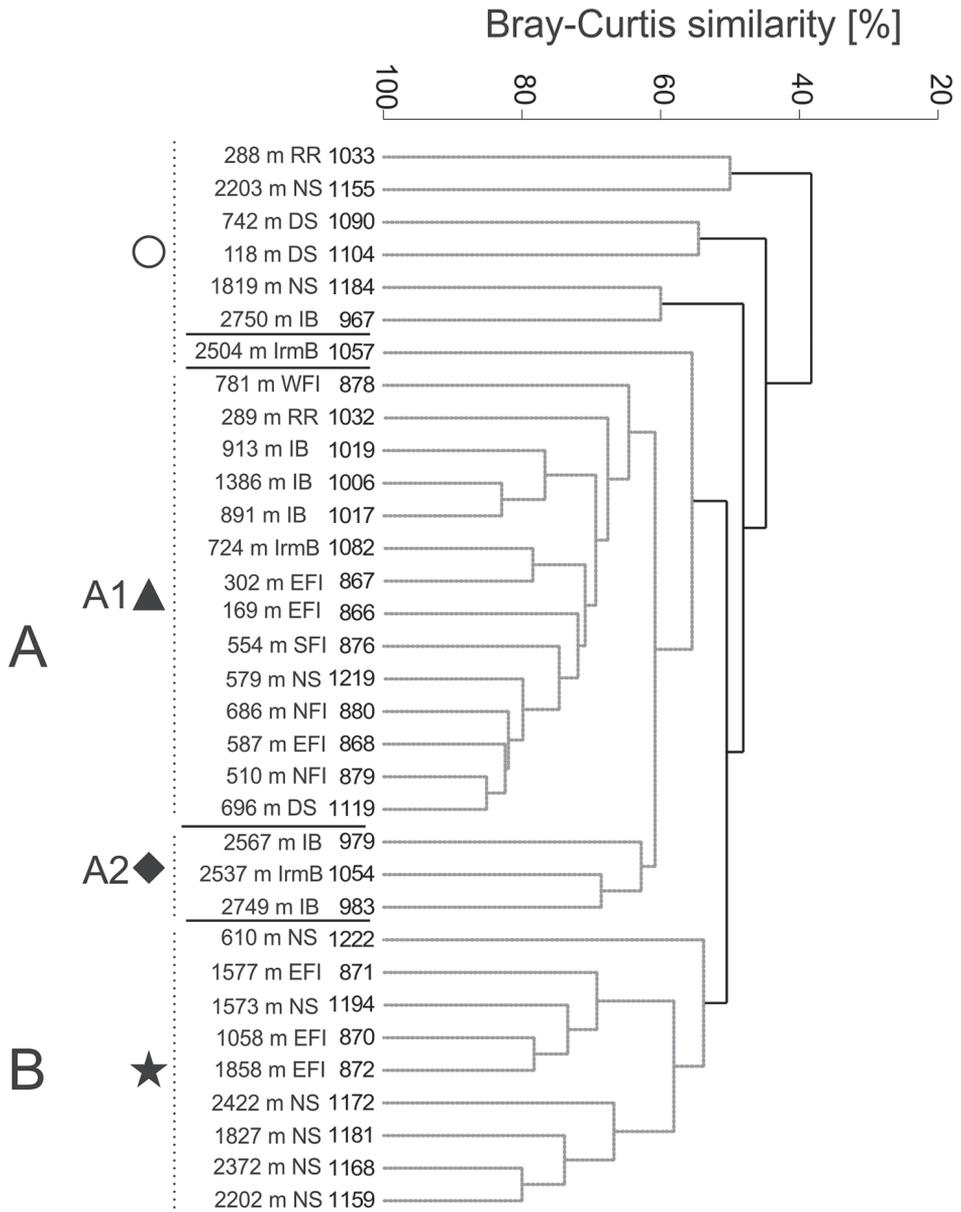


Figure 8. Dendrogram of samples for the family level data (Bray-Curtis similarity, group average grouping method and presence/absence transformed data). Abbreviations: RR - Reykjanes Ridge, NS - Norwegian Sea, DS - Denmark Strait, IB - Iceland Basin, IrmB - Irminger Basin, WFI - west off Faroe Islands, EFI - east off Faroe Islands, SFI - South of Faroe Islands, NFI - North of Faroe Islands. (Grey spotted lines indicate the samples that cannot be significantly differentiated by SIMPROF.) Regions are named based on the habitats defined by Meißner et al. (2014).

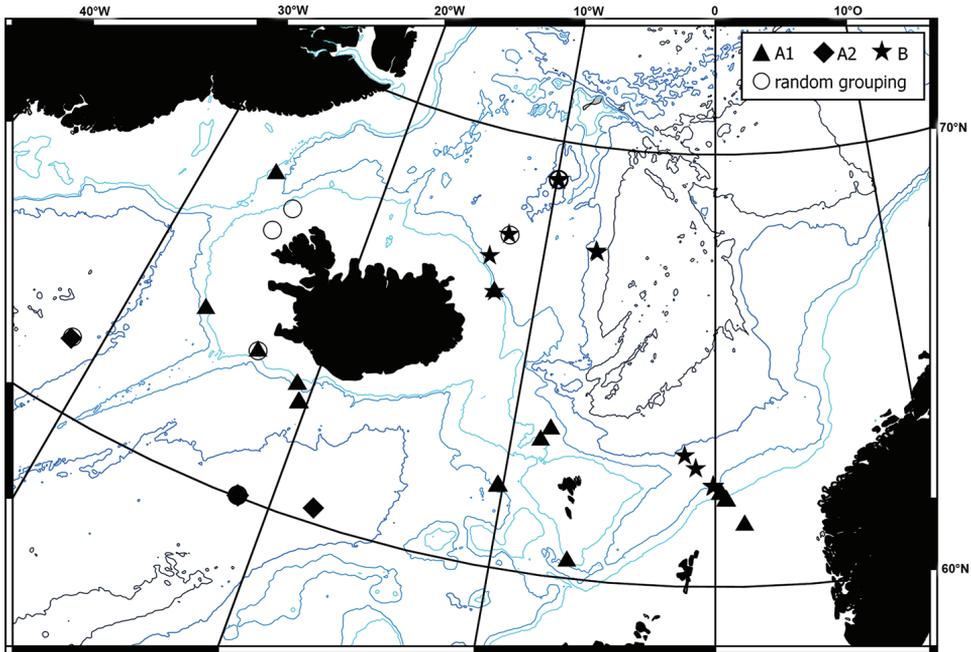


Figure 9. The spatial distribution of the clusters can be associated with the hydrography of the region. Symbols of the clusters from figure 8 are plotted on the station map.

2018). In the case of subcluster A2 (see Figure 9), the Iceland Scotland Overflow Water, which is a deep-water, cold current moving from north east into the Iceland Basin and later flowing along the Reykjanes Ridge into the Irminger Basin seems to be responsible for shaping the observed assemblage (Ostmann et al. 2014). Finally, the third group recognised consists of deep (middle and deep bathyal) samples from the Norwegian Sea and the east Faroe Islands and may be associated with cold Norwegian Sea deep water (Ostmann et al. 2014). The samples of cluster B have lower diversity in comparison to subcluster A1 and similar differences between Norwegian Sea and northernmost part of North Atlantic Ocean were observed previously for Isopoda (Svavarsson 1997).

Species level data (Amphilochidae and Oedicerotidae)

Figure 10–14

For the IceAGE Amphilochidae, similarity analysis demonstrated two larger groups of samples both at relatively low levels of similarity (Figure 10). Amphilochid cluster E, (40% similarity), groups deep-sea samples from different locations (Norwegian Sea, Irminger Basin, and Iceland Basin), and is characterised by a low diversity and dominated by *Amphilochus anoculus* Tandberg & Vader, 2018 (Tandberg and Vader 2018). Amphilochid cluster

F (21% similarity) contains mostly shallower samples, 118 to 891 m, in alignment with three deeper samples from 1058 to 2372 m, from various locations. Amphilochid cluster F is dominated by *Amphilochus tenuimanus* Boeck, 1871 and *Amphilochus manudens* Spence Bate, 1862. All 13 species of Amphilochidae were found in the samples forming this cluster.

In the analysis of Amphilochidae from BIOICE (Figure 11), the similarity analysis yielded two larger clusters at low levels of similarity (cluster H – 30% similarity and cluster I – 15% similarity), both containing samples from a similar depth range (from 63 to 772 m) and one smaller group of samples, amphilochid cluster G, collected in a deeper area 1048 to 1407 m and a single sample from 776 m. Amphilochid cluster G (100% similarity), is characterised by the consistent presence of one species *Amphilochopsis hamatus* Stephensen, 1925. Amphilochid cluster H is characterised by high abundance and frequency of *Amphilochus manudens* and *Amphilochus tenuimanus*, while amphilochid cluster I is dominated by *Gitanopsis arctica* Sars, 1892. BIOICE and IceAGE Amphilochidae were analysed in two different datasets due to different abiotic information between the two projects. Overall, the BIOICE amphilochid cluster H corresponds with the IceAGE amphilochid cluster F, while BIOICE amphilochid cluster G is consistent with IceAGE Amphilochidae cluster E (Figure 11), where the depth ranges and common species are the same. Thus, both datasets do show the same pattern.

Although *Gitana* was recorded as a deep and cold-water associated genus in the IceAGE samples, it is known to occur commonly at shallow depths in the North Sea (Beermann and Franke 2011) and the Mediterranean Sea (Krapp-Schickel 1982). However, an affinity with deep and cold water is recognised for the very widely distributed new species *Amphilochus anoculus* (Tandberg and Vader 2018) and *Amphilochopsis hamatus*. *Amphilochus manudens* seems to be limited to the upper 1000 m, with conspicuous abundance at all stations from both BIOICE and IceAGE samples from south-west of the Reykjanes Peninsula (Figure 13). The most abundant amphilochid species, *Amphilochus tenuimanus*, was sampled mainly from shallow waters to the shelf edge (139–905 m, with one record from 1384 m). It is worth highlighting, however, the distinct possibility that *Amphilochus manudens* might be a cryptic species complex (Jazdzewska et al. 2018, Tandberg and Vader 2018).

More detailed analysis of the family Oedicerotidae yields two weakly marked clusters at low levels of similarity (cluster C – 19%, cluster D – 4%; Figure 12). Overall, distribution patterns observed for the Oedicerotidae reflected those seen for the higher family-level analysis. In oedicerotid cluster C there is a subcluster of deep-sea samples collected in the Norwegian Sea (C1 - at 62% similarity). This oedicerotid cluster C1 largely corresponds with the family level cluster B. Samples from oedicerotid subcluster C1 are dominated by *Paroediceros curvirostris* (Hansen, 1888), *Deflexilodes tenuirostratus* (Boeck, 1871), *Arrhis phyllonyx* (Sars M, 1858) and *Paroediceros propinquus* (Göes, 1866). Shallower samples are grouped in the oedicerotid cluster D but are also spread across various other subclusters. Oedicerotid cluster D samples are consistently from the continental shelf depths, 118 to 587m, but notably from different regions (Iceland Basin, Reykjanes Ridge, Denmark Strait, north of Faroe Islands). Oedicerotid cluster D is dominated by *Synchelidium haplocheles* (Grube, 1864) and *Monoculodes pallidus* Sars,

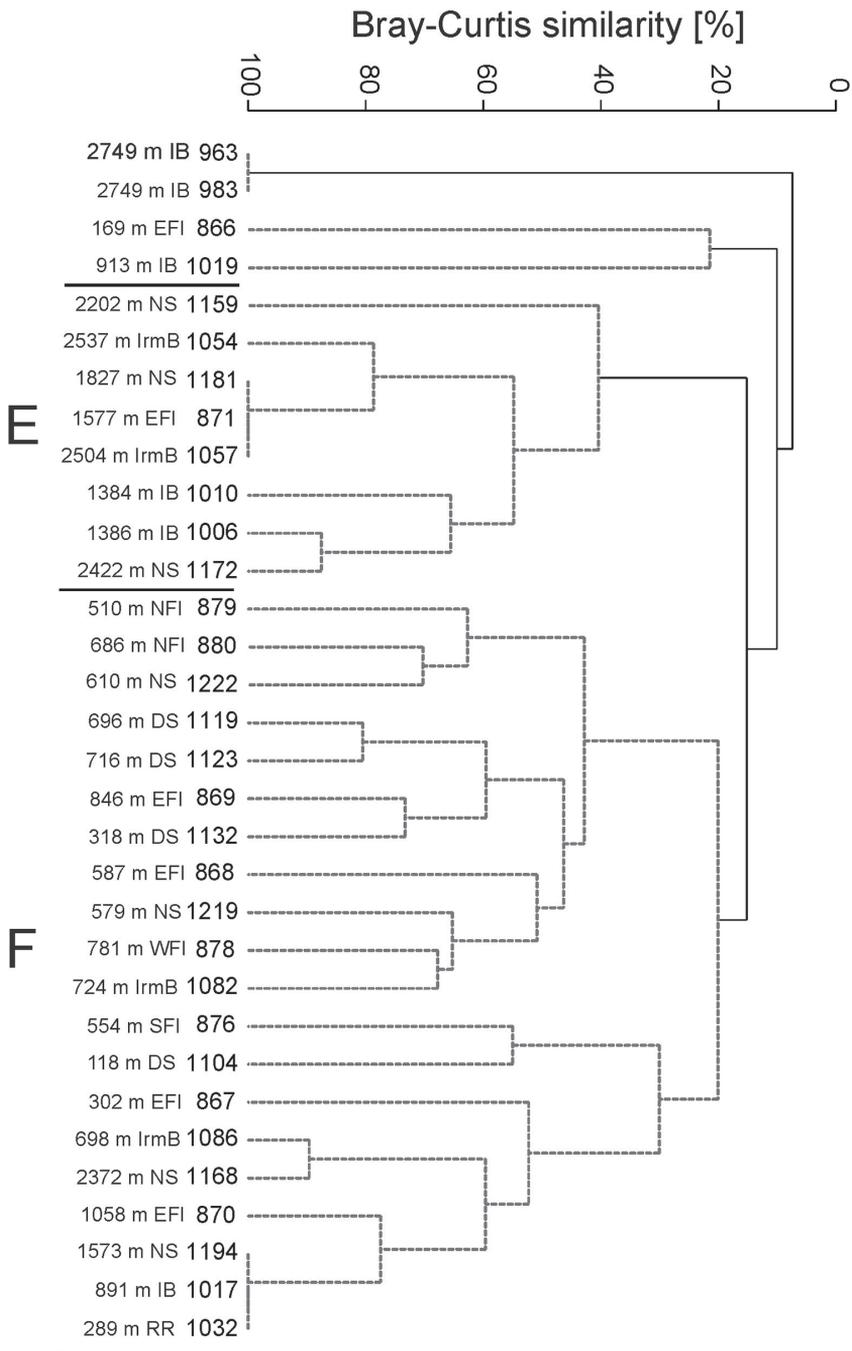


Figure 10. Dendrogram of samples for the Amphilochidae (Bray-Curtis similarity, group average grouping method standardised and square root transformed data). RR - Reykjanes Ridge, NS - Norwegian Sea, DS - Denmark Strait, IB - Iceland Basin, IrmB - Irminger Basin, WFI - west off Faroe Islands, EFI - east off Faroe Islands, SFI - South of Faroe Islands, NFI - North of Faroe Islands. Grey spotted lines indicate the samples that cannot be significantly differentiated by SIMPROF.

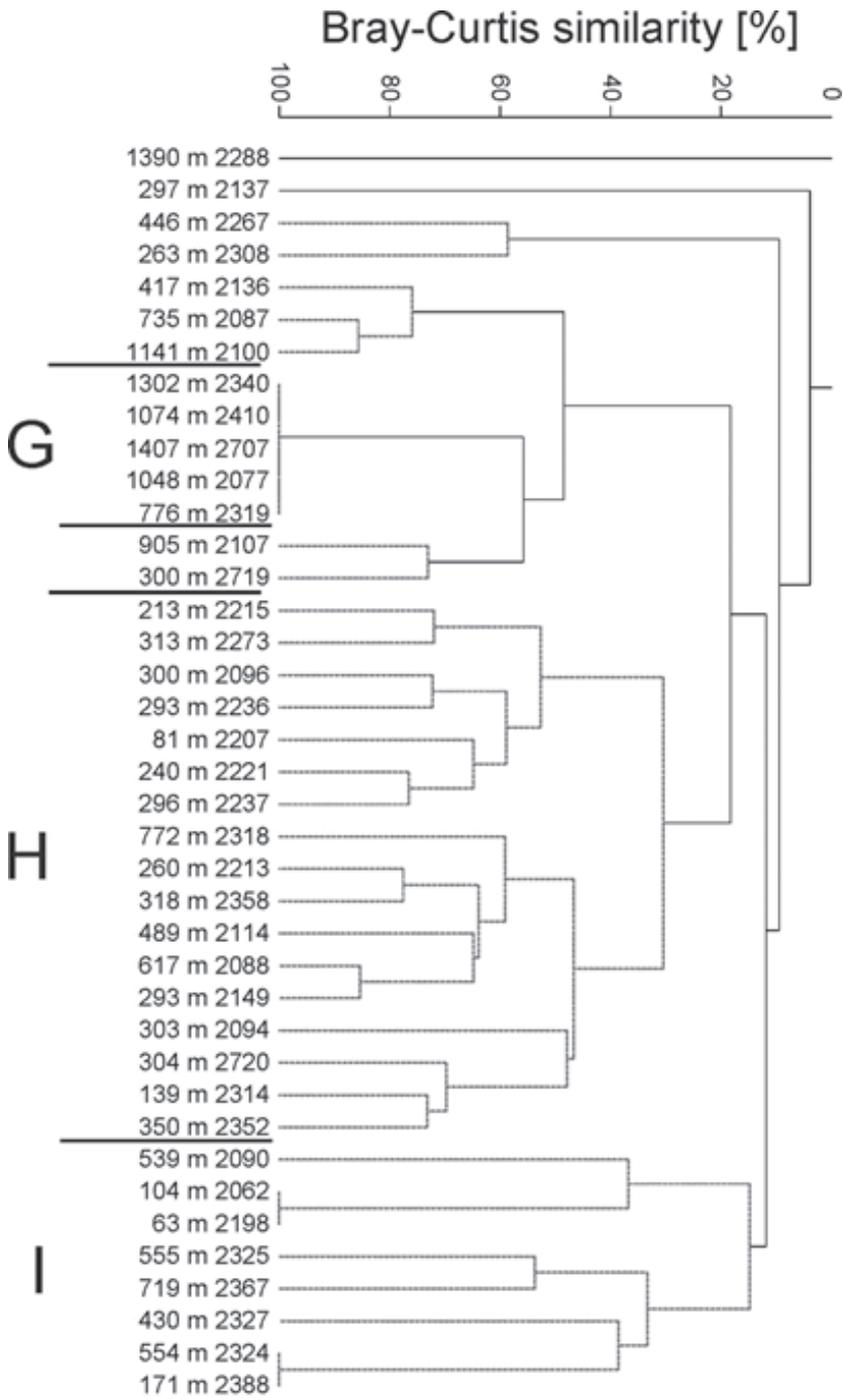


Figure 11. Amphilochidae BIOICE Dendrogram of samples for the Amphilochidae collected during BIOICE project (Bray-Curtis similarity, group average grouping method standardised and square root transformed data). Grey spotted lines indicate the samples that cannot be significantly differentiated by SIMPROF.

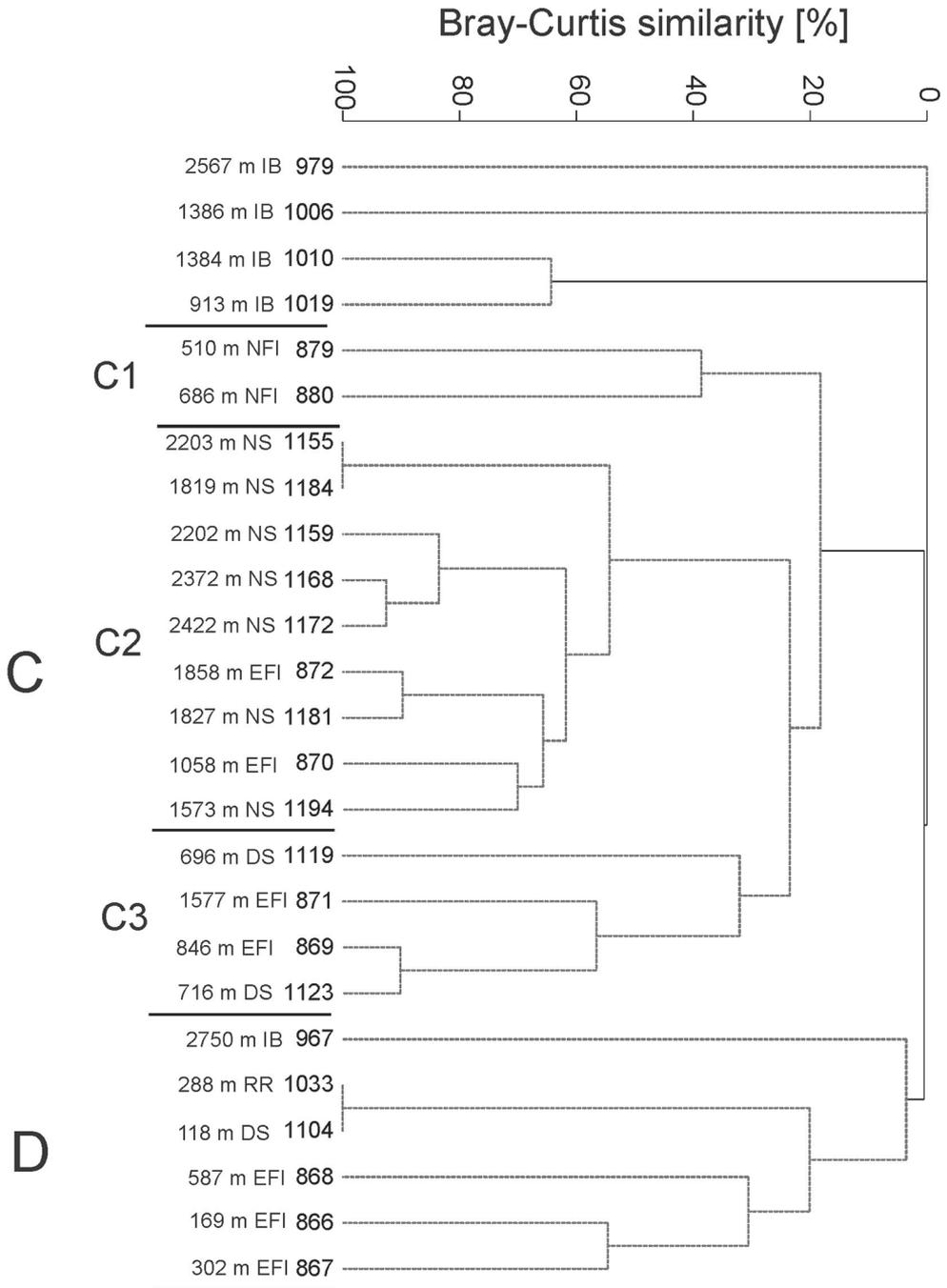


Figure 12. Dendrogram of samples for the Oedicerotidae (Bray-Curtis similarity, group average grouping method standardised and square root transformed data). Abbreviations: RR - Reykjanes Ridge, NS - Norwegian Sea, DS - Denmark Strait, IB - Iceland Basin, IrmB - Irminger Basin, WFI - west off Faroe Islands, EFI - east off Faroe Islands, SFI - South of Faroe Islands, NFI - North of Faroe Islands. Grey spotted lines indicate the samples that cannot be significantly differentiated by SIMPROF.

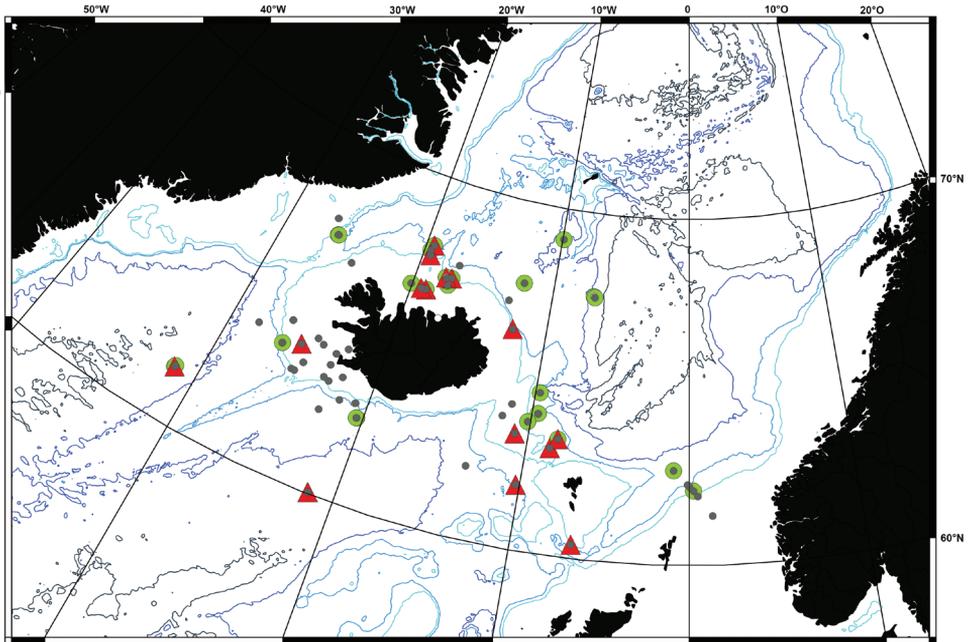


Figure 13. Amphilochidae found at BIOICE and IceAGE stations plotted together (grey circles) with the distribution of *Gitana abyssalis* (red triangle) and *Amphilochus tenuimanus* (green circle) at these stations.

1892. This cluster is also typified by the absence of four species which were dominant in oedicerotid cluster C, namely *Paroediceros curvirostris*, *Deflexilodes tenuirostratus*, *Arrhis phyllonyx*, and *Paroediceros propinquus*. Eleven of the 21 species of Oedicerotidae have abundances between one and five individuals in the samples.

In assessing the Oedicerotidae species distribution patterns within the IceAGE material (for examples see Figure 14), a more diverse species assemblage is apparent in the northern sampling localities. The two species of *Westwoodilla*, *W. caecula* (Spence Bate, 1857) and *W. megalops* (Sars, 1883) were present in Norwegian Channel only, as were both species of *Synchelidium*, although *S. intermedium* Sars, 1892 was represented by only eleven specimens across two sites. *Deflexilodes subnudus* (Norman, 1889) (*Monoculodes falcatus*) was present at a single Norwegian Channel site with 17 specimens. *Monoculoides packardi* Boeck, 1871 was recorded at three sites only in the Norwegian Channel, again with one sample represented by a single specimen. A total of 72 specimens were recorded across two regions, the Norwegian Channel and Denmark Strait, for *Deflexilodes tenuirostratus* (Boeck, 1871). A similar split between the Norwegian Channel and Denmark Strait was seen for 217 individuals of *Paroediceros curvirostratus* (Hansen, 1888), yet one of the two Norwegian Channel sites had the majority of individuals, with 110 specimens, while the second site had just three specimens. In the Denmark Strait sites, *P. curvirostratus* specimens were more evenly spread across sites. *Paroediceros propinquus* (Goës, 1866) and *Arrhis phyllonyx* (Sars M., 1858)

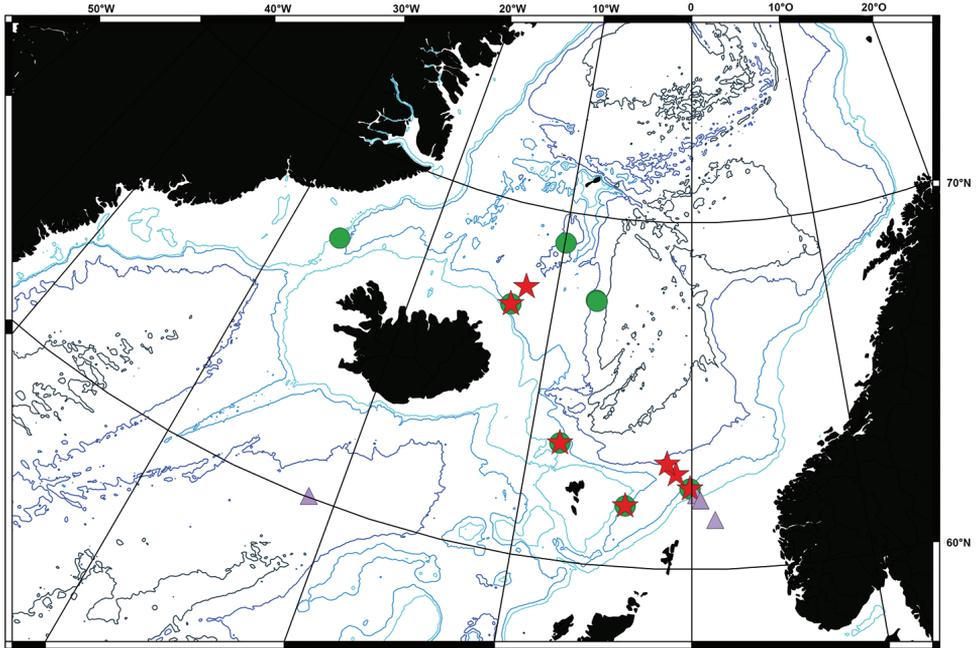


Figure 14. Distribution of selected Oedicerotidae species showing different distribution patterns: *Arrhis phyllonyx* (green circle), *Synchelidium haplocheles* (lilac triangle), *Paroediceros curvirostris* (red star).

were present across the Norwegian Channel and Iceland-Faroe Ridge, as well as the Denmark Strait to Norwegian Sea (Figure 14). *Arrhis phyllonyx* also showed high numbers of individuals (42 specimens) at a single Norwegian Channel station, considering a total of 74 specimens reported across all stations.

Oedicerotidae genera and species have the highest diversity in the North Atlantic. As the family has not received intensive study in other regions, with the exception of the north east Pacific, it is difficult to know if this is a biodiverse region for Oedicerotidae or an artefact of taxonomic treatment. Generic level review would be meaningful to address the taxonomic errors in the literature and to better understand relationships where few characters separate groups (Barnard and Karaman 1991). In most genera a full complement of subadult, male, and female specimens have not been assessed, and this is problematic for defining generic level characters, i.e., *Bathymedon* (Just 1980). The distinction between intra- and interspecific variation is not well studied. Some authors accept a 0.1 variation in ratios as an acceptable species-level character even when less than five individuals were available for study and large sample sizes show high degree of overlap and standard error (Jansen 2002). The position of the eye(s) and shape of the rostrum is cited as having high intraspecific variability, e.g., the widely reported *Westwoodilla caecula*, while rostrum shape and size is also used to separate species of *Westwoodilla* (Jansen 2002). The family would benefit from a holistic generic and species level review to more adequately represent evolutionary relationships.

General findings

The shelf-edge, especially in the Norwegian Channel, is particularly diverse. One possibility for this might be that the two northbound water masses (deep and cold, shallow and warm) mix in this zone, making possible habitats and more abundant food sources for a larger and more diverse set of species. The diversity maximum for gastropod molluscs was found to be between 400 and 450 m (Høisæter 2010). Høisæter's data (2010) for gastropods showed a very similar pattern reported from the Faroe Channel, but with a maximum diversity 200 m deeper along the Norwegian slope close to the Norwegian Channel (North Sea Fan). This zone coincides with a high fluctuation in temperature, where both, positive and negative values, were observed, indicating a varying depth of thermocline. This diversity peak was previously interpreted as an overlap of the upper and lower assemblages (Gage 2004). The factors structuring bathymetric patterns in different ocean basins and slopes may differ from those affecting other taxa in the same area.

While substantial parts of Arctic waters north of Iceland, as well as the North Atlantic south of Iceland, belong to the deep sea, reaching below 3000 m on the abyssal plains, the BIOICE dataset includes only a few stations at these depths. The dataset used here contains several samples below 1000 m. The Icelandic shallow water fauna is well documented, particularly for crustaceans (Sars 1890–1895, Svavarsson 1997, Svavarsson et al. 1993) though information declines with depth. In the case of peracarid crustaceans, in the Arctic Ocean the numbers of individuals of each species is high, while overall diversity is low. Conversely, for the North Atlantic Isopoda, diversity is high, while the number of individuals per species is comparably low (Svavarsson et al. 1993). Svavarsson et al. (1993) demonstrated considerable differences in recent isopod faunal characteristics between the shallow and deep waters North of Iceland. Here, the number of species declines by 50% at 1000 m and to one third of species at depths greater than 2000 m. The degree of Arctic endemism is seen to increase with depth.

Other groups show similar depth patterns. In the case of deep-sea prosobranchs from the North Atlantic (Porcupine Seabight and Abyssal Plain) Olabarria (2006) found depth to be a significant predictor of diversity with rates of species succession increasing rapidly with increasing depth, indicating four possible depths of faunal turnover: 700; 1600; 2800 and 4100 m. The study of Olabarria (2006) was based on data from 71 epibenthic sledge samples between 150 and 4915 m. The turnover depths differed from other taxa in the Porcupine Basin and also from other areas which would indicate a lack of global consistency in such depth-related diversity patterns. The decrease in diversity observed by Olabarria (2006) correlates with the permanent thermocline from about 600 to 1400 m. Rex (1981) and Etter and Rex (1990) found diversity maxima at depths between 2000 to 3000 m for polychaetes, gastropods, protobranchs, and cumaceans. Paterson and Lambshead (1995) found diversity maxima at around 1800 m for polychaetes at the Hebridian Slope. Flach and Bruin (1999) observed increasing diversity with increasing depth in molluscs. On the Scottish Slope macrozoobenthos diversity is low at 400 m and highest at around 1400 m (Bett 2001).

The unimodal relationship between diversity and depth with a peak at intermediate depths (2000–3000 m) is not universal and particular abiotic processes can modify the trend (Ramirez-Llodra et al 2010). A recent global biogeography “Global Open Ocean and Deep Seabed” (GOODS) describes 37 benthic provinces divided into four depth ranges (Ramirez-Llodra et al. 2010).

Conclusions

The sorting effort of two workshops on IceAGE expedition material has enabled the identification of more than 20,000 amphipod specimens to the family level from Icelandic and adjacent waters. Several families were identified further to species level. Distribution maps of occurrences have been provided in a preliminary investigation of regional amphipod family distributions. Statistical analyses at the family level revealed a depth related pattern, which was supported by species level data for two abundant families in the samples, the Amphilochidae and Oedicerotidae. In all three datasets (family level, Oedicerotidae and Amphilochidae) diversity was highest at slope depths where due to upwelling effects, cold water mixes with warmer water and phytoplankton/zooplankton are more abundant, supporting previous hypotheses that thermoclines play an important role in shaping species diversity and distribution patterns in the Icelandic benthic ecosystem (Høisæter 2010).

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References

- Allredge AL, King JM (1977) Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. *Marine Biology* 41(4): 317–333. <https://doi.org/10.1007/BF00389098>
- Amsler MO, McIntock JB, Amsler CD, Angus RA, Baker BJ (2009) An evaluation of sponge-associated amphipods from the Antarctic Peninsula. *Antarctic Science* 21(6): 579–589. <https://doi.org/10.1017/S0954102009990356>
- Ariyama H (2016) Five species of the family Cyproideidae (Crustacea: Amphipoda) from Japan, with the description of a new genus and two new species. *Zootaxa* 4097(3): 301–331. <https://doi.org/10.11646/zootaxa.4097.3.1>
- Azman BAR (2009) Cyproideidae. In: Lowry JK, Myers AA (Eds) *Benthic Amphipoda (Crustacea: Peracarida) of the Great Barrier Reef, Australia*. *Zootaxa* 2260: 380–392.
- Bachelet G, Dauvin JC, Sorbe JC (2003) An updated check-list of marine and brackish water Amphipoda (Crustacea, Peracarida) of the southern Bay of Biscay. *Cahiers de Biologie Marine* 44: 121–151.
- Barnard JL (1961) Gammaridean Amphipoda from depths of 400–6000 meters. *Galathea Report* 5: 23–128. [figs 1–83]
- Barnard JL (1972a) A review of the family Synopiidae (= Tironidae), mainly distributed in the deep-sea (Crustacea, Amphipoda). *Smithsonian Contributions to Zoology* 124: 1–94. <https://doi.org/10.5479/si.00810282.124>
- Barnard JL (1972b) Gammaridean Amphipoda of Australia, Part I. *Smithsonian Contributions to Zoology* 103: 1–333. <https://doi.org/10.5479/si.00810282.103>
- Barnard JL (1973) Deep-sea Amphipoda of the genus *Lepechinella* (Crustacea). *Smithsonian Contributions to Zoology* 133: 1–32. <https://doi.org/10.5479/si.00810282.133>
- Barnard JL (1974) Gammaridean Amphipoda of Australia. Part. II *Smithsonian Contributions to Zoology* 139: 1–148. <https://doi.org/10.5479/si.00810282.139>
- Barnard JL, Karaman G (1991) The families and genera of marine Gammaridean Amphipoda (except marine Gammaroids). *Records of the Australian Museum* 13(1–2): 1–866.
- Barnard KH (1916) Contributions to the crustacean fauna of South Africa (5) – The Amphipoda. *Annals of the South African Museum* 15: 105–302. [pls 26–28]. <https://doi.org/10.5962/bhl.title.10646>
- Beermann J, Franke HD (2011) A supplement to the amphipod (Crustacea) species inventory of Helgoland (German Bight, North Sea): indication of rapid recent change. *Marine Biodiversity Records* 4(e41): 1–15. <https://doi.org/10.1017/S1755267211000388>

- Bellan-Santini D, Dauvin JC (1988) Elements de synthese sur les *Ampelisca* du Nord-Est Atlantique. *Crustaceana* supplement 13: 20–60.
- Bellan-Santini D, Dauvin JC (1997) Ampeliscidae (Amphipoda) from Iceland with a description of a new species (Contribution to the BIOICE Research Program. *Journal of Natural History* 31: 1157–1173. <https://doi.org/10.1080/00222939700770621>
- Bellan-Santini D, Dauvin JC (2008) Contribution to knowledge of the genus *Haploops*, a new location for *Haploops lodo* (Crustacea: Amphipoda: Ampeliscidae) from the bathyal North Atlantic Ocean with a complement to the description of the species. *Journal of Natural History* 42(13–14): 1064–1077.
- Bellan-Santini D, Thurston MH (1996) Amphipoda of the hydrothermal vent along the mid-Atlantic Ridge. *Journal of Natural History* 30(8): 685–702. <https://doi.org/10.1080/00222939600770381>
- Berge J (2003) The taxonomy of the amphipod genus *Stilipes* (Crustacea: Amphipoda: Stilepididae), with description of one new species. *Organisms Diversity & Evolution* 316: 1–10. [electronic supplement]
- Berge J, Vader W (1997) Stegocephalid (Crustacea, Amphipoda) species collected in the BIO-FAR and BIOICE programmes. *Sarsia* 82: 347–370. <https://doi.org/10.1080/00364827.1997.10413662>
- Bett BJ (2001) UK Atlantic Margin Environmental Survey: introduction and overview of bathyal benthic ecology. *Continental Shelf Research* 21: 917–956. [https://doi.org/10.1016/S0278-4343\(00\)00119-9](https://doi.org/10.1016/S0278-4343(00)00119-9)
- Birstein YA, Vinogradov ME (1962) Notes on the family Pardaliscidae (Amphipoda) with the description of a new genus. *Crustaceana* 3: 249–258. <https://doi.org/10.1163/156854062X00490>
- Błażewicz-Paszkowycz M, Jennings RM, Jesulke K, Brix S (2014) Discovery of swimming males of Paratanaoidea (Tanaidacea). *Polish Polar Research* 35(2):415–453. <https://doi.org/10.2478/popore-2014-0022>
- Boeck A (1861) Bemerkninger angaaende de ved de norske Kyster forekommende Amphipoder. *Forhandlinger ved de Skandinaviske Naturforskeres. Mode Kiobenhavn* 8–14 Juli 1860(8): 631–677.
- Boeck A (1871) Crustacea amphipoda borealia et arctica. *Forhandlinger i Videnskabs-Selskabet i Christiania* 1870: 83–280.
- Bonnier J (1896) Édriophthalmes. In: Koehler R (Ed.) Résultats scientifiques de la campagne du “Caudan” dans le Golfe de Gascogne. Édriophthalmes. *Annales de l’ Université de Lyon* 26: 527–689. [pls 28–40]
- Bousfield EL (1978) A revised classification and phylogeny of amphipod crustaceans. *Transactions of the Royal Society of Canada (Series 4)* 16: 343–390.
- Bousfield EL (1982) Amphipoda. In: Parker SP (Ed.) *Synopsis and classification of living organisms*. MC Graw Hill Book Company, New York, 254–294.
- Bousfield EL, Hendrycks EA (1994) A revision of the family Pleustidae (Amphipoda: Gammaridea). Part 1. Systematics and biogeography of component subfamilies. *Amphipacific* 1(1): 17–57.

- Bousfield EL, Hendrycks EA (1995) The amphipod superfamily Eusiroidea in the North American Pacific region. I. Family Eusiridae: systematics and distributional ecology. *Amphipacifica* 1(4): 3–59.
- Bousfield EL, Hendrycks EA (1997) The amphipod superfamily Eusiroidea in the North American Pacific Region. II. Family Calliopiidae. Systematics and distributional ecology. *Amphipacifica* 2(3): 3–66.
- Bousfield EL, Kendall JA (1994) The amphipod superfamily Dexaminoidea on the North American Pacific coast; families Atylidae and Dexaminidae: systematics and distributional ecology. *Amphipacifica* 1(3): 3–66.
- Bovallius C (1886) Amphipoda Synopidea. *Acta Society Upsala*, series 3, 13(9): 1–33. [3 pls]
- Brandt A (1993) Composition, abundance, and diversity of peracarid crustaceans on a transect of the Kolbeinsey Ridge, north of Iceland. *Polar Biology* 13: 565–576. <https://doi.org/10.1007/BF00236399>
- Brandt A (1997a) Abundance, diversity and community patterns of epibenthic- and benthic-boundary layer peracarid crustaceans at 75°N off East Greenland. *Polar Biology* 17: 159–174. <https://doi.org/10.1007/s003000050118>
- Brandt A (1997b) Biodiversity of peracarid crustaceans (Malacostraca) from the shelf down to the deep Arctic Ocean. *Biodiversity and Conservation* 6: 1533–1556. <https://doi.org/10.1023/A:1018318604032>
- Brandt A, Brenke N, Andres H-G, Brix S, Guerrero-Kommritz J, Mühlenhardt-Siegel U, Wägele J-W (2005) Diversity of peracarid crustaceans (Malacostraca) from the abyssal plain of the Angola Basin. *Organisms, Diversity and Evolution* 5: 105–112. <https://doi.org/10.1016/j.ode.2004.10.007>
- Brandt A, Elsner N, Brenke N, Golovan O, Malyutina MV, Riehl T, Schwabe E, Würzberg L (2013) Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems. *Deep Sea Research Part II: Topical Studies in Oceanography* 86: 43–55. <https://doi.org/10.1016/j.dsr2.2012.07.039>
- Brandt A, Elsner N, Malyutina MV, Brenke N, Golovan OA, Lavrenteva A, Rhiel T (2015) Abyssal macrofauna of the Kuril-Kamchatka Trench area (Northwest Pacific) collected by means of a camera-epibenthic sledge. *Deep-Sea Research II* 111: 175–187. <https://doi.org/10.1016/j.dsr2.2014.11.002>
- Brandt A, Piepenburg D (1994) Peracarid crustacean assemblages of the Kolbeinsey Ridge, north of Iceland. *Polar Biology* 14: 97–105. <https://doi.org/10.1007/BF00234971>
- Brandt A, Vassilenko S, Piepenburg D, Thurston M (1996) The species composition of the Peracarida fauna (Crustacea, Malacostraca) of the NE water Polynya (Greenland). *Meddelelser om Grönland. Bioscience* 44: 1–31.
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349. <https://doi.org/10.2307/1942268>
- Brenke N (2005) An epibenthic sledge for operations on marine soft bottom and bedrock. *Marine Technology Society Journal* 39(2): 10–21. <https://doi.org/10.4031/002533205787444015>
- Brix S, Meißner K, Stransky B, Halanych KM, Jennings RM, Kocot K, Svavarsson J (2014a) The IceAGE project – a follow up of BIOICE. *Polish Polar Research* 35(2): 141–150.

- Brix S, Svavarsson J (2010) Distribution and diversity of desmosomatid and nannoniscid isopods (Crustacea) on the Greenland–Iceland–Faeroe Ridge. *Polar Biology* 33(4): 515–530. <https://doi.org/10.1007/s00300-009-0729-8>
- Brix S, Svavarsson J, Leese F (2014b) A multi-gene analysis reveals multiple highly divergent lineages of the isopod *Chelator insignis* (Hansen, 1916) south of Iceland. *Polish Polar Research* 35 (2): 225–242. <https://doi.org/10.2478/popore-2014-0015>
- Brix S, Stransky B, Maljutina M, Pabis K, Svavarsson J, Riehl T (in review) Distributional patterns of isopods (Crustacea) in Icelandic and adjacent waters. *Marine Biodiversity*.
- Buchholz R (1874) Die zweite deutsche Nordpolarfahrt in den Jahren 1869 und 1870 unter Führung des Kapitan Koldewey. *Svenska Vetenskaps-akademiens Handlingar* 2, 8: 262–270; 294–338.
- Buhl-Jensen L (1986) The benthic amphipod fauna of the west-Norwegian continental shelf compared with the fauna of five adjacent fjords. *Sarsia* 71: 193–208. <https://doi.org/10.1080/00364827.1986.10419690>
- Buhl-Mortensen L (1996) Amphipod fauna along an offshore-fjord gradient. *Journal of Natural History* 30(1): 23–49. <https://doi.org/10.1080/00222939600770031>
- Buhl-Mortensen L, Olafsdottir SH, Buhl-Mortensen P, Burgos JM, Ragnarsson SA (2015a) Distribution of nine cold-water coral species (Scleractinia and Gorgonacea) in the cold temperate North Atlantic: effects of bathymetry and hydrography. *Hydrobiologia* 759: 39–61. <https://doi.org/10.1007/s10750-014-2116-x>
- Buhl-Mortensen L, Buhl-Mortensen P, Dolan MF, Holte B (2015b) The MAREANO programme—A full coverage mapping of the Norwegian off-shore benthic environment and fauna. *Marine Biology Research* 11(1): 4–17. <https://doi.org/10.1080/17451000.2014.952312>
- Buhl-Mortensen L, Tandberg AH, Buhl-Mortensen P, Gates AR (2016) Behaviour and habitat of *Neobela monstrosa* (Boeck 1861) (Amphipoda, Corophiida) in Norwegian Sea deep water. *Journal of Natural History* 50: 323–337. <https://doi.org/10.1080/00222933.2015.1062152>
- Caine EA (1989) Relationship between wave activity and robustness of caprellid amphipods. *Journal of Crustacean Biology* 9: 425–431. <https://doi.org/10.2307/1548567>
- Campean AJ, Coleman CO (2017) A new species of *Sicafodia* Just, 2004 (Crustacea, Amphipoda, Sicafodiidae) from the North Atlantic. *Mar Biodiv*. <https://doi.org/10.1007/s12526-017-0635-1>
- Chevreaux E (1899) Sur deux espèces géantes d’amphipodes provenant des campagnes du yacht Princesse Alice. *Bulletin de la Société Zoologique de France* 24: 152–158. [figs 1–6] <https://doi.org/10.5962/bhl.part.24435>
- Chevreaux E (1908) Diagnossis d’Amphipodes nouveaux provenant des Campagnes de la Princesse-Alice dans l’Atlantique Nord. *Bulletin de la Société Zoologique de France* 121: 1–15.
- Clarke KR, Gorley RN (2015) Primer v7: User Manual/Tutorial. Primer-E Ltd, Plymouth, 296 pp.
- Coleman O (2015) Taxonomy in times of the taxonomic impediment - Examples from the community of experts on amphipod crustaceans. *Journal of Crustacean Biology* 35(6): 729–740. <https://doi.org/10.1163/1937240X-00002381>
- Coleman CO, Barnard JL (1991) Revision of Iphimediidae and similar families (Amphipoda: Gammaridea). *Proceedings of the Biological Society of Washington* 104: 253–268.

- Corbari L, Sorbe J-C (2017) First observations of the behaviour of the deep-sea amphipod *Dulichlopsis diana* sp. nov. (Senticaudata, Dulichiidae) in the vicinity of the hydrothermal vent site TAG (Mid-Atlantic Ridge). *Marine Biodiversity*. <https://doi.org/10.1007/s12526-017-0788-y>
- Cummings VJ, Thrush SF, Hewitt JE, Turner SJ (1998) The influence of the pinnid bivalve *Atrina zelandica* (Gray) on benthic macroinvertebrate communities in soft-sediment. *Journal of Experimental Marine Biology and Ecology* 228: 227–240. [https://doi.org/10.1016/S0022-0981\(98\)00028-8](https://doi.org/10.1016/S0022-0981(98)00028-8)
- d'Udekem d'Acoz C (2006) On a new *Melphidippa* species from Svalbard (Amphipoda, Melphidippidae). *Crustaceana* 79 (4): 489–499. <https://doi.org/10.1163/156854006777554839>
- d'Udekem d'Acoz C (2010) Contribution to the knowledge of European Liljeborgiidae (Crustacea, Amphipoda), with considerations on the family and its affinities. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie* 80: 127–259.
- d'Udekem d'Acoz C (2012) On the genus *Halirages* (Crustacea, Amphipoda), with the description of two new species from Scandinavia and Arctic Europe. *European Journal of Taxonomy*. Muséum national d'Histoire naturelle: Paris 2012(7): 1–32. <https://doi.org/10.5852/ejt.2012.7>
- d'Udekem d'Acoz C, Vader W, Legezinska J (2007) On a new diminutive *Rhachotropis* species from the North Sea, with a key to European *Rhachotropis* (Crustacea, Amphipoda, Eusiridae). *Bollettino del Museo Civico di Storia Naturale di Verona* 31: 31–49.
- Dana JD (1849) Synopsis of the genera of Gammaracea. *The American Journal of Science and Arts Series 2*, 8(22): 135–140.
- Dana JD (1852) On the classification on the Crustacea Choristopoda or Tetradecapoda. *American Journal of Science and Arts Series 2*, 14(appendix): 297–316.
- Dana JD (1853) Crustacea. Part II. United States Exploring during years 1838–1842 under the command of Charles Wilkes, USN: 689–1618. [atlas of 1696 plates]
- Dauby P, Scailteur Y, De Broyer C (2001) Trophic diversity within the eastern Weddell Sea amphipod community. *Hydrobiologia* 443: 69–86. <https://doi.org/10.1023/A:1017596120422>
- Dauvin JC (1996) Ampeliscidae from the Faroe Islands. Contribution to the Biofar programme. *Bollettino del Museo Civico di Storia Naturale di Verona* 20(1): 47–60.
- Dauvin JC, Sorbe JC (1995) Suprabenthic amphipods from the southern margin of the Cap-Ferret canyon (Bay of Biscay, northeastern Atlantic Ocean): abundance and bathymetric distribution. *Polskie Archiwum Hydrobiologii* 42: 441–460.
- Dauvin JC, Sorbe JC, Weppe A, Guðmundsson G (2012) Diversity and zoogeography of Icelandic deep-sea Ampeliscidae (Crustacea: Amphipoda). *Deep Sea Research Part I* 68: 12–23. <https://doi.org/10.1016/j.dsr.2012.04.013>
- Dayrat B (2005) Towards integrative taxonomy. *Biological Journal of the Linnean Society* 85(3): 407–415. <https://doi.org/10.1111/j.1095-8312.2005.00503.x>
- De Broyer C, Chapelle G, Duchesne PA, Munn R, Nyssen F, Scailteur Y, van Roozendaal F, Dauby P (2003) Structural and ecofunctional biodiversity of the amphipod crustacean benthic taxocenoses in the Southern Ocean. *Belgian Scientific Research Programme on the Antarctic, phase 4*: 1–58.

