

Clinging onto Arctic Benthos: Biogeography of *Amathillopsis spinigera* Heller