- Elizalde M, Sorbe JC, Dauvin JC (1993) Las comunidades suprabentónicas batiales del golfo de Vizcaya (margen sur del cañón de Cap-Ferret: composición faunística y estructura). *Publicaciones especiales del Instituto Español de Oceanografía* 11: 247–258.
- Enequist P (1949) Studies on the soft-bottom amphipods of the Skagerrak. PhD thesis, *Zoologiska bidrag från Uppsala* 28: 297–492.
- Etter R, Rex M (1990) Population differentiation decreases with depth in deep-sea gastropods. *Deep Sea Research Part A* 37(8): 1251–1261. [https://doi.org/10.1016/0198-0149\(90\)90041-S](https://doi.org/10.1016/0198-0149(90)90041-S)
- Fabricius O (1780) *Fauna Groenlandica: systematice sistens animalia Groenlandiae occidentalis hactenus indagata, quoad nomen specificum, triviale, vernaculumque: synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturamque singuli, prout detegendi occasio fuit: maxima parte secundum proprias observationes. Impensis Ioannis Gottlob Rothe.*
- Flach E, de Bruin W (1999) Diversity patterns in macrobenthos across a continental slope in the NE Atlantic. *Journal of Sea Research* 42(4): 303–323. [https://doi.org/10.1016/S1385-1101\(99\)00034-9](https://doi.org/10.1016/S1385-1101(99)00034-9)
- Forward RB (1986) Behavioral responses of a sand-beach amphipod to light and pressure. *Journal of Experimental Marine Biology and Ecology* 102: 55–74. [https://doi.org/10.1016/0022-0981\(86\)90126-7](https://doi.org/10.1016/0022-0981(86)90126-7)
- Frutos I, Sorbe JC (2014a) Bathyal suprabenthic assemblages from the southern margin of the Capbreton Canyon (“Kostarrenkala” area), SE Bay of Biscay. *Deep-Sea Research II* 104: 291–309. <https://doi.org/10.1016/j.dsr2.2013.09.010>
- Frutos I, Sorbe JC (2014b) A new bathyal suprabenthic *Stilipes* (Amphipoda: Stilipedidae: Stilipedinae) from the NE Atlantic Ocean. Fourteenth International Symposium on Oceanography of the Bay of Biscay, Bordeaux (France), June 2014, 54 pp.
- Gage JD (2004) Diversity in deep-sea benthic macrofauna: the importance of local ecology, the larger scale, history and the Antarctic. *Deep Sea Research Part II* 51(14): 1689–1708. <https://doi.org/10.1016/j.dsr2.2004.07.013>
- Goës A (1866) Crustacea Amphipoda maris Spetsbergiam alluentis, cum speciebus aliis arcticis enumerat. *Ofversigt af Kongliga Vetenskaps-Akademiens Forhandlingar* 8(1865): 517–536. [pls 36–41]
- Golovan OA, Błażewicz-Paszkowycz M, Brandt A, Budnikova LL, Elsner NO, Ivin VV, Lavrenteva AV, Malyutina MV, Petryashov VV (2013) Diversity and distribution of peracarid crustaceans (Malacostraca) from the continental slope and the deep-sea basin of the Sea of Japan. *Deep-Sea Research II* 86–87: 66–78. <https://doi.org/10.1016/j.dsr2.2012.08.002>
- Grube AE (1864) Die Insel Lussin und ihre Meeresfauna. Nach einem sechswochentlichen Aufenthalte. F. Hirt, Breslau, 116 pp. [1 pl.]
- Guerra-García JM (2001) Habitat use of the Caprellidea (Crustacea: Amphipoda) from Ceuta, North Africa. *Ophelia* 55: 27–38. <https://doi.org/10.1080/00785236.2001.10409471>
- Guerra-García JM (2003) Two new species of deep-water caprellids (Crustacea: Amphipoda) from northeastern Brazil. *Cahiers de Biologie Marine* 44: 171–184.

- Guerra-García JM (2004) Deep-sea Caprellidea (Crustacea, Amphipoda) from Azores with the description of three new species. *Zoosystema* 26(2): 235–362.
- Guerra-García JM, García-Gomez JC (2003) A new species of *Caprella* (Amphipoda, Caprellidea) from deep seawaters. *Crustaceana* 76: 581–590. <https://doi.org/10.1163/156854003322316218>
- Guerra-García JM, Sorbe JC, Frutos I (2008) A new species of *Liropus* (Crustacea, Amphipoda, Caprellidae) from the Le Danois bank (Southern Bay of Biscay). *Organisms Diversity and Evolution* 7: 1–12.
- Hansen HJ (1888) Malacostraca marina Groenlandiæ occidentalis. Oversigt over det vestlige Grønlands Fauna af malakostrake Havkrebsdyr. Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn, Aaret 1887 (series 4) 9: 5–226. [6 pls]
- Havermans C, Sonet G, d’Udekem d’Acoz C, Nagy ZT, Martin P, Brix S, Riehl T, Agrawal S, Held C (2013) Genetic and Morphological Divergences in the Cosmopolitan Deep-Sea Amphipod *Eurythenes gryllus* Reveal a Diverse Abyss and a Bipolar Species. *PLoS ONE* 8(9): e74218. <https://doi.org/10.1371/journal.pone.0074218>
- Heller C (1875) Die Crustaceen, Pycnogoniden und Tunicaten der k.k. österr.-ungar. Nordpol-Expedition. Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 35: 25–46. [pls 1–5]
- Hendrycks EA, Conlan KE (2003) New and unusual abyssal gammaridean Amphipoda from the north-east Pacific. *Journal of Natural History* 37(19): 2303–2368. <https://doi.org/10.1080/00222930210138926>
- Holman H, Watling L (1983) A revision of the Stilipedidae (Amphipoda). *Crustaceana* 44: 27–53. <https://doi.org/10.1163/156854083X00037>
- Holmes SJ (1908) The Amphipoda collected by the U.S. Bureau of Fisheries Steamer “Albatross” off the West Coast of North America, in 1903 and 1904, with descriptions of a new family and several new genera and species. *Proceedings of the United States National Museum* 35(1654): 489–543. [46 figs]
- Horton T, Thurston M (2013) *Hirondellea namarensis* (Crustacea: Amphipoda: Lysianassoidea: Hirondelleidae), a new deep-water scavenger species from the Mid-Atlantic Ridge. *Marine Biology Research* 9: 554–562. <https://doi.org/10.1080/17451000.2012.749994>
- Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO, Daneliya M, Dauvin JC, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Holsinger J, Hughes L, Jaime D, Jazdzewski K, Just J, Kamaltynov RM, Kim YH, King R, Krapp-Schickel T, LeCroy S, Lörz AN, Senna AR, Serejo C, Sket B, Tandberg AH, Thomas J, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (2017) World Amphipoda Database. <http://www.marinespecies.org/amphipoda> [2017-07-31]
- Høisæter T (2010) The shell-bearing, benthic gastropods on the southern part of the continental slope off Norway. *Journal of Molluscan Studies* 76(3): 234–244. <https://doi.org/10.1093/mollus/eyq003>
- Jamieson A (2015) *The Hadal Zone. Life in the Deepest Oceans*. Oxford University Press, 382 pp. <https://doi.org/10.1017/CBO9781139061384>
- Jansen T (2002) A taxonomic revision of *Westwoodilla* Bate, 1862 (Crustacea: Amphipoda) including descriptions of two new species. *Steenstrupia* 27(1): 83–136.

- Jaume D, Sorbe JC (2001) A new bathyal amphipod from the Bay of Biscay: *Carangolia barnardi* sp. nov. (Gammaridea: Urothoidae). Journal of Marine Biological Association United Kingdom 81: 49–59. <https://doi.org/10.1017/S0025315401003393>
- Jązdżewska AM, Corbari L, Driskell A, Frutos I, Havermans C, Hendrycks E, Hughes L, Lörz A-N, Stransky B, Tandberg AHS, Vader W, Brix S (2018) A genetic fingerprint of Amphipoda from Icelandic waters – the baseline for further biodiversity and biogeography studies. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project). ZooKeys 731: 55–73. <https://doi.org/10.3897/zookeys.731.19931>.
- Jązdżewska A (2015) Kuril-Kamchatka deep sea revisited – insights into the amphipod abyssal fauna. Deep-Sea Research II 111: 294–300. <https://doi.org/10.1016/j.dsr2.2014.08.008>
- Johansen PO, Vader W (2015) New and little known species of *Lepechinella* (Crustacea, Amphipoda, Lepechinellidae) and allied new genus *Lepesubchela* from the North Atlantic. European Journal of Taxonomy 127: 1–35. <https://doi.org/10.5852/ejt.2015.127>
- Just A (1978) Taxonomy, biology, and evolution of the circumarctic genus *Acanthonotozoma* (Amphipoda) with notes on *Panoploeopsis*. Acta Arctica 20: 1–140.
- Just J (1980) Amphipoda (Crustacea) of the Thule area, Northwest Greenland: Faunistics and Taxonomy. Meddelelser om Gronland, Bioscience, 2: 1–63.
- Just J, Wilson GDF (2004) Revision of the *Paramunna* complex (Isopoda: Asellota: Paramunidae). Invertebrate Systematics 18(4): 377–466. <https://doi.org/10.1071/IS03027>
- Karaman GS (1974) Revision of the family Pardaliscidae with diagnosis of genera, distribution of species and bibliography. Acta Adriatica, Institut za Oceanografiju I Ribarstvo 15(7): 3–46.
- Kim YH, Hendrycks EA, Lee KS (2011) The genus *Guernea* Chevreux, 1887 from Korean waters (Crustacea: Amphipoda: Dexaminidae). Zootaxa 3098: 1–25.
- Krapp-Schickel G (1982) Family Amphilochidae. In Ruffo S. (ed.) The Amphipoda of the Mediterranean. Monaco: Mémoires de l'Institut Océanographique 13: 70–93.
- Krapp-Schickel T (2005) Cressidae (Crustacea: Amphipoda) collected by the BIOFAR and BIOICE programmes near the Faroes and Iceland (N-Atlantic). Biofar proceedings, 150–166.
- Krapp-Schickel T (2011) New Antarctic stenothoids sensu lato (Amphipoda, Crustacea). European Journal of Taxonomy 2: 1–17
- Krapp-Schickel T (2018) *Leucothoe vaderotti*, a new Atlantic *Leucothoe* (Crustacea, Amphipoda) belonging to the “*spinicarpa*-clade” (Crustacea, Amphipoda). In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project). ZooKeys 731: 135–144. <https://doi.org/10.3897/zookeys.731.19813>
- Krapp-Schickel T, Vader W (2015) Stenothoids living with or on other animals (Crustacea, Amphipoda). Zoosystematics and Evolution 91(2): 215–246. <https://doi.org/10.3897/zse.91.5715>
- Krøyer H (1842) Nye nordiske slægter og arter af amphipodernes orden, henhørende til familien Gammarina. (Forelobigt uddrag af et større arbejde). Naturhistorisk Tidsskrift 4: 141–166.
- Krøyer H (1845) Bidrag til Kundskab om Pycnogoniderne eller Søspindlerne. Naturhistorisk Tidsskrift, Kjøbenhavn (2) 1: 90–139.
- Laetz E, Coleman CO, Christa G, Wägele H (2013) Behavioural interactions between *Tritaeta gibbosa* (Crustacea, Amphipoda) and *Ocnus planci* (Echinodermata, Holothuroidea). Vie et Milieu – Life and Environment 63: 105–117.

- Lagardère JP (1977) Recherches sur la distribution verticale et sur l'alimentation des Crustacés Décapodes benthiques de la pente continentale du golfe de Gascogne. Analyse des groupements carcinologiques. Bulletin du Centre d'Etudes et de Recherches Scientifiques, Biarritz 11: 367–440.
- Laubitz DR (1977) A revision of the genera *Dulichia* Krøyer and *Paradulichia* Boeck (Amphipoda, Podoceridae). Canadian Journal of Zoology 55(6): 942–982. <https://doi.org/10.1139/z77-123>
- Laubitz DR (1979) Phylogenetic relationships of the Podoceridae (Amphipoda, Gammaridea). Bulletin of the Biological Society of Washington 3: 144–152.
- Laubitz D, Sorbe JC (1996) Deep-water caprellids (Amphipoda: Caprellidea) from the Bay of Biscay: a new species and a new locality record. Journal of Crustacean Biology 16: 626–632. <https://doi.org/10.2307/1548754>
- Laval P (1980) Hyperiid amphipods as crustacean parasitoids associated with gelatinous plankton. Oceanography and Marine Biology, Annual Review 18: 11–56.
- Leach WE (1814) Crustaceology. Brewster's Edinburgh Encyclopaedia 7: 383–437.
- Leaché AD, Koo MS, Spencer CL, Papenfuss TJ, Fisher RN, McGuire JA (2009) Quantifying ecological, morphological, and genetic variation to delimit species in the coast horned lizard species complex (*Phrynosoma*). Proceedings of the National Academy of Sciences 106(30): 12418–12423. <https://doi.org/10.1073/pnas.0906380106>
- Ledoyer M (1986) Crustacés Amphipodes Gammariens. Familles des Haustoriidae à Vitjazianidae. Faune de Madagascar 59(2): 599–1112. [figs 227–415]
- Lilljeborg W (1865) Bidrag till kännedomen om underfamiljen Lysianassina inom underordningen Amphipoda bland kräftdjuren. Nova Acta Regiae Societatis Scientiarum Upsaliensis, Ser. 3.
- Lincoln RJ (1979) British Marine Amphipoda: Gammaridea. British Museum (Natural History), London, No 818, 658 pp. [280 figs]
- Lörz AN, Bamber RN (2010) Peracarid assemblages of benthic soft sediments around Moreton Island, Queensland. In: Davie PJF, Phillips JA (Eds) Proceedings of the Thirteenth International Marine Biological Workshop, Nature 54(3): 385–399.
- Lörz A-N, Tandberg AHS, Willassen E, Driskell A (2018) *Rhachotropis* (Eusiroidea, Amphipoda) from the North East Atlantic. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project). ZooKeys 731: 75–101. <https://doi.org/10.3897/zookeys.731.19814>
- Lowry J (2006) New families and subfamilies of amphipod crustaceans. Zootaxa 1254: 1–28.
- Lowry JK, Azman BAR (2008) A new genus and species of cyproideid amphipod associated with unstalked crinoids on the Great Barrier Reef, Australia. Zootaxa 1760: 59–68.
- Lowry JK, Myers AA (2017) A phylogeny and classification of the Amphipoda with the establishment of the new order Ingolfiellida (Crustacean: Peracarida). Zootaxa 4265(1): 1–89. <https://doi.org/10.11646/zootaxa.4265.1.1>
- Lowry JK, Stoddart H (1983) The shallow-water gammaridean Amphipoda of the subantarctic islands of New Zealand and Australia: Lysianassoidea. Journal of the Royal Society of New Zealand 13: 279–394. <https://doi.org/10.1080/03036758.1983.10420804>
- Lowry JK, Stoddart HE (2003) Crustacea: Malacostraca: Peracarida: Amphipoda, Cumacea, Mysidacea. In: Beesley PL, Houston WWK (Eds) Zoological Catalogue of Australia (Vol 19.2B). CSIRO Publishing, Melbourne, 531 pp.

- Martin JW, Pettit G (1998) *Caprella bathytatos* new species (Crustacea, Amphipoda, Caprellidae), from the mouthparts of the crab *Macroregonia macrochira*, Sakai (Brachyura, Majidae) in the vicinity of deep-sea hydrothermal vents off British Columbia. *Bulletin of Marine Science* 63(1): 189–198.
- Mattson S, Cedhagen T (1989) Aspects of the behaviour and ecology of *Dyopedos monacanthus* (Metzger) and *D. porrectus* Bate, with comparative notes on *Dulichia tuberculata* Boeck (Crustacea: Amphipoda: Podoceridae). *Journal of Experimental Marine Biology and Ecology* 127: 253–272. [https://doi.org/10.1016/0022-0981\(89\)90078-6](https://doi.org/10.1016/0022-0981(89)90078-6)
- McCloskey LR (1970) A new species of *Dulichia* (Amphipoda, Podoceridae) commensal with a sea urchin. *Pacific Science* 24: 90–98.
- Meißner K, Brenke N, Svavarsson J (2014) Benthic habitats around Iceland investigated during IceAGE expeditions. *Polish Polar Research* 35(2): 177–202. <https://doi.org/10.2478/popore-2014-0016>
- Metzger A (1875) Zoologische Ergebnisse der Nordseefahrt. 10. Crustaceen aus den Ordnungen Edriophthalmata und Podophthalmata. *Jahresbericht der Commission zur Wissenschaftlichen Untersuchung der Deutschen Meere in Kiel* 2(3): 277–310.
- Meyer-Rochow VB, Stephan H, Moro SD (1991) Morphological and anatomical observations on the hairy eyes of males and females of the marine amphipod *Dulichia porrecta* (Crustacea, Amphipoda, Podoceridae). *Italian Journal of Zoology* 58(1): 59–69.
- Miers EJ (1881) On a small collection of Crustacea and Pycnogonida from Franz-Josef Land, collected by B. Leigh Smith, Esq. *Annals and Magazine of Natural History, (series 5)* 7: 45–51.
- Milne Edwards H (1830). Extrait de recherches pour servir à l'histoire naturelle des crustacés amphipodes. 1–48.
- Miskov-Nodland K, Buhl-Mortensen L, Høisæter T (1999) Has there been a fauna change in the Skagerrak? A comparison of the present amphipod fauna with observations from 1933/37. *Sarsia* 84: 137–155. <https://doi.org/10.1080/00364827.1999.10420441>
- Montagu G (1813) Descriptions of several new or rare animals, principally marine, discovered on the south coast of Devonshire. *Transactions of the Linnean Society of London* 11: 1–26. [pls 21–25] <https://doi.org/10.1111/j.1096-3642.1813.tb00035.x>
- Moore PG (1981) A functional interpretation of coxal morphology in *Epimeria cornigera* (Crustacea: Amphipoda: Paramphithoidae) *Journal of the Marine Biological Association of the United Kingdom* 61(3): 749–757. <https://doi.org/10.1017/S0025315400048189>
- Moore PG, Earll R (1985) Sediment “whips”: amphipod artefacts from the rocky sublittoral in Britain. *Journal of Experimental Marine Biology and Ecology* 90(2): 165–170. [https://doi.org/10.1016/0022-0981\(85\)90117-0](https://doi.org/10.1016/0022-0981(85)90117-0)
- Myers AA (1985) Shallow water, coral reef and mangrove Amphipoda (Gammaridea) of Fiji. *Records of the Australian Museum, Supplement* 5: 1–143. <https://doi.org/10.3853/j.0812-7387.5.1985.99>
- Myers AA (1998) New and little known Corophioidea (Amphipoda: Gammaridea) from Faroese and Icelandic waters. *Journal of the Marine Biological Association of the United Kingdom* 78: 211–222. <https://doi.org/10.1017/S0025315400040030>
- Myers AA, Lowry JK (2003) A phylogeny and a new classification of the Corophiidea Leach, 1814 (Amphipoda). *Journal of Crustacean Biology* 23: 443–485. <https://doi.org/10.1163/20021975-99990353>

- Negoescu I, Svavarsson J (1997) Anthurideans (Crustacea, Isopoda) from the North Atlantic and the Arctic Ocean. *Sarsia* 82: 159–202. <https://doi.org/10.1080/00364827.1997.10413650>
- Norman AM (1867) Report on the Crustacea. *Natural History Transactions of Northumberland and Durham* 1: 12–29.
- Norman AM (1868) On Crustacea Amphipoda new to science or to Britain. *Annals and Magazine of Natural History* 4(2): 411–421. <https://doi.org/10.1080/00222936808695843>
- Norman AM (1869) Shetland final dredging report.- Part II. On the Crustacea, Tunicata, Polyzoa, Echinodermata, Actinozoa, Hydrozoa, and Porifera. Report of the thirty-eighth meeting of the British Association for the advancement of Science 1868: 247–336.
- Norman AM (1889) Notes on British Amphipoda – I *Megaluropus*, n. g., and some Oediceridae. *Annals and Magazine of Natural History (ser 6)* 3: 445–460. [pls. 18–20]
- Olabarria C (2006) Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from northeastern Atlantic. *Biodiversity and Conservation* 15: 3685–3702. <https://doi.org/10.1007/s10531-005-1344-9>
- Oliver JS, Oakden JM, Slattery PN (1982) Phoxocephalid amphipod crustaceans as predators on larvae and juveniles in marine soft-bottom communities. *Marine Ecology Progress Series* 7: 179–184. <https://doi.org/10.3354/meps007179>
- Oliver JS, Slattery PN (1985) Effects of crustacean predators on species composition and population structure of soft-bodied infauna from McMurdo Sound, Antarctica. *Ophelia* 24: 155–175. <https://doi.org/10.1080/00785326.1985.10429725>
- Ortiz M, Lalana R, Sánchez-Díaz A (2000) Una nueva especie de anfípodo espongícola del género *Hoplopheonoides* Shoemaker, 1956 (Gammaridea, Cyproideidae) de Cuba. *Avicennia* 12(13): 63–68.
- Ostmann A, Schnurr S, Martínez Arbizu P (2014) Marine environment around Iceland: hydrography, sediments and first predictive models of Icelandic deep-sea sediment characteristics. *Polish Polar Research* 35(2): 151–176. <https://doi.org/10.2478/popore-2014-0021>
- Padial JM, Miralles A, De La Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology* 7: 1–16. <https://doi.org/10.1186/1742-9994-7-16>
- Palerud R, Vader W (1991) Marine Amphipoda Gammaridea in North-East Atlantic and Norwegian Arctic. *TROMURA, Naturvitenskap* 68: 1–97.
- Paterson GLJ, Lamshead PJD (1995) Bathymetric patterns of polychaete diversity in the Rockall Trough, northeast Atlantic. *Deep Sea Research Part I* 42(7): 1199–1214. [https://doi.org/10.1016/0967-0637\(95\)00041-4](https://doi.org/10.1016/0967-0637(95)00041-4)
- Peart RA (2018) Ampeliscidae (Crustacea, Amphipoda) from the IceAGE expeditions. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project)*. *ZooKeys* 731: 145–173. <https://doi.org/10.3897/zookeys.731.19948>
- Pirlot JM (1934) Les amphipodes de l'expédition du Siboga. Deuxième partie. Les amphipodes gammarides II. Les amphipodes de la mer profonde 2. (Hyperioptidae, Pardaliscidae, Astyridae nov. fam., Tironidae, Calliopiidae, Paramphithoidae, Amathillopsidae nov. fam., Eusiridae, Gammaridae, Aoridae, Photidae, Ampithoidae, Jassidae). *Siboga-Expeditie, Monographie* 33d: 167–235.

- Premke K, Muyakshin S, Klages M, Wegner J (2003) Evidence for long-range chemoreceptive tracking of food odour in deep-sea scavengers by scanning sonar data. *Journal of Experimental Marine Biology and Ecology*: 285–286, 283–284. [https://doi.org/10.1016/S0022-0981\(02\)00533-6](https://doi.org/10.1016/S0022-0981(02)00533-6)
- Raith DS (1938) A collection of benthic Amphipoda from Icelandic waters and its relation to similar material from the North Sea. *Proceedings of the Linnean Society of London* 150: 95–98. <https://doi.org/10.1111/j.1095-8312.1938.tb00155.x>
- Ramirez-Llodra EZ, Brandt A, Danovaro R, De Mol B, Escobar E, German CR, Levin LA, Martinez Arbizu P, Menot L, Buhl-Mortensen P, Narayanaswamy BE, Smith CR, Tittensor DP, Tyler PA, Vanreusel A, Vecchione M (2010) Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences* 7: 2851–2899. <https://doi.org/10.5194/bg-7-2851-2010>
- Rauschert M (1990) *Pseudodulichia*, eine neue Gattung der Podoceridae aus der Antarktis (Crustacea: Amphipoda: Gammaridea). *Mitteilungen aus dem Zoologischen Museum in Berlin* 66(2): 371–374. <https://doi.org/10.1002/mmzn.19900660210>
- Rex M (1981) Community structure in the deep-sea benthos. *Annual Review of Ecology and Systematics* 12(1): 331–53. <https://doi.org/10.1146/annurev.es.12.110181.001555>
- Riehl T, Brenke N, Brix S, Driskella A, Kaiser S, Brandt A (2014) Field and laboratory methods for DNA studies on deep-sea isopod crustaceans. *Polish Polar Research* 35(2): 203–224. <https://doi.org/10.2478/popore-2014-0018>
- Ross JC (1835) Marine invertebrate animals. In: Appendix to the narrative of a second voyage in search of a north-west passage and of residence in the arctic regions during the years 1829–1833 (Sir John Ross, captain). A.W. Webster, London, 81–150. [2 pls]
- Rothlisberg PC, Percy WG (1977) An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea). *Fisheries Bulletin* 74(4): 994–997.
- Sars GO (1876) *Prodromus descriptionis crustaceorum et pycnogonidarum, quae in expeditione Norvegica anno 1876, observavit*. *Archiv for Mathematik og Naturvidenskab* 2: 227–271.
- Sars GO (1879) *Crustacea et Pycnogonida nova in itinere 2do et 3tio expeditionis Norvegicae anno 1877 & 78 collecta (prodromus descriptionis)*. *Archiv for Mathematik og Naturvidenskab* 4: 427–476.
- Sars GO (1883) *Oversigt af Norges Crustaceer med forelobige Bemærkninger over de nye eller Mindre bekjendte Arter. I. (Podophthalmata-Cumacea-Isopoda-Amphipoda)*. *Forhandlinger Vidensk abselskabs I Christiania* 18: 124 pp. [6 pls]
- Sars GO (1890–95) *Amphipoda. An Account of the Crustacea of Norway With Short Descriptions and Figures of All the Species* 1: 1–711. [240 pls, 8 supplementary pls]
- Sars M (1858) *Oversigt over de i den norsk-arctiske Region forekommende Krebsdyr*. *Christiana Videnskabs-Selskabs Forhandlinger* 1858: 122–163.
- Schellenberg A (1926) *Die Gammariden der Deutschen Sudpolar-Expedition 1901–1903*. *Deutsche Sudpolar-Expedition 1901–1903* 18(10): 235–414.
- Scott T, Scott A (1893) On some new or rare Crustacea from Scotland. *Annals and Magazine of Natural History, series* 6(12): 237–246. [pls 11–13] <https://doi.org/10.5962/bhl.title.38107>

- Sites JW, Marshall JC (2004) Operational Criteria for Delimiting Species. *Annual Review of Ecology, Evolution and Systematics* 35: 199–227. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130128>
- Sittrop DJ, Serejo CS, Souza-Filho JF, Senna AR (2015) New genera and species of Urothoidae (Amphipoda) from the Brazilian deep sea, with the re-assignment of *Pseudurothoe* and *Urothopsis* to Phoxocephalopsidae. *Journal of Natural History* 49(9–10): 527–552. <https://doi.org/10.1080/00222933.2014.953227>
- Smith SI (1883) Review of the marine Crustacea of Labrador. *Proceedings of the United States National Museum* 6: 223–232. <https://doi.org/10.5479/si.00963801.375.223>
- Sorbe JC (1984) Contribution à la connaissance des peuplements suprabenthiques néritiques sud-Gascogne. Thèse Doctorat d'Etat, Université de Bordeaux 1, n° 798, 225 pp.
- Sorbe JC, Elizalde M (2014) Temporal changes in the structure of a slope suprabenthic community from the Bay of Biscay (NE Atlantic Ocean). *Deep-Sea Research II* 106: 179–191.
- Sorbe JC, Weber O (1995) Influence de la profondeur et des sédiments superficiels sur la structure des communautés suprabenthiques bathyales sud-Gascogne. *Actas del IV Coloquio Internacional sobre Oceanografía del Golfo de Vizcaya*, 183–194.
- Spence Bate CS (1857) British Amphipoda. *Annals and Magazine of Natural History*, series 2, 19: 271.
- Spence Bate CS (1862) Catalogue of the specimens of amphipodous Crustacea in the collections of the British Museum. Taylor & Francis, London, 399 pp.
- Stebbing TR (1885) VIII.—Description of a new English Amphipodous Crustacean. *Journal of Natural History* 15(85): 59–62. <https://doi.org/10.1080/00222938509459296>
- Stebbing TRR (1888) Report on the amphipoda collected by H.M.S. Challenger during the years 1873–1876. Report on the Scientific results of the Voyage of H.M.S. Challenger during the years 1873–76. *Zoology* 29: 1–1737.
- Stebbing TRR (1899) Revision of Amphipoda (continued). *Annals and Magazine of Natural History* (series 7) 4: 205–211.
- Stebbing TRR (1906) Amphipoda I: Gammaridea. *Das Tierreich* 21: 1–806.
- Stebbing TRR (1908) On two new species of northern Amphipoda. *Journal of the Linnean Society of London, Zoology* 30: 191–197, pls 27–28. <https://doi.org/10.1111/j.1096-3642.1908.tb02133.x>
- Stephensen K (1925) Crustacea Malacostraca. VI. The order Amphipoda, part 2. Gammaridea. *The Danish Ingolf Expedition* 3(9): 101–178.
- Stephensen K (1931) Crustacea Malacostraca. VII. (Amphipoda III). *Danish Ingolf Expedition* 3(11): 179–290. [figs. 54–81]
- Stephensen K (1933) The Godthaab Expedition, 1928. Amphipoda. *Meddelelser om Grønland* 79(7): 1–88. [figs. 1–33]
- Stephensen K (1938) The Amphipoda of N Norway and Spitsbergen with adjacent waters. *Tromsø Museums Skrifter* 3(2): 141–278.
- Stephensen K (1940) Marine Amphipoda. *The Zoology of Iceland* 3(36): 1–111.
- Stephensen K (1944) Crustacea Malacostraca VIII: Amphipoda IV. *Danish Ingolf Expedition* 3(13): 1–51.

- Stimpson W (1853) Synopsis of the marine Invertebrata of Grand Manan: or the region about the mouth of the Bay of Fundy, New Brunswick (Vol. 50). Smithsonian Contributions to Knowledge 6: 1–66. [pls 1–3]
- Svararsson J (1997) Diversity of isopods (Crustacea): new data from the Arctic and Atlantic Oceans. *Biodiversity and Conservation* 6: 1571–1579. <https://doi.org/10.1023/A:1018322704940>
- Svararsson J, Stromberg JO, Brattegard T (1993) The deep-sea asellote (Isopoda, Crustacea) fauna of the Northern Seas: species composition, distributional patterns and origin. *Journal of Biogeography* 20(5): 537–555. <https://doi.org/10.2307/2845725>
- Tandberg AHS, Vader W (2018) On a new species of *Amphilocheus* from deep and cold Atlantic waters, with a note on the genus *Amphilocheopsis* (Amphipoda, Gammaridea, Amphilocheidae). In: Brix S, Lörz A-N, Stransky B, Svararsson J (Eds) Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project). *ZooKeys* 731: 103–134. <https://doi.org/10.3897/zookeys.731.19899>.
- Thiel M (1997) Reproductive biology of an epibenthic amphipod (*Dyopedos monacanthus*) with extended parental care. *Journal of the Marine Biological Association of the United Kingdom* 77: 1059–1072. <https://doi.org/10.1017/S0025315400038625>
- Thiel M (1998) Population biology of *Dyopedos monacanthus* (Crustacea: Amphipoda) on estuarine soft-bottoms: importance of extended parental care and pelagic movements. *Marine Biology* 132: 209–221. <https://doi.org/10.1007/s002270050387>
- Thomas JD (1999) *Moolapheonoides utmas*, new species, from Coral Reefs in the Madang Lagoon, Papua New Guinea (Amphipoda, Cyproideidae). *Bulletin of Marine Science* 65(2): 515–521.
- Thurston MH (1980) Abyssal benthic Amphipoda (Crustacea) from the East Iceland Basin 2. *Lepechinella* and an allied new genus. *Bulletin of the British Museum of Natural History (Zoology)* 38(1): 69–87.
- Vader W (1984) Notes on Norwegian marine Amphipoda. 8. Amphipods found in association with sponges and tunicates. *Fauna Norvegica, Series A* 5: 16–21.
- Vader W (1995) *Liljeborgia* species (Amphipoda, Liljeborgiidae) as associates of hermit crabs. *Polskie Archiwum Hydrobiologii* 42(4): 517–525.
- Vader W, Brattegard T, Buhl-Mortensen L, Larsen KM (1997) Order Amphipoda, suborder Gammaridea (phylum Crustacea) – gammaridean amphipods. In: Brattegard T, Holthe T (Eds) Distribution of marine, benthic macro-organisms in Norway. Directorate of nature management report no. 1997–1: 191–213.
- Vader W, Tandberg AHS (2013) A survey of amphipods associated with molluscs. *Crustaceana* 86(7–8): 1038–1049. <https://doi.org/10.1163/15685403-00003210>
- Vader W, Tandberg AHS (2015) Amphipods as Associates of other Crustacea: A Survey. *Journal of Crustacean Biology* 35(4): 522–532. <https://doi.org/10.1163/1937240X-00002343>
- Vinogradov GM (1999a) Amphipoda. In: Boltovskoy D (Ed.) *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, 1141–1240.
- Vinogradov GM (1999b) Deep-sea near-bottom swarms of pelagic amphipods Themisto: observations from submersibles. *Sarsia* 84: 465–467. <https://doi.org/10.1080/00364827.1999.10807352>

- Walker AO (1904) Report on the Amphipoda collected by Professor Herdman, at Ceylon, in 1902. Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, with supplementary reports upon the marine biology of Ceylon. The Royal Society, London, Part II: 229–300. [8 pls]
- Weisshappel JBF (2000) Distribution and diversity of the hyperbenthic amphipod family Eusiridae in the different seas around the Greenland-Iceland-Faeroe-Ridge. *Sarsia* 85: 227–236. <https://doi.org/10.1080/00364827.2000.10414575>
- Weisshappel JBF (2001) Distribution and diversity of the hyperbenthic amphipod family Calliopiidae in the different seas around the Greenland-Iceland-Faeroe-Ridge. *Sarsia* 86: 143–151. <https://doi.org/10.1080/00364827.2001.10420469>
- Weisshappel JBF, Svavarsson J (1998) Benthic amphipods (Crustacea: Malacostraca) in Icelandic waters: diversity in relation to faunal patterns from shallow to intermediate deep Arctic and North Atlantic Oceans. *Marine Biology* 131: 133–143. <https://doi.org/10.1007/s002270050304>
- White KN (2011) A taxonomic review of the Leucothoidae (Crustacea: Amphipoda). *Zootaxa* 3078: 1–113.
- Wildish DJ, Peer D (1981) Tidal current speed and production of benthic macrofauna in the lower Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* 40 (suppl. 1): 309–321. <https://doi.org/10.1139/f83-292>

Supplementary material I

Table 1. Samples used for present study.

Authors: Saskia Brix, Anne-Nina Lörz, Anna M. Jażdżewska, Lauren Hughes, Anne Helene S. Tandberg, Krzysztof Pabis, Bente Stransky, Traudl Krapp-Schickel, Jean-Claude Sorbe, Edward Hendrycks, Wim Vader, Inmaculada Frutos, Tammy Horton, Krzysztof Jażdżewski, Rachael Peart, Jan Beermann, Charles Oliver Coleman, Lene Buhl-Mortensen, Laure Corbari, Charlotte Havermans, Ramiro Tato, Anali Jimenez Campean
Data type: occurrence

Explanation note: Stations are organised according to the percentage of amphipods identified to the family level. Only the stations marked in green were used for primer analysis, while all were the basis for map preparation. Amphipod taxa are presented from the most to the least abundant in all samples.

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Link: <https://doi.org/10.3897/zookeys.731.19854.suppl1>

Supplementary material 2

Table 2. BIOICE and IceAGE stations used for Primer analysis of Amphilochidae including information about species distribution/number of specimens per station.

Authors: Saskia Brix, Anne-Nina Lörz, Anna M. Jażdżewska, Lauren Hughes, Anne Helene S. Tandberg, Krzysztof Pabis, Bente Stransky, Traudl Krapp-Schickel, Jean-Claude Sorbe, Edward Hendrycks, Wim Vader, Inmaculada Frutos, Tammy Horton, Krzysztof Jażdżewski, Rachael Peart, Jan Beermann, Charles Oliver Coleman, Lene Buhl-Mortensen, Laure Corbari, Charlotte Havermans, Ramiro Tato, Anali Jimenez Campean
Data type: occurrence

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Link: <https://doi.org/10.3897/zookeys.731.19854.suppl2>

Supplementary material 3

Table 3. IceAGE stations used for Primer analysis of Oedicerotidae including information about species distribution/number of specimens per station.

Authors: Saskia Brix, Anne-Nina Lörz, Anna M. Jażdżewska, Lauren Hughes, Anne Helene S. Tandberg, Krzysztof Pabis, Bente Stransky, Traudl Krapp-Schickel, Jean-Claude Sorbe, Edward Hendrycks, Wim Vader, Inmaculada Frutos, Tammy Horton, Krzysztof Jażdżewski, Rachael Peart, Jan Beermann, Charles Oliver Coleman, Lene Buhl-Mortensen, Laure Corbari, Charlotte Havermans, Ramiro Tato, Anali Jimenez Campean
Data type: occurrence

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A genetic fingerprint of Amphipoda from Icelandic waters – the baseline for further biodiversity and biogeography studies

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Abstract

Amphipods constitute an abundant part of Icelandic deep-sea zoobenthos yet knowledge of the diversity of this fauna, particularly at the molecular level, is scarce. The present work aims to use molecular methods to investigate genetic variation of the Amphipoda sampled during two IceAGE collecting expeditions. The mitochondrial cytochrome oxidase subunit 1 (COI) of 167 individuals originally assigned to 75 morphospecies

was analysed. These targeted morphospecies were readily identifiable by experts using light microscopy and representative of families where there is current ongoing taxonomic research. The study resulted in 81 Barcode Identity Numbers (BINs) (of which >90% were published for the first time), while Automatic Barcode Gap Discovery revealed the existence of 78 to 83 Molecular Operational Taxonomic Units (MOTUs). Six nominal species (*Rhabdotropis helleri*, *Arrhis phyllonyx*, *Deflexilodes tenuirostratus*, *Paroediceros propinquus*, *Metopa boeckii*, *Astyra abyssii*) appeared to have a molecular variation higher than the 0.03 threshold of both p-distance and K2P usually used for amphipod species delineation. Conversely, two Oedicerotidae regarded as separate morphospecies clustered together with divergences in the order of intraspecific variation. The incongruence between the BINs associated with presently identified species and the publicly available data of the same taxa was observed in case of *Paramphithoe hystrix* and *Amphilochus manudens*. The findings from this research project highlight the necessity of supporting molecular studies with thorough morphology species analyses.

Keywords

Amphipoda, COI barcoding, deep sea, North Atlantic

Introduction

Within the Class Malacostraca, the Order Amphipoda is currently represented by around 9000 described species, among which 80% are marine (Väinölä et al. 2008). Due to their high diversity and often large abundances (see e.g. Brandt 1997, Brandt et al. 2005, Plaisance et al. 2009), amphipods play a significant role in the food web throughout the world's oceans (Dauby et al. 2001, 2003).

Studies on the marine zoobenthos around Iceland started in the late 19th Century with the Danish Ingolf Expeditions of 1895 and 1896 (Wandel 1899). These early pioneering cruises included sampling of amphipod fauna and resulted in the published records on amphipod species diversity and distributions (Stephensen 1931, Sæmundsson 1937). In the Century which followed very few articles were produced on the marine amphipods from the Icelandic region. The few papers covered topics of both taxonomy and shallow-water communities (Thurston 1980a, b, Ingólfsson 1996). It was not until the late 1900's that the Icelandic region received further attention, namely through two large scale research programs, BIOFAR sampling from 1987–1990 (Nørrevang et al. 1994) and BIOICE sampling from 1991–2004 (Brix et al. 2014a). Both these programs were devoted to make an inventory of the marine fauna of the Faroe and Icelandic seas. Successful research continues to be generated from these collections and to-date specific studies of Amphipoda from BIOFAR and BIOICE have included taxonomic works of several families (Larsen 1996, Berge and Vader 1997, Bellan-Santini and Dauvin 1997, Myers 1998, Coleman 1999, Krapp-Schickel 2005, Dauvin et al. 2012), along with zoogeographical and ecological studies which incorporate the abundant and diverse amphipod fauna (Brandt and Piepenburg 1994, Brandt 1997, Weissshappel and Svavarsson 1998, Weissshappel 2000, 2001). Despite the large scale sampling efforts of the BIOFAR and BIOICE programs, it was recognized that large parts of the marine seafloor surrounding Greenland, Iceland and the Norwegian seas were still poorly known. To fill this knowledge gap a research program entitled:

Icelandic marine Animals – Genetics and Ecology (IceAGE), was established to further sample and develop our understanding of the North Atlantic marine fauna (Brix et al. 2014a). From the epibenthic sledge samples collected during the IceAGE Expeditions, the Amphipoda are again recognised as an especially abundant and diverse part of the North Atlantic zoobenthos (Brix et al. 2018).

As part of the greater North Atlantic and subarctic region, the special oceanographic conditions associated with the Iceland region and its adjacent waters are particularly interesting (Hansen and Osterhus 2000, Schnurr et al. 2014, Brix et al. 2014a). The marine region around Iceland includes several water masses and a conspicuous submarine mountain chain – the Greenland-Scotland-Ridge (GSR). The ridge topography influences marine habitats and presents a physical barrier separating the Arctic deep-sea basins from the North Atlantic proper. The complex hydrography which occurs across the ridge plays a key role in global thermohaline circulation (Hansen and Osterhus 2000) and is fundamental to the regional Northern European climate. Approaching from the north and engulfing Iceland from both the east and western sides are cold, deep water currents. In contrast, to this deep water encircling, warmer surface waters move around Iceland in a south-west to north-east direction (Ostmann et al. 2014, Schnurr et al. 2014). Although these hydrographical conditions may shape distributions for some isopod groups (Brix and Svavarsson 2010), yet in broader analyses of regional assemblages temperature seen to be less important when compared to other abiotic factors (Schnurr et al. 2014).

Since the proposal of the DNA barcoding concept by Hebert et al. (2003) the use of molecular methods in species recognition has become broadly applied and often supplements morphological taxonomy (e.g. Hubert and Hanner 2015, Seefeldt et al. 2017). The most commonly used molecular marker, is the mitochondrial cytochrome c oxidase subunit 1 (COI) for which there are several protocols available using either universal or specific primers (e.g. Folmer et al. 1994, Geller et al. 2013 and references therein). The use of molecular markers has highlighted the existence of many overlooked species within the Order Amphipoda both in freshwater as well as marine environments (e.g. Lörz et al. 2009, Havermans et al. 2013, Mamos et al. 2016, Verheye et al. 2016). Due to a high diversity and abundance of amphipods within faunal assemblage and the proportionally small number of scientists working on the group, most amphipod studies are restricted to a particular family/species or cover a limited spatial range (see papers cited above). The paper is the first to undertake a broader multi-family and species level approach for studying the molecular diversity of Icelandic amphipods.

Comparative studies on the Icelandic marine fauna have demonstrated a higher than expected molecular diversity for common and widely distributed isopod species (Brix et al. 2014b, Brix et al. in review). A similar pattern may be expected in the case of other peracarid crustaceans, namely the Amphipoda.

The aim of the present study is to use molecular methods to investigate the genetic variation of Icelandic amphipods and understand if changes in molecular diversity reflect the known characteristics of the regional benthic topography and hydrological conditions. The results from this study are a baseline for further research of species diversity and distribution in Icelandic and adjacent waters.

Material and methods

Sampling

The sampling area covered a wide depth range (from 117 to 2780 m) of the Denmark Strait, Irminger, Iceland and Norwegian basins, as well as the Faroe and Norwegian Channels (Figure 1). Detailed environmental data from each station were also gathered (Brix et al. 2014a).

Samples were taken during IceAGE expeditions 1 and 2 with R/V *Meteor* (M85/3) and R/V *Poseidon* (POS456) in 2011 and 2013 using two types of epibenthic sleds (EBS, Rothlisberg and Percy 1977, Brenke 2005). All samples were fixed in pre-cooled (-20°C) 96% undenatured ethanol and treated as described in Riehl et al. (2014).

During two “IceAGE amphipod determination workshops” held at the German Centre for Marine Biodiversity Research (DZMB) in Wilhelmshaven, Germany in July 2016 and in the field station of the University of Lodz in Spała, Poland in May 2017 representatives of recognized families/species were chosen for molecular analysis. Individuals were then determined to species level using Leica (MZ 6, 8 & 12.5) and Nikon (SMZ 800, 1500) dissecting microscopes. World Register of Marine Species (WoRMS) systematic division was followed. Each specimen was separated from the sample and was given a voucher identification number (voucher ID) and will be registered in the ZMH Hamburg. Individuals were subsequently stored at 4°C at the DZMB Hamburg, and DNA extracts are stored at the Smithsonian Institution at -80°C .

One hundred sixty-seven individuals from 27 stations initially assigned by amphipod taxonomists to 75 morphospecies (21 families) were used for molecular analysis (Suppl. material 1). One to six individuals per taxon were chosen. Extraction, PCR and sequencing protocols followed Riehl et al. (2014). Molecular work was conducted by LGC Genomics and the Smithsonian. In the case of individuals from the superfamily Lysianassoidea as well as from families Stegocephalidae and Hyperiopidae the extraction and PCR protocols of Havermans (2016) were used. For the PCR products, both forward and reverse strands were sequenced using the sequencing services of EUROFINS (Germany).

Data analyses

Sequences were edited using Geneious 10.1.2 resulting in 167 sequences of length of 621–658 bp excluding primers. All sequences were deposited in GenBank with the accession numbers MG264740–MG264881, KY072917–KY072920 and MG521122–MG521157 (Suppl. material 1). Relevant voucher information, taxonomic classifications, and sequences are accessible through the public data sets “DS-AMPIA” ([dx.doi.org/10.5883/DS-AMPIA](https://doi.org/10.5883/DS-AMPIA)) and “DS-RHACHOTR” (<https://doi.org/10.5883/DS-RHACHOTR>) on the Barcode of Life Data Systems (BOLD; www.boldsystems.org) (Ratnasingham and Hebert 2007).

The sequences were aligned with MAFFT v7.308 algorithm with default settings (Katoh et al. 2002, Katoh and Standley 2013) in Geneious 10.1.2 resulting in a 599

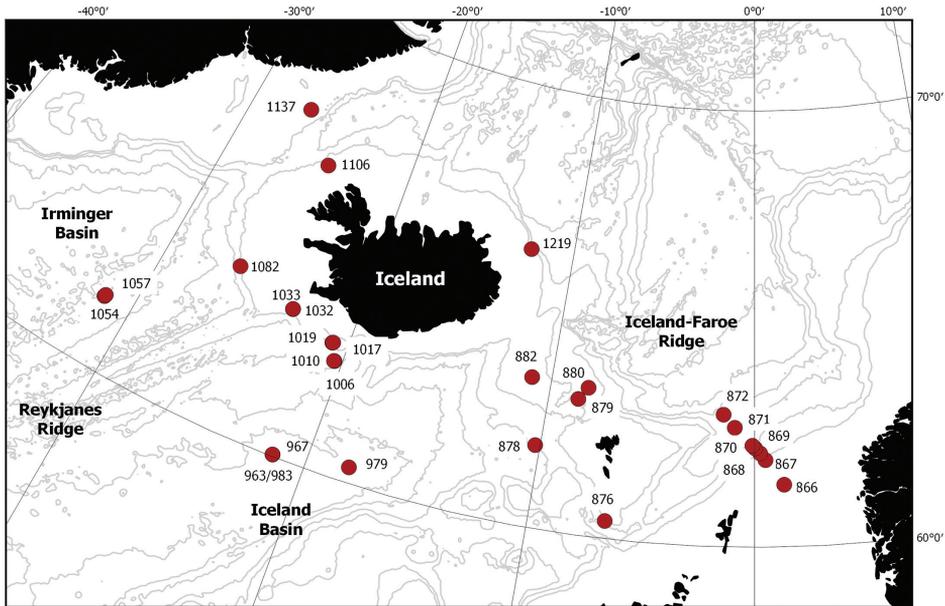


Figure 1. Sampling stations. Depth contours are the following: 500 m, 1000 m, 1500 m, 2000 m, 2500 m, 3000 m. Station details are in Suppl. material 1.

bp alignment used for further analyses. Uncorrected p-distance and the Kimura 2-parameter (K2P) model (Kimura 1980) were used to determine sequence divergence in MEGA V7.0.18 (Kumar et al. 2016). A Neighbour-Joining (NJ) tree was built based on K2P using the default parameters (transition and transversion substitutions included and pairwise deletion). Node support was inferred with a bootstrap analysis (1000 replicates). The COI sequence of *Pleuropriion hystrix* (G.O. Sars, 1877) (Isopoda) from one of the stations sampled within IceAGE project was used as outgroup.

Two distance-based methods for species delimitation were applied in order to assess the number of MOTUs that could represent putative cryptic species. The first one, Barcode Index Number (BIN) System (Ratnasingham and Hebert 2013), compares newly submitted sequences with the sequences already available in BOLD. They are clustered according to their molecular divergence using algorithms aiming at finding discontinuities between clusters. Each cluster receives a unique and specific code (Barcode Index Number or BIN), either already available or new if submitted sequences do not cluster with already known BINs. The second method, Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012), uses pairwise distance measures. With this method, the sequences are partitioned into groups (MOTUs), such that the distance between two sequences from two different groups will always be larger than a given threshold distance (i.e. barcode gap). One of the critical parameters of the ABGD method is the prior maximum divergence of intraspecific diversity (P). The prior P values were set from the default value of 0.001 to 0.03. The latter is commonly used for species delimitation in arthropods and particularly in Amphipoda (e.g. Hebert et

al. 2003, Costa et al. 2007, 2009, Raupach et al. 2015, Lobo et al. 2017). Both uncorrected p-distance and K2P were used to calculate species distances. Due to a very wide spectrum of taxa used in this study, representing many different families, as well as the presence of large number of singletons our data were not suitable for the phylogenetic approach to species delimitation analysis.

Results

Among the 75 morphologically identified species, 81 Barcode Identity Numbers (BIN) were ascribed by BOLD (Figure 2, Suppl. material 1). Fifty-eight of these are unique for the database, while 23 are shared with other studies. Within the second group, nine are held in private datasets and another nine are left identified at the order level. As a result, only five are public and are associated with known species names. In total, 94% of the BINs in the present study are published for the first time.

The ABGD method allowed for recognition of 79 to 83 MOTUs when using K2P distance and 78–79 MOTUs for p-distance analysis. In the case of K2P the most stable division over a wide range of the prior maximum divergence values ($P= 0.004-0.03$) was 79 MOTUs and thus only this division is presented in Figure 2.

The number of haplotypes for each BIN ranged from one to five, the latter being the case in *Dulichlopsis cf. macera* (G.O. Sars, 1879) (Table 1). The intraspecific variation expressed by both p-distance and K2P were similar within each BIN and generally low. The highest values were recorded for *Bruzelia cf. diodon* K.H. Barnard, 1916 and *Rhachotropis thordisae* Thurston, 1980 (0.019 and 0.010, respectively). As many as 43 MOTUs were singletons.

Four species identified on the basis of morphology (*Rhachotropis helleri* (Boeck, 1871), *Arrhis phyllonyx* (M. Sars, 1858), *Deflexilodes tenuirostratus* (Boeck, 1871), *Metopa boeckii* G.O. Sars, 1892) showed intraspecific variation considerably exceeding the values commonly used for amphipod species delimitation (Table 2) indicating potential cryptic diversity. For another two species (*Paroediceros propinquus* (Goës, 1866) and *Astyra abyssii* Boeck, 1871) those values were very close to the threshold.

The NJ tree showed the existence of different lineages within the above-mentioned species (Figure 2). Also it revealed that some individuals morphologically identified as *Paroediceros propinquus* have clustered with *Paroediceros curvirostris* (Hansen, 1888).

Figure 2. Neighbour-joining (NJ) tree of COI sequences (Suppl. material 1) based on Kimura 2-parameter. Triangles indicate the relative number of individuals studied (height) and sequence divergence (width). The asterisk (*) symbolizes taxa having already published sequences in BOLD/GenBank identified to species level. The numbers in front of the nodes indicate bootstrap support (1000 replicates, only values higher than 50% are presented). The vertical bars represent species delimitations taxonomies obtained from morphology and different species delimitation methods. The same colour indicates the same nominal species. Only the cases where incongruence between different delimitation methods were observed are shown. Note that this tree is not the reconstruction of evolutionary history of presented taxa.

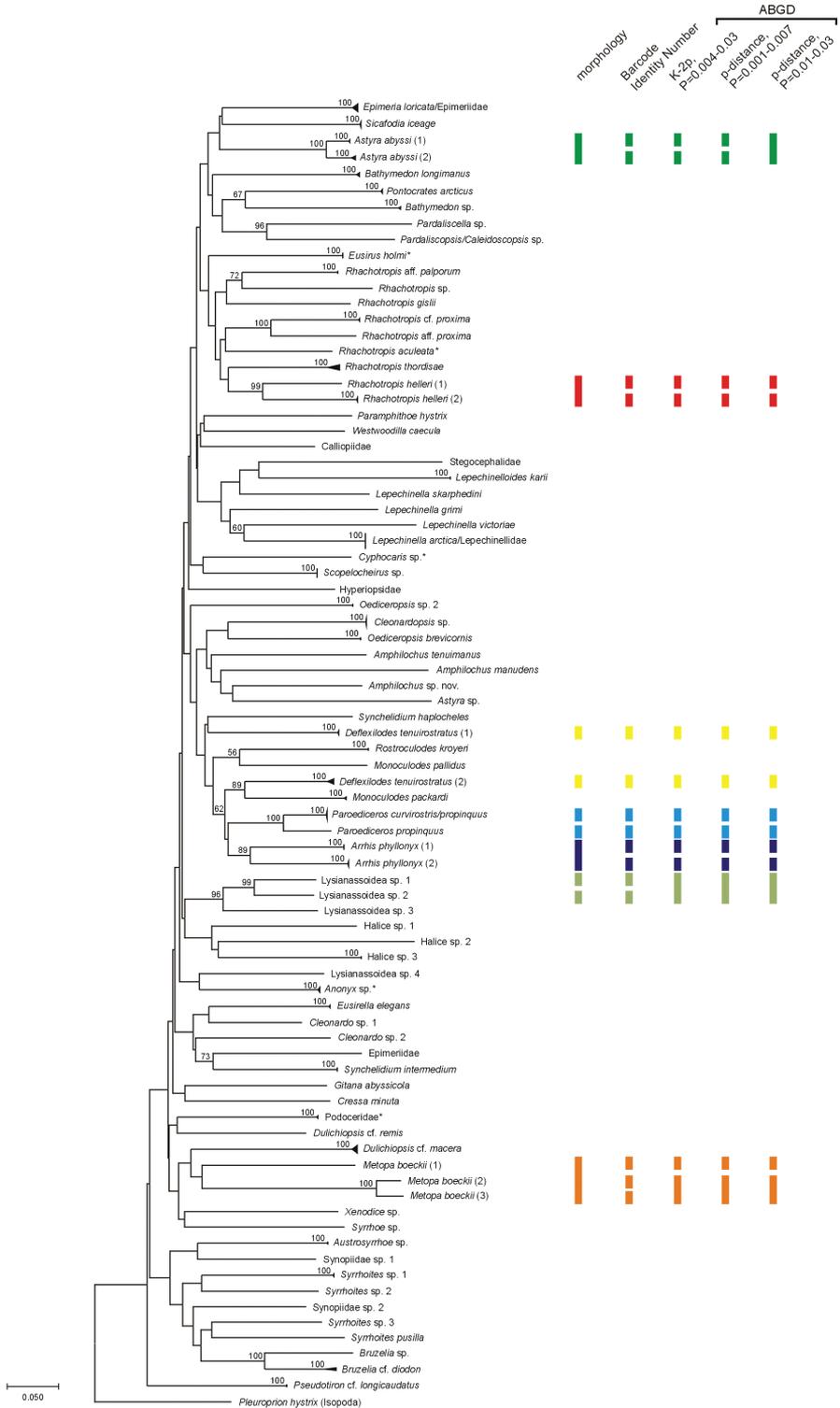


Table 1. The intraspecific variation within BINs obtained, calculated using uncorrected p-distance and Kimura 2-parameter (K2P). Taxa represented by a single sequence are not listed.

Family	Taxon	No. of ind.	No. of haplotypes	p-distance	K2P
Amathillopsidae	<i>Cleonardopsis</i> sp.	5	2	0.001	0.001
Dulichiiidae	<i>Dulichioipsis</i> cf. <i>macera</i> (G.O. Sars, 1879)	6	5	0.005	0.005
Epimeriidae	<i>Epimeria loricata</i> G.O. Sars, 1879	6	4	0.006	0.006
Eusiridae	<i>Eusirella elegans</i> Chevreux, 1908	2	2	0.002	0.002
Eusiridae	<i>Eusirus bolmi</i> Hansen, 1887	4	1	0.000	0.000
Eusiridae	<i>Rhachotropis</i> aff. <i>palporum</i> Stebbing, 1908	2	1	0.000	0.000
Eusiridae	<i>Rhachotropis</i> cf. <i>proxima</i> Chevreux, 1911	2	2	0.002	0.002
Eusiridae	<i>Rhachotropis thordisae</i> Thurston, 1980	4	2	0.010	0.010
Eusiridae	<i>Rhachotropis helleri</i> (2) (Boeck, 1971)	3	2	0.001	0.001
Lepechinellidae	<i>Lepechinella arctica</i> Schellenberg, 1926/Lepechinellidae	12	1	0.000	0.000
Lepechinellidae	<i>Lepechinelloides kariii</i> Thurston, 1980	2	1	0.000	0.000
Oedicerotidae	<i>Arrbis phyllonyx</i> (1) M. Sars, 1858	4	1	0.000	0.000
Oedicerotidae	<i>Arrbis phyllonyx</i> (2) M. Sars, 1858	4	2	0.001	0.001
Oedicerotidae	<i>Bathymedon longimanus</i> (Boeck, 1871)	3	2	0.003	0.003
Oedicerotidae	<i>Bathymedon</i> sp.	2	2	0.003	0.003
Oedicerotidae	<i>Deflexilodes tenuirostratus</i> (1) (Boeck, 1871)	3	2	0.001	0.001
Oedicerotidae	<i>Deflexilodes tenuirostratus</i> (2) (Boeck, 1871)	4	4	0.008	0.008
Oedicerotidae	<i>Monoculodes packardii</i> Boeck, 1871	2	2	0.003	0.003
Oedicerotidae	<i>Oediceropsis brevicornis</i> (Lilljeborg, 1865)	2	1	0.000	0.000
Oedicerotidae	<i>Oediceropsis</i> sp. 2	2	1	0.000	0.000
Oedicerotidae	<i>Paroediceros curvirostris</i> (Hansen, 1888)/ <i>P. propinquus</i> (Goës, 1866)	6	2	0.001	0.001
Oedicerotidae	<i>Pontocrates arcticus</i> G.O. Sars, 1895	3	3	0.002	0.002
Oedicerotidae	<i>Rostroculodes kroyeri</i> (Boeck, 1870)	2	1	0.000	0.000
Oedicerotidae	<i>Synchelidium intermedium</i> (Grube, 1864)	3	1	0.000	0.000
Pardaliscidae	<i>Halice</i> sp. 3	2	1	0.000	0.000
Podoceridae	Podoceridae	2	2	0.002	0.002
Scopelocheiridae	<i>Scopelocheirus</i> sp.	7	1	0.000	0.000
Sicafodiidae	<i>Sicafodia iceage</i> (Campean & Coleman, 2017)	4	2	0.001	0.001
Stilipedidae	<i>Astyra abyssi</i> (1) Boeck, 1871	2	2	0.002	0.002
Stilipedidae	<i>Astyra abyssi</i> (2) Boeck, 1871	3	3	0.006	0.006
Synopiidae	<i>Austrosyrrhoë</i> sp.	2	1	0.000	0.000
Synopiidae	<i>Bruzelia</i> cf. <i>diodon</i> K.H. Barnard, 1925	2	2	0.019	0.019
Synopiidae	<i>Pseudotiron</i> cf. <i>longicaudatus</i> Pirlot, 1934	2	1	0.000	0.000
Synopiidae	<i>Syrrhoites pusilla</i> Enequist, 1949	2	2	0.002	0.002
Uristidae	<i>Anonyx</i> sp.	4	2	0.002	0.002

It confirmed also the identity of six individuals originally left identified at the family level (Lepechinellidae) as aligning with specimens identified as *Lepechinella arctica* Schellenberg, 1926.

Table 2. The values of uncorrected p-distance, Kimura 2-parameter (K2P) and Barcode Identity Numbers (BINs) for nominal species presenting the highest intraspecific variation.

Family	Species	No of ind.	No of haplotypes	p-distance	K2P	BIN
Eusiridae	<i>Rhachotropis helleri</i>	4	3	0.076	0.085	ADE3179, ADE4377
Oedicerotidae	<i>Arrhis phyllonyx</i>	8	3	0.093	0.106	AAG7255, ADG9371
Oedicerotidae	<i>Deflexilodes tenuirostratus</i>	7	6	0.118	0.139	ADH2072, ADH2071
Oedicerotidae	<i>Paroediceros propinquus</i>	3	2	0.056	0.060	ADG8965, ACV0335
Stenothoidae	<i>Metopa boeckii</i>	3	3	0.198	0.245	ADH5455, ADH5456, ADH5457
Stilipedidae	<i>Astyra abyssi</i>	5	5	0.032	0.033	ADG9308, ADG9037

Incongruence between morphological species identification and different species delimitation methods was observed in the case of two representatives of Lysianassoidea (sp. 1 and sp. 2) (Figure 2). Based on their morphology they were determined as two separate units, which was confirmed by assignment of two different BINs. However, the ABGD method on both p-distance and K2P treated them as a single MOTU. When both sequences were considered together the distance value between them is 0.106 and 0.118 for p-distance and K2P, respectively. In this case the ABGD method seemed to fail, artificially treating two very divergent sequences (and as a result two species) as a single unit.

Discussion

The present study gives a first “glimpse” into the molecular diversity of Icelandic Amphipoda and provides a baseline for future studies. Further research is needed for where molecular diversity is not congruent with morphological identification. Re-examination of material for characters in consideration of clear alignment of lineages with topology, hydrology and depth stratification is also required. In considering the number of more than 21500 amphipod specimens identified to family level during IceAGE determination workshops (see Brix et al. 2018), only about 170 specimens, 0.7%, of these were selected for barcoding. The specimens targeted for molecular analysis were material identified as in good morphological condition (majority of limbs intact), material which was readily identifiable using light microscopy (did not require dissection and slide preparation for mouth parts), but where largely defined as groups of scientific interest to the experts and where there is current ongoing taxonomic research. The relatively high number of representatives of Eusiridae, Oedicerotidae or Synopiidae reflects the intention of particular scientists to analyse these taxa further. It does not represent the diversity of Icelandic and adjacent waters, as the super abundant and speciose groups such as Phoxocephalidae or Lysianassoidea are acknowledged as underrepresented in this paper. Knowing the limitations associated with the size of the material used for the study it is still possible to define the emerging issues and propose directions for further studies.

1. Recognizing amphipod species diversity in Icelandic waters

Based on the material studied 81 BINs were recognized. Only five of the BINs are identified to the species level and publically available, while 94% are either unique, held in private datasets, or without detailed identification. That proportion indicates the extent to which knowledge of this important group of marine zoobenthos is still poorly known. In another barcoding study of Crustacea from Gulf of St. Lawrence (North Atlantic) new barcodes accounted for 75 percent of studied sequences (Radulovici et al. 2009). In the eight years since the release of this earlier study, there is still large gaps in the knowledge of genetic diversity including the deeper parts of the ocean as demonstrated here for the Icelandic and adjacent waters in the North Atlantic. Within the acknowledge limitations of DNA barcoding approach, the present results show that biodiversity studies in Icelandic waters can strongly benefit from the usage of molecular method. According to Ratnasingham and Hebert (2013) the BIN corresponds a distance-based COI sequence cluster that might represent single species. Another species delimitation method (ABGD) revealed the existence of 78 to 79 MOTUs (Figure 2). These differences might be explained by methodological difference or alternately by insufficient sampling. The majority of studied taxa were represented by a two or three sequences, which may have prevented proper discrimination between intra and interspecific variation. Based on the present study it is not possible to conclusively assess which of these species delimitation methods gives the most reliable results. The number of individuals per taxon presently studied was low and half of the morphospecies were represented by single sequence only. The most commonly used value for barcode gap was applied here as a threshold to divide species, but there are some works that mentioned higher intraspecific diversity within deep-sea amphipods than previously expected (Knox et al. 2012).

The present study allowed for obtaining barcodes for species newly described from Icelandic waters: *Sicafodia iceage* Campean & Coleman, 2017 and *Amphilochus anoculus* Tandberg & Vader, 2018 (Campean and Coleman 2017, Tandberg and Vader 2018). Additionally, based on the combination of morphological and molecular data some species belonging to the genera *Rhachotropis*, *Bruzelia*, *Austrosyrrhoe* and *Syrrhoites* have been recognized as putatively new to science.

It is important to point out that the taxonomic and molecular diversity that can be seen in the NJ tree does not reflect the complete amphipod family and species diversity of Icelandic and adjacent waters, but reflects only a small representation, less than 1% of processed samples, were investigated here for genetic analysis.

2. Morphological versus molecular species identification

The molecular results are generally congruent with the morphological identification of studied species. The existence of potential cryptic (or pseudocryptic) species has been observed within three taxa of Oedicerotidae as well as one taxon in the families: Eusiridae, Stilipedidae and Stenothoidae.

Two clearly distinct clades have been observed within *Rhachotropis helleri* (Eusiridae). The specimens representing both lineages were collected at similar depths (ca. 300 m) but from very different localities: the Iceland-Faroe Ridge and the Iceland Basin. As the genus *Rhachotropis* is the subject of another publication in this issue (Lörz et al. 2018) the details of taxonomic rank of *R. helleri* are not presented here.

In *Arrhis phyllonyx* (Oedicerotidae) two different lineages have been recognised for this study. *Arrhis phyllonyx* is a species commonly reported from North Atlantic waters with a wide depth range from 100 to 2680 m (Sars 1890, Vader unpublished data). Some morphological variability has been observed and might be associated with the depth distribution of this taxon. Morphological studies have previously documented the subspecies—*A. phyllonyx arcticus* Bryazgin, 1974—from the Barents Sea (Bryazgin 1974). In the present study, all specimens were collected in the Iceland-Faroe Ridge area at neighbouring stations, including 510 m depth (lineage 1) and 158 to 686 m depth (lineage 2). Further detailed study of the morphology variation along with molecular analyses is required.

Two different clades of *Deflexilodes tenuirostratus* have been observed where genetic separation aligns with difference in sampling locality, with clade 1 sampled from the Iceland Basin and clade 2 sampled from the Iceland-Faroe Ridge. Given the clear geographic distinction between clades additional research is required to more closely investigate the morphology to assess if there could exist two cryptic species within this taxon.

Smaller yet consistent sequence differences were also noted in *Paroedicerus propinquus*. All individuals sequenced were collected from similar depths at neighbouring stations on the Iceland-Faroe Ridge. Moreover, the sequences of *P. propinquus* forming clade 1 appeared to share haplotypes with another species in this genus, namely *P. curvirostris* indicating that the morphological characters require closer examination to see if these BINs can be supported with additional morphological character states.

The results for the family Oedicerotidae will be further studied using additional genes and material from other localities (Hughes pers. com.). It is worth noting that similar results were recently observed in the case of some other North Atlantic amphipod species reported as having wide distribution range for six out of the 68 identified morphospecies (Lobo et al. 2017). In their case study the incongruence between the morphological identification and genetic variability was explained by geographic distance in four of the disparate morphospecies. In the remaining two amphipods, *Corophium multisetosum* Stock, 1952 and *Dexamine spiniventris* (Costa, 1853) the species presented high genetic divergence were collected in the same area. A lack of morphological characters differentiating two sympatrically distributed lineages of a single recognised morphospecies was observed also in *Leucothoe vulgaris* White & Reimer, 2012 (White et al. 2015). With morphologically conservative yet genetically defined species appearing across amphipod families the disparate results from these methods prompt more fine scale morphological and broader molecular investigation.

High genetic diversity was also observed in one species from the family Stenothoidae: *Metopa boeckii*. Depending on the species delimitation method, two (ABGD) or three (BINs) MOTUs have been revealed. Some morphological variability within this species

has already been observed and further morphological studies could result in new species description. All individuals of this nominal species were collected in the same geographic area at similar depths, but on opposite sides of Iceland-Faroe Ridge: *M. boeckii* lineage 1 occurred south of the topographic barrier while lineages 2 and 3 were collected from the north side. The representatives of Stenothoidae are often known to occur in association with other invertebrates (Brix et al. 2018). A further examination of host data could reveal if its dispersal limitation is potentially defined by the host invertebrate. The Island-Faroe Ridge has been demonstrated as a defining feature to dispersal for the North Atlantic isopods from the genus *Oecidiobanchus* (Brix et al. in review).

With the family Stilipedidae delimiting the species *Astyra abyssi* can be seen as either one or two species depending on the methodology applied. The values of p-distance and K2P are just over the threshold that is commonly used to discriminate species of arthropods and amphipods in particular (Hebert et al. 2003, Costa et al. 2007, 2009). *Astyra abyssi* was represented by five individuals in this study, and further molecular analysis of individuals would be needed to confirm if the observed diversity represents high intraspecific variation or of the presence of two species, one of which is cryptic. The two lineages are seen to be depth stratified with *A. abyssi* lineage 1 (2 individuals) occurred at ~300 m south of Iceland, while the lineage 2 are from two deeper water station of 724 m and 1385 m, respectively in the Irminger and Iceland basins.

These two deeper water stations, the Irminger and Iceland basins, are separated by the Reykjanes Ridge, a topological feature. However, these separated locations could be connected by the movement of water masses around Iceland, as this pattern is also seen in other deep-sea peracarids (Svavarsson et al. 1993; Svavarsson 1997, Negoescu and Svavarsson 1997). The lack of genetic separation of the populations collected from both sides of Reykjanes Ridge are also known for the isopod *Chelator insignis* (Hansen, 1916) species complex (Brix et al. 2014b). Both deep-water stations are situated in areas influenced by deep, cold currents flowing from the northeast and passing by the Reykjanes Ridge (Ostmann et al. 2014). The representatives of the family Stilipedidae are regarded as having good swimming abilities, with some species considered as pelagic (Berge 2003). By contrast, *Astyra abyssi* in lineage 1 is from a more shallow water station with an area of warm surface water current (Ostmann et al. 2014). The influence of vertical distribution on genetic divergence is known for the deep sea amphipod *Eurythenes gryllus* (Lichtenstein in Mandt, 1822) with clear separation between lineages inhabiting bathyal and abyssal depths (Havermans et al. 2013; Havermans 2016). The separation of lineages associated with depth and related to different water masses was observed in the case of pelagic siphonophore species in Sagami Bay, Japan (Grossmann et al. 2013) where two molecularly distinct populations of *Lenisia achilles* Totton, 1941 were correlated with warm subtropical and cold subarctic water masses.

The present study assisted with delimiting specimens suspected to be juvenile forms to be evaluated to a species level along side congeneric BINs. Several juvenile lepechinellids initially identified only to the family level (Lepechinellidae) were able to be assigned to *Lepechinella arctica*. In this way molecular analyses was useful where ontogenetic stage restricts morphological identification of individuals.

3. Comparison of IceAGE barcodes with publicly available content

Molecular methods proved to be a useful tool in cryptic species recognition, and the existence of several amphipod species complexes has been already reported (Lörz et al. 2009, Havermans et al. 2013, Mamos et al. 2016, Verheye et al. 2016). Species initially treated as taxa with wide geographic distributions are often reviewed following genetic analyses, especially where genetic lineages show distributions divergent in association with topography, hydrology or depth. The existence of a species complex was observed in *Paramphithoe hystrix* (Ross, 1835) (Schnabel and Hebert 2003). In the present study the *P. hystrix* sequence obtained was recognized as a unique BIN for BOLD, therefore this study contributes another lineage to this known *P. hystrix* complex. At present the complex is not supported by a morphological assessment which would allow comparison of the voucher specimens. Vouchered taxonomic identifications are essential for genetic studies, as once the mistake appears in barcoding database it is easily repeated by further users of the online genetic resources. Without currently published information on the morphology associated with these lineages, at present there can be no further comparison of this species complex as MOTUs (BINs) with the morphological concept of *P. hystrix* in the taxonomic literature.

For *Amphilochus manudens* Spence Bate, 1862 it appears also, that the individual which was assigned to this species from IceAGE sampling represents a different BIN than the specimens collected from the North Sea and ascribed to the same taxon. The sequence divergence is large (0.228 p-distance and 0.278 K2P) much higher than the present concept for intraspecific variation. The two MOTUs observed within the nominal *A. manudens* have different geographic and bathymetric distributions. The specimen from IceAGE was collected in the area of the Iceland-Faroe Ridge at 500 m depth, while the previously reported material came from a shallow station (50 m) in southeast North Sea (Raupach et al. 2015). Further studies of voucher material should be conducted to assess the comparative morphology of the material and possibly that of type material.

Conclusion

DNA barcoding can help considerably in recognition of species diversity in the deep sea by indicating the existence of cryptic or pseudocryptic species and allowing the taxonomists to focus on the novel morphological and genetic incongruence. However, the accuracy of the taxonomic identification of records in molecular databases is crucial to make those databases reliable for further users. The current study of Amphipoda from Icelandic and adjacent water in the North Atlantic strongly recognises that molecular methods need to be supplemented by comprehensive taxonomical analysis of species morphology in order to provide an expert certified baseline for further biodiversity studies.

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References

- Bellan-Santini D, Dauvin JC (1997) Ampeliscidae (Amphipoda) from Iceland with a description of a new species (Contribution to the BIOICE research programme). *Journal of Natural History* 31(8): 1157–1173. <http://dx.doi.org/10.1080/00222939700770621>
- Berge J (2003) The taxonomy of the amphipod genus *Stilipes* (Crustacea: Amphipoda: Stilepididae), with description of one new species. *Organisms, Diversity and Evolution* 3, Electr. Suppl. 16: 1–10.
- Berge J, Vader W (1997) Stegocephalid (Crustacea, Amphipoda) species collected in the BIOFAR and BIOICE programmes. *Sarsia* 82: 347–370. <https://doi.org/10.1080/00364827.1997.10413662>
- Brandt A (1997) Biodiversity of peracarid crustaceans (Malacostraca) from the shelf down to the deep Arctic Ocean. *Biodiversity and Conservation* 6: 1533–1556. <https://doi.org/10.1023/A:1018318604032>
- Brandt A, Brenke N, Andres H-G, Brix S, Guerrero-Kommritz J, Mühlenhardt-Siegel U, Wägele J-W (2005) Diversity of peracarid crustaceans (Malacostraca) from the abyssal plain of the Angola Basin. *Organisms, Diversity and Evolution* 5: 105–112. <https://doi.org/10.1016/j.ode.2004.10.007>
- Brandt A, Piepenburg D (1994) Peracarid crustacean assemblages of the Kolbeinsey Ridge, north of Iceland. *Polar Biology* 14: 97–105. <https://doi.org/10.1007/BF00234971>
- Brenke N (2005) An epibenthic sledge for operations on marine soft bottom and bedrock. *Marine Technology Society Journal* 39: 10–21. <https://doi.org/10.4031/002533205787444015>

- Brix S, Jennings RM, Bober S, Svavarsson J, Driskell A (in review) More diverse than expected: Distributional patterns of the genus *Oecidiobranthus* Hessler, 1970 on the Greenland-Iceland-Faroe Ridge based on molecular markers. *Marine Biodiversity*.
- Brix S, Lörz A-N, Jążdżewska AM, Hughes L, Tandberg AHS, Pabis K, Stransky B, Krapp-Schickel T, Sorbe JC, Hendrycks E, Vader W, Frutos I, Horton T, Jążdżewski K, Peart R, Beermann J, Coleman CO, Buhl-Mortensen L, Corbari L, Havermans C, Tato R, Campean AJ (2018) Amphipod family distributions around Iceland. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology* (IceAGE Amphipoda project). *ZooKeys* 731: 41–53. <https://doi.org/10.3897/zookeys.731.19854>
- Brix S, Meißner K, Stransky B, Hallanych KM, Jennings RM, Kocot KM, Svavarsson J (2014a) Preface: The IceAGE project – a follow up of BIOICE. *Polish Polar Research* 35(2): 141–150. doi: <https://doi.org/10.2478/popore-2014-0010>
- Brix S, Svavarsson J (2010) Distribution and diversity of desmosomatid and nannoniscid isopods (Crustacea) on the Greenland–Iceland–Faeroe Ridge. *Polar Biology* 33(4): 515–530. doi: [10.1007/s00300-009-0729-8](https://doi.org/10.1007/s00300-009-0729-8)
- Brix S, Svavarsson J, Leese F (2014b) A multi-gene analysis reveals multiple highly divergent lineages of the isopod *Chelator insignis* (Hansen, 1916) south of Iceland. *Polish Polar Research* 35(2): 225–242. doi: <https://doi.org/10.2478/popore-2014-0015>
- Bryazgin VF (1974) Dopolnenija k faune Gammaridea (Amphipoda) Barentzeva morja. *Zoologicheskij Zhurnal* 53(9): 1417–1420.
- Campean AJ, Coleman CO (2017) A new species of *Sicafodia* Just, 2004 (Crustacea, Amphipoda, Sicafodiidae) from the North Atlantic. *Marine Biodiversity*. doi.org/10.1007/s12526-017-0635-1
- Coleman CO (1999) On *Laothoes* (Crustacea, Amphipoda; Eusiridae) from the North Atlantic Ocean, with description of a new species. *Journal of Natural History* 33: 799–811. doi: <http://dx.doi.org/10.1080/002229399300119>
- Costa FO, deWaard JR, Boutillier J, Ratnasingham S, Dooh RT, Hajibabaei M, Hebert PDN (2007) Biological identifications through DNA barcodes: the case of the Crustacea. *Canadian Journal of Fisheries and Aquatic Science* 64: 272–295. <https://doi.org/10.1139/f07-008>
- Costa FO, Henzler CM, Lunt DH, Whiteley NM, Rock J (2009) Probing marine *Gammarus* (Amphipoda) taxonomy with DNA barcodes. *Systematics and Biodiversity* 7: 365–379. doi: <http://dx.doi.org/10.1017/S1477200009990120>
- Dauby P, Nyssen F, De Broyer C (2003) Amphipods as food sources for higher trophic levels in the Southern Ocean: a synthesis. In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff WJ (Eds) *Antarctic Biology in a Global Context*, Backhuys Publishers, Leiden, the Netherlands, 129–134.
- Dauby P, Scailteur Y, De Broyer C (2001) Trophic diversity within the eastern Weddell Sea community. *Hydrobiologia* 443: 69–86. <https://doi.org/10.1023/A:1017596120422>
- Dauvin J-C, Alizier S, Weppe A, Guðmundsson G (2012) Diversity and zoogeography of Icelandic deep-sea Ampeliscidae (Crustacea: Amphipoda). *Deep-Sea Research I* 68: 12–23. <https://doi.org/10.1016/j.dsr.2012.04.013>

- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3(5): 294–299.
- Geller J, Meyer C, Parker M, Hawk H (2013) Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Molecular Ecology Resources* 13(5): 851–861. doi: 10.1111/1755-0998.12138
- Grossmann MM, Lindsay DJ, Collins AG (2013) The end of an enigmatic taxon: *Eudoxia macra* is the eudoxid stage of *Lensia cossack* (Siphonophora, Cnidaria). *Systematics and Biodiversity* 11(3): 381–387. <http://dx.doi.org/10.1080/14772000.2013.825658>
- Hansen B, Osterhus S (2000) North Atlantic-Nordic Seas exchanges. *Progress in Oceanography* 45: 109–208. [https://doi.org/10.1016/S0079-6611\(99\)00052-X](https://doi.org/10.1016/S0079-6611(99)00052-X)
- Havermans C (2016) Have we so far only seen the tip of the iceberg? Exploring species diversity and distribution of the giant amphipod *Eurythenes*. *Biodiversity* 17(1-2): 12–25. <https://doi.org/10.1080/14888386.2016.1172257>
- Havermans C, Sonet G, d'Udekem d'Acoz C, Nagy ZT, Martin P, Brix S, Riehl T, Agrawal S, Held C (2013) Genetic and morphological divergences in the cosmopolitan deep-sea amphipod *Eurythenes gryllus* reveal a diverse abyss and a bipolar species. *PLoS ONE* 8(9): e74218. <https://doi.org/10.1371/journal.pone.0074218>
- Hebert PD, Ratnasingham S, deWaard JR (2003) Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London B* 270: S96–S99. <https://doi.org/10.1098/rsbl.2003.0025>
- Hubert N, Hanner R (2015) DNA Barcoding, species delineation and taxonomy: a historical perspective. *DNA Barcodes* 3: 44–58. <https://doi.org/10.1515/dna-2015-0006>
- Ingólfsson A (1996) The distribution of intertidal macrofauna on the coasts of Iceland in relation to temperature. *Sarsia* 81: 29–44. doi: <http://dx.doi.org/10.1080/00364827.1996.10413609>
- Katoh K, Misawa K, Kuma K, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30(14): 3059–3066. <https://doi.org/10.1093/nar/gkf436>
- Katoh K, Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution* 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kimura M (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120. <https://doi.org/10.1007/BF01731581>
- Knox MA, Hogg ID, Pilditch CA, Lörz A-N, Hebert PDN, Steinke D (2012) Mitochondrial DNA (COI) analyses reveal that amphipod diversity is associated with environmental heterogeneity in deep-sea habitats. *Molecular Ecology* 21: 4885–4897. <https://doi.org/10.1111/j.1365-294X.2012.05729.x>
- Krapp-Schickel T (2005) Cressidae (Crustacea: Amphipoda) collected by the BIOFAR and BIOICE programmes near the Faroes and Iceland. *BIOFAR Proceedings* 2005, 150–166.

- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33(7): 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Larsen K (1996) A redescription of *Protellina ingolfi* (Crustacea, Amphipoda, Caprellidae) from the North-Eastern Atlantic. *Journal of the Marine Biological Association of the UK* 76: 657–664. <https://doi.org/10.1017/S0025315400031362>
- Lobo J, Ferreira MS, Antunes IC, Teixeira MA, Borges LM, Sousa R, Gomes PA, Costa MH, Cunha MR, Costa FO (2017) Contrasting morphological and DNA barcode-suggested species boundaries among shallow-water amphipod fauna from the southern European Atlantic coast. *Genome* 60(2): 147–157. <https://doi.org/10.1139/gen-2016-0009>
- Lörz AN, Maas EW, Linse K, Coleman CO (2009) Do circum-Antarctic species exist in peracarid Amphipoda? A case study in the genus *Epimeria* Costa, 1851 (Crustacea, Peracarida, Epimeriidae). *ZooKeys* 18: 91–128. <https://doi.org/10.3897/zookeys.18.103>
- Lörz A-N, Tandberg AHS, Willassen E, Driskell A (2018) Rhachotropis (Eusiroidea, Amphipoda) from the North East Atlantic. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project)*. *ZooKeys* 731: 75–101. <https://doi.org/10.3897/zookeys.731.19814>
- Mamos T, Wattier R, Burzyński A, Grabowski M (2016) The legacy of a vanished sea: a high level of diversification within a European freshwater amphipod species complex driven by 15 My of Paratethys regression. *Molecular Ecology* 25(3): 795–810. <https://doi.org/10.1111/mec.13499>
- Myers AA (1998) New and little known Corophioidea (Amphipoda: Gammaridea) from Faroese and Icelandic waters. *Journal of the Marine Biological Association of the UK* 78: 211–222. <https://doi.org/10.1017/S0025315400040030>
- Negoescu I, Svavarsson J (1997) Anthurideans (Crustacea, Isopoda) from the North Atlantic and the Arctic Ocean. *Sarsia* 82: 159–202. <https://doi.org/10.1080/00364827.1997.10413650>
- Nørrevang A, Brattegard T, Josefson AB, Sneli J-A, Tendal OS (1994) List of BIOFAR stations. *Sarsia* 79: 165–180. doi: <http://dx.doi.org/10.1080/00364827.1994.10413557>
- Ostmann A, Schnurr S, Martínez Arbizu P (2014) Marine environment around Iceland: hydrography, sediments and first predictive models of Icelandic deep-sea sediment characteristics. *Polish Polar Research* 35(2): 151–176. doi: <https://doi.org/10.2478/popore-2014-0021>
- Plaisance L, Knowlton N, Paulay G, Meyer C (2009) Reef-associated crustacean fauna: biodiversity estimates using semi-quantitative sampling and DNA barcoding. *Coral Reefs* 28: 977–986. doi:10.1007/s00338-009-0543-3
- Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* 21(8): 1864–1877. <https://doi.org/10.1111/j.1365-294X.2011.05239.x>
- Radulovici AE, Sainte-Marie B, Dufresne F (2009) DNA barcoding of marine crustaceans from the Estuary and Gulf of St Lawrence: a regional-scale approach. *Molecular Ecology Resources* 9 (suppl 1): 181–187. doi: <https://doi.org/10.1111/j.1755-0998.2009.02643.x>

- Ratnasingham S, Hebert PD (2013) A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. *PLoS ONE* 8(7): e66213. <https://doi.org/10.1371/journal.pone.0066213>
- Ratnasingham S, Hebert PD (2007) BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Notes* 7(3): 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Raupach MJ, Barco A, Steinke D, Beermann J, Laakmann S, Mohrbeck I, Neumann H, Kihara TC, Pointner K, Radulovici A, Segelken-Voigt A, Wesse C, Knebelberger T (2015) The application of DNA barcodes for the identification of marine crustaceans from the North Sea and adjacent regions. *PLoS ONE* 10(9), e0139421. <https://doi.org/10.1371/journal.pone.0139421>
- Riehl T, Brenke N, Brix S, Driskell A, Kaiser S, Brandt A (2014) Field and laboratory methods for DNA studies on deep-sea isopod crustaceans. *Polish Polar Research* 35(2): 203–224. doi: <https://doi.org/10.2478/popore-2014-0018>
- Rothlisberg PC, Percy WG (1977) An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea). *Fishery Bulletin* 74: 994–997.
- Sars GO (1890) Amphipoda. An account of the Crustacea of Norway with short descriptions and figures of all the species. Alb. Cammermeyer, Kristiana. Volume 1, 711 pp.
- Schnabel KE, Hebert PDN (2003) Resource-associate divergence in the arctic marine amphipod *Paramphithoe hystrix*. *Marine Biology* 143: 851–857. <https://doi.org/10.1007/s00227-003-1126-4>
- Schnurr S, Brandt A, Brix S, Fiorentino D, Malyutina M, Svavarsson J (2014) Composition and distribution of selected munnopsid genera (Crustacea, Isopoda, Asellota) in Icelandic waters. *Deep Sea Research Part I* 84: 142–155. <https://doi.org/10.1016/j.dsr.2013.11.004>
- Seefeldt MA, Weigand AM, Havermans C, Moreira E, Held C (2017) Fishing for scavengers: an integrated study to amphipod (Crustacea: Lysianassoidea) diversity of Potter Cove (South Shetland Islands, Antarctica). *Marine Biodiversity*. <https://doi.org/10.1007/s12526-017-0737-9>
- Stephensen K (1931) Crustacea Malacostraca. VII. The order Amphipoda, part 3. Gammaridea. The Danish Ingolf Expedition 3: 176–293.
- Svavarsson J (1997) Diversity of isopods (Crustacea): new data from the Arctic and Atlantic Oceans. *Biodiversity and Conservation* 6: 1571–1579. <https://doi.org/10.1023/A:1018322704940>
- Svavarsson J, Strömberg JO, Brattegard T (1993) The deep-sea asellote (Isopoda, Crustacea) fauna of the Northern Seas: species composition, distributional patterns and origin. *Journal of Biogeography* 20: 537–555. <https://doi.org/10.2307/2845725>
- Sæmundsson B (1937) Icelandic Malacostraca in the Museum of Reykjavik. *Vísindafélag Íslendinga* 20: 1–34.
- Tandberg AHS, Vader W (2018) On a new species of *Amphilochus* from deep and cold Atlantic waters, with a note on the genus *Amphilochopsis* (Amphipoda, Gammaridea, Amphilochidae). In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology* (IceAGE Amphipoda project). *ZooKeys* 731: 103–134. <https://doi.org/10.3897/zookeys.731.19899>

- Thurston MH (1980a) Abyssal benthic Amphipoda (Crustacea) from the East Iceland Basin. 1. The genus *Rhachotropis*. Bulletin of the British Museum (Natural History). Zoology 38(1): 43–67.
- Thurston MH (1980b) Abyssal benthic Amphipoda (Crustacea) from the East Iceland Basin. 2. *Lepechinella* and an allied new genus. Bulletin of the British Museum (Natural History). Zoology 38(1): 69–87.
- Väinölä R, Witt JDS, Grabowski M, Bradbury JH, Jażdżewski K, Sket B (2008) Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. Hydrobiologia 595: 241–255. <https://doi.org/10.1007/s10750-007-9020-6>
- Verheyde ML, Backeljau T, d’Acoz CDU (2016) Looking beneath the tip of the iceberg: diversification of the genus *Epimeria* on the Antarctic shelf (Crustacea, Amphipoda). Polar Biology 39(5): 925–945. <https://doi.org/10.1007/s00300-016-1910-5>
- Wandel CF (1899) Report of the voyage. The Danish Ingolf Expedition 1: 1–21.
- Weisshappel JB (2000) Distribution and diversity of the hyperbenthic amphipod family Eusiridae in the different seas around the Greenland-Iceland-Faeroe-Ridge. Sarsia 85: 227–236. <http://dx.doi.org/10.1080/00364827.2000.10414575>
- Weisshappel JB (2001) Distribution and diversity of the hyperbenthic amphipod family Calliopidae in the different seas around the Greenland-Iceland-Faeroe-Ridge. Sarsia 86: 143–151. <http://dx.doi.org/10.1080/00364827.2001.10420469>
- Weisshappel JBF, Svavarsson J (1998) Benthic amphipods (Crustacea: Malacostraca) in Icelandic waters: diversity in relation to faunal patterns from shallow to intermediate deep Arctic and North Atlantic Oceans. Marine Biology 131: 133–142. <https://doi.org/10.1007/s002270050304>
- White KN, Reimer JD, Lorion J (2015): Preliminary analyses reveal strong genetic structure in populations of *Leucothoe vulgaris* (Crustacea: Amphipoda: Leucothoidae) from Okinawa, Japan. Systematics and Biodiversity 14(1): 55–62. <https://doi.org/10.1080/14772000.2015.1078856>

Supplementary material I

Table S1

Authors: Anna M. Jażdżewska, Laure Corbari, Amy Driskell, Inmaculada Frutos, Charlotte Havermans, Ed Hendrycks, Lauren Hughes, Anne-Nina Lörz, Bente Stran-sky, Anne Helene S. Tandberg, Wim Vader, Saskia Brix

Data type: molecular data

Explanation note: Amphipod and outgroup accession numbers in BOLD, GenBank and station data.

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Rhachotropis (Eusiroidea, Amphipoda) from the North East Atlantic

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Abstract

The genus *Rhachotropis* has the widest geographic and bathymetric distribution of all amphipod genera worldwide. Molecular and morphological investigations of specimens sampled around Iceland and off the Norwegian coast allow the first insights into the relationships of North East Atlantic *Rhachotropis*. The 31 cytochrome oxidase subunit I (COI) sequences generated for this study were assigned 13 Barcode Index Numbers (BINs) in the Barcode of Life database (BOLD), of which 12 are new to the database. Molecular analyses of COI and 16S sequences could not confirm a theory that depth has a greater influence on the phylogeny of *Rhachotropis* than geographic distance. Although the North East Atlantic is a well-studied area, our molecular investigations revealed the genus *Rhachotropis* may contain cryptic species, which indicates a higher biodiversity than currently known. For example, the specimens which key to *Rhachotropis helleri* is a complex of three COI clades, two of which cannot be identified with morphological traits. One specimen of each of the clades in the cladogram was documented by high definition photographs. A special focus was on the visual morphology of the eyes, as this character shows interspecific differences within the genus *Rhachotropis* in response to fixation in ethanol. Detailed morphological investigation showed that some clades thought to be indistinguishable can be separated by minute but consistent morphological characters. Datamining Genbank to examine all registered COI-sequences of *R. aculeata*, the only previously known *Rhachotropis* BIN in the North Atlantic and sub-Arctic, showed *R. aculeata* to be subdivided by an Arctic and a North Atlantic population.

Keywords

Amphipoda, Eusiridae, North Atlantic, IceAGE, NorAmph, COI, 16S

Introduction

Eusiridae are fast moving predators with a worldwide distribution. The genus *Rhachotropis* has the widest geographic (all oceans) and bathymetric (0–9460 m) distribution of all amphipod genera (Lörz et al. 2012). Currently, the genus *Rhachotropis* (Eusiridae) contains 61 species (World Amphipod Database, Horton et al. 2017).

Expeditions to the North East (NE) Atlantic via the programs IceAGE (Icelandic Animals Genetics & Ecology), Mareano and several smaller Norwegian mapping projects (Norwegian and Spitsbergen economic waters) sampled various Amphipoda during the last 10 years. Almost all amphipod collections yielded members of Eusiridae. *Rhachotropis* was the dominant genus in eusirid samples, along with three other genera: *Eusirus*, *Cleonardo* and *Eusirella*.

As the material was suitable for DNA analysis we investigated the relationships of freshly collected *Rhachotropis* from the NE Atlantic to each other via analysis of the cytochrome oxidase I (COI) and 16S gene regions. We then set these new specimens in context to *Rhachotropis* from Norway and other parts of the world.

Twenty-one of the 61 described *Rhachotropis* species are known from the NE Atlantic and Arctic region: *Rhachotropis aculeata* (Lepechin, 1780); *R. arii* Thurston, 1980; *R. distincta* (Holmes, 1908); *R. faeroensis* Stephensen, 1944; *R. gislui* Thurston, 1980; *R. gloriosae* Ledoyer, 1982; *R. gracilis* Bonnier, 1896; *R. grimaldii* (Chevreux, 1887); *R. helleri* (Boeck, 1971); *R. inflata* (Sars, 1883); *R. aff. kergueleni* Stebbing, 1888; *R. leucophthalma* Sars, 1883; *R. lomonosovi* Gurjanova, 1934; *R. macropus* Sars, 1883; *R. northriana* d’Udekem d’Acoz, Vader & Legezynska, 2007; *R. oculata* (Hansen, 1887); *R. palporum* Stebbing, 1908; *R. proxima* Chevreux, 1911; *R. rostrata* Bonnier, 1896; *R. thordisae* Thurston, 1980; *R. thorkelli* Thurston, 1980.

Lörz et al. (2012) hypothesized that depth might have a greater influence on the phylogeny of the genus *Rhachotropis* than geographic distances. The large amount of freshly collected *Rhachotropis* from the NE Atlantic allowed us to test this theory. Here we consider this theory using new data from specimens from 110 m to 2750 meters depth in the NE Atlantic. We ask and discuss the following questions:

- 1) What are the phylogenetic relationships of NE Atlantic and Arctic *Rhachotropis*?
- 2) Do relationships among specimens from the shallow (Norwegian Channel) and deep (Icelandic Basin and Norwegian Sea) stations indicate biogeographic processes such as submergence or emergence?
- 3) Does depth have a bigger influence on the phylogeny of *Rhachotropis* than geographic distance?

Material and methods

The detailed description of the Icelandic study area is presented in the introduction of this volume (Brix et al. 2018). Large amphipod specimens were immediately sorted on deck, fixed in 98% ethanol and later transferred to 96% ethanol. Samples were

decanted and the decant bulk fixed. The Norwegian amphipods were collected as parts of several mapping and teaching cruises and all examined through the Norwegian Biodiversity Information Centre financed project NorAmph at the University of Bergen. Material from the mapping projects “Mareano” and “Sognefjord” were sampled using RP-sleds where the material was decanted immediately and the decant bulk-fixed in 97% ethanol (Buhl-Mortensen et al. 2015). The high-arctic material from the Spitsbergen region was collected during student-cruises at the University Centre of Svalbard. Samples were sorted by teachers and students before being stored in 96% ethanol and kept in the cold-room for transport to land.

Morphological identification and documentation

Specimens were examined and dissected under a Leica MZ12.5 stereomicroscope. Small appendages (e.g. mouthparts, uropods, telson) were temporarily mounted in glycerin and examined using a LeicaDM2500 compound microscope. The body lengths of specimens examined were measured by tracing an individual’s mid-trunk lengths (tip of the rostrum to end of telson).

Photos of material held at the Deutsches Zentrum für Marine Biodiversität (DZMB) were taken with a Canon EOS 5 Mark III with a Canon MP-E65 macro lens mounted for stacking. The stacking programme software used was Zerene Stacker 1.04 (setting P-max). Photos of the Norwegian material (all stored at the University Museum of Bergen) were assembled using a Leica DFC425 camera fitted with a motorised stacker on a Leica M205 binocular, and Leica LAS 3.8 software for taking photos. Compilation of stacked photos was done with Zerene Stacker 1.04 (P-max). Larger specimens were photographed using a Canon EOS 60D with Canon MP-E-65 (f2.8) lens.

In order to examine the eye, *Rhachotropis oculata* AMPIV228-17 was selected for confocal laser scanning microscopy (CLSM). To produce auto-fluorescence of the surfaces, 405 nm laser lines with emission filters set to 421–499 nm and 488 nm laser lines with filters set to 489–607 nm were used. The head was scanned using a Leica DM2500 with a Leica TCS SPE at a resolution of 2480 × 2480 pixels at 10×. The software package LEICA LAS X was used for recording the image from the scans, the topmost seven photo-stack layers were removed to make the ommatidia visible. The image stacks were further processed and finalized in Adobe Photoshop CS5.

IceAGE material is held at the Zoological Museum University of Hamburg, Centre of Natural History (CeNak), Germany.

NorAmph material is held at the University Museum of Bergen, Natural History Collections, Norway.

DNA extraction and analyses

DNA was extracted from the IceAGE specimens using an Autogen Prep 965 phenol-chloroform automated extractor following the manufacturer’s protocol for animal tis-

sue. The barcode region of COI gene was amplified using primer pair jgLCO1490/jgHCO2198 (Geller et al. 2013) or the pair COIFamp (TTTTCTACTAAYCAYAAA-GATATYGG) and COIRamp (TAAACTTCIGGGTGICCAAAAAAYC) (K. Macdonald, pers. comm.). The PCR reaction mix was comprised of 0.3 μ M of each primer, 0.1 uL 10 mg/mL BSA (Promega) and 5 units of GoTaqFlexi DNA polymerase mix (Promega). The 16S gene was amplified using the primer pair 16Sar/16Sbr (Palumbi et al. 1991) or the pair 16Sft_amp (GCRGTATYTRACYGTGCTAAGG) and 16SRt_amp2 (CTGGCTTAAACCGRTYTGAAGT) (K. Macdonald, pers. comm.). PCR reaction mix and cycling conditions for both gene regions were as follows: 35 cycles of 30 sec at 95° C, 30 sec at 50° C, 45 sec at 72° C. PCR products were purified with ExoSAP-IT (Affymetrix). Sequencing was performed using the BigDye Terminator 3.1 Cycle Sequencing Kit (Applied Biosystems).

Amphipod tissue samples of material from NorAmph, usually consisting of two or three pleopods, were prepared for the NORBOL-consortium following the procedures of the Barcode of Life Database (BOLD) system (Ratnasingham and Hebert 2007). These samples were sequenced in both directions by the Canadian Centre of DNA Barcoding (CCDB) using the primer pair C_LepFolF/C_LepFolR for both PCR and Sanger sequencing of COI (Hernández-Triana et al. 2014, Ratnasingham and Hebert 2007). The CCDB standard PCR for invertebrates is initial denaturation at 94°C for 2 min, 5 cycles of 94°C for 30 sec, annealing at 45°C for 40 sec, and extension at 72°C for 1 min, 35 cycles of 94°C for 30 sec, annealing at 51°C for 40 sec, and extension at 72°C for 1 min, and a final extension at 72°C for 10 min. Voucher specimens for these sequences are stored in the Invertebrate Collections of the University Museum of Bergen, Norway. Sequences with voucher pictures and metadata are available from the BOLD website (boldsystems.org) using the accession codes provided in Table 1 and Suppl. material 1, or <https://doi.org/10.5883/DS-RHACHOTR>.

In addition to these new sequences, we used previously published sequences from *Rhachotropis* (Lörz et al. 2012) and *Eusirus holmii* as outgroup in the phylogenetic analyses.

Sequences were assembled with the software package Geneious (version 10.0.9) (Kearse et al. 2012) and aligned with the MAFFT plugin (Katoh and Standley 2013, Katoh et al. 2002).

We used MEGA7 (Kumar et al. 2016) to group sequences according to morphology based identifications and to compute p-distances within and between groups with standard errors estimated from 1000 bootstrap replicates.

We used FastTree2 ver. 2.1.5 (Price et al. 2010) with the GTR plus gamma model and 20 rate categories to estimate initial gene trees from the sequences. Support values for nodes were calculated with the Shimodaira-Hasegawa (Shimodaira and Hasegawa 1999) test and 1000 resamples.

We used MrBayes ver 3.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) with the mixed gamma function command to simultaneously search for the optimal model and tree set by sampling across the space of the General Time Reversible model (GTR). The data were partitioned into two parts, one comprised by first and second codon positions, the second by third codon positions. Model

Table 1. Overview of Rhachotropis sequences produced for this work, with BOLD accession numbers and BIN numbers (BOLD). The dataset can be accessed using <https://doi.org/10.5883/DS-RHACHOTR>

Species name	BOLD number	16S	COI	BIN number (BOLD)
<i>Rhachotropis aculeata</i> (Lepechin, 1780)	AMPIV200-17	x	x	AAB3310
<i>Rhachotropis aculeata</i> (Lepechin, 1780)	AMPNB077-13		x	
<i>Rhachotropis aff inflata</i> (Sars, 1883)	AMPNB524-17		x	–
<i>Rhachotropis aff palporum</i> Stebbing, 1908	AMPIV033-17	x	x	ADH1827
<i>Rhachotropis aff palporum</i> Stebbing, 1908	AMPIV003-17	x	x	
<i>Rhachotropis aff proxima</i> Chevreux, 1911	AMPIV005-17	x	x	ADH1828
<i>Rhachotropis cf proxima</i> Chevreux, 1911	AMPIV001-17	x	x	ADH1784
<i>Rhachotropis cf proxima</i> Chevreux, 1911	AMPIV002-17	x	x	
<i>Rhachotropis gislui</i> Thurston, 1980	AMPIV004-17	x	x	ADH0956
<i>Rhachotropis aff helleri</i> (Boeck, 1871)	AMPIV010-17	x	x	ADE3179
<i>Rhachotropis aff helleri</i> (Boeck, 1871)	AMPIV011-17	x	x	
<i>Rhachotropis aff helleri</i> (Boeck, 1871)	AMPNB277-15		x	
<i>Rhachotropis aff helleri</i> (Boeck, 1871)	AMPNB278-15		x	
<i>Rhachotropis aff helleri</i> (Boeck, 1871)	AMPNB279-15		x	ADE1120
<i>Rhachotropis aff helleri</i> (Boeck, 1871)	AMPNB481-17		x	
<i>Rhachotropis helleri</i> (Boeck, 1871)	AMPIV233-17	x	x	ADE4377
<i>Rhachotropis helleri</i> (Boeck, 1871)	AMPNB276-15		x	
<i>Rhachotropis helleri</i> (Boeck, 1871)	AMPNB381-16		x	
<i>Rhachotropis inflata</i> (Sars, 1883)	AMPIV070-17	x		–
<i>Rhachotropis inflata</i> (Sars, 1883)	AMPNB078-13		x	ACF8625
<i>Rhachotropis lomonosovi</i> Gurjanova, 1934	AMPNB352-15		x	ACW7325
<i>Rhachotropis macropus</i> Sars, 1893	AMPNB413-16		x	ADD5182
<i>Rhachotropis macropus</i> Sars, 1893	AMPNB420-16		x	
<i>Rhachotropis macropus</i> Sars, 1893	AMPNB424-16		x	
<i>Rhachotropis macropus</i> Sars, 1893	AMPNB387-16		x	
<i>Rhachotropis macropus</i> Sars, 1893	AMPNB443-16		x	
<i>Rhachotropis macropus</i> Sars, 1893	AMPNB444-16		x	
<i>Rhachotropis macropus</i> Sars, 1893	AMPNB466-16		x	
<i>Rhachotropis macropus</i> Sars, 1893	AMPNB526-17		x	
<i>Rhachotropis northriana</i> d'Udekem d'Acoz, Vader & Legezinska, 2007	AMPIV227-17	x		–
<i>Rhachotropis northriana</i> d'Udekem d'Acoz, Vader & Legezinska, 2007	AMPIV224-17	x		
<i>Rhachotropis northriana</i> d'Udekem d'Acoz, Vader & Legezinska, 2007	AMPIV225-17	x		
<i>Rhachotropis northriana</i> d'Udekem d'Acoz, Vader & Legezinska, 2007	AMPIV231-17	x		
<i>Rhachotropis northriana</i> d'Udekem d'Acoz, Vader & Legezinska, 2007	AMPIV230-17	x		
<i>Rhachotropis oculata</i> (Hansen, 1887)	AMPIV228-17	x		–
<i>Rhachotropis</i> sp. n. B	AMPIV009-17	x	x	ADH1829
<i>Rhachotropis thordisae</i> Thurston, 1980	AMPIV034-17	x	x	ADH0957
<i>Rhachotropis thordisae</i> Thurston, 1980	AMPIV007-17	x	x	
<i>Rhachotropis thordisae</i> Thurston, 1980	AMPIV008-17	x	x	
<i>Rhachotropis thordisae</i> Thurston, 1980	AMPIV226-17	x	x	
<i>Rhachotropis thorkelli</i> Thurston, 1980	AMPIV006-17	x		–
<i>Rhachotropis thorkelli</i> Thurston, 1980	AMPIV078-17	x		

parameters were estimated independently for the two. Two million generations for two parallel runs of four chains sampling every 1000 generations were monitored with the Average Standard Deviation of Split Frequencies (ASDSF) in MrBayes and with Tracer (Rambaut et al. 2013). Figtree (Rambaut 2014) was used for tree graphics.

Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012) was run via the web interphase at <http://www.wabi.snv.jussieu.fr/public/abgd/abgdweb.html>, selecting simple distances and relative gap widths ranging from 1 via 1.5 (default) to 3.0 with FastA file input of the sequence data.

Additional sequences of *R. aculeata* were downloaded from BIN AAB3310 in BOLD. We calculated a Median Joining Network with POPART (Leigh and Bryant 2015).

Geographic distances (in km) between the samples were calculated with Geographic Distance Matrix Generator (Ersts 2017).

Results

Systematics

Order AMPHIPODA Latreille, 1816

Suborder GAMMARIDEA Latreille, 1802

Family EUSIRIDAE Stebbing, 1888

Genus *Rhachotropis* S.I. Smith, 1883

***Rhachotropis* S.I. Smith, 1883: 222.**

***Gracilipes* Holmes, 1908: 526.**

We obtained sequences from 42 *Rhachotropis* specimens in our samples (Table 1). Thirty-one newly obtained sequences of COI were combined with 53 sequences available in GenBank (Fig. 1). All available information for the GenBank data, such as sampling details, can be found in the Suppl. material 1. Our new COI sequences were assigned to 13 different Barcode Index Numbers (BINs) in BOLD, of which all except AAB3310 (*Rhachotropis aculeata*) were new to the database. This greatly increased the representation of the diversity of this genus in the BOLD database.

Twenty-four *Rhachotropis* 16S sequences were generated from the recent IceAGE collections and analysed separately (Fig. 2).

Within and between-group mean p-distances with estimated standard errors are shown in Tables 2 and 3 respectively. Most of the groups are about 20 % different in pairwise comparisons. Exceptions are *R. macropus* and *R. lomonosovi* with a difference of only 9.8 % and *R. inflata* and *R. aff. inflata* with a 3.5 % difference. Within group mean distances show relatively homogenous groups: 8.7 % difference in *R. thordisae*, 5.8 % in *R. inflata*, and 5 % in *R. aff. helleri*. The BOLD BINs display results congruent with our morphological investigation: the two *R. cf. proxima* sequences belong to a different BIN than the *R. aff. proxima* (Table 1) with a p-distance of 0.15 (Table 3). The *R. aff. helleri* sequences were assigned to two different BINs by BOLD. The two groups were calculated with a p-distance

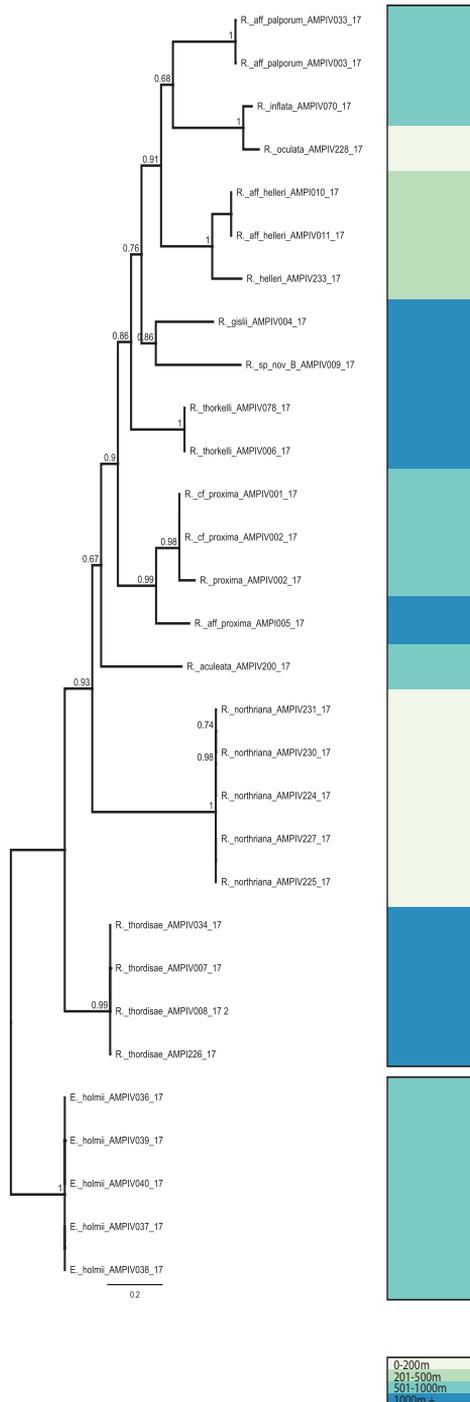


Figure 2. 16S gene tree calculated as in Fig. 1- *Rhacotropis* samples collected during IceAGE (details Supplementary Table 1). Clades are coloured for depth strata for sampling: 0–200 m light grey, 201–500 m light green, 501–1000 m turquoise, 1000+ m blue.

Table 2. Estimates of Average Evolutionary Divergence over Sequence Pairs within morphologically defined groups. The number of base differences per site from averaging over all sequence pairs within each group are shown. Standard error estimate(s) are shown in the last column. The analysis involved 82 nucleotide sequences. Codon positions included were 1st+2nd+3rd. All ambiguous positions were removed for each sequence pair. There were a total of 648 positions in the final dataset. Evolutionary analyses were conducted in MEGA7. The presence of n/c in the results denotes cases in which it was not possible to estimate evolutionary distances.

Species	p-dist	std_err
<i>Eusirus holmii</i>	0.000	0.000
<i>Rhachotropis abyssalis</i>	0.000	0.000
<i>Rhachotropis aculeata</i>	0.009	0.002
<i>Rhachotropis aff helleri</i>	0.050	0.005
<i>Rhachotropis aff inflata</i>	n/c	n/c
<i>Rhachotropis aff palporum</i>	0.000	0.000
<i>Rhachotropis aff proxima</i>	n/c	n/c
<i>Rhachotropis cf proxima</i>	0.002	0.001
<i>Rhachotropis chathamensis</i>	0.000	0.000
<i>Rhachotropis gislii</i>	n/c	n/c
<i>Rhachotropis helleri</i>	0.000	0.000
<i>Rhachotropis inflata</i>	0.058	0.005
<i>Rhachotropis lomonosovi</i>	n/c	n/c
<i>Rhachotropis macropus</i>	0.004	0.001
<i>Rhachotropis novaezealandica</i>	n/c	n/c
<i>Rhachotropis rossi</i>	n/c	n/c
<i>Rhachotropis</i> sp. n. B	n/c	n/c
<i>Rhachotropis thordisae</i>	0.011	0.003

of 8.56 % and came out as sisters in the COI gene trees (Fig. 1, Suppl. material 4), but not as monophyletic with the one we consider as the genuine *R. helleri*. The latter was assigned to a third BIN and is 15.7 % different from the former group (Table 3).

ABGD analyses returned 18 groups of *Rhachotropis* when using default relative gap width of 1.5 (Suppl. material 3), all corresponding to the clusters found with the phylogenetic analyses. When increasing the gap width to three, *R. aculeata* was additionally divided into two groups (not shown).

Model testing of the data in two partitions using the Bayesian Information Criterion (BIC) resulted in the TN93+G model both for the third codon position and for the combination of the first and second. Similar models were obtained with MrBayes.

Phylogenetic estimates with MrBayes and FastTree based on COI sequences returned very similar tree topologies (Fig. 1, Suppl. material 4.) with few exceptions, such as the position of *R. helleri*. Some of the relationships between species had posterior probabilities lower than 0.90 and were therefore not well supported.

The FastTree estimate based on 16S data was indicating somewhat similar tendencies, such as the early divergence of *R. thordisae* and the splits in the groups associated with *R. proxima* and *R. helleri*. The two gene trees were otherwise difficult to compare

because the 16S data set included sequences from *R. northbriana*, *R. oculata*, *R. aculeata* and *R. thordisae*, for which COI are missing. Likewise, 16S sequences were not obtained for many of the taxa represented in the COI data set, including *R. macropus*, *R. lomonosovi*, *R. gislui* and others (Fig. 2).

Additional COI sequences of *R. aculeata* downloaded from BIN AAB3310 in BOLD show some geographic structure. We calculated a Median Joining Network with five geographical groups in POPART (Leigh and Bryant 2015). The species appears to have a special cluster in the Atlantic, including the Canadian West Atlantic and Norwegian Sea, whereas the Svalbard specimen clusters with the Arctic populations of North America (Fig. 3).

Photographs were taken of at least one representative of each clade (Figs 4–6).

Discussion

Overall the morphological differentiation of the *Rhachotropis* sampled in the NE Atlantic is mirrored in the differentiation of our mitochondrial DNA markers and reflected both in gene tree topology and genetic distances. However, both *R. aff. helleri* and *R. inflata* have diverged into groups that were unnoticed *a priori* from morphology and *R. aff. inflata* clusters with one of the latter lineages. The taxonomic status of *R. aff. helleri* versus *R. helleri* must be examined further with more data. There is also considerable COI divergence in the *R. proxima* group.

Our DNA sequence data are shedding new light on the species relationships of *Rhachotropis*, although based on one gene fragment only the phylogenetic trees should certainly be interpreted with caution. The difference between gene trees and species trees has been an important topic in theoretical phylogenetics since the seminal publication by Maddison (1997). The phenomenon of lineage sorting and deep coalescence certainly also has implications for our understanding of species, particularly with respect to the idea of divergent monophyletic lineages and of species delimitation based on a single mitochondrial marker (Degnan and Rosenberg 2006, 2009, Knowles and Kubatko 2010). While the DNA barcoding campaign has sparked an excess of new species discoveries, it should be remembered that gene trees are representation of genetic structure and that non-monophyletic or genetically distant subclades are not necessarily separate species (Sukumaran and Knowles 2017). We have found that there is generally good correspondence between morphological species assignments and genetic structure in *Rhachotropis* but that there are also several examples of haplotype clusters that are candidates for broader systematic examination with multiple genes and morphological analyses.

The following discussion is divided according to three questions asked.

1) *What are the phylogenetic relationships of North East Atlantic and Arctic Rhachotropis?* The FastTree approach and the Bayesian method returned very similar tree topologies with minimum exceptions. In both cases there was strong support for most of the spe-

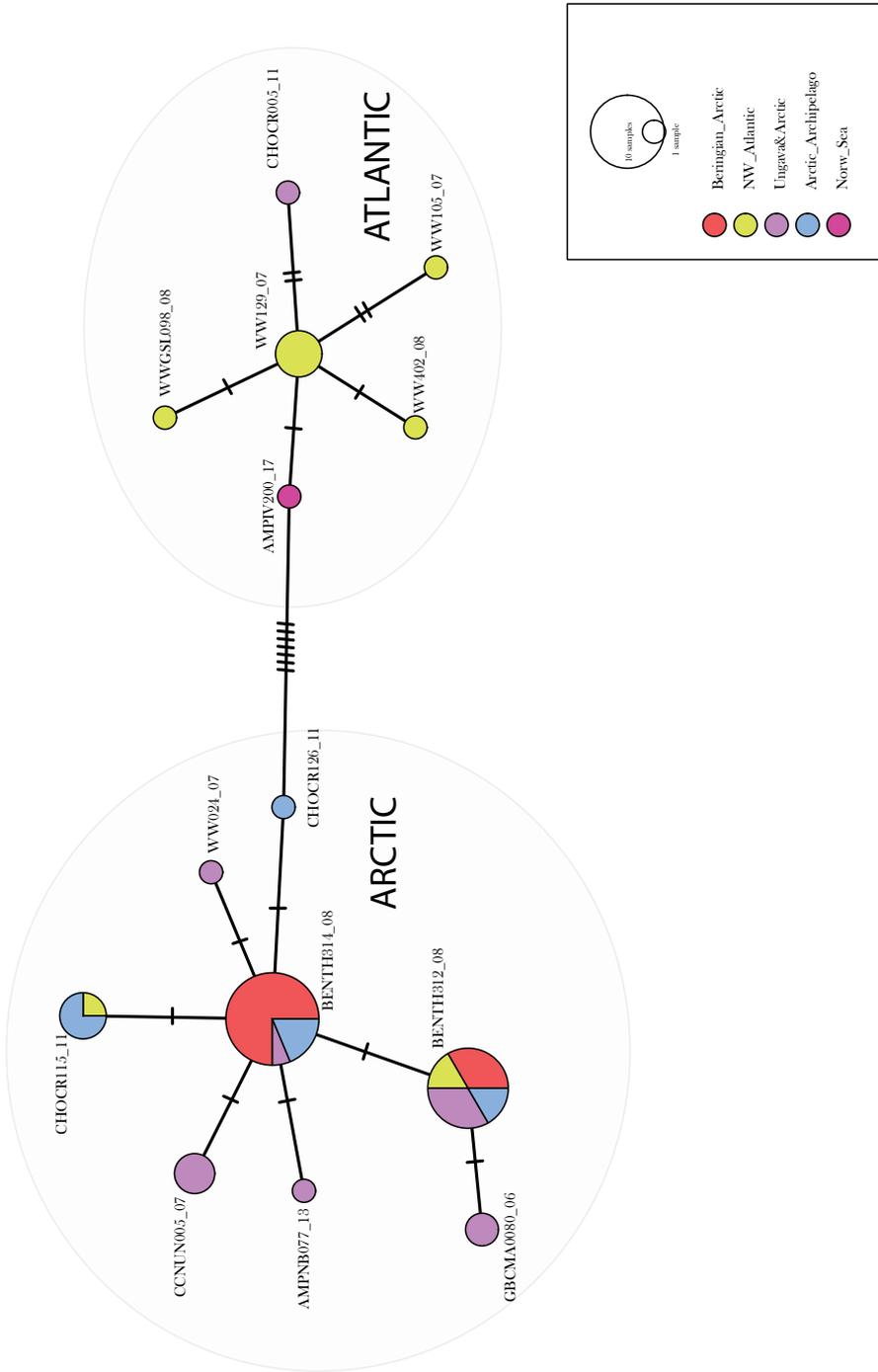


Figure 3. Median joining haplotype network of *Rhachotropis aculeata* calculated with POPART (Leigh and Bryant 2015) using five geographical clusters.



Figure 4. Lateral view photos of IceAGE material representing different clades in the analyses. **A** *Rhachotropis gislui* AMPIV004-17 **B** *R. belleri* AMPIV233-17 **C** *R. aff. belleri* AMPIV011-17 **D** *R. inflata* AMPIV070-17 **E** *R. northbriana* AMPIV225-17 **F** *R. oculata* AMPIV228-17 **G** *R. aff. palporum* AMPIV033-17 **H** *R. aff. proxima* AMPIV005-17 **I** *R. cf. proxima* AMPIV002-17 **J** *R. sp. B* AMPIV009-17 **K** *R. thordisae* AMPIV007-17 **L** *R. thorkelli* AMPIV078-17.



Figure 4. Continued.

cies clades and also for some sister species relationships. However, many of the deeper branches were less well supported, which should be kept in mind when inferring the evolutionary history of ecological and biogeographical events.

Only three species occurred in both sampling sets from our two collecting groups in Icelandic and Norwegian waters: *R. aculeata* (Fig. 6A), *R. helleri* (Figs 4B, 5B, 6B) and *R. inflata* (Figs 4D, 5D). Eight species were only sampled during the IceAge project, four species only during NorAmph. However, we assume that the species collected in certain depth strata could be found in the corresponding depth area of other areas. We assume that depth and temperature have a greater effect than other characteristics, e.g. sediment type; for example *Rhachotropis helleri* was found on the Reykjanes ridge in 289 m (Fig. 4B), the Lofoten area off Norway in 850 m, in the Sognefjord 307 m (Fig. 6B) and the Norwegian channel 203 m (see Table 1). The dominant sediment of the Reykjanes ridge is muddy sand with a small proportion of gravel (Meißner et al. 2014), whereas the *R. helleri* off Norway were collected on sediments dominated by sandy mud with little gravel.

Weissappel (2000) investigated the biogeographic distribution of Eusiridae species around Iceland and found a marked separation along the Greenland-Iceland-Faroe (GIF) Ridge. Weissappel assumed that eusirids followed relatively sharp boundaries between water masses of different origin lying on and adjacent to the GIF ridge or within the area on each side of the ridge.

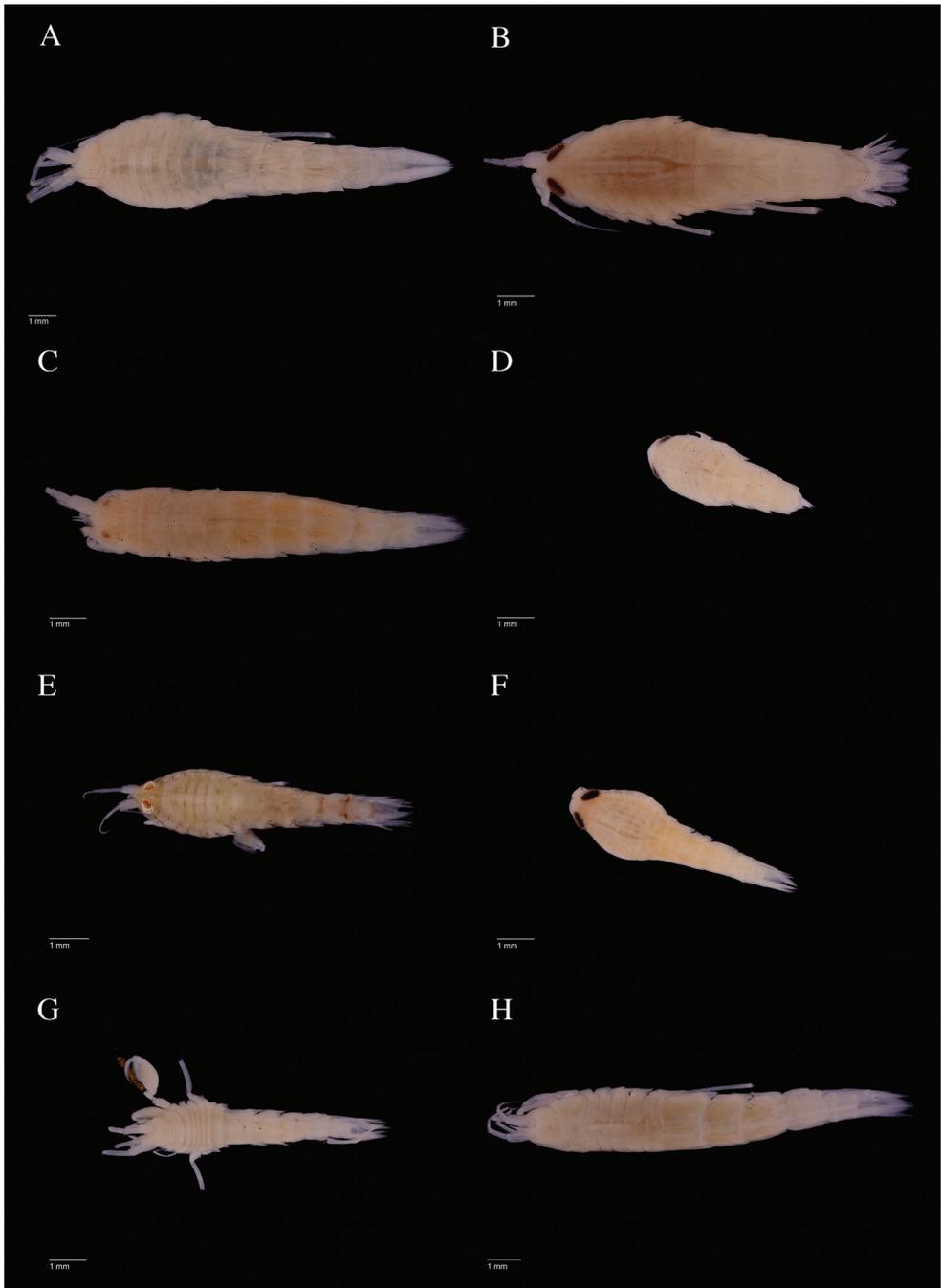


Figure 5. Dorsal view photos of IceAGE material representing different clades in the analyses. **A** *Rhachotropis gislui* AMPIV004-17 **B** *R. belleri* AMPIV233-17 **C** *R. aff. belleri* AMPIV011-17 **D** *R. inflata* AMPIV070-17 **E** *R. northriana* AMPIV225-17 **F** *R. oculata* AMPIV 228-17 **G** *R. aff. palporum* AMPIV033-17 **H** *R. aff. proxima* AMPIV005-17 **I** *R. cf. proxima* AMPIV002-17 **J** *R. sp. B* AMPIV009-17 **K** *R. thordisae* AMPIV007-17 **L** *R. thorkelli* AMPIV078-17.



Figure 5. Continued.

Weisshappel (2000) showed that most eusirid species are restricted to certain combinations of bottom water temperatures and bottom depths, 28 out of 36 were found within a single water mass. Different Eusiridae species show different biogeographic preferences. *Eusirus holmii*, for example shows a very narrow temperature distribution – it is only collected in waters colder than 1°C – but has a very wide depth range, 400 to 1600 m. *R. aculeata* is the opposite: it has a wide temperature tolerance (-1°C to +6°C), and a relative narrow depth distribution, 100-600 m. There seems to be some divergence (Fig. 3) between Atlantic and Arctic populations. Whereas the *R. aculeata* specimen from Spitzbergen Isfjord at 123 m cluster with the latter group, the *R. aculeata* from 580 m in the Norwegian Sea is closer to the COI haplotypes occurring in Canadian West Atlantic waters.

An even more temperature-tolerant species is *R. inflata* which only occurs in shallow waters above 400 m, but tolerating temperatures from 0°C to 9°C (Weisshappel 2000 and current study). Morphological separation of *R. inflata* (Figs 4D, 5D) and *R. aff. inflata* (Fig. 6D) is minute: a dent on urosomite 1 in contrast to a non-dented urosomite 1. When applying these two morphology based groups in computation of p-distance, the mean divergence is only 3.5 % (Table 3). However, COI data divides *R. inflata* into two distinct clusters, one also including *R. aff. inflata*, the latter which clusters with sequences of *R. inflata* from Nunavut. The mean p-distance between the two *R. inflata* clades is actually 15 %, so these clades are clearly candidates for critical

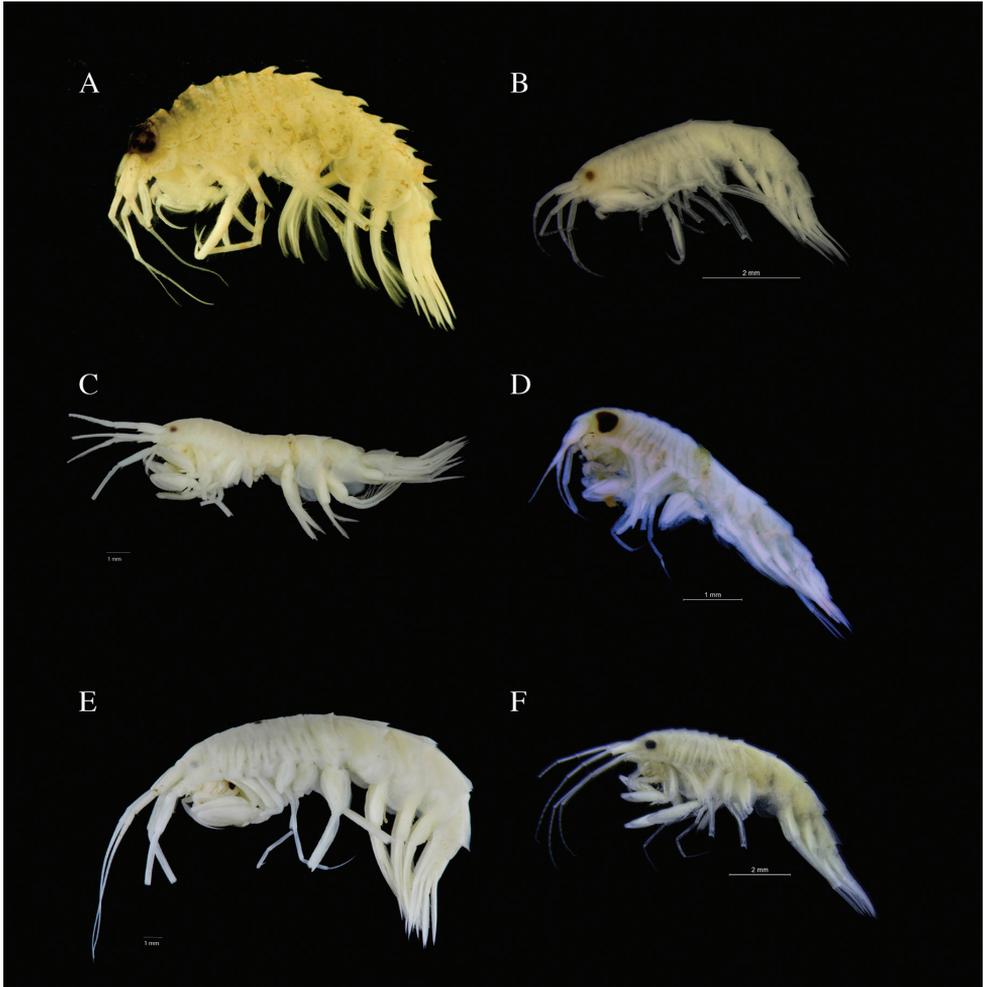


Figure 6. Lateral view photos of NorAmph material representing different clades in the analyses. **A** *Rhachotropis aculeata* AMPNB077-13 **B** *R. helleri* AMPNB276-15 **C** *R. aff. helleri* AMPNB279-15 **D** *R. aff. inflata* AMPNB524-17 **E** *R. lomonosovi* AMPNB352-15; **F** *R. macropus* AMPNB443-16.

taxonomic examination with multiple gene data. Not enough material was available for a study of the character development in different growth stages in both genders within the framework of this study.

DNA barcoding revealed three clades within a species that keyed out to *Rhachotropis helleri*. The original description of *R. helleri* was provided by Boeck (1871); one brief paragraph in latin with no illustrations. Sars (1895) illustrated *R. helleri* in detail. We regard the specimens illustrated and described by Sars as corresponding to the species named by Boeck. Further morphological investigation of our *R. helleri* samples revealed two *helleri* groups. The first group has a smooth dorsal seventh pereonite and eyes larger than 50 % of head (see Figs 4B, 5B, 6B) – this we named *R. helleri* as it

closely matches the drawings provided by Sars (1895). The second group specimens bear a small distinct spine on their seventh pereonite and have a smaller eye, covering a maximum of 20 % of the head. We provisionally named these *R. aff. helleri* (Figs 4C, 5C, 6C). The specimens of the *R. aff. helleri* group split into two molecularly distinct clades (Fig. 1, Suppl. material 3) with a p-distance of 8.56 %. We were not able to find a morphological differentiation in this group.

We conclude that the two *aff. helleri* groups therefore either represent a single species, which contains widely-divergent COI sequence, or that the two clades may be two species, which are genuinely cryptic rather than pseudo-cryptic (Janosik and Halanych 2010; Brandt et al. 2014). Although there may be good reasons to flag potentially new species to attract further attention (Wägele 1994), we do not propose the formal erection of a new species here because the *aff. helleri* can be only distinguished by the presence-absence of one spine and eye size, characters that can vary with sex and body size, and the two *aff. helleri* can currently only be reliably identified by DNA sequencing.

R. macropus (Fig. 6F) and *R. lomonosovi* (Fig. 6E) show the smallest interspecific distance of 9.8 % (Table 2). *R. macropus* and *R. lomonosovi* are genetically (Table 3) and morphologically (Fig. 6E, 6F) very similar. *R. macropus* is known to be very numerous along the Norwegian coast and in Svalbard (d'Udekem et al. 2007). While generally found at moderate depths of 200–700 m, we have two specimens from 1230 m in our samples, which extends the depth range by 500 m. *R. lomonosovi* is a true Arctic species, common at depths of 1000–1500 m (d'Udekem et al. 2007). Our single representative of this *R. lomonosovi* is from the lower Arctic/ Norwegian northern coast (outer Lofoten area), from a depth of 823 m, but from a water temperature of -0.58°C .

2) Do relationships between the shallow (Norwegian Channel) and the deep (Icelandic Basin and Norwegian Sea) amphipods indicate biogeographic processes such as submergence or emergence?

Generally more species are currently known from the shelf and upper slope area. However, the observed depth pattern is heavily collection biased: areas with more stations show more species (Lörz et al. 2012). Bousfield and Hendrycks (1995) attempted a phylo-biogeographic analysis of *Rhachotropis* of the North Pacific. Some of the species, such as *R. aculeata*, *R. helleri*, *R. macropus*, *R. oculata*, *R. inflata* and *R. distincta* are known from both the North Pacific and the North Atlantic, but these distribution data are based on literature using morphological data only. Bousfield and Hendrycks (1995) postulated that species such as *R. aculeata* and *R. macropus* belong to more primitive forms. Characters considered plesiomorphic by Bousfield and Hendrycks (1995) were, for example, an elongate telson, long rostrum, strongly toothed pleon and urosome. These so-called primitive species have a large body size (10.5–40 mm). In contrast the more advanced *oculata-inflata* groups have small body lengths (3.8–12 mm), smooth urosome and short telson. While the primitive large species were generally coastal shelf species, the species become smaller, more weakly spinose and anoculate in most abyssal members. Bousfield and Hendrycks (1995) assume submergence as the primary biogeographic pattern amongst the *Rhachotropis* species in general and amongst the

North Pacific in particular. Our findings cannot confirm this. Neither can we agree that shallow = large, spiny species. Our most abundant species was collected at the shallowest station, *R. northriana*. This is a very small, not very spinose species with a relatively large telson. Several abyssal species are known to reach large body sizes, such as *R. rossi* (12 mm) or *R. abyssalis* (13 mm). Although some of the deeper nodes in our phylogeny (Fig. 1, Suppl. material 4) are not well supported, we also cannot agree that *R. aculeata* and *R. macropus* are the most primitive forms, as in our molecular analysis of COI and 16S they are not in a basal position. When observing depth distributions of *Rhachotropis* clades, there does not seem to be a directional trend in terms of emergence or submergence of during speciation.

Eyes

The genus *Rhachotropis* is known to have a diversity of “eye phenotypes”. *R. leucophthalma* G. O. Sars, 1893 is a white-eyed species – this feature is so prominent that it provided its name; its eyes become colourless and hard to see in alcohol (d’Udekem et al. 2007), whereas the true arctic species *R. lomonosovi* Gurjanova, 1934 also has white eyes when alive, but they turn black in alcohol. (This is sadly not easily seen in Fig. 6F, as the specimens cuticulum has loosened from the ommatidia leaving the eye colour an indistinct grey.) *Rhachotropis oculata* has kidney-shaped eyes which keep their colour, eg. AMPIV228-17 Figs 4E, 5E and for the ommatidia Fig. 7B. (Our specimens match the description of *R. oculata* by Hansen, 1887, but differ in various characters from *R. oculata* pictured by Bousfield and Hendrycks 1995.)

Rhachotropis helleri (AMPIV233-17) has distinct red eyes, even after being preserved in 98% ethanol for more than 4 years (Fig. 7A). The ommatidia are clearly hexagonal in shape. After 6 years of preservation the eye colour and the outline fade, e.g. AMPIV011-17 Figs 4C, 5C. Here there is a clear difference between the *R. helleri* (largish eyes, and clearly defined Figs 4B, 5B, 6B) and the *R. aff. helleri* (see also Fig. 6C) which have much smaller eyes and no clearly visible edge of the eye.

R. northriana has distinct red eyes also clearly visible after being preserved in ethanol for several years (eg. AMPIV225-17, Figs 4E, 5E).

Another species which maintains clearly visible dark eyes in preservation is *R. inflata* (eg. AMPIV070-17 Figs 4D, 5D).

We therefore think it unlikely that the ancestral *Rhachotropis* was a blind inhabitant of the deep sea. We assume that submergence has led to the loss of eyes in truly deep sea or abyssal species such as *R. thordisae* (Fig 4K) and *R. thorkelli* (Fig. 4L). The latter species prove that *Rhachotropis* can hunt without eyesight, however all species collected in the photic zone have well developed eyes.

3) Does depth have a bigger influence on the phylogeny of *Rhachotropis* than geographic distance?

Rhachotropis specimens are found in all major oceans of the world: Arctic, Atlantic Ocean, Mediterranean Sea, Caribbean Sea, Indian Ocean, Pacific Ocean and the Southern Ocean (Lörz et al. 2012). *Rhachotropis* specimens have been collected in all water depths, from the shelf (e.g d’Udekem et al. 2007, Lowry and Springthorpe

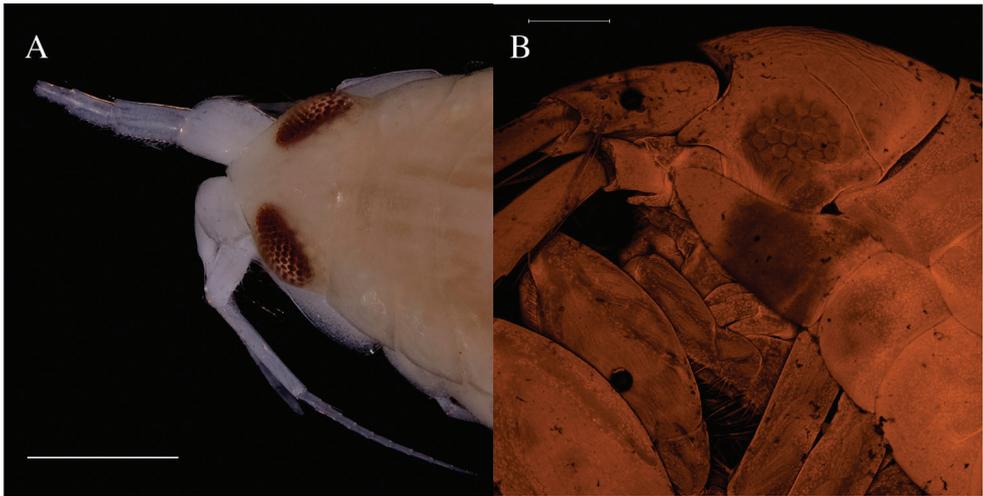


Figure 7. Eyes of, **A** *Rhachotropis helleri* AMPIV233-17, ommatidia (Photo) **B** *Rhachotropis oculata* AMPIV228-17 (CLSM), 7 stack-layers have been removed in the eye-region to reveal the ommatidia beneath the cuticulum.

2005, Lörz 2015) to abyssal and hadal sampling sites (Thurston 1980, Lörz 2010), in trenches (Dahl 1959), as well as around hydrothermal vents (e.g. Bellan-Santini 2006). Based on molecular data (COI) Lörz et al. (2012) predicted that depth had a greater influence on phylogeny than geographic distance.

The genetic distance between shallow species such as *Rhachotropis aculeata* from 600 m and deep sea species such as *R. thordisae* from 2750 m is only 16 %, the shallow water *R. inflata* from 123 m and the deep sea *R. thorkelli* is 20.7 %. The two deep sea species *R. gislii* and *R. thordisae* were collected at the same station at 2750 m depth and show a similar genetic distance of 22 % as the two species *R. cf. proxima* and *R. aff. inflata* (21%) both later collected around 900 m (Table 3). The smallest genetic distance was observed amongst the species *R. lomonosovi* and *R. macropus*, which were collected in 823 m and between 300 m and 1230 m respectively. Potentially our sampled depth band in the North Atlantic is not wide enough to sufficiently illuminate biogeographic questions. It is likely that samples from abyssal and hadal depths will heavily influence the interpretation of distribution patterns. However, when we include *Rhachotropis* samples from GenBank not collected in the NE Atlantic the lack of correlation between genetic distance and depth as well as the lack of correlation between genetic distance and geographic distance continues. *R. abyssalis* was sampled at 3210 m and its genetic distance to *R. cf. proxima* from South Iceland at 900 m is only 19 % – the same distance as to *R. rossii*, which was collected below 3000 m in the Ross Sea.

The intraspecific distance is around 5 % in *R. aff. helleri*, and less than 1 % in *R. aff. palporum*, *R. chathamensis* and *R. macropus*, even though the latter was sampled in a depth range of 330–1260 m. Recent investigations by Brix et al. (2014) of the eurybathic isopod species *Chelator insignis* off Iceland presented a different picture: the isopods collected in different depth strata had high genetic distances over 20%, indicating

narrow vertical distribution ranges of cryptic species and highlighting bathymetry as key player in speciation processes. Jażdżewska et al. (2018) provide the first insight into cryptic amphipods off Iceland revealed by DNA barcoding.

A characteristic species, *R. aculeata* (Fig. 6A), was selected for further investigation via COI sequences available online. For a better visualization of genetic distances a haplotype network was calculated from the COI alignment (Fig. 3). The network shows 13 haplotypes of *R. aculeata*, but the maximum distance is only seven mutation steps between haplotypes, proving *R. aculeata* to have a remarkable truly circum-arctic distribution. The haplotype network shows that the Svalbard specimen clusters with the population in the Canadian Arctic (Fig. 3). The geographic distance between these population is thousands of km. Even though *Rhachotropis* are known to be good swimmers, this is a tremendous distribution for an animal with no larval stage. Due to their predatory feeding behaviour it is unlikely that *R. aculeata* clings to drifting algae or ice.

Conclusion

Morphologically separated groups of *Rhachotropis* are well supported by the genetic markers COI and 16S, with possible cryptic species in *Rhachotropis* aff. *helleri*. We recommend a morphological study of allometry in this genus, where many species often are collected in large numbers. Our present data lead us to support the theory that *Rhachotropis* originated in shallow (photic) seas, and has subsequently submerged to greater (subphotic) depths, with loss of eyes for the abyssal species. The question about geographic versus bathymetric distance as a driver for genetic distance is harder to answer, as there is no clear picture for the entire genus.

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References

- Bellan-Santini D (2006) *Rhachotropis* species (Crustacea: Amphipoda: Eusiridae) of hydrothermal vents and surroundings on the Mid-Atlantic Ridge, Azores Triple Junction Zone. *Journal of Natural History* 40(23-24): 1407–1424. <https://doi.org/10.1080/00222930600956809>
- Boeck A (1871) Crustacea Amphipoda Borealia et Arctica. *Videnskaps Selskapets Forhandling* for 1870, 1–222.
- Bonnier J (1896) Résultats scientifiques de la campagne du Caudan dans le golfe de Gascogne. Vol. 3. Édriophthalmes. *Annales de l'Université de Lyon* 26: 527–689.
- Bousfield EL, Hendrycks EA (1995) The amphipod superfamily Eusiroidea in the North American Pacific region. I. Family Eusiridae: systematics and distributional ecology. *Amphipacifica* 1(4): 3–59.
- Buhl-Mortensen L, Hodnesdal H, Thorsnes T (Eds) (2015) The Norwegian Sea Floor – New Knowledge from MAREANO for Ecosystem-Based Management. MAREANO, 192 pp.
- Brandt A, Brix S, Held C, Kihara T (2014) Molecular differentiation in sympatry despite morphological stasis: deep-sea *Atlantoserolis* Wägele, 1994 and *Glabroserolis* Menzies, 1962 from the south-west Atlantic (Crustacea: Isopoda: Serolidae) *Zoological Journal of the Linnean Society* 172: 318–359. <https://doi.org/10.1111/zoj.12178>
- Brix S, Lörz A-N, Jażdżewska AM, Hughes L, Tandberg AHS, Pabis K, Stransky B, Krapp-Schickel T, Sorbe JC, Hendrycks E, Vader W, Frutos I, Horton T, Jażdżewski K, Peart R, Beermann J, Coleman CO, Buhl-Mortensen L, Corbari L, Havermans C, Tato R, Campan AJ (2018) Amphipod family distributions around Iceland. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project)*. *ZooKeys* 731: 41–53. <https://doi.org/10.3897/zookeys.731.19854>
- Brix S, Svavarsson J, Leese F (2014) A multi-gene analysis reveals multiple highly divergent lineages of the isopod *Chelator insignis* (Hansen, 1916) south of Iceland. *Polish Polar Research* 35 (2): 225–242. <https://doi.org/10.2478/popore-2014-0015>
- Cartes JE, Sorbe C (1999) Deep-water amphipods from the Catalan Sea slope (western Mediterranean): bathymetric distribution, assemblage composition and biological characteristics. *Journal of Natural History* 33(8): 113–1158. <https://doi.org/10.1080/002229399299978>
- Chevreaux E (1887) Crustacés amphipodes nouveaux dragués par l'Hirondelle, pendant sa campagne de 1886. *Bulletin de la Société zoologique de France* 12: 566–580.
- Chevreaux E (1911) Diagnoses d'Amphipodes nouveaux provenant des Campagnes de la *Princesse-Alice* dans l'Atlantique nord. *Bulletin de l'Institut Océanographique, Monaco*, 204: 1–13.
- Dahl E (1959) Amphipoda from depths exceeding 6000 m. *Galathea reports*, 211–240.
- Degnan JH, Rosenberg NA (2006) Discordance of species trees with their most likely gene trees. *PLoS genetics* 2(5): e68. <https://doi.org/10.1371/journal.pgen.0020068>
- Degnan JH, Rosenberg NA (2009) Gene tree discordance, phylogenetic inference and the multispecies coalescent. *Trends in Ecology and Evolution* 24(6): 332–40. <https://doi.org/10.1016/j.tree.2009.01.009>

- Ersts PJ (2017) Geographic Distance Matrix Generator(version 1.2.3). American Museum of Natural History, Center for Biodiversity and Conservation. Available from http://biodiversityinformatics.amnh.org/open_source/gdmg [Accessed on 2017-7-4]
- Geller J, Meyer CP, Parker M, Hawk H (2013) Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Molecular Ecology Resources* 13(5): 851–861. <https://doi.org/10.1111/1755-0998.12138>
- Gurjanova EF (1934) Neue Formen von Amphipoden des Karischen Meeres. *Zoologischer Anzeiger* 108: 122–130.
- Hansen HJ (1887) Malacostraca marina Groenlandiae occidentalis. Oversigt over det vestlige Grønlands fauna af malakostrake havkrepsdyr. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, (1887): 5–226.
- Hernández-Triana LM, Chaverri LG, Rodríguez-Pérez MA, Prosser SWJ, Hebert PDN, Gregory TR, Johnson N (2014) DNA barcoding of Neotropica black flies (Diptera: Simuliidae) Species identification and discovery of cryptic diversity in Mesoamerica. *Zootaxa* 3936(1): 93–114. <https://doi.org/10.11646/zootaxa.3936.1.5>
- Holmes SJ (1908) The Amphipoda collected by the U.S. Bureau of Fisheries steamer “Albatross” off the west coast of North America, in 1903 and 1904, with descriptions of a new family and several new genera and species. *Proceedings of the United States National Museum* 35(1654): 489–543. <https://doi.org/10.5479/si.00963801.35-1654.489>
- Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO, Daneliya M, Dauvin JC, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Holsinger J, Hughes L, Jaume D, Jazdzewski K, Just J, Kamal'tynov RM, Kim YH, King R, Krapp-Schickel T, LeCroy S, Lörz A-N, Senna AR, Serejo C, Sket B, Tandberg AH, Thomas J, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (2017) World Amphipoda Database. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=489869> [on 2017-05-29]
- Huelsenbeck J, Ronquist F (2001) MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17. <https://doi.org/10.1093/bioinformatics/17.8.754>
- Janosik AM, Halanych KM (2010) Unrecognized Antarctic biodiversity: a case study of the genus *Odontaster* (Odontasteridae; Asteroidea). *Integrative and Comparative Biology* 50: 981–992. <https://doi.org/10.1093/icb/icq119>
- Jazdzewska AM, Corbari L, Driskell A, Frutos I, Havermans C, Hendrycks E, Hughes L, Lörz A-N, Stransky B, Tandberg AHS, Vader W, Brix S (2018) A genetic fingerprint of Amphipoda from Icelandic waters – the baseline for further biodiversity and biogeography studies. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology* (IceAGE Amphipoda project). *ZooKeys* 731: 55–73. <https://doi.org/10.3897/zookeys.731.19931>
- Katoh K, Misawa K, Kuma KI, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–66. <https://doi.org/10.1093/nar/gkf436>

- Katoh K, Standley DM (2013) MAFFT Multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*. <https://doi.org/10.1093/molbev/mst010>
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*. <https://doi.org/10.1093/bioinformatics/bts199>
- Knowles LL, Kubatko KS (2010) *Estimating Species Trees: Practical and Theoretical Aspects*. Wiley-Blackwell, 232 pp.
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33(7):1870–4. <https://doi.org/10.1093/molbev/msw054>
- Ledoyer M (1982) Family Eusiridae. In: Ruffo (Ed.) *The Amphipoda of the Mediterranean*. Mémoires de l'Institut Océanographique 13(1): 233–244.
- Leigh JW, Bryant D (2015) POPART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6: 1110–1116. <http://dx.doi.org/10.1111/2041-210X.12410>
- Lepechin I (1780) *Tres oniscorum species descriptae*. Acta Academiae Scientiarum Imperialis Petropolitanae.
- Lörz AN (2010) Deep-sea *Rhachotropis* (Crustacea: Amphipoda: Eusiridae) from New Zealand and the Ross Sea with key to the Pacific, Indian Ocean and Antarctic species. *Zootaxa* 2482: 22–48.
- Lörz AN, Linse K, Smith PJ, Steinke D (2012) First Molecular Evidence for Underestimated Biodiversity of *Rhachotropis* (Crustacea, Amphipoda), with Description of a New Species. *PLoS ONE* 7(3): e32365. <https://doi.org/10.1371/journal.pone.0032365>
- Lörz, AN (2015) An enigmatic *Rhachotropis* (Crustacea: Amphipoda: Eusiridae) from New Zealand. *Zootaxa* 4006(2): 383–391. <https://doi.org/10.11646/zootaxa.4006.2.9>
- Lowry JK, Springthorpe RT (2005) New calliopiid and eusirid amphipods from eastern Australian waters (Crustacea: Amphipoda: Calliopiidae: Eusiridae). *Proceedings of the Biological Society Washington* 118: 38–47. [https://doi.org/10.2988/0006-324X\(2005\)118\[38:NCAEAF\]2.0.CO;2](https://doi.org/10.2988/0006-324X(2005)118[38:NCAEAF]2.0.CO;2)
- Maddison WP (1997) Gene trees in species trees. *Systematic Biology* 46(3): 523–536. <https://doi.org/10.1093/sysbio/46.3.523>
- Meißner K, Brenke N, Svavarsson J (2014) Benthic habitats around Iceland investigated during the IceAGE expedition. *Polish Polar Research* 35(2): 177–202. <https://doi.org/10.2478/popore-2014-0016>
- Palumbi S, Martin A, Romano S, McMillan WO, Stice L, Grabowski G (1991) *The Simple Fool's Guide to PCR, Version 2*. Department of Zoology and Kewalo Marine Laboratory, University of Hawaii, Honolulu.
- Price MN, Dehal PS, Arkin AP (2010) FastTree 2 – Approximately Maximum-Likelihood trees for large alignments. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0009490>
- Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, automatic barcode gap discovery for primary species delimitation. *Molecular Ecology* 21: 1864–1877. <https://doi.org/10.1111/j.1365-294X.2011.05239.x>

- Rambaut A (2014) FigTree v. 1.4.2 <http://tree.bio.ed.ac.uk/>
- Rambaut A, Suchard M, Drummond A (2013) Tracer v.1.6. <http://tree.bio.ed.ac.uk/software/tracer/>
- Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). Molecular Ecology Notes. <https://doi.org/10.1111/j.1471-8286.2006.01678.x>
- Ronquist F, Huelsenbeck J (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models.
- Sars GO (1883) Oversigt af Norges Crustaceer med foreløbige Bemærkninger over de nye eller mindre bekjendte Arter. I. (Podophthalmata – Cumacea – Isopoda – Amphipoda). Forhandling i Videnskabs Selskabet i Christiania, year 1882(18): 1–124.
- Sars GO (1890–1895) An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. 1. Amphipoda. Alb. Cammermeyers forlag, Christiania, 978 pp.
- Shimodaira CH, Hasegawa M (1999) Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution 16: 1114–16. <https://doi.org/10.1093/oxfordjournals.molbev.a026201>
- Smith SI (1883) List of Crustacea dredged on the coast of Labrador by the expedition under the direction of W. A. Stearns, in 1882. Proceedings of the United States National Museum 7: 218–222. <https://doi.org/10.5479/si.00963801.374.218>
- Stebbing TRR (1888) Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76. Zoology 29, 1737 pp.
- Stebbing TRR (1908) On two new species of northern Amphipoda. Linnaean Journal of Zoology 30: 191–196. <https://doi.org/10.1111/j.1096-3642.1908.tb02133.x>
- Stephensen K (1944) Crustacea Malacostraca VIII (Amphipoda IV). The Danish Ingolf-Expedition 3(13): 1–51.
- Sukumaran J, Knowles LL (2017) Multispecies coalescent delimits structure, not species. Proceedings of the National Academy of Sciences USA 114(7): 1607–1612. <https://doi.org/10.1073/pnas.1607921114>
- Thurston MH (1980) Abyssal benthic Amphipoda (Crustacea) from the East Iceland Basin. Bulletin of the British Museum (Natural History) 38(1): 43–67.
- d’Udekem d’Acoz C, Vader W, Legezińska J (2007) On a diminutive *Rhachotropis* species from the North Sea, with a key to European *Rhachotropis* (Crustacea, Amphipoda, Eusiridae). Bollettino del Museo Civico di Storia Naturale di Verona 31: 31–49.
- Wägele JW (1994) Notes on Antarctic and South American Serolidae (Crustacea, Isopoda) with remarks on the phylogenetic biogeography and a description of new genera. Zoologische Jahrbücher. Abteilung für Systematik 121: 3–69.
- Weisshappel JB (2000) Distribution and diversity of the hyperbenthic amphipod family Eusiridae in the different seas around the Greenland-Iceland-Faeroe-Ridge. Sarsia 85: 227–236. <https://doi.org/10.1080/00364827.2000.10414575>

Supplementary material 1

Table S1. Extended overview of all samples used in analyses with geographical and environmental details

Authors: Anne-Nina Lörz, Anne Helene Tandberg, Endre Willassen, Amy Driskell

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Depths indicated in red have been found using the latitude and longitude information with the datapoint and the bathymetry-layer on Google Earth Pro.

Depths indicated in blue are inferred from the general depths in the named (no latitude or longitude given) geographical location, given bathymetry-layer on Google Earth Pro.

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Link: <https://doi.org/10.3897/zookeys.731.19814.suppl1>

Supplementary material 2

Table S2. Geographic distances between stations (sample name) in km.

Authors: Anne-Nina Lörz, Anne Helene Tandberg, Endre Willassen, Amy Driskell

Data type: Microsoft Excel Worksheet (.xlsx)

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Link: <https://doi.org/10.3897/zookeys.731.19814.suppl2>

Supplementary material 3

Figure S1. Tree showing COI sequence cluster derived from ABGD (Automatic Barcode Gap Discovery) analysis using simple distances and default parameter settings.

Authors: Anne-Nina Lörz, Anne Helene Tandberg, Endre Willassen, Amy Driskell

Data type: Adobe Acrobat Document (.pdf)

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Supplementary material 4

Figure S2. Bayesian consensus tree from COI sequences. Numbers on branches are posterior probabilities. See text for further information.

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On a new species of *Amphilochus* from deep and cold Atlantic waters, with a note on the genus *Amphilochopsis* (Amphipoda, Gammaridea, Amphilochidae)

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Abstract

Amphilochus manudens and *Amphilochopsis hamatus* are redescribed based on specimens from the BioIce, Mareano, and IceAGE programmes. The new species *Amphilochus anoculus* **sp. n.** is described based on material from the IceAGE programme and the preceding BioIce programme; it is separated from the closely related *Amphilochus manudens* by the absence of eyes, a symmetrically bilobed labrum, four setae on the maxilla 2 outer plate, a rounded corner of epimeral plate 3, and a robust seta at the tip of the telson. There are also clear differences in depth and temperature ranges. *Amphilochopsis hamatus* is shown to be closely related to *Amphilochus manudens* and *A. anoculus* and transferred to *Amphilochus* s. str.

Keywords

Amphilochus, Amphipoda, BioIce, IceAGE, Mareano, new species, North Atlantic, taxonomy

Introduction

The amphipod family Amphilochidae consists today of 15 genera, of which several are monotypic. There are ninety species, of which most are assigned to the possi-

bly paraphyletic (Hoover and Bousfield 2001) genera *Gitanopsis* and *Amphilochus* (Horton et al. 2017). The family is cosmopolitan with the small genera seemingly restricted to specific geographic areas. Historically, the definition of Amphilochidae has been much like what Barnard and Karaman (1991) use as their diagnosis: "Coxa 4 immensely broadened, coxae 2–4 with contiguous overlapping, not rabbeted, coxa 2 not hidden; coxa 1 very small and hidden by coxa 2. Peduncle of uropod 3 elongate. Telson entire, elongate."

During the sorting of Amphilochidae material from the BioIce programme for a Master thesis in 2000, it became apparent that three groups of specimens had an anterodistal tooth on the propodus of pereopod 2. *Amphilochus manudens* and *Amphilochopsis hamatus* were already known from the literature (Sars 1890–95; Stephensen 1925; Gurjanova 1951), but the last group of specimens; with an anterodistal tooth and seemingly no eyes did not fit any of the described species. Specimens with the same morphological traits have since been found by the authors in amphipod material from Spitsbergen, the Faroe Islands, the Norwegian coast and in newly collected Icelandic material from the follow-up programme to BioIce: IceAGE (for information on IceAGE amphipod collections, see Brix et al. 2014; 2018). We therefore find it timely to describe a new species for the observed morphotype with the anterodistal tooth and no visible eyes. To be able to fully distinguish the new species from the known species it most resembles, morphological redescriptions of these are included, and the three species are genetically barcoded (COI-gene, Folmer et al. 1994) to show a clear separation of species both collected from Iceland (Jazdzewska et al. (2018)) and Norway (Boldsystems.org).

Materials and methods

The material examined in this study comes from the programme BioIce in the years 1991–1997, the IceAGE-programme, and material in the collections of the University museums of Tromsø and Bergen, Norway. A few additional specimens derive from environmental monitoring studies around the Faroe Islands. For information on the collection of the material for BioIce, see Berge and Vader (1997), for the collection of IceAGE material, see Brix et al. (2014, 2018). Most of the new material at the University museum of Bergen comes from the Mareano programme; for collection of this material, see Buhl-Mortensen et al. (2015). The Amphilochidae-material from BioIce was sorted and described in Tromsø for an MSc-thesis (Tandberg 2000). Sample individuals were dissected using a binocular and mounted in rose-bengal-stained polyvinyl-lactophenol for examination under a light microscope. Pencil-drawings were made using a microscope fitted with a drawing tube; drawings were traced with ink and scanned. Digital inking on scanned hand-inked drawings followed procedures described by Coleman (2003, 2009). All scales on drawings are 0.1 mm unless otherwise stated.

Material from IceAGE and the collections from the University Museum of Bergen were identified and dissected for illustration of appendages using a Leica MZ12.5

stereo microscope. Temporary glycerine mounted and permanently mounted appendages (Faure medium) were drawn using a Leica 2500 compound microscope fitted with a camera lucida, and scanned pencil drawings were digitally inked in Adobe Illustrator following the method described by Coleman (2003, 2009). Animals used for COI-sequencing in Norway were photographed using a Leica DFC425 camera fitted with a motorised stacker on a Leica M205 binocular, and the Leica LAS 3.8 software for taking photos. Compilation of stacked photos into a single photo has been performed using Zerene Stacker 1.04 (setting P-max).

Further material for *Amphilochnus anoculus* sp. n. comes from a survey in the Faroe-Shetland Channel (Mannvik et al. 2002), the Norwegian Sea and from the polar basin north of Spitsbergen (Tromsø Museum collections). Ecological data for *Amphilochnus manudens* and *Amphilochnopsis hamatus* were also gathered from the BioFar program (Nørrevang et al. 1994).

Sequencing of COI was performed through IceAGE (for details see Jazdzewska et al. 2018) and NorBOL (The Norwegian Barcode of Life, for details see Lörz et al. 2018).

BioIce material is held at the National Museum of Iceland, Reykjavik, Iceland (IINH-numbers).

IceAGE material is held at the Zoological Museum University of Hamburg, Centre of Natural History (CeNak), Germany (ZMH K-numbers).

NorAmph and other University of Bergen material is held at the University Museum of Bergen, Natural History Collections, Norway (ZMBN-numbers).

Material from University Museum of Tromsø is held at the Natural Collections University of Tromsø, Tromsø, Norway (TSZCr-numbers).

The material from the environmental studies performed by AkvaplanNIVA was kept for five years before it was destroyed: the identification of the amphipods of the survey was performed by the first author.

Results

Taxonomy

Order AMPHIPODA Latreille, 1816

Suborder GAMMARIDEA Latreille, 1802

Family AMPHILOCHIDAE Boeck, 1871

Genus *Amphilochnus* Spence Bate, 1862

Amphilochnus Spence Bate, 1862: 107; Stebbing 1906: 149; Barnard and Karaman 1991: 96

Callimerus Stebbing, 1876: 445

***Amphilochus anoculus* sp. n.**

<http://zoobank.org/AD3ED2F5-F13B-4885-BD81-492F173B4EA1>

Material examined. from Icelandic (BioIce and IceAGE), Norwegian coastal and arctic (Svalbard) and Faroese waters. (For an extensive list of examined material see Table 1.).

Holotype: IceAGE ZMH K-47225, female 3 mm (slide).

Paratypes: Slides: BioIce 2367 male, 3 mm IINH37914; BioIce 2367 female, 3 mm IINH37915; MareanoR1225-RP112 female 4 mm ZMBN121953; IceAGE 1006 male, 3 mm ZMBN121952. Wet-sample: TSZCr 14338 (8 specimens).

Type locality. ZMH K-47225: IceAGE station 1057 (61.6417, -31.3562) (2504m).

Paratype localities. IINH37914, IINH37915: BioIce station 2367 (64.3800, -9.4300) (719m); TSZCr 14338: UNIS course-station JM 369-05 (80.5313, 10.5777) (819 m); ZMBN121953: Mareano station R1225-RP112 (70.4748, 31.7340) (401 m); ZMBN121952: IceAGE station 1006 (62.5508, -20.3750) (1386 m).

Distribution. This species is known from BioIce/IceAGE stations in deep and cold waters north and east of Iceland, from deep stations in the Faroe-Shetland Channel, several deep stations north in the Norwegian Sea and from one deep station in the polar basin. It appears to be confined to cold and deep waters (see Fig. 1).

Illustrations are all from paratypes: Figs 2–4 of ZMBN121952, except for Fig. 3 pereopod 1 dactylus (1b) which is from ZMH K-47225 and Fig. 4 uropod 3 and telson that are both from BioIce station 2367.

Description. Description is based on a composite of studied material. No observed sexual dimorphism.

Head. Rostrum subequal to peduncle article 1 of antenna 1, curved. Eyes absent. Cephalic lobes produced, broadly rounded, tips of mouthparts just visible under the edge of cephalon. Antenna 1 subequal to antenna 2; peduncle strong, longer than six-articulate flagellum; accessory flagellum absent. Setae on both peduncle and flagellum few and short. Antenna 2 peduncle longer than eight-articulate flagellum. Few and short setae distally on peduncle articles, all articles of the peduncle are longer than broad.

Labrum symmetrically bilobed. Mandible molar small but triturate, rounded cone-shaped, with setation on entire chewing area, which is ridged; incisor serrate; eleven accessory spines; palp slender, 3-articulate; article 1 is shorter than article 2, which is shorter than article 3; article 3 with setae; lacinia mobilis laterally expanded. Labium symmetrical, without inner lobes. Maxilla 1 palp biarticulate, with two apical setae; inner plate reduced, with one seta; outer plate with eight robust and six thinner setae. Maxilla 2 inner plate shorter than outer plate, nine setae on distal margin; outer plate long and thin with four distal setae. Maxilliped inner plate reaching end of merus, well separated, thin, two robust distal setae; outer plate reaches middle of carpus of palp, one robust seta and ridge of serrations; palp slim, heavily setulated on propodus.

Mesosome dorsally smooth; segment 3 is shorter than segment 4. Coxa 1 reduced and covered by coxa 2, which is longer than broad. Coxa 2 distal margin serrate and with setae. Coxa 3 and 4 distal margin not serrate, without setae. Coxa 5–7 concave.

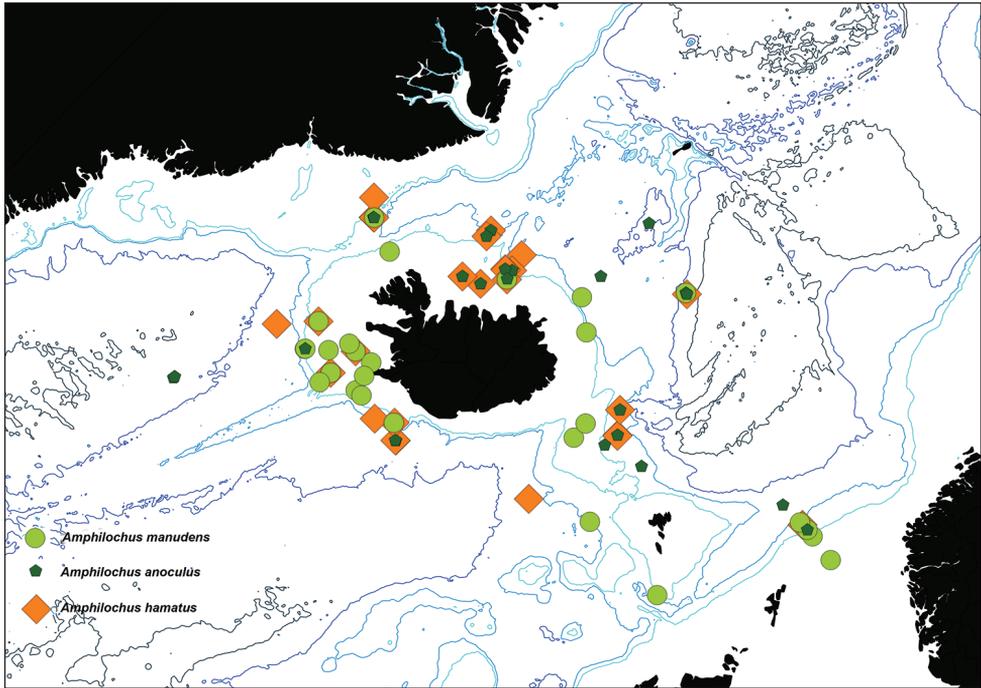


Figure 1. Map showing the Icelandic distribution of *Amphilocheus anoculus* sp. n., *Amphilocheus manudens* and *Amphilocheus hamatus* (based on BioIce and IceAGE material).

Pereopod 1 basis longer than propodus, upper half distally widened, few and short setae; carpal lobe well developed, reaching 65% of posterior margin of propodus; propodus triangular; palm oblique, serrate with setae, no seta defining palmar corner, anterodistal tooth of medium size (half as long as the base of dactylus is broad); dactylus smooth with few, thin setae on inner margin. Pereopod 2 basis little longer than propodus, upper half not as widened distally as pereopod 1; carpal lobe covers all of posterior margin of propodus; propodus elongate, palm oblique, serrate with minute setae, no setae defining the palmar corner, anterodistal tooth well developed (same size as the breadth of the base of dactylus); dactylus inner margin weakly serrate on proximal half. Pereopod 3 missing in holotype. Pereopod 4 basis with four anterior setae, dactylus half-length of propodus. Pereopod 5 with posterior lobe on basis and merus. Pereopod 6 with posterior lobe on basis; posterior lobe on merus boat-shaped; carpus shorter than propodus; dactylus more than half length of propodus. Pereopod 7, posterior lobe on basis and merus, meral lobe covers 50% of carpus; dactylus more than half-length propodus.

Metasome smooth. Epimeral plates 1 and 3 rounded; plate 2 right-angled. Urosome smooth; segment 1 long; segments 2 and 3 shorter. Uropod 1 peduncle longer than rami; outer ramus marginally longer than inner; three to four setae on outer margins. Uropod 2 peduncle longer than rami; outer ramus half-length of inner; setae on both rami. Uropod 3 peduncle with clear flange, smooth; outer ramus weakly shorter than inner ramus; uro-

Table 1. List of stations for examined species of *Amphibolochus anoculus* sp. n., *A. mamudens*, and *A. hamatus*. Asterisk* after museum-number indicates holo- and paratypes.

Species	Station name	Sampling programme	Collection number	Latitude (dec)	Longitude (dec)	Depth (m)	Temp (C)	BOLD-accession number	Note
	BioIce 2087	BioIce		67,257	-17,446	735,0	-0,40		
	BioIce 2088	BioIce		67,239	-17,857	617,0	-0,40		
	BioIce 2094	BioIce		67,034	-17,570	303,0	1,70		
	BioIce 2100	BioIce		68,001	-19,421	1141,0	-0,60		
	BioIce 2107	BioIce		67,836	-19,555	905,0	-0,60		
	BioIce 2136	BioIce		66,726	-18,953	417,0	0,60		
	BioIce 2149	BioIce		66,749	-20,086	293,0	3,00		
	BioIce 2318	BioIce	IINH 37886 (wet), IINH37916 (slide)	64,070	-9,030	996,0			
	BioIce 2325	BioIce		63,750	-10,183	555,0			
	BioIce 2367	BioIce	IINH37888, IINH37914*, IINH37915*	64,380	-9,430	719,0			Paratype (slides)
	3-1	Akvaplan NIVA Faroe project		60,348	-5,167	1088,0			
	8-1	Akvaplan NIVA Faroe project		60,591	-5,309	825,0			
	9-1	Akvaplan NIVA Faroe project		60,538	-5,206	921,0			
	13-2	Akvaplan NIVA Faroe project		60,483	-4,932	1022,0			
	15-1	Akvaplan NIVA Faroe project		60,553	-4,937	1055,0			
	15-3	Akvaplan NIVA Faroe project		60,553	-4,937	1055,0			
	81 03211	Tromsø Museum Collection tours	TSZCr 15516	63,167	4,817	860,0			
	14968	Tromsø Museum Collection tours	TSZCr 14968	70,850	15,383	2100,0			
	JM 369-05	UNIS AB321-2005	TSZCr 14338*	80,531	10,578	819,0			Paratypes (wet)
	R405 RP59	Mareano	ZMBN_111537	72,140	15,346	902,4	-0,41	AMPNB487-17	
	R479 RP156	Mareano		68,653	10,301	2744,2	-0,82		
	R573 RP28	Mareano		70,872	16,933	916,5	-0,64		
	R642 RP104	Mareano	ZMBN_104532	68,241	9,243	2346,6	-0,84	AMPNB354-15	
	R653 RP108	Mareano		67,608	8,392	1750,7	-0,84		
	R671 RP111	Mareano	ZMBN_104531	67,891	9,875	777,2	-0,52	AMPNB353-15	
	R1180 RP86	Mareano		71,609	32,992	304,9	2,84		

Amphibolochus anoculus sp. n.

Species	Station name	Sampling programme	Collection number	Latitude (dec)	Longitude (dec)	Depth (m)	Temp (C)	BOLD-accession number	Note
	R1200 RP90	Mareano		70,854	32,507	248,9	3,74		
	R1225 RP112	Mareano	ZMBN121953 *	70,475	31,734	401,4	5,45		Paratype (slide)
	R1225 RP112	Mareano	ZMBN121959, ZMBN121960	70,475	31,734	401,4	5,45		slides
	IceAGE 1010	IceAGE	ZMH K-47220	62,552	-20,395	1384,8			
	IceAGE 1010	IceAGE	ZMH K-47221	62,552	-20,395	1384,8			
	IceAGE 1054	IceAGE	ZMH K-47222	61,603	-31,377	2537,3			
	IceAGE 880	IceAGE	ZMBN121954	63,389	-8,157	686,0			
	IceAGE 880	IceAGE	ZMH K-47223	63,389	-8,157	686,0		AMPIV181-17	
	IceAGE 1010	IceAGE	ZMBN121955	62,552	-20,395	1384,8			
	IceAGE 1010	IceAGE	ZMH K-47224	62,552	-20,395	1384,8			
	IceAGE 1057	IceAGE	ZMH K-47225*	61,642	-31,356	2504,7			Holotype (slide)
	IceAGE 1168	IceAGE	ZMH K-47226	67,606	-7,001	2372,6			
	IceAGE 1123	IceAGE	ZMH K-47227	67,214	-26,208	716,5			
	IceAGE 1172	IceAGE	ZMH K-47228	67,578	-6,935	2422,4			
	IceAGE 1181	IceAGE	ZMBN121956	67,658	-12,227	1827,0			
	IceAGE 1119	IceAGE	ZMBN121957	67,214	-26,242	696,9			
	IceAGE 871	IceAGE	ZMBN121958	62,737	-0,946	1577,4			
	IceAGE 1168	IceAGE	ZMH K-47229	67,606	-7,001	2372,6			
	IceAGE 1123	IceAGE	ZMH K-47230	67,214	-26,208	716,5			
	IceAGE 1172	IceAGE	ZMH K-47231	67,578	-6,935	2422,4			
	IceAGE 1172	IceAGE	ZMH K-47232	67,578	-6,935	2422,4		DNA-voucher: ZMH K-47232	
	IceAGE 1054	IceAGE	ZMH K-47233	61,603	-31,377	2537,3		DNA-voucher: ZMH K-47233	
	IceAGE 1159	IceAGE	ZMH K-47234	69,111	-9,917	2202,8			
	IceAGE 868	IceAGE	ZMH K-47235	62,152	0,259	587,4			
	IceAGE 1123	IceAGE	ZMH K-47236	67,214	-26,208	716,5			
	IceAGE 1010	IceAGE	ZMH K-47237	62,552	-20,395	1384,8		DNA-voucher: ZMH K-47237	
	IceAGE 1006	IceAGE	ZMBN121952*	62,551	-20,375	1386,8			Paratype (slide)

Amphilocheus
anoculus sp. n.

Species	Station name	Sampling programme	Collection number	Latitude (dec)	Longitude (dec)	Depth (m)	Temp (C)	BOLD-accession number	Note
<i>Amphilocheus manudens</i> Spence Bate, 1862	BioIce 2096	BioIce		67,018	-17,578	300,0	1,70		
	BioIce 2207	BioIce	IINH37889	67,011	-22,596	81,0	8,30		
	BioIce 2213	BioIce		64,155	-23,971	260,0	7,00		
	BioIce 2215	BioIce	IINH37887	64,157	-24,261	213,0	6,90		
	BioIce 2221	BioIce		63,917	-25,273	240,0	6,50		
	BioIce 2236	BioIce		63,450	-24,680	293,0	6,90		
	BioIce 2237	BioIce	IINH37885	63,270	-24,408	293,0	6,90		
	BioIce 2273	BioIce		63,140	-24,983	313,0	7,00		
	BioIce 2288	BioIce		62,387	-22,677	1390,0	3,40		
	BioIce 2308	BioIce		63,250	-22,790	263,0	7,10		
	BioIce 2314	BioIce		63,703	-23,058	139,0	7,60		
	BioIce 2352	BioIce		63,783	-11,817	350,0			
	BioIce 2358	BioIce		63,167	-11,533	318,0			
	BioIce 2720	BioIce		64,430	-26,403	304,0	5,60		
	R405 RP59	Mareano		72,137	15,341	899,6	-0,41		
	R423 RP69	Mareano		71,872	17,142	355,3	5,53		
	R474 RP154	Mareano		71,073	18,543	251,0	7,52		
	R503 RP51	Mareano		71,772	25,975	321,1	4,42		
	R534 RP60	Mareano		70,675	18,622	364,6	6,34		
	R608 RP87	Mareano		70,958	21,120	149,0	6,57		
R613 RP90	Mareano		70,769	20,818	246,8	6,42			
R618 RP91	Mareano		70,701	21,025	258,8	6,38			
R621 RP93	Mareano		70,673	20,852	195,6	7,28			
R631 RP99	Mareano		70,805	19,702	178,6	6,87			
R636 RP102	Mareano		70,622	20,104	289,7	6,98			
R657 RP109	Mareano		67,343	8,638	849,6	-0,84			
R721 RP126	Mareano		67,841	11,809	183,2	6,87			
R733 RP128	Mareano	ZMIBN_94864	67,720	10,272	219,2	7,34	AMPNB115-14		
R754 RP132	Mareano		67,803	9,685	823,5	-0,56			
R786 RP10	Mareano		67,953	9,589	1315,4	-0,84			

Species	Station name	Sampling programme	Collection number	Latitude (dec)	Longitude (dec)	Depth (m)	Temp (C)	BOLD-accession number	Note
<i>Amphilocheus manudens</i> Spence Bate, 1862	R782 RP11	Mareano		68,059	9,468	1712,0	-0,81		
	R821 RP13	Mareano	ZMBN_104481	67,021	8,223	556,0		AMPNB303-15	
	R870 RP19	Mareano		67,387	11,622	128,3	6,29		
	R849 RP21	Mareano		67,401	10,822	179,6	7,51		
	R1137 RP77	Mareano		72,574	32,386	272,3	2,09		
	R1146 RP80	Mareano		72,103	34,287	288,9	2,18		
	R1150 RP82	Mareano		72,093	33,701	249,5	2,83		
	R1174 RP85	Mareano		71,618	32,225	296,5	3,39		
	R1180 RP86	Mareano		71,609	32,992	304,9	2,84		
	R1186 RP87	Mareano		71,421	32,859	281,5	4,47		
	R1196 RP89	Mareano		71,187	32,243	226,0	4,27		
	R1200 RP90	Mareano		70,854	32,507	248,9	3,74		
	R1205 RP92	Mareano		70,574	32,273	297,3	4,22		
	R1213 RP93	Mareano		70,771	30,785	376,1	4,62		
	R1230 RP95	Mareano		70,117	31,350	303,9			
	IceAGE 868	IceAGE	ZMH K-47238	62,152	0,259	587,4			
	IceAGE 1082	IceAGE	ZMH K-47239	63,702	-26,394	724,4			
	IceAGE 1017	IceAGE	ZMH K-47240	62,931	-20,774	891,7			
	IceAGE 1032	IceAGE	ZMH K-47241	63,309	-23,158	289,4			
	IceAGE 878	IceAGE	ZMH K-47242	61,897	-10,230	781,4			
IceAGE 868	IceAGE	ZMH K-47243	62,152	0,259	587,4				
IceAGE 1086	IceAGE	ZMH K-47244	63,709	-26,384	698,1				
IceAGE 1219	IceAGE	ZMH K-47245	66,289	-12,347	579,1				
IceAGE 1086	IceAGE	ZMH K-47246	63,709	-26,384	698,1				
IceAGE 876	IceAGE	ZMH K-47247	60,406	-6,615	554,3				
IceAGE 876	IceAGE	ZMH K-47248	60,406	-6,615	554,3			AMPIV183-17	
IceAGE 878	IceAGE	ZMH K-47249	61,897	-10,230	781,4				
IceAGE 878	IceAGE	ZMH K-47250	61,897	-10,230	781,4				
IceAGE 878	IceAGE	ZMH K-47251	61,897	-10,230	781,4				
IceAGE 1168	IceAGE	ZMH K-47252	67,606	-7,001	2372,6				

Species	Station name	Sampling programme	Collection number	Latitude (dec)	Longitude (dec)	Depth (m)	Temp (C)	BOLD-accession number	Note
<i>Amphilocheus manudens</i> Spence Bate, 1862	IceAGE 1104	IceAGE	ZMH K-47253	66,643	-24,533	118,8			
	IceAGE 1194	IceAGE	ZMH K-47254	67,078	-13,055	1573,5			
	IceAGE 1172	IceAGE	ZMH K-47255	67,578	-6,935	2422,4			
	IceAGE 867	IceAGE	ZMH K-47256	61,997	0,507	302,5			
	IceAGE 866	IceAGE	ZMH K-47257	61,427	1,351	169,1			
	IceAGE 870	IceAGE	ZMH K-47258	62,329	-0,102	1058,4			
	IceAGE 867	IceAGE	ZMH K-47259	61,997	0,507	302,5			
	IceAGE 1123	IceAGE	ZMH K-47260	67,214	-26,208	716,5			
	IceAGE 1082	IceAGE	ZMH K-47261	63,702	-26,394	724,4		DNA-voucher: ZMH K-47261	
	IceAGE 866	IceAGE	ZMH K-47262	61,427	1,351	169,1			
	IceAGE 867	IceAGE	ZMH K-47263	61,997	0,507	302,5			
	IceAGE 868	IceAGE	ZMH K-47264	62,152	0,259	587,4			
	IceAGE 1086	IceAGE	ZMH K-47265	63,709	-26,384	698,1		DNA-voucher: ZMH K-47265	
IceAGE 867	IceAGE	ZMH K-47266	61,997	0,507	302,5				
IceAGE 867	IceAGE	ZMH K-47267	61,997	0,507	302,5		DNA-voucher: ZMH K-47267		
<i>Amphilocheus hamattus</i> (Stephensen, 1925)	BioIce 2077	BioIce	IINH37894	67,405	-17,104	1048,0	-0,50		
	BioIce 2087	BioIce		67,257	-17,446	735,0	-0,40		
	BioIce 2088	BioIce	IINH37892	67,239	-17,857	617,0	-0,40		
	BioIce 2090	BioIce	IINH37893	67,222	-17,816	539,0	-0,40		
	BioIce 2096	BioIce	IINH37891	67,018	-17,578	300,0	1,70		
	BioIce 2100	BioIce		68,001	-19,421	1141,0	-0,60		
	BioIce 2107	BioIce	IINH37890	67,836	-19,555	905,0	-0,60		
	BioIce 2136	BioIce	IINH37896	66,726	-18,953	417,0	0,60		
	BioIce 2149	BioIce		66,749	-20,086	293,0	3,00		
	BioIce 2213	BioIce	IINH37897	64,155	-23,971	260,0	7,00		
	BioIce 2236	BioIce	IINH37898	63,450	-24,680	293,0	6,90		
	BioIce 2237	BioIce		63,270	-24,408	293,0			

Species	Station name	Sampling programme	Collection number	Latitude (dec)	Longitude (dec)	Depth (m)	Temp (C)	BOLD-accession number	Note
<i>Amphilochus hamatus</i> (Stephensen, 1925)	BioIce 2317	BioIce	IINH37889	64,117	-9,050	996,0			
	BioIce 2318	BioIce	IINH37900	64,070	-9,030	996,0			
	BioIce 2319	BioIce	IINH37901	64,017	-9,617	776,0			
	BioIce 2340	BioIce	IINH37902	62,133	-13,333	1302,0			
	BioIce 2367	BioIce	IINH37903	64,380	-9,430	719,0			
	BioIce 2410	BioIce	IINH37904	62,860	-21,735	1074,0	4,00		
	BioIce 2707	BioIce	IINH37905	63,922	-28,270	1407,0	3,70		
	BioIce 2719	BioIce	IINH37906	64,428	-26,403	300,0	5,60		
	R671 RP111	Mareano	ZMBN_104542	67,891	9,875	777,2	-0,52	AMPNB364-15	
	R877 RP3	Mareano	ZMBN_104479	68,475	9,785	2561,4	-0,80	AMPNB301-15	
	R776 RP4	Mareano		68,186	10,354	799,9	-0,74		
	IceAGE 869	IceAGE	ZMH K-47268	62,270	0,020	846,4			
	IceAGE 1006	IceAGE	ZMH K-47269	62,551	-20,375	1386,8			
	IceAGE 1006	IceAGE	ZMH K-47270	62,551	-20,375	1386,8			
	IceAGE 1019	IceAGE	ZMH K-47271	62,939	-20,744	913,6			
	IceAGE 1132	IceAGE	ZMH K-47272	67,641	-26,755	318,1			
	IceAGE 1172	IceAGE	ZMH K-47273	67,578	-6,935	2422,4			
	IceAGE 1123	IceAGE	ZMH K-47274	67,214	-26,208	716,5			
	IceAGE 1119	IceAGE	ZMH K-47275	67,214	-26,242	696,9			
	IceAGE 1119	IceAGE	ZMH K-47276	67,214	-26,242	696,9		DNA-voucher: ZMH K-47276	
IceAGE 1010	IceAGE	ZMH K-47277	62,552	-20,395	1384,8				
IceAGE 1010	IceAGE	ZMH K-47278	62,552	-20,395	1384,8			DNA-voucher: ZMH K-47278	
IceAGE 1172	IceAGE	ZMH K-47279	67,578	-6,935	2422,4			DNA-voucher: ZMH K-47279	
IceAGE 869	IceAGE	ZMH K-47280	62,270	0,020	846,4				
IceAGE 1010	IceAGE	ZMH K-47281	62,552	-20,395	1384,8				

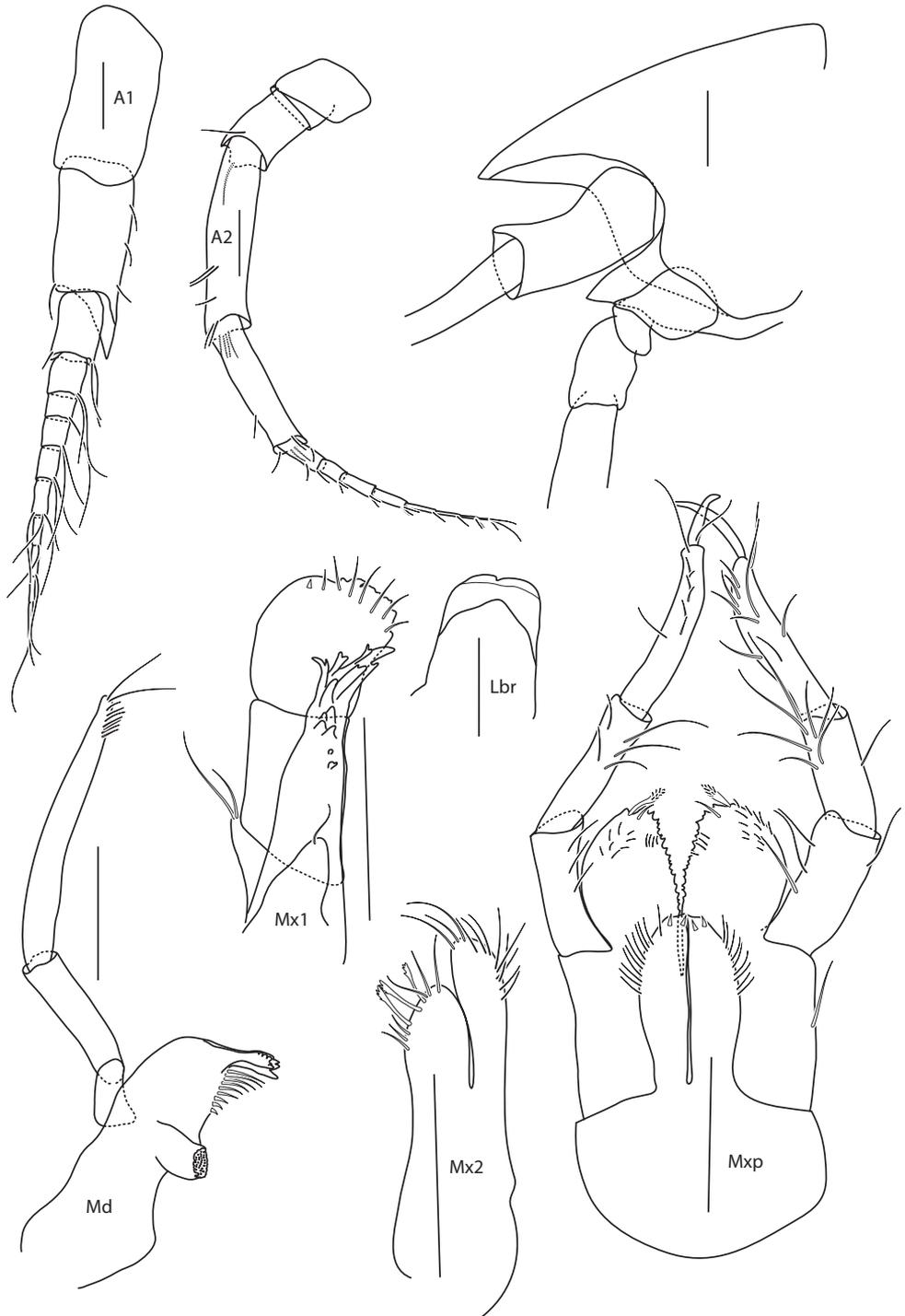


Figure 2. *Amphilochus anoculus* sp. n. Head and mouthparts. ZMBN121952. Scale bars: 0.1 mm.

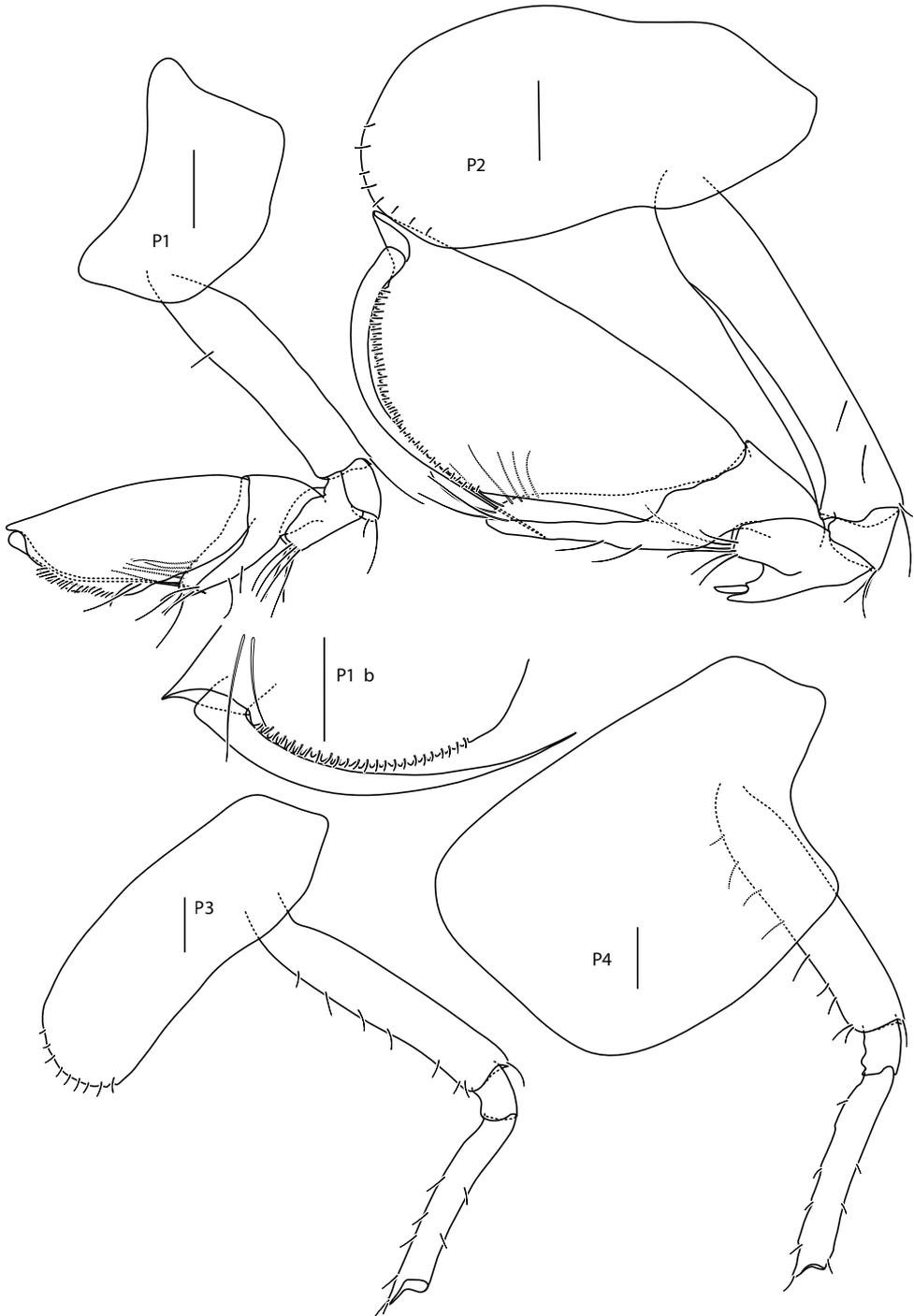


Figure 3. *Amphilochus anoculus* sp. n. Pereopods 1, 2, 3 and 4. ZMBN121952. Pereopod 1 dactylus from ZMH K-47225. Scale bars: 0.1 mm.

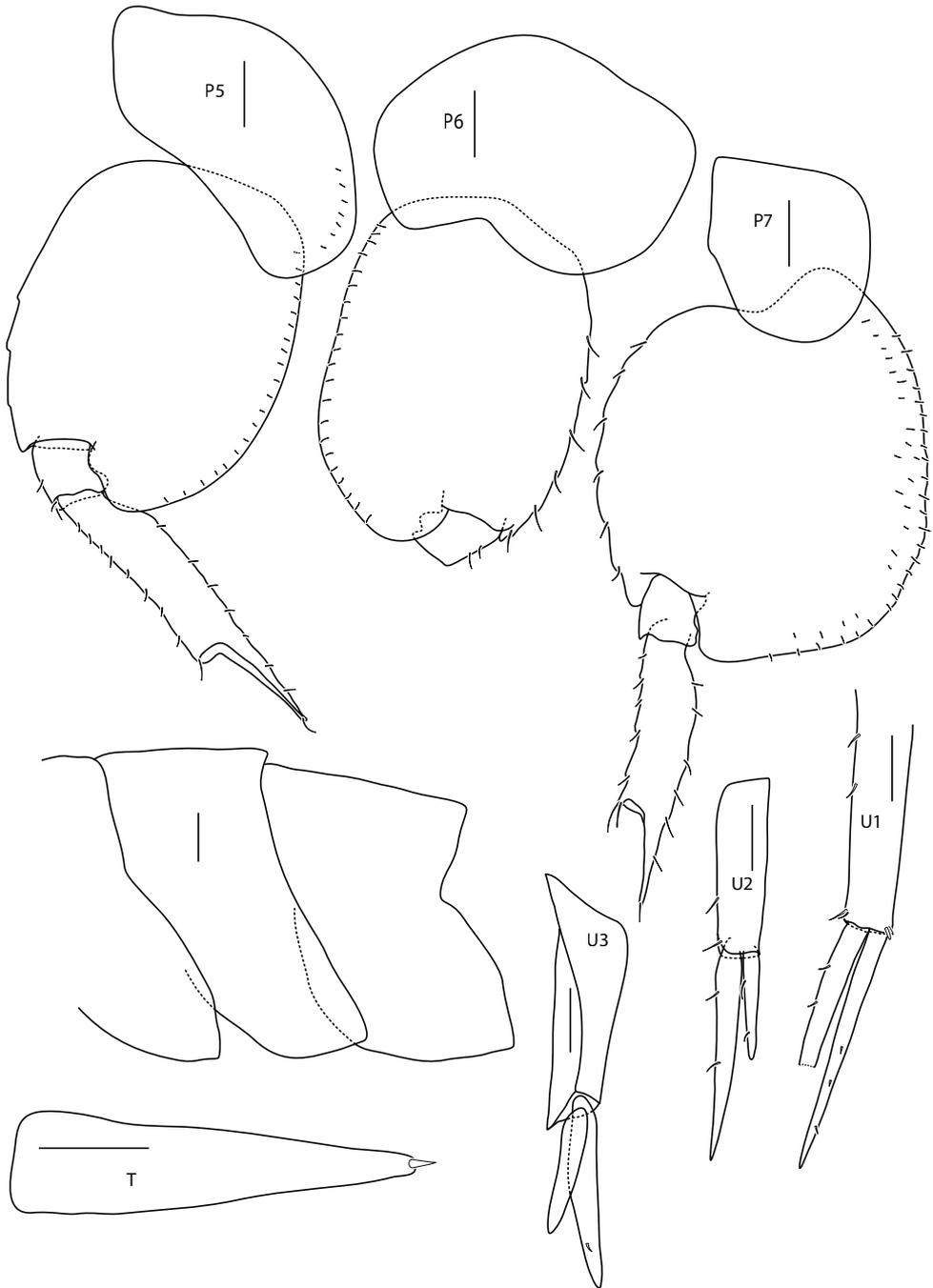


Figure 4. *Amphilochus anoculus* sp. n. Pereopods 5, 6 and 7, Epimeral plates, Uropods 1, 2 from ZMBN121952. Uropod 3 and telson from BioIce station 2367. Scale bars: 0.1 mm.

Table 2. Comparison of character states between *Amphilochus anoculus* sp. n., *A. manudens*, and *A. hamatus*.

Character	<i>Amphilochus anoculus</i> sp. n.	<i>Amphilochus manudens</i>	<i>Amphilochus hamatus</i>
Cephalic lobes	rounded	acute	rounded
Labrum	symmetrically bilobed	asymmetrically bilobed	asymmetrically bilobed
Mandible	molar rounded	molar conical	molar conical
1st Maxilla	palp 2-articulate	palp 2-articulate	palp 1-articulate
2nd Maxilla	outer plate with 4 setae	outer plate with 3 setae	outer plate with 3 setae
Labium	tooth on inner edge of outer plate	no tooth on inner edge of outer plate	tooth on inner edge of outer plate
Eyes	absent	round, strongly coloured	ill defined, bean-shaped or oval
Gnathopod 2	elongate	subtriangular	elongate
Oostegites on P6	present	absent	present
Epimeral plate 1	rounded	angular	angular
Epimeral plate 3	rounded	with clear tooth	rounded
Uropod 3	with flange on peduncle	no flange on peduncle	no flange on peduncle
Telson	tip with robust seta	tip smooth	tip tridentate – all lobes rounded.
Temperature (°C)	-0.6 to +1.7	+1.7 to +7	-0.85 to +7
Depth (m)	303m to 1055m	81m to 350m (single specimens at 772m and 1390m)	260m to 1407m

pod 3 longer than telson. Gills on segments 2 to 7; oostegites on segments 2 to 6. Telson elongate and boat-shaped; distal end entire, acute and with one seta.

Living colour. Semi-transparent, virtually colourless.

Distribution. Iceland, Faroe Channel, Norwegian Sea, Polar basin. Has only been found in cold and deep water.

Remarks. This species is easily recognized because it lacks eyes and has an anterodistal tooth on the propodi of pereopods 1 and 2. *Amphilochus manudens* and *A. hamatus* are the only other Amphilochidae having this tooth, but unlike *Amphilochus anoculus* sp. n., they both have eyes. The telson has a robust seta distally, a character not seen in any other Amphilochidae. The flange on the distal end of uropod 3 peduncle is also a good character-state to use when separating it from *A. hamatus*. A synoptic list of characters separating the three species is shown in Table 2.

Biology. This species appears to be restricted to cold water (it is only found at a temperature range of -0.6 °C to +1.7 °C. Three stations from the Mareano-project have higher temperatures than this (stations R1180 RP86, R1200 RP90 and R1225 RP112). These are also the three of the shallowest stations where this species has been found, and constitute a statistical outlier in the dataset. They are all in the eastern Barents Sea, an area where winter-temperatures are much colder, and thus still might fall within the proposed ecological niche of the species. It has been found north and east of Iceland, south of the Faroe Islands, north in the Norwegian Sea and in the

Polar basin, at depths ranging from 303 to 2100 meters. In contrast, the closely related *Amphilochus manudens* has, during BioIce, IceAGE, and several other collection efforts in the area been found mainly at depths from 81 to 360 meters, with single specimens found at 772 and 1390 meters (see Fig 1 for specimens from BioIce and IceAGE). No *Amphilochus manudens* were found in the Faroe-samples from AkvaplanNiva.

Derivatio nominis. The name *anoculus* (*an* = no, *oculus* = eye) refers to the absence of eyes. It is a noun in apposition.

Amphilochus manudens Spence Bate, 1862

Amphilochus manudens Spence Bate, 1862:107, pl 17 fig 6; Sars 1890-95: 217, pl 74; Chevreux and Fage 1925: 114, fig 109; Lincoln 1979: 150, fig 65 e-f, fig 66 a-d; Krapp-Schickel 1982: 75, fig 51.

Remarks. Although *Amphilochus manudens* is one of the best described species within the Amphilochidae (Sars 1890–95; Lincoln 1979; KrappSchickel 1982), we have included a redescription of material from Iceland, to facilitate direct comparison with the new species.

Material examined. all drawings are made from specimens found during the BioIce program. For the complete set of drawings (Figs 5–8) we have used specimens IINH37889 (BioIce 2207), IINH37887 (BioIce 2215) and IINH37885 (BioIce 2237). Type material not examined. Additional material of *Amphilochidae* from a Statoil funded baseline survey of some Faroe waters has been examined, and only *Amphilochus anoculus* and *Amphilochus tenuimanus* were found. We have also examined all Amphilochidae from the BioFar program, and only *Amphilochus manudens* was found (no *Amphilochus anoculus* sp. n.). During a cruise in the Polar basin in 2005 both *Amphilochus manudens* and *Amphilochus anoculus* sp. n. were found, but at different stations (see discussion below). Material from several Norwegian surveys (summarised in the project NorAmph) and the IceAGE project included several *Amphilochus manudens*. For information about the specific sample-stations, see Table 1.

Description. *Head.* Rostrum curved, smaller than peduncle article 1 of antenna 1. Eyes round, no ommatidial framing, small, deep brown-red in colour. Cephalic lobe produced, distally acute. Antenna 1 subequal to antenna 2; peduncle article 1 is longer than article 2, which is longer than article 3; peduncle is longer than six-articulate flagellum; accessory flagellum absent. Antenna 2 peduncle longer than eight-articulate flagellum; peduncle articles have few short setae.

Labrum asymmetrically bilobed. Mandible molar small but triturative, cone-shaped, with a row of short setae around the ridged chewing area; incisor serrate; nine accessory spines; palp slender, 3-articulate; article 1 is shorter than article 2, which is longer than article 3; article 3 with two long setae distally and distal third of margin serrate; lacinia mobilis laterally expanded. Labium symmetric; inner lobes reduced. Maxilla 1 palp 2-articulate, with eight setae; inner plate reduced, with 1 seta; outer plate with six strong

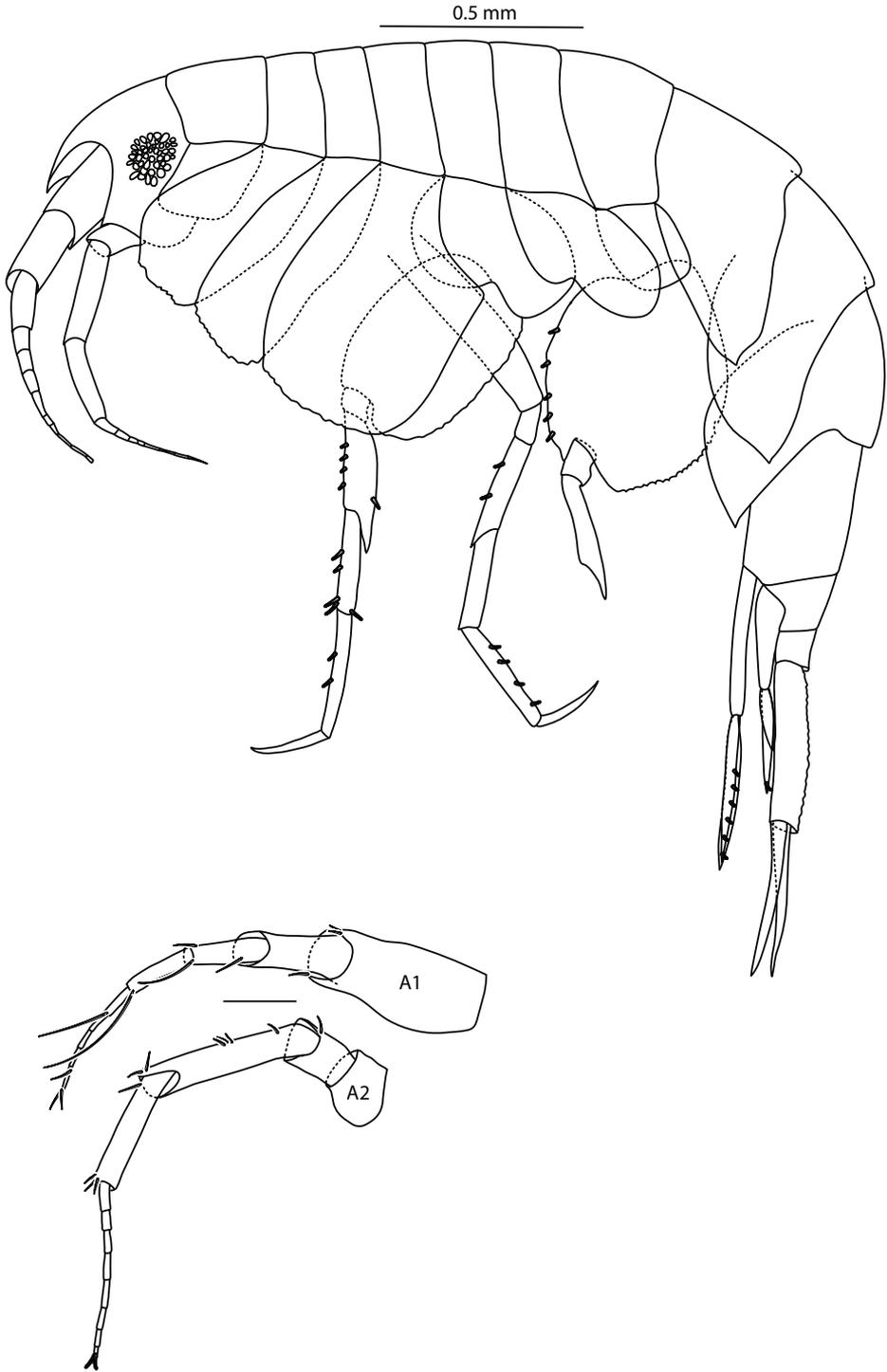


Figure 5. *Amphilochus manudens*. Habitus and antennae. IINH37889. Scale bar habitus 0.5 mm, other scale bars 0.1 mm.

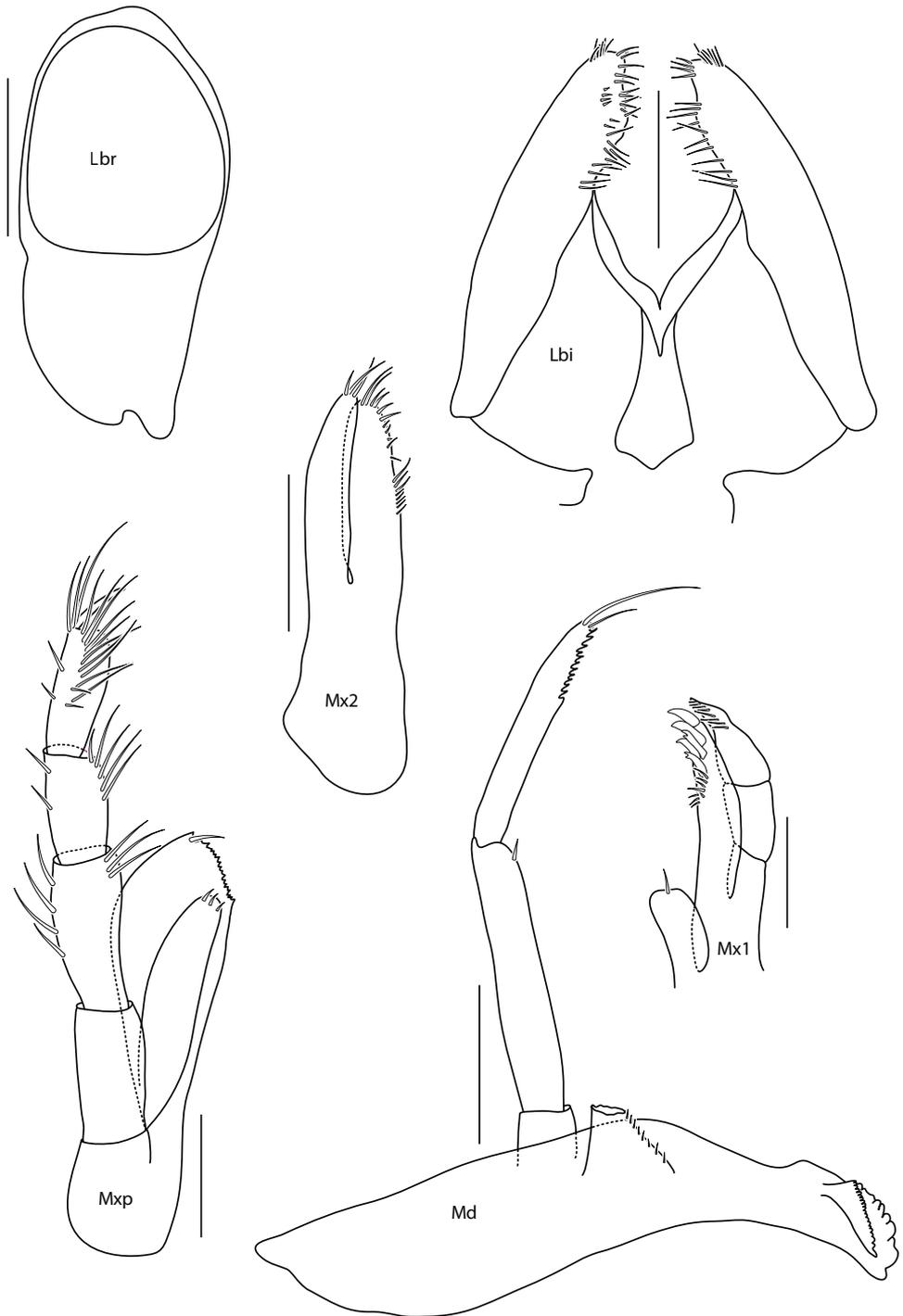


Figure 6. *Amphilochus manudens*. Mouthparts. IINH37887. Scale bars: 0.1 mm.



Figure 7. *Amphilocheus manudens*. Pereopods. IINH37885. Scale bars: 0.1 mm.



Figure 8. *Amphilocheus manudens*. Appendages from pleon and urosome. IINH37885. Scale bars: 0.1 mm.

setae and two rows with four and three smaller setae. Maxilla 2 inner plate shorter than outer plate, six long setae distally and a row of five short, three long and five short setae; outer plate is long and thin with three distal setae. Maxilliped inner plate is long and thin, well separated, three short and strong setae distally; outer plate reaches just past merus of palp; palp slim, heavily setulated on carpus and propodus.

Mesosome dorsally smooth; length segment 3 is smaller than segment 4. Coxa 1 reduced and covered by coxa 2, which is longer than broad. Coxa 2 distal margin serrate, with setae. Coxa 3 concave; distal margin serrate, without setae. Coxa 4 distal margin serrate; without setae. Coxa 5–7 concave.

Pereopod 1 basis longer than propodus, upper half distally widened, few and short setae on anterior margin, longer setae on posterior margin; carpal lobe well developed, 50% of posterior margin of propodus; propodus subtriangular, proximal half of oblique palm serrate, distal half with short evenly spaced setae, no seta defining palm, anterodistal tooth strong; dactylus longer than palm, narrow and acute, apparently smooth. Pereopod 2 basis longer than propodus, linear, several short setae; one robust seta distally on ischium; merus with small distal 'hook'; carpal lobe covers 100% of posterior margin of propodus, lined with setae posteriorly, small crown of setae distally; propodus elongate with a regularly convex serrate palm without seta, anterodistal tooth strong; dactylus longer than palm, narrow, apparently smooth. Pereopod 3 coxa elongate, pereopod 4 coxa posteriorly produced, both with basis to propodus anterior edge lined with short setae, dactylus more than half propodus. Pereopod 5 to 7 basis and merus with posterior lobes; carpus shorter than propodus; dactylus longer than half propodus.

Metasome smooth. Epimeral plate 1 with small, blunt posterodistal tooth, distal margin convex; plate 2 angular, distal margin convex; plate 3 with clear posterodistal tooth, distal margin weakly concave. Urosome smooth; segment 1 as long as segments 2 and 3 together. Uropod 1 peduncle and rami subequal; rami subequal; setae on outer ramus. Uropod 2 peduncle subequal to inner ramus; outer ramus about half-length of inner ramus; setation on both rami. Uropod 3 peduncle longer than rami; outer ramus is shorter than inner ramus; rami longer than telson; rami with setae.

Gills on segments 2 to 6. Oostegites on segments 2 to 5. Telson elongate; distal end entire and acute; no setae.

Distribution. North East Atlantic and Arctic Ocean (Lincoln, 1979); Barents Sea and Murmansk area (Gurjanova 1951; Vader and Bryazgin 1998; Vader et al. 2001); Spitsbergen (Stephensen 1935; Vader et al. 2001); Mediterranean (Marseilles, Capri) (Krapp-Schickel 1982); amphi-Atlantic (Watling 1979); Gulf of St Lawrence (Brunel et al. 1998).

***Amphilochus hamatus* (Stephensen, 1925), comb. n.**

Amphilochopsis hamatus Stephensen, 1925: 173, figs 52–53; Gurjanova 1951: 402, fig. 246; Barnard and Karaman 1991: 95.

Material examined. Drawings are made from IINH37894 (BioIce 2077), IINH37898 (BioIce 2236), IINH37900 (BioIce 2318) and IINH37903 (BioIce 2367). Material from IceAGE and NorAmph has been used for molecular sequencing and comparisons. For a list of stations for the material, see Table 1. Type material not examined. The drawings are shown on Figs 9–12.

Description. *Head.* Rostrum curved, reaches tip of article 1, antenna 1. Eyes not evident, but an ill-defined eye-patch can be seen. Cephalic lobe produced distally and rounded. Antenna 1 shorter than antenna 2; second peduncle-article with a triangular

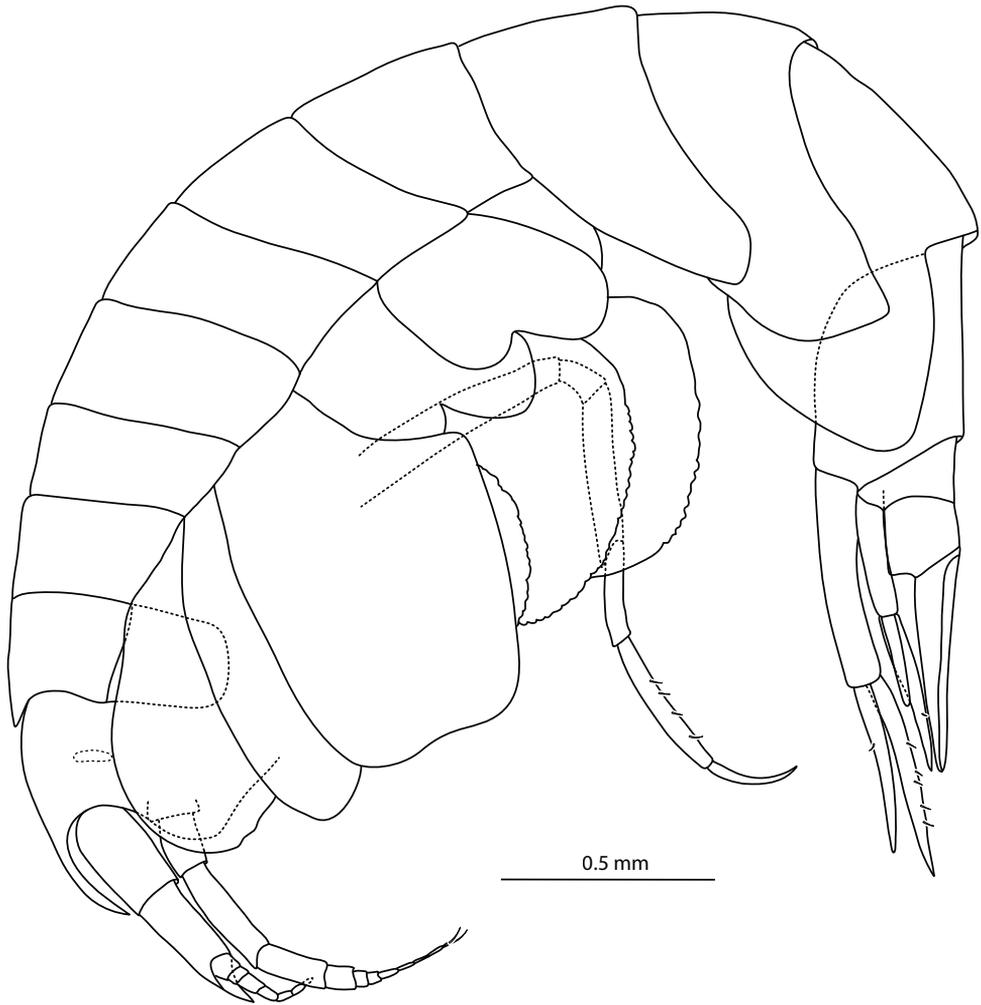


Figure 9. *Amphilochus hamatus*. Habitus. IINH37900. Scale bar: 0.5 mm.

production on the apex the size of third peduncle article; peduncle subequal to ten-articulate flagellum; no accessory flagellum. Antenna 2 peduncle longer than flagellum; short setae on peduncle, and a pair of long setae at tip of flagellum.

Labrum asymmetrically bilobed. Mandible molar small but triturative, cone-shaped; incisor serrate; ten accessory spines; palp slender, 3-articulate with series of short setae on article 3, one long seta at tip; lacinia mobilis laterally expanded. Labium symmetric, with inner lobe reduced; sharp tooth making tip of outer lobe look dentate. Maxilla 1 palp 1-articulate, with a crown of two robust setae and a serrate distal margin; inner plate reduced, 1 seta; outer plate with four and eight heavy and five smaller setae. Maxilla 2 long and thin; inner plate shorter than outer plate; three heavy setae and eight smaller setae on outer plate; inner plate with seven short setae distally and

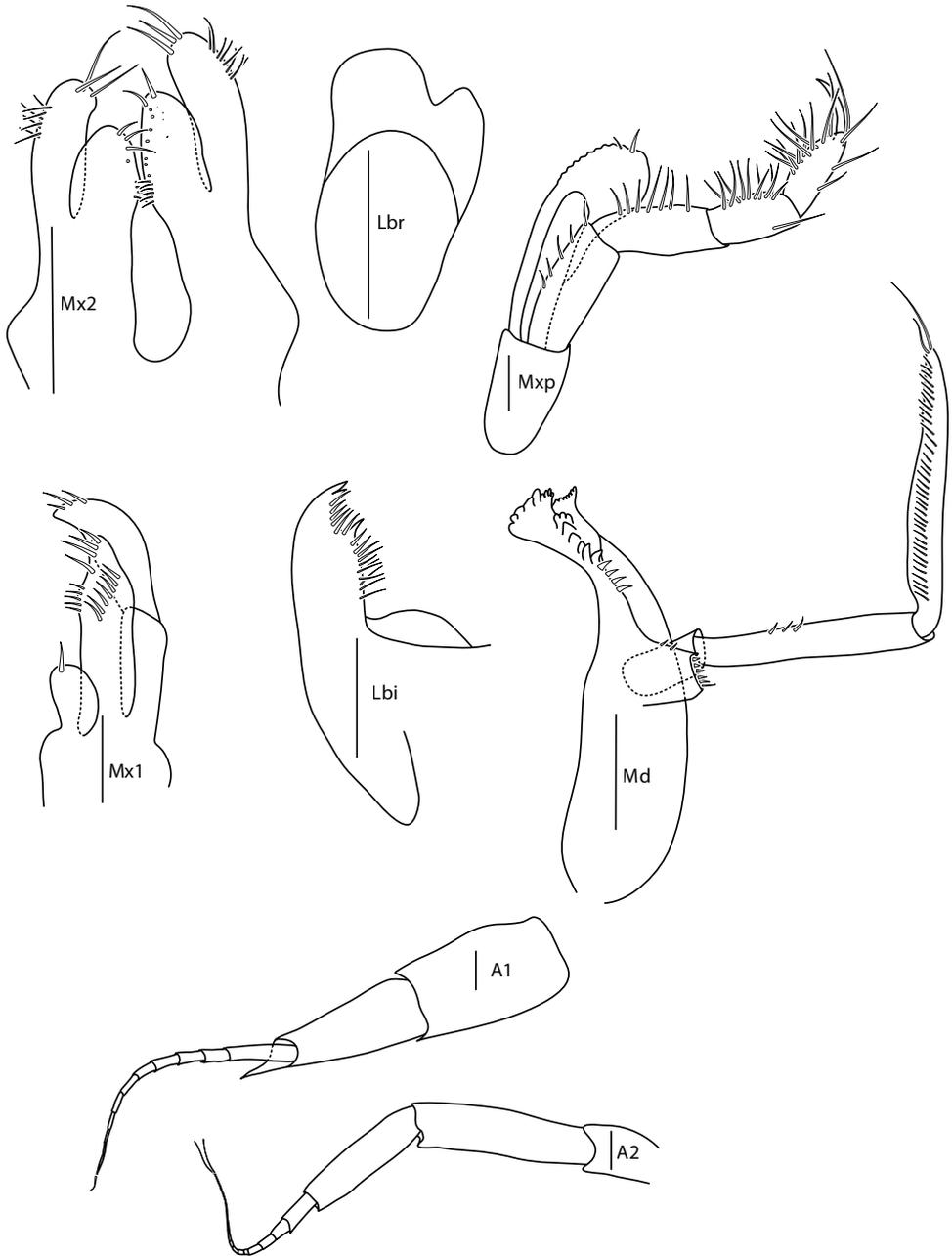


Figure 10. *Amphilochus hamatus*. Mouthparts. IINH37894. Scale bars: 0.1 mm.

one to two thin setae medially. Maxilliped inner plate small and thin, well separated, just reaching past ischium; outer plate reaching mid-merus, two strong setae distally, serrations on inner margin; palp slim, heavily setulated on carpus and propodus.



Figure 11. *Amphilocheus hamatus*. Pereopods 1 and 2, uropods. IINH37898 and IINH37903. Scale bars: 0.1 mm.

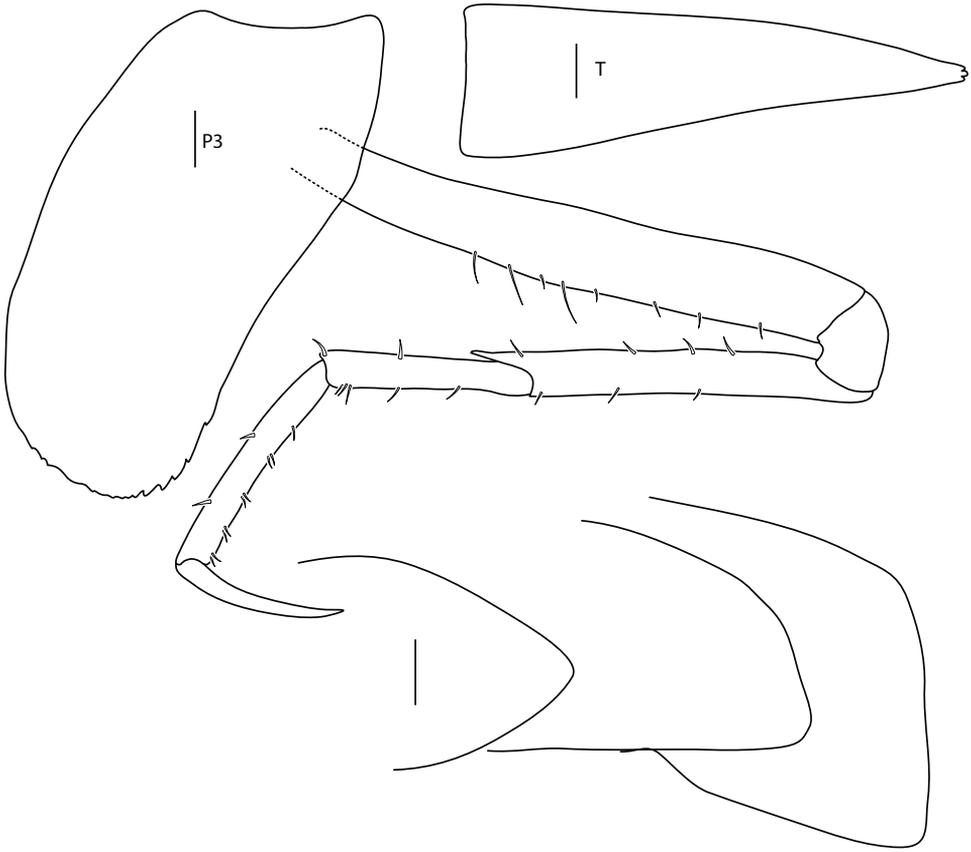


Figure 12. *Amphilochus hamatus*. Pereopod 3, epimeral plates, telson. IINH37898 and IINH37894. Scale bars: 0.1 mm.

Mesosome dorsally smooth; segment 3 shorter than segment 4. Coxa 1 reduced, subquadratic and covered by coxa 2, which is longer than broad. Coxa 2 distal margin smooth, no setae. Coxa 3 concave, smooth, with setae on distal margin. Coxa 4 distal margin smooth with setae. Coxa 5–7 concave.

Pereopod 1 basis subequal to propodus length, upper half distally widened, three long setae posteriorly; carpal lobe 65% of propodus posterior margin; propodus subtriangular, palm oblique, serrate, no setae defining palmer corner, anterodistal tooth of medium size; dactylus with inner margin partly serrate. Pereopod 2 basis weakly longer than propodus, linear; merus with a clearly defined “hook” on posterior side, close to carpus; carpal lobe 100% of propodus posterior margin, boat-shaped with a row of setae on margin; propodus subovate, palm oblique, defined mostly by its serration and upper third with small setae, no setae defining palmar corner, anterodistal tooth large (same size as breadth of the base of dactylus); dactylus inner margin with a row of small and strong setae, otherwise smooth. Pereopod 3 posterior margin of basis with

an even row of slender setae; merus with small lobe. Pereopod 4 basis with very thin setae. Pereopods 5 and 6 basis and merus with posterior lobes; dactylus longer than half-length propodus. Pereopod 7, basis and merus with posterior lobes.

Metasome smooth. Epimeral plates rounded, no teeth. Urosome smooth; segment 1 long; segments 2 and 3 short. Uropod 1 peduncle subequal to rami; rami subequal; both peduncle and outer ramus with marginal setae. Uropod 2 peduncle subequal to inner ramus; outer ramus half-length of inner ramus; setation on peduncle and rami. Uropod 3 peduncle marginally longer than rami; outer ramus half-length of inner ramus; rami shorter than telson; setation on peduncle and rami. Gills on segments 2 to 6. Oostegites on segments 2 to 6. Telson elongate, longer than broad; distal end entire and tridentate, all lobes rounded; no setae.

Distribution. This species appears to have a wide depth range based on our collections (206 to 1407 m), although Stephensen (1925) found it only in deep water (700 to 2702 m). The temperatures it has been found at range from -0.6 to +7.0 °C. It is also recorded from the deep Norwegian Sea (Dahl 1979), the Arctic basin (Gurjanova 1951), Greenland (Brandt et al. 1996) and the deep polar basin (Tzvetkova and Golikov 2001).

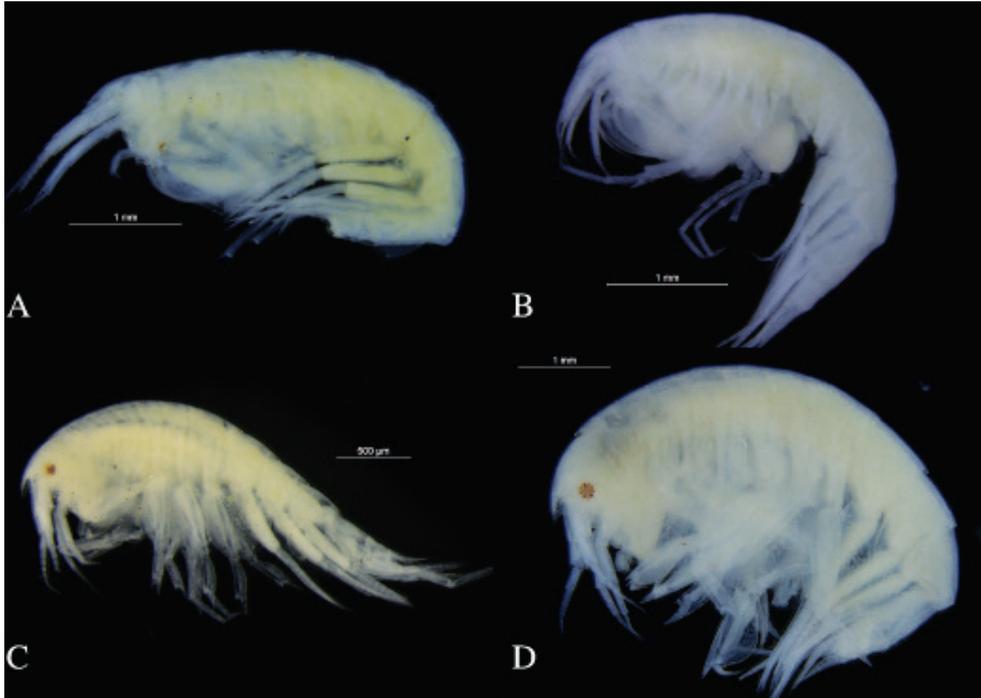
Discussion

Genetic delimitation of the species

Examinations of the COI-gene (Folmer segment) of *Amphilochus manudens*, *Amphilochus anoculus* sp. n. and *Amphilochopsis hamatus* from both IceAGE (Icelandic waters) and NorBol (Norwegian waters) show a clear separation of the new species *Amphilochus anoculus* from other Amphilochidae tested. (Jazdzewska et al. 2018; NorAmph in Barcode of Life Project (BOLD) www.boldsystems.org). Using Barcode Identification Numbers (BIN) to make a quick check on species delimitation gives four different BINs for *Amphilochus manudens* from the two projects, as well as separate BINs for *Amphilochus anoculus* and *Amphilochopsis hamatus*. It has, however, been very difficult to get good sequences for *A. anoculus*; after thorough scrutiny we only found one non-ambiguous sequence. Many of our discarded sequences were removed from the analyses from being too short, but the parts we have are identical to the full COI-sequence we tested, and that thoroughly separates it from all clades of *A. manudens* and *A. hamatus*. Calculating the distance between groups using Mega7 (Kumar et al. 2015) shows this (Table 3), even though it must be noted that since *A. manudens* separated into several clades, the within-distance for this group was also very large (0.283). Clearly, a more thorough genetic analysis and possibly a larger sample-pool (especially a larger genetic sample pool) will reveal if we have further new species to be separated from *Amphilochus manudens*, but for this study it will suffice to note that *Amphilochus manudens* may constitute a species complex. Specimens of *Amphilochus manudens* assigned to two of the different BINs as well as *Amphilochus anoculus* sp. n. and *Amphilochopsis hamatus* are photographed (Fig 13).

Table 3. P-distances between groups (species) of Amphilochidae from NorAmph and IceAGE projects.

<i>Amphilochoides boeckii</i>	0,426					
<i>Amphilochus anoculus</i>	0,343	0,359				
<i>Amphilochus hamatus</i>	0,331	0,302	0,196			
<i>Amphilochus manudens</i>	0,388	0,400	0,335	0,279		
<i>Amphilochus sp1</i>	0,336	0,317	0,223	0,095	0,238	
<i>Amphilochus tenuimanus</i>	0,357	0,327	0,312	0,285	0,378	0,294

**Figure 13.** Photographs of habitus **A** *Amphilochus anoculus* sp. n. ZMBN_104532 **B** *Amphilochus hamatus* ZMBN_104479 **C** *Amphilochus manudens* ZMBN_103989 **D** *Amphilochus manudens* UMBerger_NBamph_123.

The status of the genus *Amphilochopsis* Stephensen, 1925

The genus *Amphilochopsis* was erected by Stephensen (1925) for the species *A. hamatus*. Stephensen wrote: ‘The present genus is very closely allied to *Amphilochus*, but is characterised especially in having the molar of the maxillae (*sic!*) well developed (but not very large) and in having only one joint in the palp of maxilla 1’. The type species of the relatively large (Barnard and Karaman 1991) and probably not monophyletic (Hoover and Bousfield 2001) genus *Amphilochus* Spence Bate, 1862 is *Amphilochus manudens* Spence Bate, 1862; this species is usually described as having a non-triturative molar on the mandible, but in reality the molar, although much reduced in size and conical in

form, has a small flat triturating surface on top (see Fig. 6). *Amphilochus manudens* has a 2-articulate palp on maxilla 1. Later authors have often allied the genus *Amphilochopsis* with the basic amphilochid genus, the also extremely variable *Gitanopsis* G.O. Sars. This is probably mainly because in keys to the genera the first dichotomy usually concerns the molar, and *Amphilochopsis* is deemed to have a well-developed molar, while *Amphilochus* is judged to have a feebly developed, non-triturative molar. Thus Barnard and Karaman (1991) write in their monograph for *Amphilochopsis* sub ‘Relationship’: ‘Differing from *Gitanopsis* in the 1-articulate palp of maxilla 1’, and also Hoover and Bousfield (2001), in their phenograms, ally *Amphilochopsis* closely to *Gitanopsis*.

In reality the molar of *Amphilochus manudens* is only quantitatively different from that of *Amphilochopsis hamatus*, with the new species *A. anoculus* in an intermediate position between the two. These molars are completely different from the well-developed cylindrical molars of *Gitanopsis* and *Gitana* species, as well as from the almost completely reduced molars of many other species in *Amphilochus* s.l. A number of other species in *Amphilochus* s. l., e.g. the west Atlantic *A. casahoya* and *A. delacaya*, both described by McKinney (1978), and the Hawaiian species described by Barnard in 1970, have the same type of ‘intermediate’ molar as *A. manudens*.

Amphilochopsis hamatus has a clearly 1-articulate palp on mx 1, while all *Amphilochus* species that we have seen have a 2-articulate palp. This type of character-state has been used extensively elsewhere in the division of genera in the Amphilochidae (cf. the discussion in Barnard (1962)). We feel, however, that this difference alone is not sufficient to warrant a separate genus for *A. hamatus*, especially as the articulation of the palp in some *Amphilochus* species, i.e., *A. anoculus*, is not always easy to perceive and may even be incomplete.

As shown by Hoover and Bousfield (2001) who in their ‘partial revision’ split up *Amphilochus* s. l. and erected the genus *Apolochus* for some of its species, *Amphilochus* s. l. is definitely not a monophyletic genus, and is in great need of a complete revision. A preliminary phylogenetic analysis of amphilochid species, based on literature data (Tandberg 2000) came to the same conclusion: species of *Amphilochus* and *Gitanopsis* were scattered over the entire cladogram. The cladogram did, however, show a clear clade around *Amphilochus manudens*, the type species of *Amphilochus*, and thus *Amphilochus* s. str.: this clade included, besides *A. manudens*, the new species *A. anoculus*, *A. opunake* Barnard, 1972 from New Zealand, the Mediterranean *A. planierensis* Ledoyer, 1977, and *Amphilochopsis hamatus*.

An easily observed and spectacular character of *A. hamatus* is the characteristic hook on the merus of P2, from which its name is derived. However, this same hook occurs, albeit in greatly reduced form, in both *A. manudens* and *A. planierensis*. The new species described above, *A. anoculus*, also has a meral hook on P2; this is another character where the character state present in *A. anoculus* falls between the more extreme versions of the states in *A. manudens* and *A. hamatus*. We therefore do not think the meral hook on P2 to be of more than specific value.

For these reasons, we have decided to transfer *Amphilochopsis hamatus* to *Amphilochus* s. str. and to submerge the genus *Amphilochopsis* as a junior synonym of *Amphilochus* s. str.

Ecology of the species

In Icelandic waters, *Amphilocheus manudens* and *Amphilocheus hamatus* seem to be confined to shallower and warmer waters. The only parameter that seems to be limiting is temperature – they are only found in “warm” waters: + 1,7°C to +7°C. *Amphilocheus manudens* is common, and from the literature known to be found mostly on gravel and silty sand, and on hydroids (Jones 1948; Schellenberg 1942).

Given the distribution-data on *Amphilocheus manudens* from BioIce, BioFar, IceAGE and other studies in the Faroe channel and our surveys in the Norwegian Sea and Polar basin, it seems that *Amphilocheus anoculus* sp. n. replaces *Amphilocheus manudens* in cold waters. Temperatures for the stations in the Faroe channel and a few in the Norwegian Sea were not reported, but Westerberg (1990) has shown that the general benthic temperatures in this area are always lower than 0.5 °C and temperatures in the deep waters of the Norwegian Sea are lower than 1 °C, which supports our hypothesis that *A. anoculus* replaces *A. manudens* at temperatures below 1.7 °C.

Key to *Amphilocheidae* in the North-East Atlantic

A pictorial key, loosely based on Stephensen (1935) with the new species added, is shown in Fig 14.

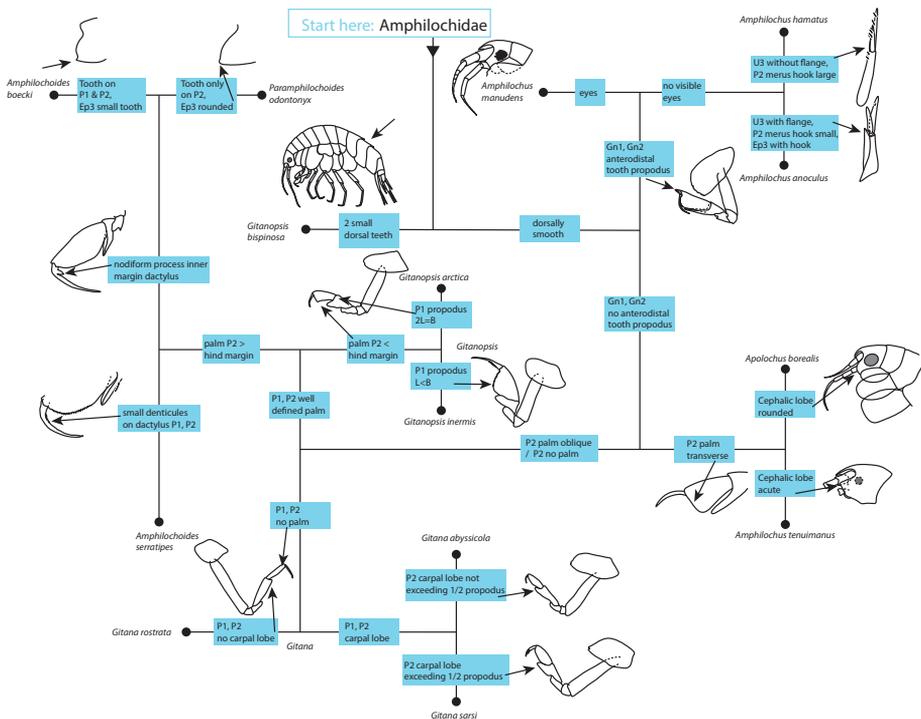


Figure 14. Pictorial key to Amphilocheidae in the NE Atlantic.

Acknowledgements

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References

- Barnard JL (1962) Benthic marine Amphipoda of southern California: families Amphilochidae, Leucothoidae, Stenothoidae, Argissidae, Hyalidae. *Pacific Naturalist* 3: 116–163.
- Barnard JL (1970) Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands. *Smithsonian Contributions to Zoology* 34: 1–296. <https://doi.org/10.5479/si.00810282.34>
- Barnard JL, Karaman GS (1991) The families and genera of marine gammaridean Amphipoda (except marine gammaroids). Part 1. Records of the Australian Museum Supplement 13(1): 1–417. <https://doi.org/10.3853/j.0812-7387.13.1991.91>
- Berge J, Vader W (1997) Stegocephalid (Crustacea, Amphipoda) species collected in the BIOFAR and BIOICE programmes. *Sarsia* 82: 347–370. <https://doi.org/10.1080/00364827.1997.10413662>
- Boeck A (1871) Crustacea Amphipoda Borealia et Arctica. *Videnskabs Selskapets forhandling*, Kristiania 1870: 1–222.
- Boeck A (1873) *De skandinaviske og arktiske amfipoder*. Christiania, 864 pp.
- Brandt A, Vassilenko S, Piepenburg D, Thurston M (1996) The species composition of the Peracarid fauna (Crustacea, Malacostraca) of the Northeast Water Polynya (Greenland). *Meddelelser om Grønland Bioscience* 44: 1–30.
- Brix S, Meißner K, Stransky B, Halanych KM, Jennings RM, Kocot K, Svavarsson J (2014) The IceAGE project – a follow up of BIOICE. *Polish Polar Research* 35(2): 141–150.
- Brix S, Lörz A-N, Jazdzewska AM, Hughes L, Tandberg AHS, Pabis K, Stransky B, Krapp-Schickel T, Sorbe JC, Hendrycks E, Vader W, Frutos I, Horton T, Jazdzewski K, Peart R, Beermann J, Coleman CO, Buhl-Mortensen L, Corbari L, Havermans C, Tato R, Campean AJ (2018) Amphipod family distributions around Iceland. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project)*. *ZooKeys* 731: 41–53. <https://doi.org/10.3897/zookeys.731.19854>

- Brunel P, Bossé L, Lamarche G (1998) Catalogue of the Marine Invertebrates of the Estuary and Gulf of Saint Lawrence. Canadian Special Publication of Fisheries Aquatic Sciences 126: 1–405.
- Buhl-Mortensen L, Hodnesdal H, Thorsnes T (Eds) (2015) The Norwegian Sea Floor – New Knowledge from MAREANO for Ecosystem-Based Management. MAREANO, 192 pp.
- Chevreaux ME, Fage L (1925) Amphipodes. Faune de France 9: 1–487.
- Coleman CO (2003) “Digital inking” How to make perfect line drawings on computers. *Organisms Diversity & Evolution* 3(4): 1–14. <https://doi.org/10.1078/1439-6092-00081>
- Coleman CO (2009) Drawing setae the digital way. *Zoosystematics and Evolution* 85(2): 305–310. <https://doi.org/10.1002/zoos.200900008>
- Dahl E (1979) Amphipoda Gammaridea from the deep Norwegian Sea. A preliminary report. *Sarsia* 64: 57–59. <https://doi.org/10.1080/00364827.1979.10411363>
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3(5): 294–299.
- Gurjanova EF (1951) [Amphipods of the USSR seas and adjacent waters (Amphipoda - Gammaridea).] *Izdatelstvo Akademii Nauk SSSR* 41: 1–1031. [In Russian]
- Hoover PM, Bousfield EL (2001) The amphipod superfamily Leucothoidea on the Pacific coast of North America: Family Amphilochidae: Systematics and distributional ecology. *Amphipacifica* 3(1): 3–28.
- Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO, Daneliya M, Dauvin JC, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Holsinger J, Hughes L, Jaume D, Jazdzewski K, Just J, Kamalynov RM, Kim YH, King R, Krapp-Schickel T, LeCroy S, Lörz AN, Senna AR, Serejo C, Sket B, Tandberg AH, Thomas J, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (2017) World Amphipoda Database. <http://www.marinespecies.org/amphipoda> [on 2017–07–20]
- Jazdzewska AM, Corbari L, Driskell A, Frutos I, Havermans C, Hendrycks E, Hughes L, Lörz A-N, Stransky B, Tandberg AHS, Vader W, Brix S (2018) A genetic fingerprint of Amphipoda from Icelandic waters – the baseline for further biodiversity and biogeography studies. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project)*. *ZooKeys* 731: 55–73. <https://doi.org/10.3897/zookeys.731.19931>
- Jones NS (1948) The ecology of the Amphipoda of the South of the Isle of Man. *The Journal of the Marine Biological Association of the United Kingdom* 27: 400–439. <https://doi.org/10.1017/S0025315400025455>
- Krapp-Schickel G (1982) Family Amphilochidae. In: Ruffo S (Ed) *The Amphipoda of the Mediterranean*. *Family Amphilochidae*. *Mémoires de l’Institut Océanographique* 13: 70–93.
- Kumar S, Stecher G, Tamura K (2015) MEGA7: Molecular Evolutionary GENetic Analysis version 7.0. *Molecular Biology and Evolution*. <http://www.megasoftware.net>
- Ledoyer M (1977) Contribution à l’étude de l’écologie de la faune vagile profonde de la Méditerranée nord occidentale. I. Les Gammariens (Crustacea, Amphipoda). *Bolletino del Museo Civico di Storia Naturale di Verona* 4: 321–421.
- Lörz A-N, Tandberg AHS, Willassen E, Driskell A (2018) Rhachotropis (Eusiroidea, Amphipoda) from the North East Atlantic. In: Brix S, Lörz A-N, Stransky B, Svavarsson J (Eds) *Icelandic marine Animals: Genetics and Ecology (IceAGE Amphipoda project)*. *ZooKeys* 731: 75–101. <https://doi.org/10.3897/zookeys.731.19814>

- Lincoln RJ (1979) *British Marine Amphipoda: Gammaridea*. British Museum (Natural History), London, 658 pp.
- McKinney LD (1978) Amphilochidae (Crustacea: Amphipoda) from the western Gulf of Mexico and Caribbean Sea. *Gulf Research Reports* 6: 137–143. <https://doi.org/10.18785/grr.0602.04>
- Mannvik HP, Pettersen A, Carrol JL (2002) Environmental baseline survey of the Faroe offshore licence areas 001–004 in the Faroe-Shetland Channel, 2001. Akvaplan-niva reports, APN-411.2201.03.
- Nørrevang A, Brattegard T, Josefson AB, Sneli JA, Tendal OS (1994) List of BioFar stations. *Sarsia* 79: 165–180. <https://doi.org/10.1080/00364827.1994.10413557>
- Sars GO (1890–95) *Amphipoda. An Account of the Crustacea of Norway With Short Descriptions and Figures of All the Species*, 1, Al. Cammermeyer, Christiania, 717 pp.
- Schellenberg A (1942) *Krebstiere oder Crustacea. IV. Flohkrebse oder Amphipoda*. *Die Tierwelt Deutschlands* 40: 1–252.
- Spence Bate C (1862) *Catalogue of the specimens of amphipodous Crustacea in the collection of the British Museum*. British Museum of Natural History, London.
- Stebbing TRR (1876) On some new and little-known amphipodous Crustacea. *Annals and Magazine of Natural History*, series 4, 18: 443–449. <https://doi.org/10.1080/0022293-7608682076>
- Stebbing TRR (1906) *Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen. Amphipoda. 1. Gammaridea*, 1–854.
- Stephensen K (1925) *Crustacea Malacostraca. VI. (Amphipoda. II.)*. *The Danish Ingolf-Expedition* 3: 101–178.
- Stephensen K (1935) *The Amphipoda of N. Norway and Spitsbergen with adjacent waters*. *Tromsø Museums Skrifter* 3: 1–140.
- Tandberg AHS (2000) *Studies on Amphilochidae (Amphipoda, Gammaridea), With a Phylogenetic Analysis of the Family, and a Description of a New Species*. MSc Thesis, Univ of Tromsø: 1–82.
- Tzvetkova NL, Golikov AA (2001) List of species of free-living invertebrates of Eurasian Arctic Seas and adjacent deep water. *Amphipoda, (Explorations of the seas)* 51: 79–94.
- Vader W, Brattegard T, Buhl-Mortensen L, Miskov Larsen K (2001) Chapter “Amphipoda, suborder Gammaridea”. In: Brattegard T, Holthe T (2001) *Distribution of marine benthic macroorganisms in Norway. A tabulated catalogue*. Update of Direktoratet for Naturforvaltning Utredning 1997–1: 183–207.
- Vader W, Bryazgin VF (1998) *Karelian-Norwegian Cooperation on the Crustacea Amphipoda of the Barents Sea Area, With a Preliminary Checklist of Amphipoda Gammaridea*. Proceedings of the Scientific Conference held in Karelian Research Centre RAS within the framework of the Days of Norway in Republic of Karelia, Petrozavodsk, 28–31 May, 1997. Russian Academy of Science Karelian Research Centre, 40–45.
- Watling L (1979) Zoogeographic affinities of northeastern North American gammaridean Amphipoda. *Bulletin of the Biological Society of Washington* 3: 256–282.
- Westerberg H (1990) *Benthic Temperature in the Faroe Area*. Report from the Department of Oceanography, University of Gothenburg 51: 1–19.

Leucothoe vaderotti, a new Atlantic *Leucothoe* (Crustacea, Amphipoda) belonging to the “*spinicarpa*-clade” (Crustacea, Amphipoda)

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Abstract

Within the international IceAGE project (Icelandic marine Animals: Genetics and Ecology) some leucothoid amphipods (Crustacea) were collected, among them a rather small new species, belonging to the “*Leucothoe spinicarpa*-clade.”

Keywords

Amphipoda, Atlantic Ocean, IceAGE, Leucothoidae, new species, taxonomy

Introduction

Within the IceAGE-collections (a follow-up of BIOICE, see for example Berge and Vader, 1997) some rather small specimens of the genus *Leucothoe* were collected, similar to the ones described in Krapp-Schickel and Vader (2012) from the Norwegian Sea, called “*Leucothoe* aff. *spinicarpa*”. This genus is extremely easy to recognize as such, but its many species are differentiated from each other only by subtle characters, which has traditionally led to a wholesale lumping of many species under just a few names, especially *Leucothoe spinicarpa* (Abildgaard, 1789). In the last years, it has become clear that the genus, with many of its species living commensally, is a very speciose one and there is no doubt a considerable number of as-yet undescribed species to be discovered (cf. Thomas and Klebba 2007).

Material and methods

Samples were taken during IceAGE1 and IceAGE2 (with research vessels ‘Meteor’ and ‘Poseidon’; see Brix et al. 2014); they were fixed in cold 96% un-denaturated ethanol, sorted on ice, and stored at 0–4 °C after sorting. They were identified, some mounted on slides with Faure’s fluid, and drawn using a Leitz Laborlux microscope. “Inking” was done with a Wacom tablet, following Coleman, 2003.

Acronyms used in the morphological descriptions are as follows:

A 1, 2	antenna 1, 2	Ped	peduncle
Md	mandible	flag	flagellum
acc.	accessory	Pl	pleopod
Mx 1, 2	maxilla 1, 2	Gn 1, 2	gnathopod 1, 2
ad.	adult	T	telson
Mxp	maxilliped	Hd	head
art	article	U 1–3	uropod 1–3
OP	outer plate	IP	inner plate
Cx	coxal plate	UL	upper lip
P 3–7	peraeopod 3–7	LL	lower lip
Ep	epimeral plate		

Results

Leucothoidae Dana, 1852

Genus *Leucothoe* Leach, 1814

Leucothoe vaderotti sp. n.

<http://zoobank.org/BB292914-F4F1-451F-829A-4010FBCF5C31>

Figs 1, 2

Leucothoe aff. *spinicarpa* Krapp-Schickel & Vader, 2012, 386–388, fig. 3, 4

Material. *Holotype* DZMB–HH 56285 (ZMH K–46787): 1 ad. 5.5 mm, 61°59.83'–61°59.26' N, 000°30.40'–000°32.32'E, Poseidon IceAGE 2, POS 456, 24.7.2013, Norwegian Channel, North Sea, St. 867, 302.5–290 m depth, EBS Supra, 300 µm. In alcohol.

Additional material. All in alcohol; one slide DZMB–HH52415.

DZMB–HH 52177 (ZMH K–46788): juv. 2 mm; 61°53.79'N–61°53.53'N, 010°13.77'W–010°12.65'W, Poseidon IceAGE 2, POS 456, 29.7.2013, FI Ridge, St. 878–1, 781.4–775.8 m depth, EBS Supra, 300 µm.

DZMB–HH 52021 (ZMH K–46789): 1 es. 4 mm; 60°24.33'N–60°23.70'N, 006°36.91'–006°38.60'W, Poseidon IceAGE 2, POS 456, 29.7.2013, Farøer Channel South-East, St. 876–5, 554.3–674.8 m depth, shell fragments, EBS, 500 µm.

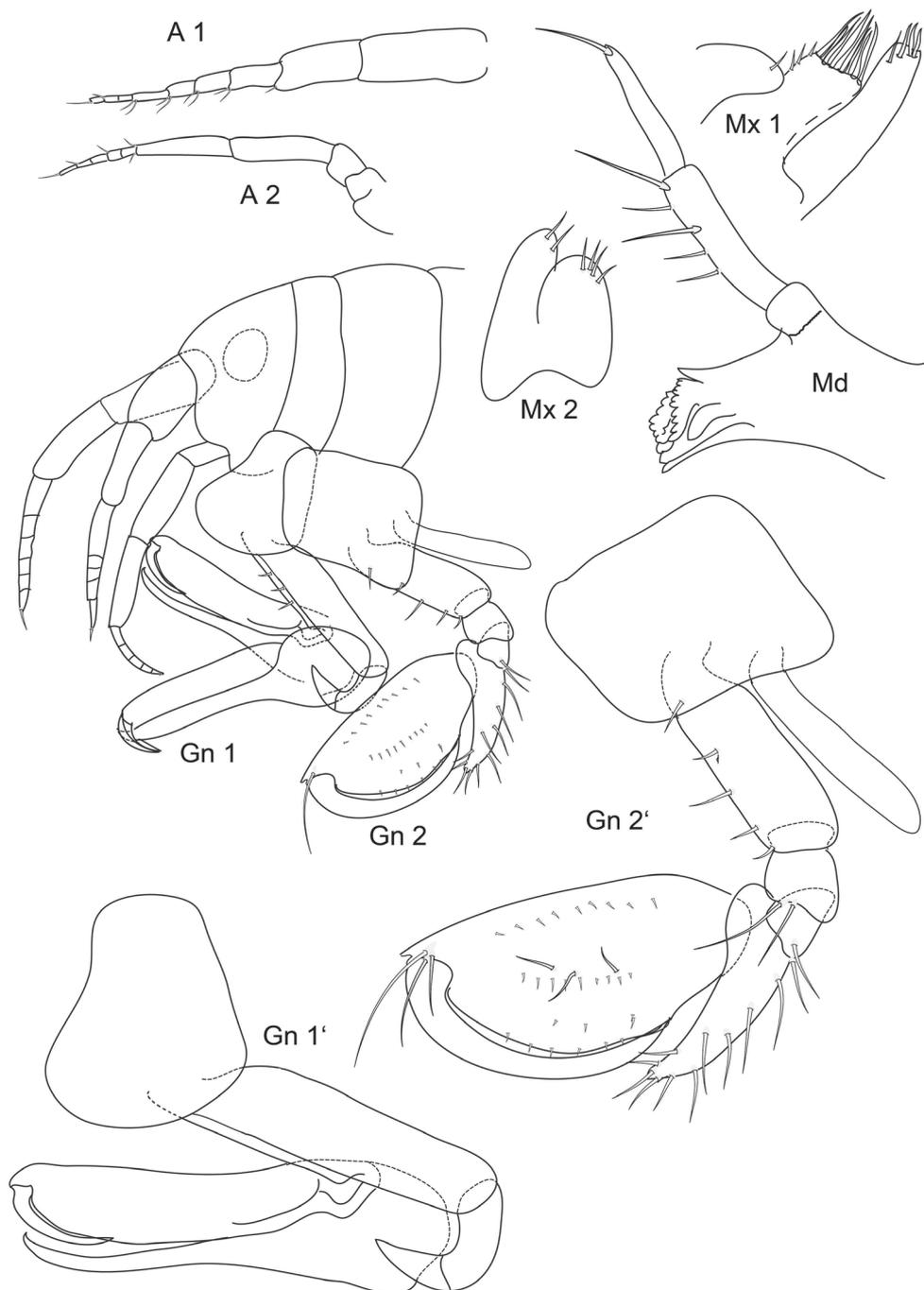


Figure 1. *Leucothoe vaderotti* sp. n. **A 1, A 2** antennae **Mx 1, Mx 2** maxillae **Gn 1, Gn 2** gnathopods **Gn 1', Gn 2'** gnathopods enlarged.

DZMB–HH 52593 (ZMHK–46790): 8 es. 3–4 mm; 61°53.79'N–61°53.53'N, 010°13.77'W–010°12.65'W, Poseidon IceAGE 2, POS 456, 29.7.2013, FI Ridge, St. 878–1, 781.4–775.8 m depth.

DZMB–HH 52617 (ZMH K–46791): 1 juv. 2.5 mm; 63°42.53'N–63°42.78'N, 026°23.05'–026°22.53'W, Meteor IceAGE, ME 85–3, 9.9. 2011, South Iceland, Irminger Basin, slope, St. 1086–1, 698.1– 678.5 m depth, 730 trawling distance, EBS Supra, 300 µm.

DZMB–HH 52667 (ZMH K–46792): 1 juv. incompl., 2 mm: 61°38.50'N–61°39.24'N, 031°21.37'–031°20.95'W, Meteor IceAGE, ME 85–3, 7.9.2011, South Iceland, Irminger Basin, Deep Sea, St. 1057–1, 2504.7–2531.8 m depth, 1983 trawling distance, EBS Supra, 300 µm.

DZMB–HH 52694 (ZMH K–46793): 3 juv. 2–3 mm; 60°24.33'N–60°23.70'N, 006°36.91'–006°38.60'W, Poseidon IceAGE 2, POS 456, 29.7.2013, Farøer Channel South-East, St. 876–5, 554.3–674.8 m depth, shell fragments, EBS, 500 µm.

DZMB–HH 52415 (ZMH K–46794): 2 es. 2–3 mm; 63°42.10'N–63°42.37'N, 026°23.64'–026°23.46'W, Meteor IceAGE, ME 85–3, 9.9.2011, South Iceland, Irminger Basin, slope, St. 1082–1, 724.4–704.9 m depth, 782 trawling distance, EBS Supra, 300 µm. Slide in Faure's medium, used for illustration.

Diagnosis. Eyes oval, dark in ethanol. Mandibular palp long and narrow, art 3 more than half the length of art 2. Cx 1 inferior margin smooth, nearly as long as wide. Gn 1 carpus distal part approximately six times longer than wide, dactylus reaching approximately 1/3 of propodus length. P 3, P 4 with narrow basis, P 5 – P 7 basis oval and broadened, with regularly rounded and finely serrated hind margin. Ep 2 posterodistally with upturned tip, Ep 3 distoposterior corner with blunt, rounded angle.

Description. Length 4–6 mm.

Head. Anterior margin rounded, anterodistal margin rectangular with rounded corner. Mid-cephalic keel with acute projection. Rostrum small.

Eyes oval. Antennae short, nearly 1/3 of body length, A 1 peduncle art 1 inferodistally with acute tooth, flagellum up to 11 arts, accessory flagellum not seen. A 2 subequal in length to A 1, peduncle art 4 > art 5, flagellum around 6 arts.

Mouthparts. Mandible lacking molars, palp 3-articulate, with long lateral and single distal setae. Art 3 with distal seta, incisors strongly dentate. Other mouthparts like in *L. spinicarpa*.

Peraeon. Cx 1–Cx 4 relative width 1: 1.2:0.8:1.

Coxa 1 smooth, length and width subequal; anterodistal margin produced, distal margin regularly rounded, facial setae absent.

Gn 1 basis not inflated, carpus distal part narrow, length to width ratio approximately 6:1; propodus straight, palm with fine short spines; dactylus curved, reaching nearly 1/3 of propodus length.

Cx 2 nearly as long as wide, subquadrangular, much wider than Cx 3, smooth; facial setae absent.

Gn 2 basis slightly inflated, on anterior margin some setae of different length; carpus reaching approx. half propodus, distally truncate, setose; propodus distally with

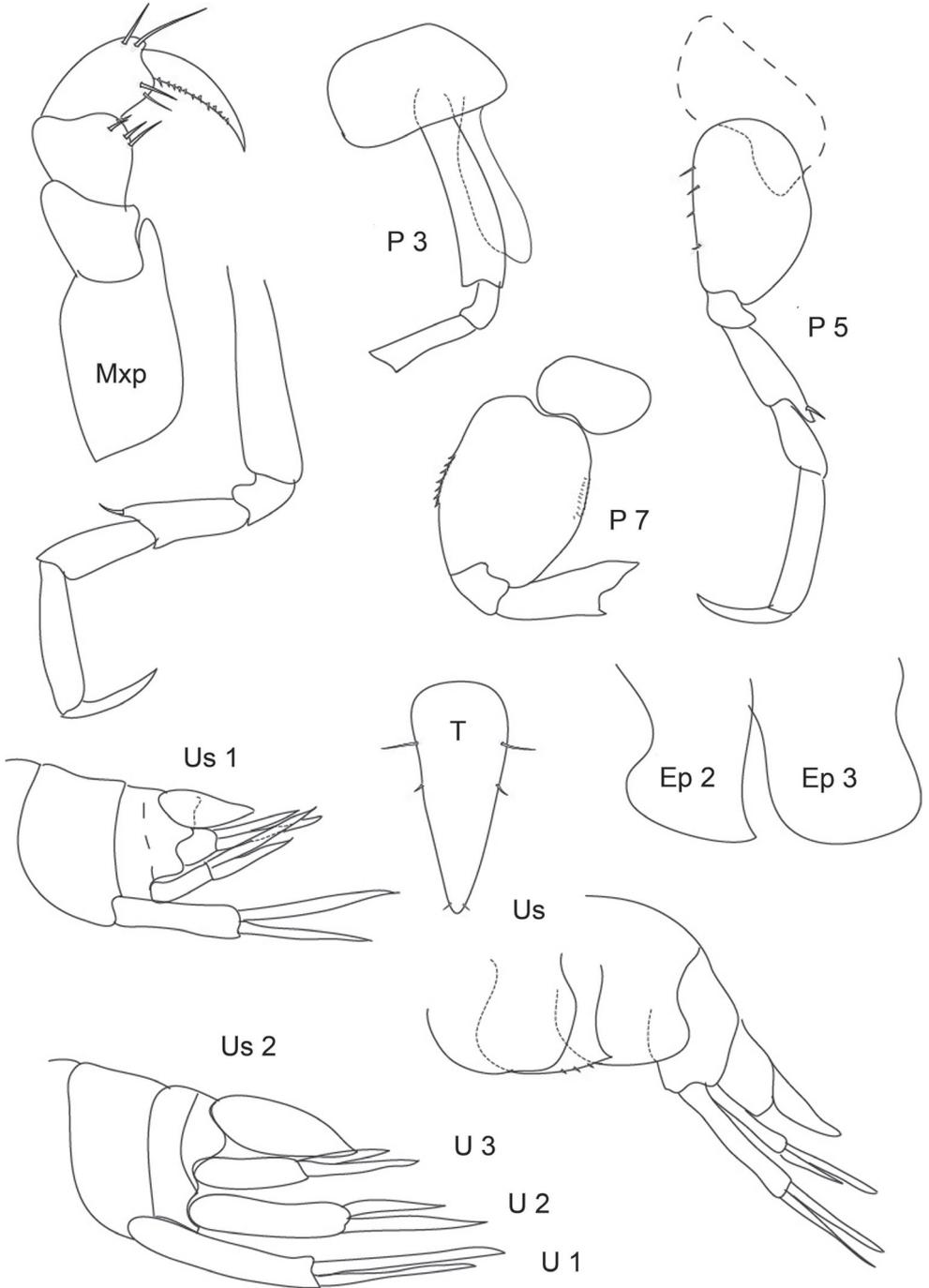


Figure 2. *Leucothoe vaderotti* sp. n. **Mxp** maxilliped **P 3, 4, 5, 7** pereopods **Ep 2, 3** epimeral plates **Us** urosome with epimeral plates, uropods and telson **Us 1, 2** other urosomites **U1, 2, 3** uropods **T** telson.

short, sharp prolongation, palm convex, regularly rounded, with weak mediofacial setal row, with a few submarginal setae; dactylus curved, smooth, reaching more than 2/3 of propodus length.

Cx 3 length greater than its width, smooth, subrectangular with straight margins and rounded corners.

Cx 4 wider than Cx 3, posterior margin shorter than anterior one, somewhat excavate.

P 3, 4 basis narrow, approx. the width of merus; dactylus reaching or surpassing half the length of propodus.

P 5 – 7 similar, basis oval, both margins with fine serration.

Pleon. Ep 1 posteroventral corner rounded. Ep 2 posterodistal corner acutely produced, Ep 3 posteroventral corner bluntly rounded.

U 1 – U 3 similar, length regularly diminishing and U 2 not considerably shorter (like in *L. spinicarpa*).

Etymology. Wim Vader completed eight decades in February 2017. He was born Dutch but having lived for much more than half of his life in Norway, he will easily guess that I used the Norwegian word *åtti* = eighty for dedicating this Atlantic species to him. Fifty years ago we began our long-lasting and harmonious collaboration, a “golden jubilee”- thank you, Wim!

Geographical distribution. South Iceland- Farøer Channel and Ridge; depth 554–2531 m.

Remarks. Together with five specimens collected 1983 between Greenland and Iceland (see Krapp-Schickel and Vader 2012) the present material of the proposed new species consists of 23 animals belonging undoubtedly to the genus *Leucothoe*. All specimens are between 2 and 5 mm, rarely up to 6 mm long. There are four specimens larger than 10 mm with all characters fitting *Leucothoe spinicarpa*, sampled in similar depths as those of the animals 2–5 mm in size. The larger specimens show some differences which are not very conspicuous. It is most probable that they belong to two different species, and it seems also quite reasonable to presume that within the period of early June to end of September these 23 specimens are not all juveniles; however, no ovigerous females were found.

Differences of the small animals compared with *Leucothoe spinicarpa* are:

- Ep 3 totally blunt (see here fig. 2 and Krapp-Schickel and Vader 2012: 390 fig. 4 Ep3) vs. not rounded, but with small but clear posterodistal corner in *L. spinicarpa* (Crowe 2006: 61 fig. 1a, 63 fig. 3e; Sars 1885 pl. 101)

- U 2 in adults reaching length of U1 (see fig. 2) vs. clearly much shorter than U1 and U3 in *L. spinicarpa* (Crowe 2006 fig. 1 and fig. 4)

- Gn 1, 2 basis anterior margin with few irregular longer or shorter setae (see here fig. 1, Krapp-Schickel and Vader 2012: 389 fig. 3) vs. dense setation in *L. spinicarpa* (Crowe 2006 fig. 61 fig. 1 b–e; Sars 1895 pl. 100)

- Gn 1 dactylus less than half the length of propodus (see above fig. 1; Krapp-Schickel and Vader 2012: 389 fig. 3) vs. more than half the length of propodus in *L. spinicarpa* (Crowe 2006 fig. 61 fig 1c; Sars 1885 pl. 100)

• sizes of 23 specimens collected between 1 June–30 September are all between 2–4 mm, with only a few reaching 6 mm; vs. size range between 10–19 mm of *L. spinicarpa* (Crowe 2006, Sars 1895, Krapp-Schickel and Menioui 2005).

These differences are significant enough to distinguish these small specimens as a new species.

Other material examined. Two other *Leucothoe* species were sampled, *L. spinicarpa* and *L. lilljeborgi*, the latter clearly in lower depths than the new species.

DZMB–HH 56264 (ZMH K–46795): 1 spec. 2.5 mm *Leucothoe lilljeborgi* 61°25.63'–61°25.05'N, 001°21.07'–001°21.66'E, Poseidon IceAGE 2, POS 456, 24.07.2013, Norwegian Channel, North Sea, St. 866, 169.1–168.8 m depth, EBS Epi, 500 µm.

DZMB–HH 56326 (ZMH K–46796): 2 spec. 2–2.5 mm *L. lilljeborgi* 61°25.63'–61°25.05'N, 001°21.07'–001°21.66'E, Poseidon IceAGE 2, POS 456, 24.7.2013, Norwegian Channel, North Sea, St. 866, 169.1–168.8 m depth, EBS Epi, 300 µm decant.

DZMB–HH 56428 (ZMH K–46797): 1 spec. 2.5 mm *L. lilljeborgi*: 61°25.63'–61°25.05'N, 001°21.07'–001°21.66'E, Poseidon IceAGE 2, POS 456, 24.7.2013, Norwegian Channel, North Sea, St. 866, 169.1–168.8 m depth, EBS Epi, 300 µm.

DZMB–HH 56500 (ZMH K–46798): 1 *L. spinicarpa* 13 mm, 2 males *L. lilljeborgi* 5.5 and 4 mm 61°59.83'–61°59.26'N, 000°30.40'–000°32.32'E, Poseidon IceAGE 2, POS 456, 24.7.2013, Norwegian Channel, North Sea, St. 867, 302.5–290 m depth, EBS Epi, 500 µm.

DZMB–HH 52362 (ZMH K–46799): 1 *L. spinicarpa* 11 mm; 63°42.53'N–63°42.78'N, 026°23.05'–026°22.53'W, Meteor IceAGE, ME 85-3, 9.9.2011, South Iceland, Irminger Basin, slope, St. 1086-1, 698,1–678.5 m depth, 730 trawling distance, EBS Supra, 300 µm.

DZMB–HH 52627 (ZMH K–46800): 1 *L. spinicarpa* 8 mm 62°33.10'N–62°33.22'N, 020°23.71'–020°22.87'W, Meteor IceAGE, ME 85-3, 2.9.2011, South Iceland, Iceland Basin, slope, St. 1010–1, 1384.8–1389 m depth, 1183 trawling distance, EBS Supra, 300 µm.

DZMB–HH 32864 (ZMH K–46801): 1 juv. *Leucothoe* sp. imperf. 2 mm, together with *Leucothoe spinicarpa* 12 mm; 61°53.79'N–61°53.53'N, 010°13.77'W–010°12.65'W, Poseidon IceAGE 2, POS 456, 29.7.2013, FI Ridge, St. 878-1, 781.4–775.8 m depth, EBS Supra, 300 µm.

Discussion

After Krapp-Schickel and Vader (2012) many *Leucothoe* species are known from the Atlantic Ocean, but mainly from warmer regions. Not much is known about their biology, but it is known that they prefer to live near, in, or with other species such as sponges, and this may also be the reason that they are often well hidden and thus overlooked when generalised ship sampling occurs.

table 1. srekj

Locality	Species	Author
West Africa	<i>Leucothoe minima</i>	Schellenberg, 1925
	<i>L. occidentalis</i>	Reid, 1951
	<i>L. brunonis</i>	Krapp-Schickel & Menioui, 2005
	<i>L. campi</i>	Mateus & Mateus, 1986
	<i>L. spinulosa</i>	Chevreux, 1920
South Africa	<i>L. miersi</i>	Stebbing, 1888
	<i>L. ctenocheir</i>	K.H. Barnard, 1925
	<i>L. dolichoceras</i>	K.H. Barnard, 1916
Caribbean, Gulf of Mexico	<i>L. wuriti</i>	Thomas & Klebba, 2007
	<i>L. flammosa</i>	Thomas & Klebba, 2007
	<i>L. hortapugai</i>	Winfried et al. 2009
	<i>L. barana</i>	Thomas & Klebba, 2007
	<i>L. ortizi</i>	Winfried et al. 2009
	<i>L. hendrickxi</i>	Winfried et al. 2009
	<i>L. saron</i>	Thomas & Klebba, 2007
	<i>L. ubouhu</i>	Thomas & Klebba, 2006
	<i>L. garigunae</i>	Thomas & Klebba, 2007
Brazil	<i>L. cheiriserra</i>	Serejo, 1998
	<i>L. libue</i>	Barnard, 1970
	<i>L. basilobata</i>	Serejo, 1998
	<i>L. urospinosa</i>	Serejo, 1998
	<i>L. leptosa</i>	Serejo, 1998
Biscaya and Azores	<i>L. cathalaa</i>	Fruos & Sorbe, 2012
	<i>L. rostrata</i>	Chevreux, 1908
Barbados, Mid Atlantic ridge	<i>L. ayrtonia</i>	Bellan-Santini, 1997
	<i>L. atosi</i>	Bellan-Santini, 1997
Great Britain, Scotland, northern Atlantic	<i>L. incisa</i>	Robertson, 1892
	<i>L. procera</i>	Bate, 1857
	<i>L. lilljeborgi</i>	Boeck, 1861
	<i>L. richiardii</i>	Lessona, 1865
	<i>L. spinicarpa</i>	Abildgaard, 1789
	<i>L. articulosa</i>	(Montagu, 1804)
	<i>L. uschakovi</i>	Gurjanova, 1951

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References

Abildgaard PC (1789) Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum. Descriptiones et Historia. Havniae, N. Möller et filius, 71 pp. [pls 81–120]

- Barnard KH (1916) Contributions to the crustacean fauna of South Africa. 5. The Amphipoda. *Annals of the South African Museum* 15(3): 105–302. [pls 26–28] <https://doi.org/10.5962/bhl.title.10646>
- Barnard KH 1925 Contributions to the crustacean fauna of South Africa No. 8 – Further additions to the list of Amphipoda. *Annals of the South African Museum* 20: 319–380.
- Bate CS (1857) A synopsis of the British edriophthalmous Crustacea. Part I. Amphipoda. *Annals and magazine of natural history* (2)19, 110: 135–152. [2 figs]
- Bate CS (1862) Catalogue of the specimens of Amphipodous Crustacea in the collections of the British Museum. Taylor & Francis, London, 399 pp. [2–58 pls]
- Bellan Santini D (1997) Amphipods of the cold seep community on the South Barbados accretionary prism. *Crustaceana* 70(1): 1–30. <https://doi.org/10.1163/156854097X00311>
- Berge J, Vader W (1997) Stegocephalid (Crustacea, Amphipoda) species collected in the BIO-FAR and BIOICE programmes. *Sarsia* 82(4): 347–370. <http://dx.doi.org/10.1080/00364827.1997.10413662>
- Boeck A (1861) Bemaerkninger angaaende de ved de norske kyster forekommende Amphipoder. *Forhandlinger ved de Skandinaviske naturforskeres ottende møde i København* 8: 631–677.
- Brix S, Meissner K, Stransky B et al. (2014) The IceAge project – a follow up of BIOICE. *Polish Polar Research* 35(2): 141–150. <https://doi.org/10.2478/popore-2014-0010>
- Chevreaux E (1908) Diagnoses d'amphipodes nouveaux provenant des campagnes de la Princesse-Alice dans l'Atlantique nord. *Bulletin de l'Institut Océanographique de Monaco* 122: 1–8. [4 figs]
- Chevreaux E (1920) Sur quelques Amphipodes nouveaux ou peu connus provenant des côtes de Bretagne. *Bulletin de la Société zoologique de France* 45: 75–87.
- Crowe SE (2006) A redescription of *Leucothoe spinicarpa* (Abildgaard, 1789) based on material from the North Atlantic (Amphipoda, Leucothoidae). *Zootaxa* 1170: 57–68.
- Frutos I, Sorbe C (2012) *Leucothoe cathalaa* sp. nov. (Crustacea: Amphipoda: Leucothoidae), a new bathyal benthic species from the Le Danois Bank ('El Cachucho' Spanish MPA), southern Bay of Biscay. *Journal of the Marine Biological Association of the United Kingdom* 93(3): 659–666. doi:10.1017/S0025315412000574
- Gurjanova E (1951) Amphipoda Gammaridea from the seas of the USSR and vicinity. *Opre-deliteli Faune SSSR Zool Inst Akad Nauk SSSR* 41: 1–1029. [In Russian]
- Krapp-Schickel T, Menioui M (2005) *Leucothoe* species from Moroccan Atlantic coasts with redefinition of some species within the *Leucothoe spinicarpa* clade. *Bollettino Museo Civico Storia Naturale Verona Botanica-Zoologia* 29: 63–83.
- Krapp-Schickel T, Vader W (2012) Leucothoid and Maerid Amphipods (Crustacea) from deep regions of the North Atlantic. *Helgoland Marine Research* 67(2): 383–396. <https://doi.org/10.1007/s10152-012-0330-3>
- Lessona M (1865) Sopra due nuove specie di animali invertebrati raccolte nel Golfo di Genova. *Atti della Società Italiana di Scienze Naturali* 8: 423–428.
- Mateus A, Mateus E (1986) Campagne de la 'Calypso' dans le Golfe de Guinée et aux Îles Principe, Sao Tomé et Annobon (1956). Amphipodes récoltés à bord de la 'Calypso'. *Anais Faculdade Ciências Porto* 66: 125–223.

- Montagu G (1804) Description of several marine animals found on the south coast of Devonshire. Transaction Linnean Society London 7: 61–85. <https://doi.org/10.1111/j.1096-3642.1804.tb00282.x>
- Reid DM (1951) Report on the Amphipoda (Gammaridea and Caprellidea) of the coast of tropical West Africa. Atlante Report 2: 189–291.
- Robertson D (1892) A second contribution towards a catalogue of the Amphipoda and Isopoda of the Firth of Clyde and west of Scotland. Proceedings and Transactions of the Natural History Society of Glasgow 3: 199–223.
- Sars GO (1885) Zoology. Crustacea I. Norke Nordhavs Expedition 1876-1878, zoologi 4, 280 pp. [21 pls]
- Sars GO (1890-95) Amphipoda. An account of the Crustacea of Norway with short descriptions and figures of all the species. I. Alb. Cammermeyer, Christiania & Copenhagen, 711 pp [vol. 7], 11 pp [vol. 9]. [+ 240–V111 pl]
- Schellenberg A (1925) Crustacea : Amphipoda. Beiträge zur Kenntnis der Meeresfauna Westafrikas, W. Michaelsen 3, 4: 113–204. [27 fig.]
- Serejo CS (1998) The genus *Leucothoe* (Crustacea, Amphipoda, Leucothoidae) on the Brazilian coast. Beaufortia 48(6): 105–135.
- Stebbing TRR (1888) Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–1876. Eyre and Spottiswoodie, London, Zoology 29: 1–1737.
- Thomas JD, Klebba KN (2006) Studies of commensal Leucothoid Amphipods: Two new sponge-inhabiting species from South Florida and the Western Caribbean. Journal of Crustacean Biology 26(1): 13–22. <https://doi.org/10.1651/C-2624.1>
- Thomas JD, Klebba KN (2007) New species and host associations of commensal leucothoid amphipods from coral reefs in Florida and Belize. Zootaxa 1494: 1–44. <https://doi.org/10.11646/zootaxa.1400.1.1>
- Thomas JD, Ortiz M (1995) *Leucothoe laurensi*, a new species of leucothoid Amphipod from Cuban waters (Crustacea: Amphipoda: Leucothoidae). Proceedings of the biological Society of Washington 108: 613–616.
- Winfield I, Alvarez F (2009) Two new species of amphipods (Peracarida, Amphipoda, Leucothoidae) from the Veracruz Coral Reef system, SW Gulf of Mexico. Crustaceana 82(1): 11–25. <https://doi.org/10.1163/156854008X36721412>

Ampeliscidae (Crustacea, Amphipoda) from the IceAGE expeditions

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Abstract

Ampeliscidae has been recorded extensively from Icelandic waters by many detailed reports. Material collected from the IceAGE (Icelandic marine animals: Genetics and Ecology) 1 and 2 expeditions has resulted in a reasonably expected collection of ampeliscid amphipod species and distributions. However, as seems to be the trend in amphipod systematics, there are ever-present species complexes. Resulting from this, two species new to the genus *Haploops* are presented. Additionally, a new species and new record and key of the genus *Byblisoides* is also presented.

Keywords

Ampelisca, *Byblisoides*, distributions, *Haploops*, Iceland, key, new species

Introduction

The family Ampeliscidae Krøyer, 1942 is a species diverse group of soft sediment, benthic dwelling amphipods. To date there are 306 described species from only four genera (Horton et al. 2017). Species from this family are known from intertidal to abyssal depths and can range in size from 3 – over 25 mm. Due to living in the first few centimetres of sediment/benthos ampeliscids are important environmental health indicators (accumulation of heavy metals) and vital components of fishery and larger mammal food webs. Some taxa can also form biogenic environments, due to their tube building behavior, providing a habitat for other organisms. Ampeliscid amphipods appear to

have a strong depth and sediment delimitation of species (Dauvin et al. 2012), which can help in assessment of geophysical environments.

Ampelisoids have a global distribution, with majority of species recorded from the northern hemisphere. This is mainly due to the extensive combined works from Drs Dauvin, Bellan-Santini and Kaïm-Malka over many years. Whilst these researchers have focused on northern Atlantic waters (along with authors such as Sars 1895, Mills 1967, 1971), there has also been work on various parts of the Pacific Ocean. These include extensive studies on the eastern and Northern Pacific (Barnard 1954, 1961, and 1967, Dickinson 1982, 1983), and the western and tropical Pacific (Gurjanova 1951, 1955, Ren 2006, Dang and Le 2013). There have been very few studies extending into the southern hemisphere.

The scope of this paper is to document the ampelisoid fauna from Icelandic waters collected from the IceAGE 1 and 2 expeditions. This fauna has been widely and elegantly documented (Sars 1895, Bellan-Santini and Dauvin 1988, 1997, 2008, Dauvin and Bellan-Santini 1988, 1990, Dauvin et al. 2012, Kaïm-Malka 2000, 2010, Kaïm-Malka et al. 2016), so there was little expectation of new fauna. Even though previous sampling was extensive and most of the known species were recorded in the current samples, three new species including a new record of the genus *Byblisoides* K.H. Barnard, 1931, not previously known from this region, are documented. Species of Ampeliscidae, like most amphipods, seem to form cryptic species complexes. These new species are often superficially similar morphologically, but as previous researchers on the group have noted the differences are complex but clear, warranting specific status (Kaïm-Malka et al. 2016).

Materials and methods

The specimens documented in this project are part of the IceAGE project (Icelandic marine Animals: Genetics and Ecology project). The project's main aim is to combine a variety of areas of biodiversity research and ecological modelling and was managed by the German Centre for Marine Biodiversity Research (**DZMB**). The specimens were collected from two expeditions following a variety of transects in Icelandic waters (see introductory paper, this issue): IceAGE 1 (ME 85-3) on the RV Meteor, sample dates of presented material 28/08/2011 – 22/09/2011; and IceAGE 2 (POS 456) on the RV Poseidon, collection dates of presented material 24/07/2013 – 31/07/2013. All the material processed was collected using Epibenthic Sledge (EBS) and was taken either from the supranet or epinet portion. The material was preserved in 96% ethanol. The amphipods were sorted to family level at two workshops, the first in July, 2016 in Wilhelmshaven, Germany and the second in April, 2017 in Spala, Poland.

Later for species taxonomic examination the material was dissected and examined in glycercol. The pencil drawings of the whole animals were made on dissecting microscope Leica MZ12.5 (with attached camera lucida) and the dissected parts drawn on compound microscope Zeiss Axioskop 2 plus (with camera lucida). Measurements were made dorsally from the tip of the rostrum to the tip of the telson.

Type and other material is deposited in the collections of the Zoological Institut and Museum at the University of Hamburg (**ZMH**) with secondary type material

and some material examined deposited in the NIWA Invertebrate Collection (NIWA), Wellington, New Zealand.

Abbreviations used include: A – antenna, UL – upper lip, LL – Lower lip, MD – mandible, MX – maxilla, MXP – maxilliped, G – gnathopod, P – pereopod, epim – epimeron, U – uropod, and T – telson.

Results

Of the 20 species previously documented from Icelandic waters (Dauvin et al. 2012), this study recorded 13 species (majority in the genus *Ampelisca*) and six species new to Icelandic waters (including three species new to science) (Table 1). Overall, 432 identifiable specimens were examined (there were also a number of damaged specimens that were unidentifiable to species but definitely in the family Ampeliscidae). Of these specimens, 228 belonged to the genus *Ampelisca* (in 9 species), 122 specimens belong to *Haploops* (in 5 species), 81 specimens belong to *Byblis* (in 4 species), and 1 specimen (and species) to *Byblisoides* (Table 1). The distribution of species (Figure 1) shows that as expected *Ampelisca* species occur at the most number of stations and with the greatest depth range. The study had relatively low abundances compared to the BIOICE (Benthic Invertebrates of Icelandic waters) study (Dauvin et al. 2012), with mostly only a few ampeliscids recorded at each station. This is potentially due to differences in sampling gear, depth ranges and number of stations sampled.

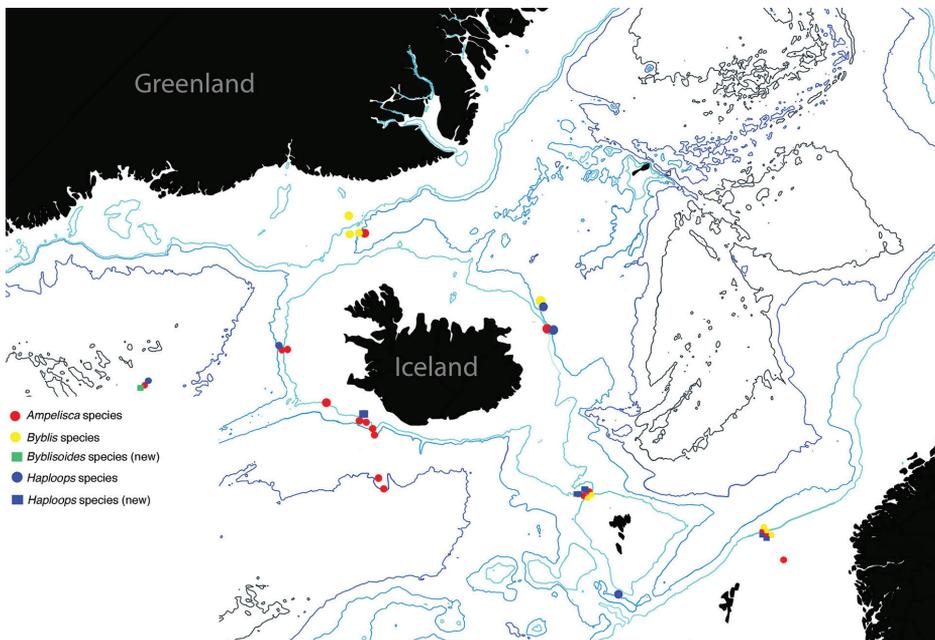


Figure 1. Map to the distribution of species from Icelandic waters in the genera of Ampeliscidae, highlighting the new species documented.

Table 1. Ampeliscidae amphipods from IceAGE 1 and IceAGE 2 epibenthic sledge collections. (E) represents samples from the epinet bucket of the epibenthic sledge; (EÜ) represents samples from the epinet above the bucket; (S) represents samples from the supranet bucket; and (SÜ) represent samples from the supranet above the bucket.

Species	Station	Locality	Depth (m)	No.	Previous records
<i>Ampelisca aequicornis</i> Bruzelius, 1859	IceAGE 1 1033-1 (E)	Reykjanes Ridge, South Iceland (shelf)	288.5–293.6	1	Skagerrak (Type), Iceland, Faroe Islands, Bay of Biscay, Norwegian Sea, Arctic North Atlantic, and Northwestern Atlantic (30–983 m)
	IceAGE 2 866-7 (E)	Norwegian Channel	168.8–169.1	4	
	867-1 (E)		290–302.5	49	
Totals			168.8–302.5	54	
<i>Ampelisca anomala</i> Sars, 1882 *	IceAGE 2 867-1 (E)	Norwegian Channel	290–302.5	6	Faroes, Bay of Biscay, Norwe- gian Sea (Type).
Totals			290–302.5	6	
<i>Ampelisca compacta</i> Norman, 1882	IceAGE 1 1010-1 (E)	Iceland Basin, South Iceland (slope)	1384.8–1389	15	Iceland, Faroe Islands (268– 2082 m)
Totals			1384.8–1389	15	
<i>Ampelisca gibba</i> Sars, 1882 *	IceAGE 2 879-5 (E)	Faroe Island Ridge - middle Norwegian Channel	500.6–510.9	12	Faroes, Bay of Biscay, Norwe- gian Seas (type)
	866-7 (E)		168.8–169.1	16	
Totals			168.8–510.9	28	
<i>Ampelisca islandica</i> Bellan-Santini & Dauvin, 1997	IceAGE 1 979-1 (S)	Iceland Basin, South Iceland (deep Sea)	2567.6–2572.2	3	Icelandic waters (type) (884– 2082 m)
	983-1 (E)	Iceland Basin, South Iceland (slope)	2568.5–2749.4	8	
	1006-1 (S)	Irmingier Basin, South Iceland (slope)	1386.8–1390.1	45	
	1010-1 (E)		1384.8–1389	14	
1082-1 (S)		704.9–724.4	12		
Totals			704.9–2749.4	82	
<i>Ampelisca macrocephala</i> Liljeborg, 1852	IceAGE 2 868-3 (S)	Norwegian Channel	587.4–614.4	1	Iceland, Faroe Islands, Norwe- gian Seas, Arctic north Atlantic, northwest Atlantic (10–797 m)
	879-5 (E)	Faroe Island Ridge - middle	500.6–510.9	8	
Totals			500.6–614.4	9	
<i>Ampelisca odontoplax</i> Sars, 1895	IceAGE 1 1017-1 (E)	Iceland Basin, South Iceland (shelf)	891.7–910.3	28	Iceland, Faroe Islands, Norwe- gian Seas (type), Arctic north Atlantic (139–1993 m)
	1033-1 (E)	Reykjanes Ridges, South Iceland (shelf)	288.5–293.6	2	
	1086-1 (E)	Irmingier Basin, South Iceland (slope)	678.5–698.1	2	
	1219-1 (E)	Norwegian Sea, East Iceland	579.1–622.4	2	
	IceAGE 2 867-1 (E)	Norwegian Channel	290–302.5	1	
880-2 (E)	Faroe Island Ridge - middle	686–687.4	2		
Totals			288.5–910.3	37	

Species	Station	Locality	Depth (m)	No.	Previous records
<i>Ampelisca uncinata</i> Chevreux, 1887	IceAGE 1 983-1 (E)	Iceland Basin, South Iceland (Deep Sea)	2568.5–2749.4	2	Iceland, Faroe Islands, Bay of Biscay, Northwestern Atlantic (130–2082 m)
	1006-1(S)	Iceland Basin, South Iceland (slope)	1386.8–1390.1	16	
	1010-1 (E)	Iceland Basin, South Iceland	1384.8–1389	24	
	1017-1 (E)	(shelf)	891.7–910.3	3	
	1019-1 (S)	Irminger Basin, South Iceland	905.9–913.6	24	
	1054-1 (S)	(Deep Sea)	2537.3–2538.1	3	
	1082-1 (S)	Irminger Basin, South Iceland (Slope)	704.9–724.4	2	
	1086-1 (E)	Denmark Strait, East Greenland	678.5–698.1	7	
	1123-1 (E)		716.5–726	1	
IceAGE 2 867-1 (E)	Norwegian Channel	290–302.5	7		
Totals			290–2749.4	89	
<i>Ampelisca eschrichtii</i> Krøyer, 1842	IceAGE 2 879-5 (E)	Faroe Island Ridge - middle	500.6–510.9	3	
	880-2 (E)	Faroe Island Ridge - middle	686–687.4	5	
Totals			500.6–687.4	8	
<i>Byblis crassicornis</i> Metzger, 1875	IceAGE 1 1194-1 (S)	Norwegian Sea, north-east Iceland	1573.5–1579.5	3	Iceland, Faroe Islands, Norwe- gian Seas, Arctic north Atlantic, northwestern Atlantic (180- 2082)
	IceAGE 2 867-1 (E)	Norwegian Channel	290–302.5	1	
	868-3 (E)		587.4–614.4	15	
	869-3 (E)	Faroe Island	846.4–868.4	1	
	879-5 (E)	Ridge - middle	500.6–510.9	3	
Totals			290–1579.5	23	
<i>Byblis erythropus</i> Sars, 1882 *	IceAGE 2 867-1 (E)	Norwegian Channel	290–302.5	11	Faroe Island, Norwegian Seas, Arctic Atlantic, northwestern Atlantic
Totals			290–302.5	11	
<i>Byblis medialis</i> Mills, 1971	IceAGE 2				Iceland, Northwest Atlantic (type), (535–2100 m)
	868-3 (EÜ)	Norwegian Channel	587.4–614.4	1	
	880-2 (E)	Faroe Island Ridge - middle	686–687.6	18	
Totals			587.4–687.6	19	
<i>Byblis minuticornis</i> Sars, 1879	IceAGE 1 1119-1 (S)	Denmark Strait, East Greenland	696.9–706.4	2	Iceland, Faroe Islands, Bay of Biscay, Norwegian Seas (type), Arctic Atlantic (69–1910 m)
	1123-1 (E)		716.5–726	2	
	1132-1 (SÜ)		316.5–318.1	1	
	IceAGE 2 868-3 (E)	Norwegian Channel	587.4–614.4	1	
	869-3 (E)		846.4–868.4	5	
	879-5 (E)	Faroe Island ridge - middle	500.9–510.9	3	
	880-2 (E)		686–687.4	14	
Totals			316.5–868.4	28	

Species	Station	Locality	Depth (m)	No.	Previous records
<i>Byblisoides bellansantini</i> sp. n.*	IceAGE 1 1054-1 (S)	Irminger Basin, South Iceland (deep sea)	2537.3–2538.1	1	
Totals			2537.3–2538.1	1	
<i>Haploops carinata</i> Liljeborg, 1855	IceAGE 1 1057-1 (E)	Irminger Basin, South Iceland	2504.7–2531.8	1	Iceland, Faroe Islands, Norwegian Seas (types) (264–1750 m)
Totals			2504.7–2531.8	1	
<i>Haploops islandica</i> Kaim-Malka, Bellan-Santini & Dauvin, 2016	IceAGE 1 1082-1 (S)	Irminger Basin, South Iceland	704.9–724.4	1	Iceland (Type), Faroe Islands (283–1727 m)
	1194-1 (S)	Norwegian Sea, north-east Iceland	1573.5–1579.5	2	
	1219-1 (E)	Norwegian Sea, east Iceland	579.1–622.4	1	
	IceAGE 2	Norwegian Channel			
	867-1 (E)	South-East Faroer Channel	290–302.5	12	
	868-3 (E)		587.4–614.4	7	
	876-5 (E)		554.3–674.8	2	
Totals			290–1579.5	25	
<i>Haploops tubicola</i> Liljeborg, 1855	IceAGE 1 1219-1 (E)	Norwegian Sea, east Iceland	579.1–622.4	1	Iceland, Faroe Islands, Norwegian Seas (type), Bay of Biscay, Arctic Atlantic, northwestern Atlantic (10–2886 m)
Totals			579.1–622.4	1	
<i>Haploops dauvini</i> sp. n.*	IceAGE 2 868-3 (S)		587.4–614.4	3	
	879-5 (E)	Norwegian Channel	500.6–510.9	8	
	880-2 (E)	Faroe Island Ridge - middle	686–687.4	1	
Totals			500.6–687.4	12	
<i>Haploops kaimmalkai</i> sp. n.*	IceAGE 1 1010-1 (E)	Iceland Basin, South Iceland (slope)	1384.8–1389	1	
	IceAGE 2	Faroe Island Ridge - middle			
	880-2 (E)		686–687.4	3	
	868-3 (E)	Norwegian channel	587.4–614.4	79	
Totals			587.4–1389	83	

*species not previously recorded in Icelandic waters

Systematics

Ampeliscidae Krøyer, 1842

Byblisoides K.H. Barnard, 1931

Diagnosis (adapted from Barnard and Karaman 1991). Antenna 1–2 flagella with less than 5 articles. Maxilliped palp article 3 not produced. Pereopod 7 basis posterior margin angled and expanding ventrally. Telson longer than broad and cleft more than half of length. Urosomite 1 produced to form large unilobed carina.

***Byblisoides bellansantinae* sp. n.**

<http://zoobank.org/ABDDCB9B-9C4E-4BE2-A986-9BC876C2465B>

Figs 2–4

Type material. Holotype, female, 14 mm, ZMH K-47035, station IceAGE 1, 1054-1, Irminger Basin, South Iceland, 031°22.60'W – 031°22.18'W, 61°36.19'N – 61°36.97'N, 2537.3 – 2538.1 m, ME85 - 3, supranet bucket of EBS, 07.09.2011.

Type locality. Irminger Basin, South Iceland.

Etymology. Named for Dr Denise Bellan-Santini, whose extensive research on the Ampeliscidae has greatly aided this study.

Diagnosis. Anteroventral margin of head rounded and produced to length of anterior margin of head. Antenna 1 short, reaching to three-quarters of antenna 2 peduncle article 4. Pereopod 7 carpus anterior margin without plumose setae. Pereopod 7 basis posteroventral corner rounded. Uropod 2 inner ramus bearing marginal robust setae. Description. Based on holotype female 14 mm length. Head anteroventral corner produced forward, reaching almost level with the anterodorsal corner, anterior margin, excavate at antenna 2 insertion, antennal lobe concave, with two acute points, rostrum absent, head longer than deep, ventral margin slightly sinuous. Antenna 1 short, reaching to three-quarters length of antenna 2 peduncle article 4; peduncle article 1 subequal in length to article 2 (1.1 ×), article 2 longer than article 3 (3 ×), article 3 shorter than article 1 (0.3 ×); flagellum shorter than peduncle, comprising of three articles (article 1 longest), ventral margin of both peduncle and flagellum with long plumose, slender setae. Antenna 2 comparatively stout, reaching to just under half of the body length; peduncular article 4 subequal in length to article 5, article 5 ventral margin slightly serrate, with long slender setae; flagellum shorter than peduncle, with 4 articles.

Mandible molar well-developed and triturating, seven plumose robust setae in accessory setal row; incisor toothed; lacinia mobilis with many teeth of different sizes; palp long, article 1 very short, article 2 longer than article 3 (2.2 ×) and curved with sparse setae, article 3 longer than article 1 (3.2 ×), moderately setose. Lower lip two lobed, inner plate half height of outer. Maxilla 1 inner plate rounded and small, covered in setules, no long setae; outer plate topped with toothed robust setae; palp with two articles, article 2 reaching to end of teeth on outer plate, tipped with five long plumose setae and five facial slender setae. Maxilla 2 inner and outer plates of equal height and width, both tipped with long plumose setae. Maxilliped inner plate very short, rounded, tipped with three long robust setae and two slender setae; outer plate twisted around palp, inner lateral margin lined with toothed robust setae becoming slender plumose setae distally; palp broad and subchelate in aspect, article 2 expanded and long bearing many strong slender plumose setae, article 3 narrow and folded over article 2, reaching only a third of the length, strongly setose, article 4 curved and acutely tipped, reaching half the length of article 3.

Gnathopod 1 coxa reaching to edge of anterior margin, coxa expanded distally, ventral margin narrowly curved lined with long plumose slender setae, plus a few medial plu-



Figure 2. *Byblisoides bellansantiniae* sp. n. Holotype, female, 14 mm, ZMH K-47035, Irminger Basin, Iceland, 2537.3–2538.1 m. Whole animal, head and epimeron. Scale for habitus represents 1 mm.

mose setae; basis narrow, lateral margins lined with long plumose, slender setae, medial setae long and plumose; merus slightly lobate and strongly setose particularly posteriorly; carpus longer than merus and longer than propodus (1.2 ×), strongly setose, particularly medially and posteriorly with long plumose setae, not lobate; propodus ovoid, weakly subchelate, palm not well defined, anterior and posterior margins lined with long plumose slender setae; dactylus short and curved, a third the length of the propodus, inner

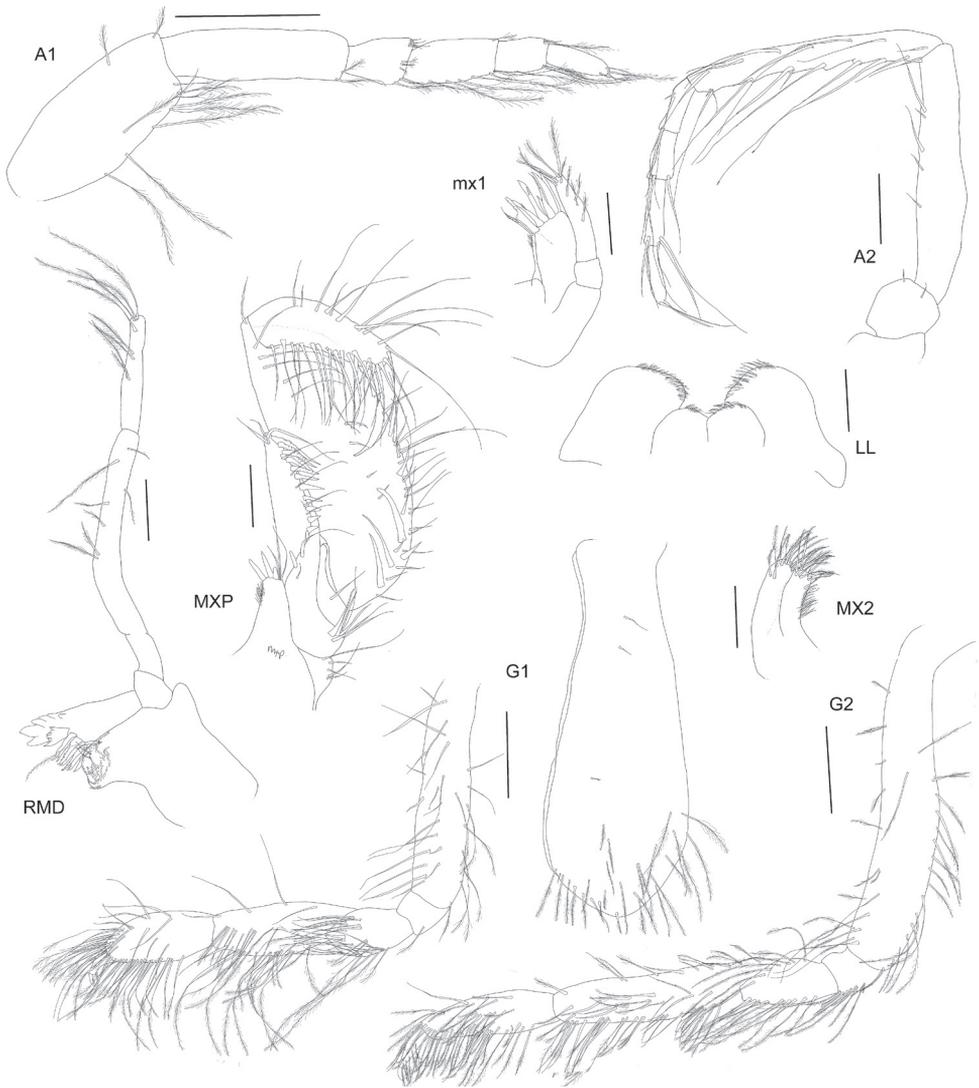


Figure 3. *Byblisoides bellansantiniæ* sp. n. Holotype, female, 14 mm, ZMH K-47035, Irminger Basin, Iceland, 2537.3–2538.1 m. Antennae 1–2, gnathopods 1–2 scales represent 0.5 mm. Mouthparts scales represent 0.2 mm.

margin with a distal tooth and sparse slender setae. Gnathopod 2 coxa similar length to coxa 1, ventral margin curved (unevenly), fringed with medial and marginal sparse long plumose setae; basis long and narrow lateral margins with long slender plumose setae, merus with subacute posterior lobe, long plumose setae on both the anterior and posterior margins; carpus longer than merus and longer than propodus, narrow and not lobate, covered in long, plumose setae; propodus narrow, covered in long plumose setae; dactylus short, about a third the length of the propodus and slightly curved, inner margin setose.

Pereopod 3 coxa similar to coxa 2; basis long and narrow, anterior margin with short sparse setae, posterior margin without setae; merus narrow, shorter than basis, subequal to carpus and propodus together, both margins with sparse long plumose setae; carpus with long plumose setae on posterior margin; propodus longer than carpus, short sparse setae on posterior margin, posterior margin slightly concave; dactylus long and narrow, slightly curved, shorter than propodus. Pereopod 4 coxa subrectangular, posterior margin with extended rounded lobe, posterior margin below lobe concave, ventral margin almost straight and sparsely setose; basis same length as coxa with setose lateral margins; ischium setose along posterior margin; merus long and narrow, shorter than basis, longer than carpus and propodus together, setose with plumose setae along complete length of posterior margin and distal half of anterior margin; carpus shorter than propodus, setose along posterior margin; propodus long and narrow, setose on proximal posterior margin; dactylus long, narrow and straight, shorter than propodus.

Pereopod 5 basis almost rounded narrow distally, anterior margin broadly rounded, lined with long plumose setae, anterior margin bilobed without setae; ischium with acute posterior lobe; merus longer than ischium with only one long plumose seta on anterior margin, no setae on posterior margin; carpus longer than merus, longer than propodus, only setose along anterior margin (all plumose), not lobate; propodus narrow, setose along anterior margin, not lobate; dactylus short, strongly curved and smooth. Pereopod 6 basis nearly circular, subquadrate distally, anterior margin lined with short slender setae, and one long plumose seta, posterior margin without setae; ischium with acute posterior lobe; merus longer than ischium, not lobate, anterior margin with one long slender seta and one long robust seta, posterior margin without setae; carpus longer than merus and longer than propodus, anterior margin lined with eight long robust setae, anterior margin no setae, distal corner with two long robust setae; propodus long and narrow not produced into a distal lobe, anterior margin lined with four short plumose robust setae, distal corner bearing three long strong setae; dactylus short, curved and smooth. Pereopod 7 basis widest distally, ovoid, rounded, medial surface setose, anterior margin with sparse setae, ventral and partly posterior margin lined with long plumose setae all the way to the junction with the ischium, posterior corner slightly serrate; ischium short and not setose, except for anterodistal corner; merus longer than ischium, not lobate, anterior margin with two long robust setae, posterior with three long plumose setae and distally with one long plumose and one robust seta; carpus narrow, longer than merus, subequal to propodus, anterior margin with three robust setae and two distal robust setae, posterior margin without marginal setae, but with four long distal robust setae; propodus long and narrow, anterior margin without setae, posterior margin with two robust setae; dactylus long, straight and narrow, slightly shorter than propodus.

Pleon. Epimeron 1 posteroventrally broadly rounded, no tooth or setae. Epimeron 2 posteroventrally broadly rounded, no tooth or setae. Epimeron 3 posteroventrally produced to form a small subacute tooth, posterior margin straight, no ventral setae. Urosomite 1 produced into a straight dorsally, curved ventrally carina, unilobed when viewed from dorsal. Uropod 1, in situ, reaching to tip of uropod 2 rami; peduncle

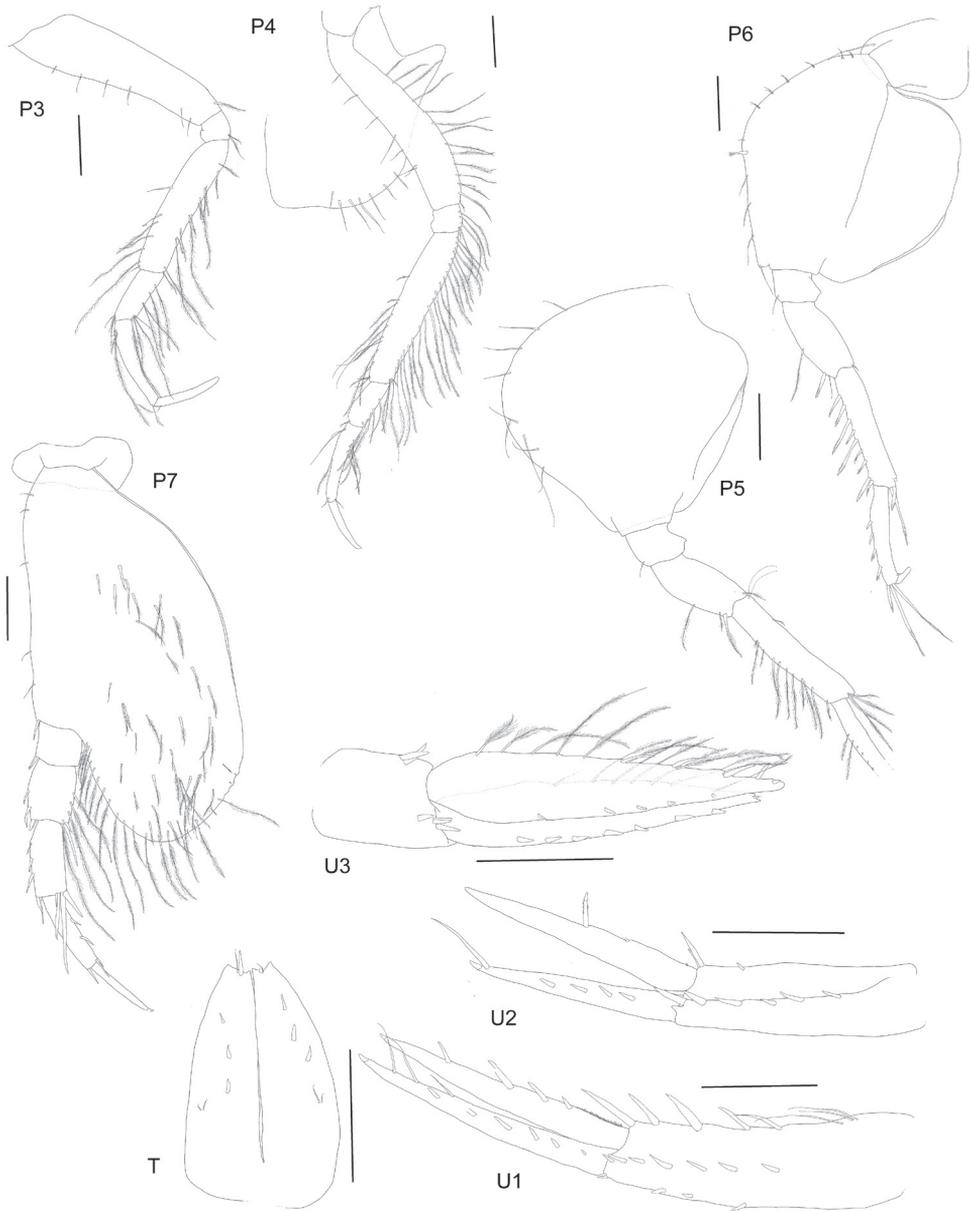


Figure 4. *Byblisoides bellansantiniae* sp. n. Holotype, female, 14 mm, ZMH K-47035, Irminger Basin, Iceland, 2537.3–2538.1 m. Scales represent 0.5 mm

longer than rami, outer margin lined with three short robust setae, inner margin lined with three proximal, long plumose setae and five long robust setae, row of seven short, robust medial setae; rami subequal in length, outer ramus lined with six robust setae and three slender setae; inner ramus with hair-like setal fringe proximally and distally

with four robust marginal setae. Uropod 2 peduncle same length as inner ramus but longer than outer ramus, inner margin with two robust lateral setae and six medial robust setae; outer ramus with four short medial robust setae, one long subterminal robust seta; inner ramus longer than outer ramus with proximal hair-like fringe and two long marginal distal robust setae. Uropod 3 peduncle much shorter than rami, with three distal, medial short robust setae, and two lateral robust setae; inner ramus slightly longer than outer, both rami leaf-shaped (broadest proximally); inner ramus lined with long slender plumose setae and four robust setae laterally (outer margin), five robust setae on inner margin; outer rami inner margin with long slender, plumose setae, outer margin with seven short robust setae laterally. Telson longer than wide (1.65 ×), 78 % cleft; each lobe concavely truncated distally, each lobe with three dorsal robust setae, two slender dorsal setae, one robust apical and one slender apical seta.

Remarks. *Byblisoides* is the smallest of the Ampeliscid genera with only seven species (including this species). However, the species fall into the same traps as the rest of the ampeliscids, in that they have relatively similar morphology needing a combination of characters to provide differences. Usually a species wouldn't be described from a single specimen, but as this is a new record for the Icelandic region and distinctly a new species it has been done. *Byblisoides bellansantinae* sp. n. fits the most recent diagnosis of the genus (Barnard and Karaman 1991) in the flagella of antennae 1 – 2 with 4 or fewer articles. Article 3 of maxilliped palp unproduced. Article 2 of pereopod 7 with posterior margin oblique and article expanding ventrally, anterior margin of posteroventral lobe near junction with article 2 usually setose. Telson much longer than broad, cleft much more than half its length.

This species also aligns to the description of the genus in the same publication, the only slight difference is with the lower part of posterior margin on coxa 4 being angled to the anterior margin (not parallel). *Byblisoides bellansantinae* sp. n. has the closest affinities to *B. profundi* Mills, 1971 from the Gay Head – Bermuda transect from a depth of 4600–4900 m. The ventral shape of the coxa and general shape of pereopod 7 basis draw these species together. However, they are distinct because of the shape of the anteroventral corner of the head (produced and rounded in *B. bellansantinae* sp. n. and not produced in *B. profundi*), and setation of basis of pereopod 7 (medially setose in *B. bellansantinae*, not setose in *B. profundi*). Other differences include the setation of the carpus and propodus of pereopods 5 and 6 (without setae *B. bellansantinae*, strong plumose setae *B. profundi*).

A key to the species of *Byblisoides* is provided below. Built on that provided by J.L. Barnard, 1961.

Distribution. Southern Iceland, North Atlantic. Depths 2500–2600 m.

Key to species of *Byblisoides*

- 1 Anterior edge of carpus of pereopod 7 with four long plumose setae.....
*B. juxtacornis* K.H. Barnard, 1931
- Anterior edge of carpus of pereopod 7 without plumose setae..... 2

- 2 Urosomite 1 not obviously produced to form a carina (from lateral view).....
 *B. esferis* J.L. Barnard, 1961
 – Urosomite 1 obviously produced to form a carina (from lateral view)3
 3 Urosomite 1 carina bilobed (from dorsal view)4
 – Urosomite 1 carina not bilobed (from dorsal view)5
 4 Uropod 2 inner ramus with robust setae *B. blasensis* J.L. Barnard, 1964
 – Uropod 2 inner ramus without robust setae... *B. arcillis* J.L. Barnard, 1961
 5 Pereopod 7 basis ventral lobe acute *B. plumicornis* Ledoyer, 1978
 – Pereopod 7 basis ventral lobe rounded6
 6 Anteroventral corner of head produced and rounded..... *B. bellansantiniæ* sp. n.
 – Anteroventral corner of head not produced..... *B. profundis* Mills, 1971

Haploops Liljeborg, 1856

Diagnosis (adapted from Barnard and Karaman 1991). Antenna 1–2 flagella with more than five articles. Maxilliped palp article 3 expanded and usually produced. Pereopod 7 basis with parallel margins (sometimes straight and sometimes concave), narrow posteroventral lobe present. Telson of varying lengths to widths, usually cleft more than half.

Haploops dauvini sp. n.

<http://zoobank.org/B1A77932-F41F-42BE-9D8A-98C6EA8403C7>

Figures 5–7

Type material. Holotype, female, 7 mm, ZMH K-47038, station IceAGE 2, 868-3, Norwegian Channel, 000°15.51'E – 000°15.86'E, 62°09.14'N – 62°10.30'N, 587.4 – 614.4 m, POS-456, from the supranet bucket of EBS, 25.07.2013. Paratypes: ZMH K-47039, female 6 mm; NIWA 123641, female, 7 mm, same collection data as holotype.

Additional material examined. ZMH K-47042, ZMH K-47043, 8 specimens, station IceAGE 2, 879-5, Faroe Island Ridge (middle), 008°34.32'W – 008°36.22'W, 63°06.10'N – 63°05.62'N, 500.6 – 510.9 m, POS-456, 31.07.2013. ZMH K-47040, 1 specimen, station IceAGE 2, 880-2, Faroe Island Ridge (middle), 008°09.42'W – 008°11.22'W, 63°23.36'N – 63°24.62'N, 686 – 687.4 m, POS-456, 31.07.2013.

Type locality. Norwegian Channel, North Atlantic Ocean.

Etymology. This species is named for Dr Jean-Claude Dauvin, whose extensive work on the family Ampeliscidae was invaluable for the description of this species.

Diagnosis. Eyes absent. Head anterior margin straight. Antenna 1 article 1 almost half the length of article 2. Antenna 2 peduncular article 4 subequal in length to article 5. Gnathopod 1 carpus subequal in length to the propodus. Gnathopods and pereopods without setal fringe. Pereopod 4 coxa broad. Pereopod 5 basis almost circular.

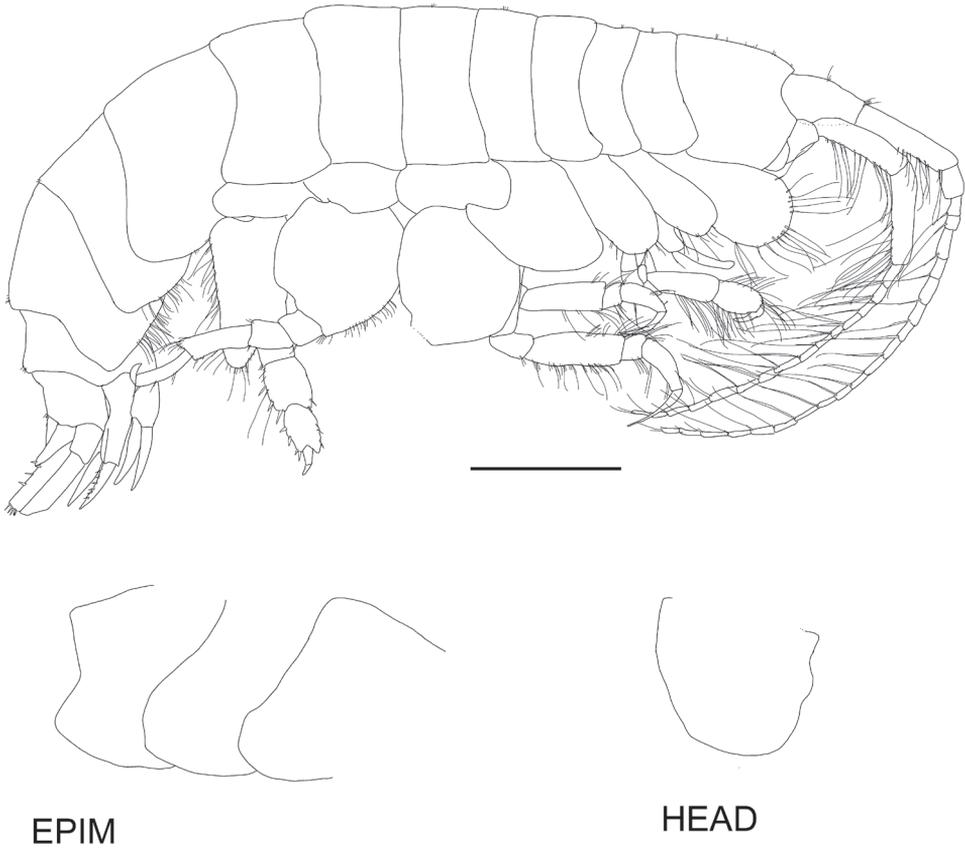


Figure 5. *Haploops dawvini* sp. n., holotype, female, 7 mm, ZMH K-47038, Norwegian Channel, 587.4–614.4 m. Whole animal, head and epimeron. Habitus scale represents 1 mm.

Pereopod 7 basis narrow. Uropod 1 rami subequal in length. Telson with 1 distal robust seta per lobe.

Description. Based on holotype adult female, 7 mm in length.

Both pereon and pleon without dorsal setae. Head almost as deep as long, rostrum absent, anterior margin straight and almost perpendicular to dorsal margin. Corneal lenses absent. Antenna 1 as long as antenna 2, close to half body length; peduncular article 1 shorter than article 2 (0.6 ×), article 2 longer than article 3 (3 ×), article 3 shorter than article 1 (0.5 ×); flagellum short with 16 articles, fringed ventrally with long, weakly plumose setae. Antenna 2 close to half the body length; peduncular article 4 approximately subequal to article 5 (0.9 ×); flagellum with 15 articles; peduncle and flagellum fringed with long, weakly plumose setae.

Upper lip distally notched, lightly setose. Mandible molar well developed and triturating, with 7 plumose robust setae in the accessory setal row; palp long, article 2 shorter than article 3 (0.85 ×); article 2 weakly setose, article 3 strongly setose with

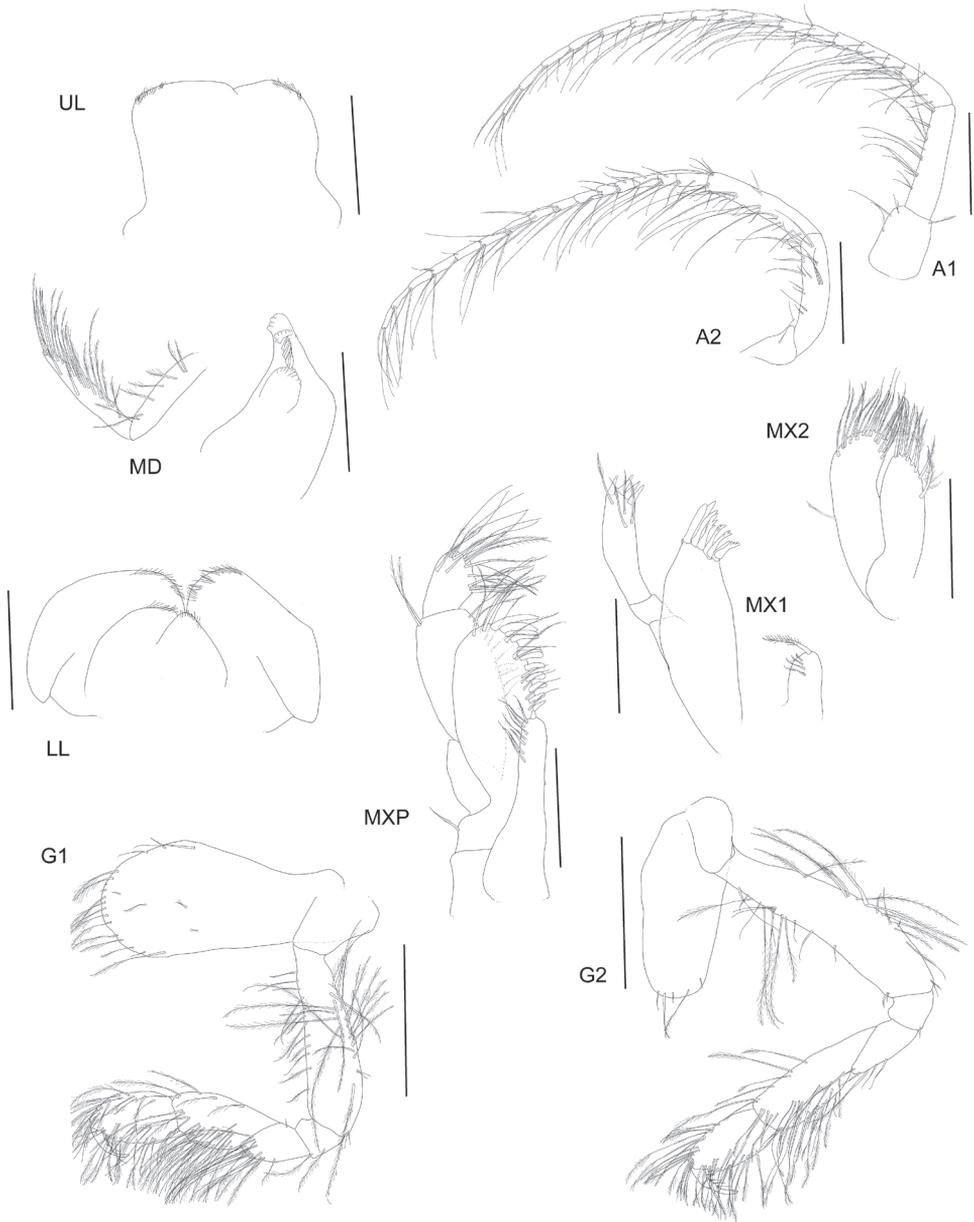


Figure 6. *Haploops dawvini* sp. n., holotype, female, 7 mm, ZMH K-47038, Norwegian Channel, 587.4–614.4 m. Antennae 1–2, gnathopods 1–2 scales represent 0.5 mm. Mouthparts scales represent 0.2 mm.

plumose setae. Lower Lip with inner and outer lobe, inner half the height of the outer. Maxilla 1 inner plate with 1 apical strong plumose seta and 4 accessory simple facial setae; palp with two articles, second article reaching past length of outer plate, with 4

robust setae distally and four slender, plumose facial setae. Maxilla 2 plates of similar widths, both with long plumose setae. Maxilliped inner plate elongated with a rounded tip with one short robust seta and nine long plumose slender facial setae; outer plate ovoid reaching to $\frac{3}{4}$ length of palp article 2, inner lateral margin with robust setae tending to long plumose setae distally; palp article 4 longer than article 3, and inserted subterminally, inner margin setose.

Pereon. Gnathopod 1 coxa roughly teardrop shape, expanded and rounded distally. In situ, reaching to level of anterior margin of head, ventral margin broadly and evenly rounded with fringe of long plumose setae, scattered setae medially; basis shorter than coxa, same length as carpus and propodus together, lateral margins and medially fringed with long plumose setae and occasional short non-plumose setae; merus slightly lobate with long plumose setae on posterior margin; carpus longer than merus, slightly longer than propodus (1.15 ×), with slight rounded posterior lobe, posterior margin bearing many long, plumose slender setae; propodus ovoid, subchelate, posterior margin slightly serrate, strongly setose on both posterior and anterior margin; dactylus long and curved, inner margin setose, reaching to half of length of propodus. Gnathopod 2 coxa $\frac{2}{3}$ length of coxa 1, narrowing slightly distally, ventral margin rounded with sparse plumose setae; basis longer than coxa, similar length to carpus and propodus combined, lateral margins with long plumose slender setae; merus non-lobate; carpus longer than merus and longer than propodus (1.6 ×), non-lobate, long plumose setae on both posterior and anterior margins (more dense on posterior margin); propodus ovoid, subchelate, palm not strongly defined, long, plumose setae on both anterior and posterior margins; dactylus shorter than propodus (0.6×), with a setose inner margin.

Pereopod 3 coxa similar in length to coxa 2, ventral margin rounded with sparse long plumose setae; basis longer than coxa, just shorter than merus + carpus + propodus, lateral margins with long, plumose setae; merus shorter than basis, longer than carpus and propodus combined, sparsely setose on both posterior and anterior margins, not inflated; carpus short with long plumose setae on the posterior margin only; propodus longer than carpus, long, plumose setae on anterior margin plus two on the posterior margin, posterior margin straight (not concave or convex); dactylus shorter than carpus and propodus combined (longer than propodus individually), not setose, straight. Pereopod 4 coxa broad with rounded extended posterior lobe, ventral margin rounded (no acute corners) with sparse, plumose setae; basis longer than coxa, fringed laterally with long, plumose setae on both margins, shorter than merus + carpus + propodus; merus narrow, longer than carpus and propodus combined, long plumose setae only at distal end of article; carpus short with posterior, long, plumose setae only; propodus longer than carpus with sparse (2 on anterior and 1 on posterior) plumose setae; dactylus shorter than propodus, straight and without setae.

Pereopod 5 basis broadly rounded, almost circular, anterior margin with a few short setae; distal articles broken off. Pereopod 6 basis almost circular, not as broad as basis 5, anterior margin with sparse small setae, posterior margin rounded; ischium with acute

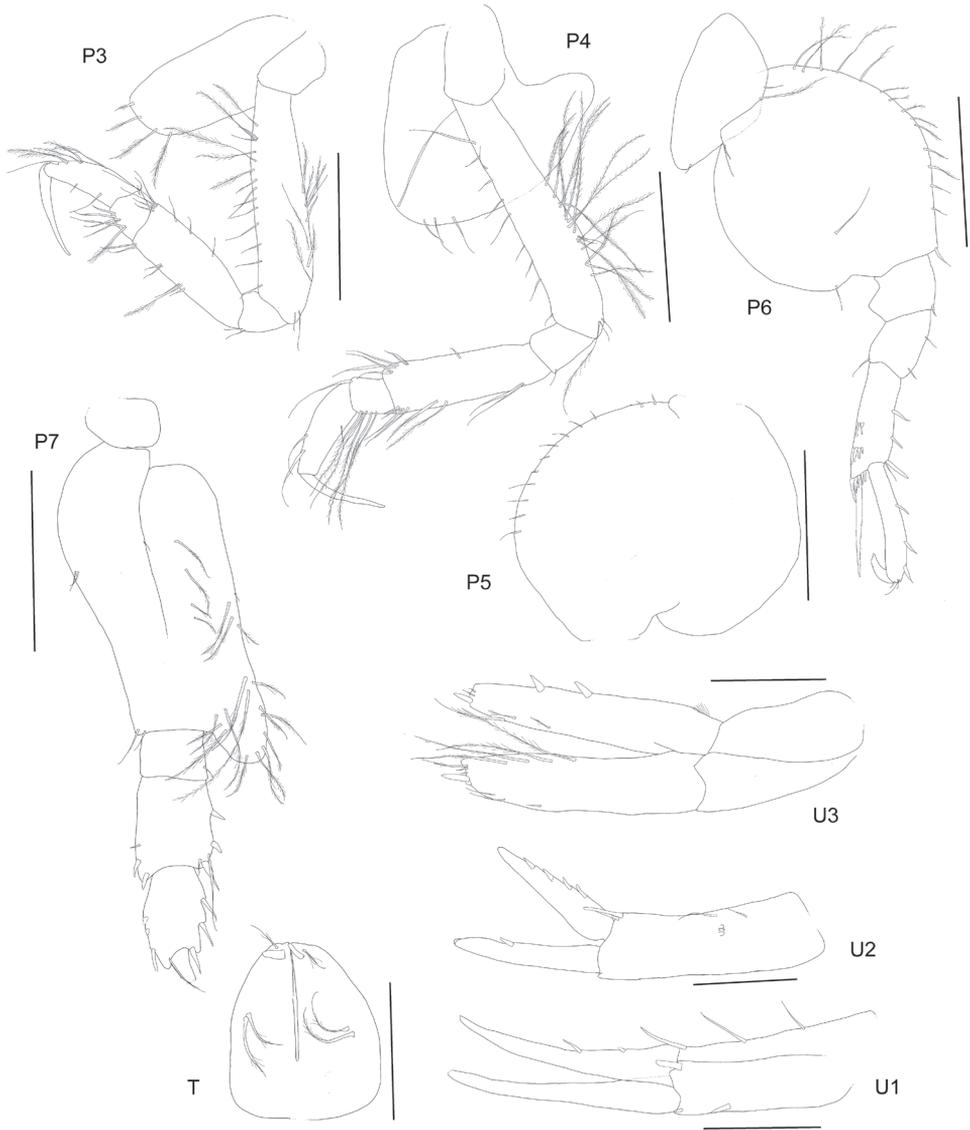


Figure 7. *Haploops dawvini* sp. n., holotype, female, 7 mm, ZMH K-47038, Norwegian Channel, 587.4–614.4 m. Pereopods 3–7 scales represent 0.5 mm. Uropods 1–3 and Telson scales represent 0.2 mm.

posterior lobe; merus same length as ischium, weakly setose; carpus longer than merus, slightly shorter than propodus ($0.85 \times$ not including posterior lobe), anterior margin with two weak robust setae, posterior margin with two rows of stout robust setae (2 and 4), and extended to form a lobe bearing 6 strong, robust setae increasing in length laterally; propodus narrower than carpus, anterior margin with two weak robust setae, posterior margin without robust setae, anterior margin produced slightly to form a

weakly setose lobe; dactylus strongly curved and smooth, much shorter than propodus. Pereopod 7 basis moderately narrow (length without lobe /width = 2.0 ×), anterior and posterior margins slightly concave, medial surface with numerous long, plumose setae, posterior-distal lobe narrow, rounded and deflected, reaching to $\frac{3}{4}$ length of ischium, with a few marginal setae; ischium without anterodistal robust setae; merus subrectangular, longer than ischium (1.8 ×), subequal in length to carpus, anterior margin with one marginal and one distal robust seta, not lobate, posterior margin not lobate with two marginal and one distal robust seta; carpus subovoid, broad (width/length = 0.75×), anterior margin slightly lobate distally, with three marginal robust setae, posterior margin not lobate with two long marginal robust setae and one distal robust seta; propodus narrow, less than half the length of the carpus, no setae; dactylus broken off.

Pleon smooth. Epimeron 1 posteroventral corner broadly rounded, no tooth. Epimeron 2 posteroventral corner broadly rounded, no tooth. Epimeron 3 subquadrate, no tooth and no setae, dorsal margin with sparse, very short setae. Urosomite 1 slightly raised to form a small rounded carina, dorsal margin bearing a few very short setae. Urosomites 2–3 fused.

Uropod 1, in situ, reaching one third of the length of uropod 2 rami; peduncle shorter than rami, outer margin with two robust setae, inner margin with three slender setae, one strong robust seta medio-distally; rami subequal in length, both curved and gently tapering to a subacute tip; outer ramus without setae; inner ramus with two robust setae. Uropod 2 peduncle longer than rami, inner margin with 2 slender setae and two long robust setae distally; rami subequal in length, narrow tapering to a rounded tip; outer ramus with one marginal robust seta; inner ramus with four marginal robust setae. Uropod 3 peduncle shorter than rami (0.65×), and without setae; rami long and narrow, even width along length, not tapering, truncated apically, subequal in length; outer ramus two robust setae distally, long plumose setae on distal half of each margin; inner ramus with two strong robust setae on outer margin and one robust seta distally, plumose setae on distal part of inner margin, hair-like fringe on proximal half of outer margin. Telson slightly longer than wide (1.2 ×), cleft to 68%, each lobe apically rounded subquadrately; each lobe with two slender dorsal setae, one apical slender setae and one apical robust seta.

Male. No males availables in the samples.

Remarks. Of the blind species in *Haploops*, this species can be most closely allied to *Haploops abyssorum* Chevreux, 1908, *H. lodo* J.L. Barnard, 1961, *H. similis* Stephensen, 1925 and *H. kaimmalkai* (current work). The similarities between these species are due to the lack of eyes and a narrow pereopod 7 basis. The differences between the five species are shown in table 2.

Even though *Haploops dawvini* sp. n. has strong similarities to the above four species, it stands as a distinct species due to the subequal proportions of gnathopod 1 carpus and propodus (carpus is longer than the propodus in the other four species), the presence of long plumose setae on the ventral margins of coxae 2 and 3 (simple and sparse setae in the other four species), uropod 1 peduncle is shorter than the

rami (longer or subequal in the other four species), pereopod 5 basis is almost circular (ovoid or irregular in the other four species), and uropod 1 rami are subequal in length (a character shared with *H. kaimmalkai*, the other three species have the inner ramus distinctly shorter than the outer ramus).

Distribution. Icelandic waters, North Atlantic. Depths ranging from 500–690 m.

***Haploops kaimmalkai* sp. n.**

<http://zoobank.org/39241512-099C-4593-BDCB-FDD31348229C>

Figures 8–10

Type material. Holotype, female, 6 mm, ZMH K-47057, station IceAGE 1, 1010-1, Iceland Basin, South Iceland (slope), 020°23.71'W – 020°22.87'W, 62°33.10'N – 62°33.22'N, 1384.8 – 1389 m, ME85-3, from the epinet bucket of the EBS, 02.09.2011. Paratypes: ZMH K-47056, 1 specimen, 6 mm; NIWA 123642, 2 specimens, 5 (female juvenile) and 7 mm (male), station IceAGE 2, 880-2, Faroe Island Ridge (middle), 008°09.42'W – 008°11.22'W, 63°23.36'N – 63°24.62'N, 686 – 687.4 m, POS-456, from epinet bucket of EBS, 31.07.2013.

Additional material examined. ZMH K-47054, ZMH K-47055, 79 specimens, station IceAGE 2, 868-3, Norwegian Channel, 000°15.51'E – 000°15.86'E, 62°09.14'N – 62°10.30'N, 587.4 – 614.4 m, POS-456, from epinet bucket of EBS, 25.07.2013.

Type locality. Iceland Basin, South Iceland, North Atlantic Ocean.

Etymology. This species is named for Dr Richard A. Kaïm-Malka, whose invaluable research has contributed greatly to this paper.

Diagnosis. Eyes absent. Head anterior margin sinusoidal. Antenna 1 article 1 almost the same length as article 2. Antenna 2 peduncular article 4 shorter than article 5. Gnathopod 1 carpus longer than the propodus. Gnathopods and pereopods with setal fringe. Pereopod 4 coxa narrow. Pereopod 5 basis sinusoidal. Pereopod 7 basis narrow. Uropod 1 rami subequal in length. Telson without distal robust seta per lobe.

Description. Based on holotype adult female, 6 mm in length.

Both pereon and pleon without dorsal setae. Head almost as deep as long, rostrum absent, anterior margin sinusoidal and almost perpendicular to dorsal margin. Corneal lenses absent.

Antenna 1 as long as antenna 2, close to half body length; peduncular article 1 shorter than article 2 (0.87 ×), article 2 longer than article 3 (2.5 ×), article 3 shorter than article 1 (0.4 ×); flagellum short with 13 articles, sparsely fringed ventrally with long, weakly plumose setae. Antenna 2 close to half the body length; peduncular article 4 shorter than article 5 (0.75 ×); flagellum with at least 11 articles (broken off); peduncle and flagellum sparsely fringed with long, weakly plumose setae.

Upper lip distally notched, lightly setose. Mandible molar well developed, large and triturating, with 6 plumose robust setae in the accessory setal row; palp long, article 2 slightly shorter than article 3 (0.9 ×); article 2 and 3 equally setose with plumose setae.

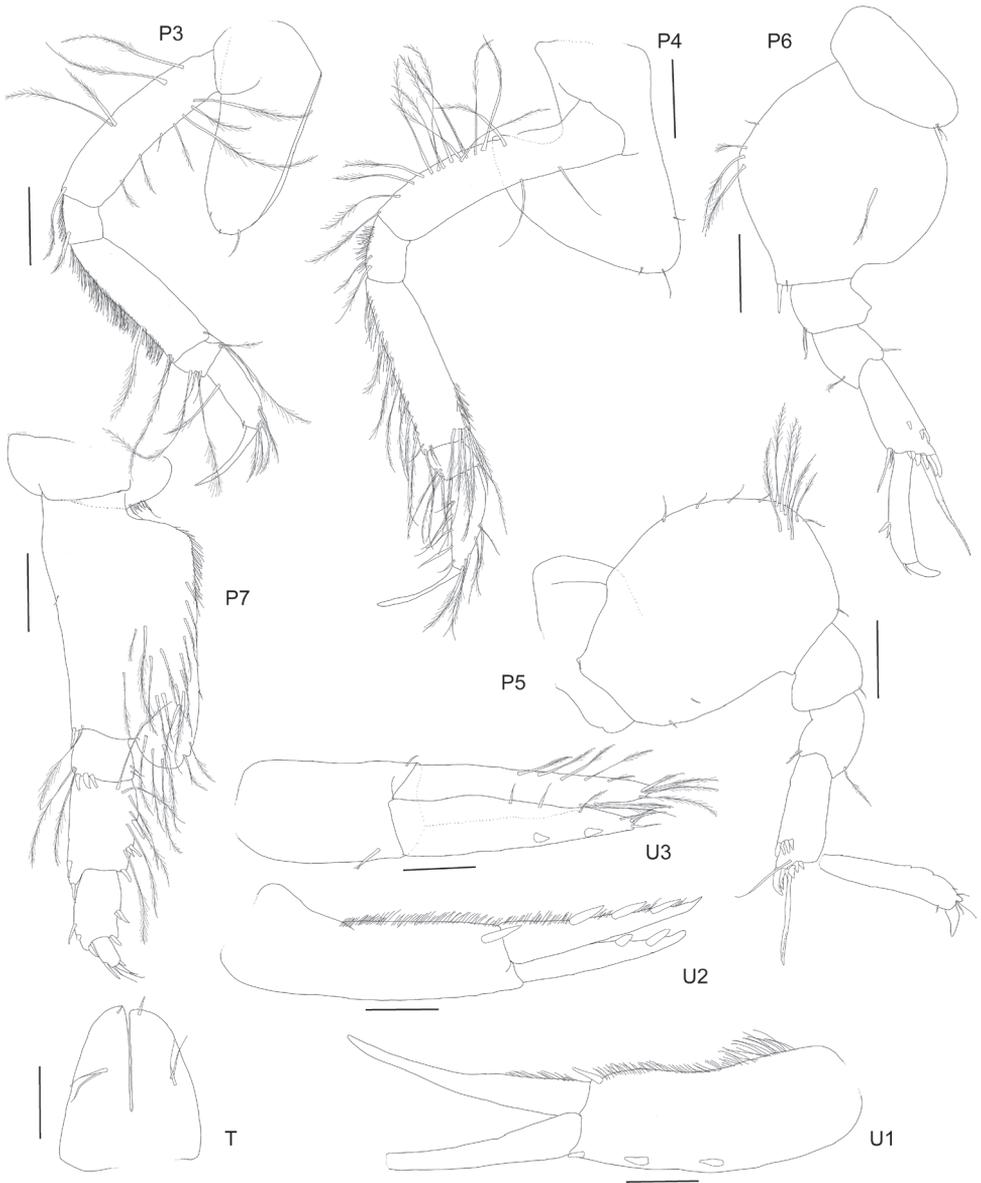


Figure 8. *Haploops kaimmalkai* sp. n. holotype, female, 6 mm, ZMH K-47057, Iceland Basin, 1384.8–1389 m. Whole animal, head and epimeron. Habitus scale represents 1 mm.

Lower Lip with inner and outer lobe, inner half the height of the outer. Maxilla 1 inner plate with 1 apical strong plumose seta and no accessory simple facial setae; palp with two articles, second article reaching past length of outer plate, with 4 robust setae distally and five slender, plumose facial setae. Maxilla 2 plates of similar widths, both with long plumose setae. Maxilliped inner plate narrow with a rounded tip with one

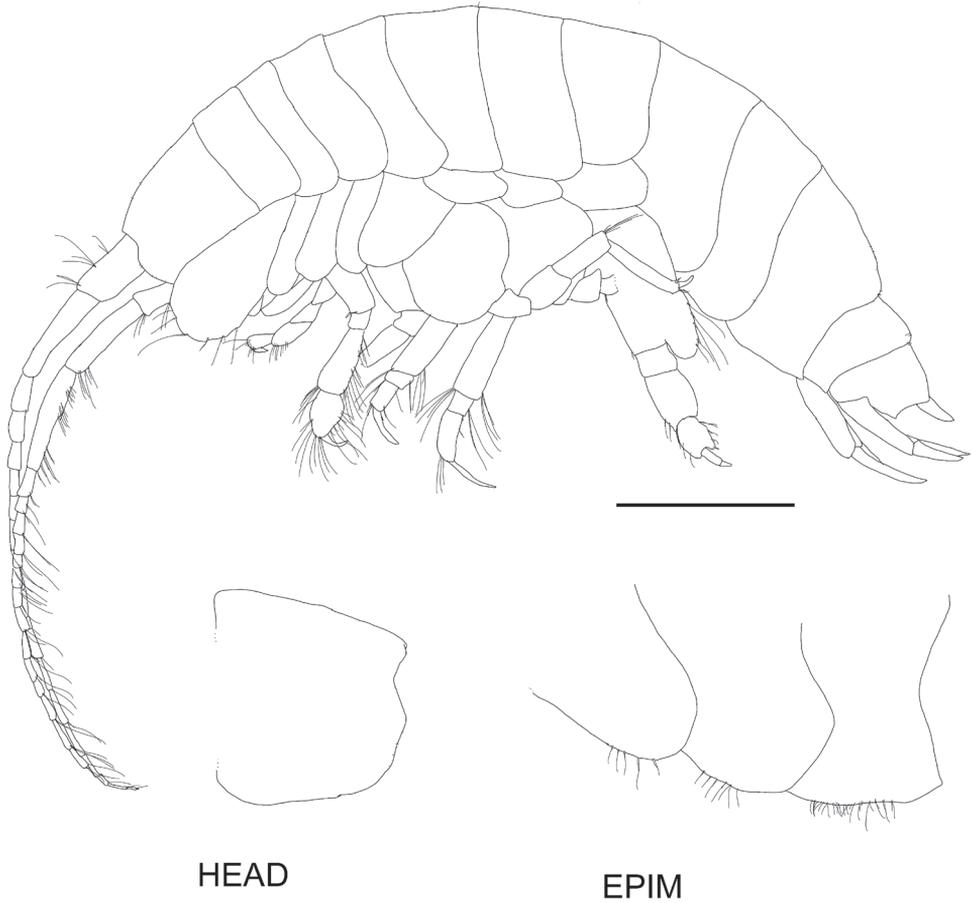


Figure 9. *Haploops kaimmalkai* sp. n. holotype, female, 6 mm, ZMH K-47057, Iceland Basin, 1384.8–1389 m. Scales represent 0.2 mm.

short robust seta and eight long plumose slender facial setae; outer plate narrowly ovoid reaching to end of palp article 2, inner lateral margin with robust setae tending to long plumose setae distally; palp article 4 subequal in length to article 3, and inserted strongly subterminally, so article 3 forms as large distally setose lobe, inner margin smooth.

Pereon. Gnathopod 1 coxa roughly teardrop shape, expanded and rounded distally. In situ, reaching just past level of anterior margin of head, ventral margin broadly and evenly rounded slightly serrate, with fringe of long plumose setae, scattered setae medially; basis shorter than coxa, longer than carpus and propodus together, lateral margins and medially fringed with long plumose setae and occasional short non-plumose setae; merus slightly lobate with long plumose setae on distal posterior margin; carpus longer than merus, longer than propodus (1.4 ×), with slight rounded posterior lobe, posterior margin bearing many long, plumose slender setae; propodus short and ovoid, subchelate, posterior margin smooth, strongly setose on both posterior and anterior

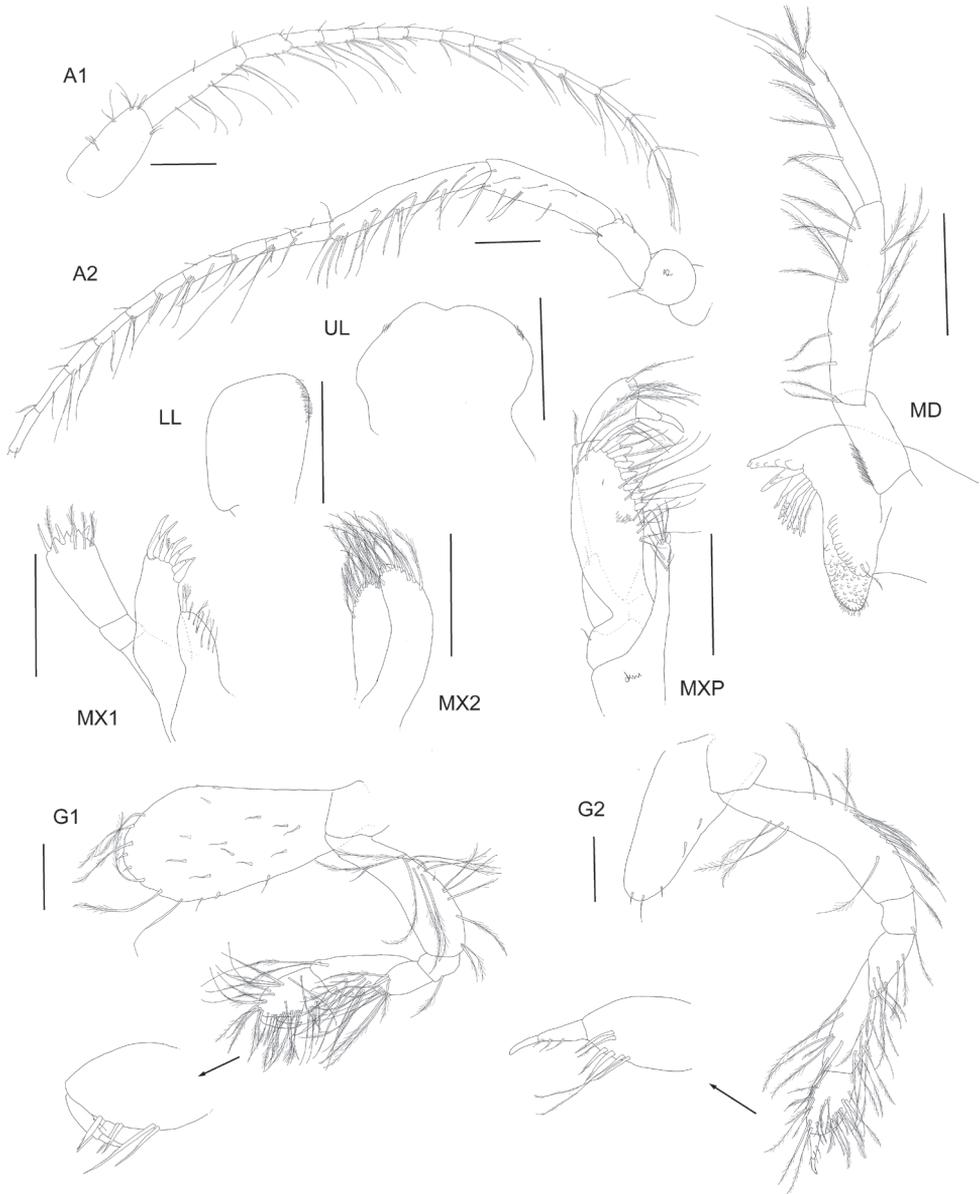


Figure 10. *Haploops kaimmalkai* sp. n. holotype, female, 6 mm, ZMH K-47057, Iceland Basin, 1384.8–1389 m. Pereopods 3–7 scales represent 0.2 mm. Uropods 1–3 and Telson scales represent 0.1 mm.

margin; dactylus long and curved, inner margin with only one seta, reaching over half of length of propodus. Gnathopod 2 coxa $2/3$ length of coxa 1, narrowing distally, ventral margin rounded with sparse setae; basis longer than coxa, longer than carpus and propodus combined, lateral margins with long plumose slender setae; merus non-lobate; carpus longer than merus and longer than propodus ($1.6 \times$), non-lobate,

long plumose setae on both posterior and anterior margins (more dense on posterior margin); propodus ovoid, weakly subchelate, palm not strongly defined, long, plumose setae on both anterior and posterior margins; dactylus shorter than propodus ($0.6\times$), with a setose inner margin.

Pereopod 3 coxa similar in length to coxa 2, ventral margin rounded, narrowing distally with sparse short setae; basis longer than coxa, shorter than merus + carpus + propodus, lateral margins with long, plumose setae; merus shorter than basis, longer than carpus and propodus combined, sparsely setose on posterior margins, not inflated; ischium and merus posterior margin with fringe of fine hair-like setae; carpus short with long plumose setae on the posterior margin only; propodus longer than carpus, long, plumose setae on distal anterior margin plus one on the posterior margin, posterior margin straight (not concave or convex); dactylus shorter than carpus and propodus combined (subequally to propodus individually), not setose, straight. Pereopod 4 coxa narrow with rounded extended posterior lobe, ventral margin rounded (no acute corners) with sparse setae; basis longer than coxa, fringed laterally with long, plumose setae on posterior margin, shorter than merus + carpus + propodus; merus narrow, longer than carpus and propodus combined, long plumose setae only at distal anterior end and along posterior margin; ischium, merus, carpus and propodus fringed with long hair-like setae along posterior margin; carpus short with posterior, long, plumose setae only; propodus longer than carpus with sparse plumose setae on each margin; dactylus shorter than propodus, straight and without setae.

Pereopod 5 basis curved shape, anterior margin broadly rounded with a few short setae and large patch of long plumose setae, posterior margin sinusoidal, with sparse setae; carpus extended to form posterior distal lobe, margin with row of 4 robust setae, distal corner with 7 robust setae increasing in length laterally; carpus shorter than propodus, propodus narrow, weakly setose, not produced to form a distal lobe. Pereopod 6 basis ovoid, anterior margin with sparse small setae, plus a patch of three long plumose slender setae, posterior margin narrowly rounded; ischium with acute posterior lobe; merus same length as ischium, not setose; carpus longer than merus, subequal in length to propodus ($0.9\times$ not including posterior lobe), anterior margin without marginal setae, posterior margin with one row of three stout robust setae, and extended to form a lobe bearing 7 strong, robust setae increasing in length laterally; propodus narrower than carpus, anterior margin with two weak robust setae, posterior margin without robust setae, anterior margin not produced distally; dactylus curved and smooth, much shorter than propodus. Pereopod 7 basis moderately narrow (length without lobe / width = $1.8\times$), anterior and posterior margins straight, medial surface with numerous long, plumose setae, proximal posterior margin with fine hairs, posterior-distal lobe narrow, rounded and not deflected, reaching to $\frac{3}{4}$ length of ischium, with a few marginal setae; ischium with three anterodistal robust setae; merus subrectangular, longer than ischium ($2.0\times$), longer than carpus, anterior margin with one marginal and one distal robust seta, slightly lobate, posterior margin not lobate with three marginal and one distal robust seta, and six long plumose slender marginal setae; carpus subrectangular, narrow (width/length = $0.67\times$), anterior margin slightly lobate distally, with two

marginal robust setae, posterior margin not lobate with two long marginal robust setae and one distal robust seta; propodus narrow, less than half the length of the carpus, two setae; dactylus narrow, half of propodus.

Pleon smooth. Epimeron 1 posteroventral corner broadly rounded, no tooth. Epimeron 2 posteroventral corner broadly rounded, no tooth. Epimeron 3 posteroventral corner subquadrate, tiny tooth, ventral margin with fringe of small setae, dorsal margin with sparse, very short setae. Urosomite 1 slightly raised to form a small rounded carina, dorsal margin bearing a few very short setae. Urosomites 2 – 3 fused.

Uropod 1, in situ, reaching half of the length of uropod 2 rami; peduncle longer than rami, outer margin with three robust setae, inner margin with one distal robust seta and fringe of hair-like setae; rami subequal in length, both curved and gently tapering to a subacute tip; outer ramus without setae; inner ramus without setae. Uropod 2 peduncle longer than rami, inner margin with fringe of hair-like setae and one long robust setae distally; outer ramus shorter than inner, narrow tapering to a rounded tip; outer ramus with two marginal robust setae; inner ramus with three marginal robust setae. Uropod 3 peduncle shorter than rami (0.68 ×), and with slender setae; rami long and narrow, even width along length, slightly tapering, rounded apically, subequal in length; outer ramus two robust setae distally, long plumose setae on distal half of each margin; inner ramus without robust setae, plumose setae on distal part of inner margin. Telson slightly longer than wide (1.2 ×), cleft to 64%, each lobe apically rounded subquadrately; each lobe with two slender dorsal setae, one apical slender setae.

Male. Varies slightly in the setation and shape of uropod 3 rami.

Remarks. This species has similarities to the other blind *Haploops* species that have a narrow pereopod 7 basis. The differences and similarities are documented in Table 2.

As with *Haploops dauvini* sp. n., this species has strong similarities to four other species, especially *H. similis*. It has been noted before that *H. similis* is probably a complex of closely related, morphologically similar species (Kannevorff 1966, Mills 1971). The differences between the original description (Stephensen 1925), the specimens documented in Mills (1971) and the current species include the shape of the head anterior margin (sinusoidal in *H. kaimmalkai* and straight in *H. similis*); the proportions of antenna 1 articles (article 1 slightly shorter than article 2 in *H. kaimmalkai* and half the length of article 2 in *H. similis*); proportions of antenna 2 peduncular articles (article 4 shorter than article 5 in *H. kaimmalkai* and subequal in length to article 5 in *H. similis*); *H. kaimmalkai* has the posterior margins of gnathopods 1 and 2 and pereopods 3 and 4 with a strong setal fringe, this is absent in *H. similis*; pereopod 7 basis has straight margins in *H. kaimmalkai* (concave in *H. similis*); epimeron 3 has a small tooth and a ventral setal fringe in *H. kaimmalkai* (no tooth and no fringe in *H. similis*); and the setation of uropods 1 – 3 and the telson differs between the two species.

These differences indicate the distinctiveness of *Haploops kaimmalkai* as a new species within the complex of species surrounding *H. similis*.

Distribution. Icelandic Basin, Norwegian Channel, North Atlantic Ocean. Ranging at depths from 587–1388 m.

Table 2. Character differences between five blind *Haploops* species.

Character	<i>H. dauvini</i>	<i>H. kaaimalkai</i>	<i>H. abyssorum</i>	<i>H. lodo</i>	<i>H. similis</i>
Head – anterior margin	straight	sinusoidal	straight	sinusoidal	straight
A1 - length	subequal to A2	subequal to A2	A1 shorter than A2, but longer than A2 peduncle	A1 shorter than A2, reaching to end of A2 peduncle	A1 shorter than A2 but longer than A2 peduncle
A1 art 1/art 2/art 3	12.4/20/6.7	17.4/20/7.8	18/20/8	15.6/20/7.1	11.5/20/6.1
A2 art 4/art 5	art 4 = art 5	art 4 < art 5	art 4 < art 5	art 4 = art 5	art 4 = art 5
MD molar	medium and triturating	large and strongly triturating	?	not documented	Medium and triturating
MXP	outer plate reaching ¾ palp art 2 (in situ)	outer plate reaching equal topalp art 2 (in situ)	?	outer plate reaching to 1/3 palp art 3 (in situ)	Outer plate reaching ¾ palp art 2 (in situ)
MXP palp article 4	inserted slightly subterminally, longer than art 3, inner margin setose	inserted considerably subterminally, subequal to art 3, inner margin smooth	?	inserted slightly subterminally, longer than art 3, inner margin setose	Inserted considerably subterminally, subequal to art 3, inner margin smooth
Gnathopod 1	reaching to head anterior margin, ventrally smooth	reaching slightly past head anterior margin, ventrally slightly serrate	reaching beyond the head anterior margin, ventrally serrate	reaching beyond the head anterior margin, ventrally smooth	position to head anterior margin unknown, ventrally smooth
Coxa	carpus subequal in length to propodus	carpus longer than propodus	carpus slightly shorter than propodus	carpus longer than propodus	carpus longer than propodus
G1	long plumose setae	short simple setae	?	short simple setae	short simple setae
Coxa 2–3 ventral margin	no strong marginal setal fringe, just clumps on both anterior and posterior margins of merus	strong posterior marginal setal fringe; anterior margin no setae	?	no strong marginal setal fringe; merus anterior margin without setae	No marginal setal fringe, posterior margin of merus with occasional plumose setae, anterior margin without setae
P4 coxa	broad	narrow	broad	broad	broad
P4 basis	plumose setae on both margins	plumose setae on posterior margin only	plumose setae on both margins	plumose setae on posterior margin only	plumose setae on posterior margin and sparsely on anterior margin
P4 distal articles posterior margin	fine setal fringe absent	fine setal fringe present	fine setal fringe absent	fine setal fringe absent	fine setal fringe absent

Character	<i>H. dauvini</i>	<i>H. kaimalkai</i>	<i>H. abyssorum</i>	<i>H. lodo</i>	<i>H. similis</i>
P4 dactylus/propodus	dactylus < propodus	dactylus < propodus	dactylus > propodus	dactylus > propodus	dactylus < propodus
P5 basis	both margins broadly rounded	anterior margin broadly rounded, posterior margin sinusoidal	?	anterior margin narrowly rounded, posterior margin straight/truncated	Anterior margin weakly rounded, posterior margin weakly rounded
P5–6	propodus produced distally to form a lobe	propodus not produced distally, no lobe	?	propodus not produced distally, no lobe	propodus not produced distally, no lobe
P7 basis	concave margins, lobe deflected	straight margins, lobe not deflected	straight margins, lobe not deflected	concave margins, lobe deflected	Concave margins, lobe not deflected
P7 ischium	no anterodistal robust setae	three anterodistal robust setae	no anterodistal robust setae	five anterodistal robust setae	four anterodistal robust setae
P7 merus posterior margin	three robust setae, no plumose setae	four robust setae plus six long plumose setae	four robust setae, no plumose setae	three robust setae, no plumose setae	two robust setae, two distal long plumose setae
P7 merus/carpus/propodus/dactylus	10.4/10/4.4/?	13.2/10/4.9/2.4	10.9/10/7.1/4.3	10.6/10/3.5/2.7	13/10/5/4
Epimeron 3: posteroventral corner	narrowly rounded, no tooth, sparse ventral setae	subquadrate, tiny tooth, ventral fringe of setae	subquadrate?	subquadrate, tiny tooth, no ventral setae	Subquadrate, no tooth, no ventral setae
Urosomite 1	weak rounded carina	weak rounded carina	carinate?	weak rounded carina	no carina
Uropod 1	peduncle shorter than rami	peduncle longer than rami	peduncle subequal to rami	peduncle slightly longer than rami	peduncle longer than rami
Uropod 1 rami length	rami subequal in length	rami subequal in length	rami subequal in length	inner ramus slightly shorter than outer	inner ramus shorter than outer
Uropod 1 inner rami	2 robust setae, no setal fringe	0 robust setae, setal fringe on proximal half	0 robust setae, no setal fringe	0 robust setae, slight setal fringe	1 robust seta (inner margin), no setal fringe
Uropod 2 rami length	rami subequal in length	outer ramus shorter than inner	outer ramus shorter than inner	outer ramus slightly longer / subequal to inner	outer ramus slightly shorter than inner
Uropod 2 inner ramus	4 robust setae, no setal fringe	3 robust setae, strong setal fringe	3 robust setae, no setal fringe	3 robust setae, no setal fringe	3 robust setae, no setal fringe
Telson	1 distal robust seta and 2 medial plumose setae per lobe	0 distal robust setae (just 1 slender seta) and 2 medial plumose per lobe	0 distal robust setae and 0 medial plumose setae per lobe	1 distal robust seta and 2 medial slender setae per lobe	1 distal robust seta and 0 medial setae per lobe

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References

- Barnard JL (1954) Amphipoda of the family Ampeliscidae collected in the eastern Pacific Ocean by the *Velero III* and *Velero IV*. Allan Hancock Pacific Expeditions 19: 1–137.
- Barnard JL (1961) Gammaridean Amphipoda from depths of 400 to 6000 meters. Galathea Report 5: 23–128.
- Barnard JL (1967) New species and records of pacific Ampeliscidae (Crustacea: Amphipoda). Proceedings of the United States National Museum 121(3576): 1–20. <https://doi.org/10.5479/si.00963801.121-3576.1>
- Barnard JL, Karaman GS (1991) The families and genera of marine gammaridean Amphipoda (except marine gammaroids) Part 1. Records of the Australian Museum, supplement 13: 84–90.
- Barnard KH (1931) Diagnosis of new genera and species of amphipod Crustacea collected during the “Discovery” Investigations, 1925–1927. Annals and Magazine of Natural History 10(7): 425–430. <https://doi.org/10.1080/00222933108673327>
- Bellan-Santini D, Dauvin JC (1988) Elements de synthese sur les Ampelisca du Nord-Est Atlantique. Crustaceana supplement 13: 20–60.
- Bellan-Santini D, Dauvin JC (1997) Ampeliscidae (Amphipoda) from Iceland with a description of a new species (Contribution to the BIOICE Research Program). Journal of Natural History 31: 1157–1173. <https://doi.org/10.1080/00222939700770621>
- Bellan-Santini D, Dauvin JC (2008) Contribution to the knowledge of the genus *Haploops*, a new location for *Haploops lodo* (Crustacea: Amphipoda: Ampeliscidae) from the bathyal North Atlantic Ocean with a complement to the description of the species. Journal of Natural History 42: 1065–1077. <https://doi.org/10.1080/00222930701877557>
- Bruzelius RM (1859) Bidrag till Kannedomen om Amphipodernas inre byggnad. Ofversigt af Kongliga [Svenska] Vetenskaps- Akademiens Forhandlingar 16(1): 1–18.
- Chevreaux E (1887) Crustaces amphipodes nouveaux dragues par “l’Hirondelle” pendant sa campagne de 1886. Bulletin de la Société Zoologique de France 12: 566–580.
- Chevreaux E (1908) Diagnoses d’amphipodes nouveaux provenant des campagnes de la “Princesse-Alice” dans l’Atlantique nord. Bulletin de l’Institut Océanographique de Monaco 117: 1–13.
- Dang NT, Le H (2013) Ampeliscid crustaceans (Amphipoda: Gammaridea: Ampeliscidae) from the Vietnam Sea. Tap Chi Sinh Hoc 35(1): 140–152. <https://doi.org/10.15625/0866-7160/v35n2.3097>

- Dauvin JC, Alizier S, Weppe A, Gudmundsson G (2012) Diversity and zoogeography of Icelandic deep-sea Ampeliscidae (Crustacea: Amphipoda). *Deep Sea Research* 1(68): 12–23. <https://doi.org/10.1016/j.dsr.2012.04.013>
- Dauvin JC, Bellan-Santini D (1988) Illustrated key to *Ampelisca* species from the North-Eastern Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 68(4): 659–676. <https://doi.org/10.1017/S0025315400028782>
- Dauvin JC, Bellan-Santini D (1990) An overview of the Amphipod genus *Haploops* (Ampeliscidae). *Journal of the Marine Biological Association of the United Kingdom* 70: 887–903. <https://doi.org/10.1017/S0025315400059129>
- Dickinson JJ (1982) The Systematics and Distributional Ecology of the family Ampeliscidae (Amphipoda, Gammaridea) in the North-eastern Pacific Region. I. The genus *Ampelisca*. National Museums of Canada, Publications in Biological Oceanography 10: 1–39.
- Dickinson JJ (1983) The Systematics and Distributional Ecology of the Superfamily Ampeliscoidea (Amphipoda, Gammaridea) in the Northeastern Pacific Region. II. The Genera *Byblys* and *Haploops*. National Museum of Canada, Publications in Natural Sciences 1: 1–6.
- Gurjanova E (1951) Bokoplyvy morei SSSR i sopredelnykh vod (Amphipoda, Gammaridea). [Amphipods of the seas of USSR and adjacent waters (Amphipoda, Gammaridea)]. *Opre-deliteli po faune SSSR, Akademiya Nauk SSSR* 41: 1–1029.
- Gurjanova E (1955) Crustacea-Malacostraca Chukotskogo Morja i Beringova Proliva [Crustacea: Malacostraca of the Chukchi Sea and Bering Strait]. *Krajniji Severo-vostochn* 2: 169–214.
- Horton T, Lowry J, De Broyer C, Costello M, Bellan-Santini D (2013) Ampeliscidae Krøyer, 1842 In: Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO, Daneliya M, Dauvin J-C, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Holsinger J, Hughes L, Jaume D, Jazdzewski K, Just J, Kamal'tynov RM, Kim Y-H, King R, Krapp-Schickel T, LeCroy S, Lör A-N, Senna AR, Serejo C, Sket B, Tandberg A.H, Thomas J, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (2017) World Amphipoda Database. World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=101364> [accessed on 2017-07-26]
- Kaïm-Malka RA (2000) Elevation of two eastern Atlantic varieties of *Ampelisca brevicornis* (Costa, 1853) (Crustacea, Amphipoda) to full specific rank with redescription of the species. *Journal of Natural History* 34 (10): 1939–1966. <https://doi.org/10.1080/00222930050144792>
- Kaïm-Malka RA (2010) *Haploops longiseta*, a new species from the Atlantic Ocean (Crustacea, Gammaridea, Ampeliscidae). [Contribution to the knowledge of the *Haploops* genus. 6.] *Zootaxa* 2356: 57–68.
- Kaïm-Malka RA, Bellan-Santini D, Dauvin JC (2016) On some *Haploops* species collected in the North Atlantic Ocean with the description of *Haploops islandica* sp. n. (Crustacea: Gammaridea: Ampeliscidae) [Contribution to the knowledge of the *Haploops* genus. 8] *Zootaxa* 4179(1): 42–76. <https://doi.org/10.11646/zootaxa.4179.1.2>
- Kanneworff E (1966) On some amphipod species of the genus *Haploops*, with special reference to *H. tubicola* Liljeborg and *H. tenuis* sp. nov. from the Oresund. *Ophelia* 3: 183–207. <https://doi.org/10.1080/00785326.1966.10409642>

- Krøyer H (1842) Nye nordiske slægter og arter af amphipodernes orden, henhørende til familien Gammarina. (Forelobigt uddrag af et større arbejde). *Naturhistorisk Tidsskrift* 4: 141–166.
- Lilljeborg W (1852) Norges Crustaceer. Ofversigt af Kongliga Vetenskaps-Akademiens Forhandlingar 8: 19–25.
- Lilljeborg W (1855) Om Hafs-Crustaceer vid Kullaberg iskane. Ofversigt af Kongliga Vetenskapsakademiens Forhandlingar, Stockholm 12(3): 444–460.
- Metzger A (1875) Crustaceen In: Bericht über die Untersuchungs-Fahrt der Pommerania. Berlin. 277–309.
- Mills EL (1967) A reexamination of some species of *Ampelisca* (Crustacea: Amphipoda) from the east coast of North America. *Canadian Journal of Zoology* 45(5): 635–652. <https://doi.org/10.1139/z67-080>
- Mills EL (1971) Deep-sea Amphipoda from the Western North Atlantic Ocean. The family Ampeliscidae. *Limnology and Oceanography* 16(2): 357–386. <https://doi.org/10.4319/lo.1971.16.2.0357>
- Norman AM (1882) Report on the Crustacea. *Proceedings of the Royal Society of Edinburgh* 11: 683–689.
- Ren X (2006) *Fauna Sinica, Invertebra. Vol. 41, Crustacea, Amphipoda, Gammaridea (I)*. Science Press, Beijing, China, 588 pp.
- Sars GO (1879) Carcinologiske Bidrag til Norges fauna. I. Monographi over de ved Norges Kyster forekommende Mysider. Pt. 3. A.W. Brøgger, Christiania, 1–131.
- Sars GO (1882) Oversigt af Norges Crustaceer med foreløbige Bemærkninger over de nye eller mindre bekjendte Arter. I. (Podopthalmata - Cumacea - Isopoda - Amphipoda). *Videnskabs-Selskabet i Christiania* 18: 1–124.
- Sars GO (1895) Amphipoda. An account of the Crustacea of Norway, with short descriptions and figures of all the species. I. Cammermeyer, Christiania, 1–711.
- Stephensen K (1925) Crustacea Malacostraca VI Amphipoda 2. *Danish Ingolf Expedition* 3: 98–180.

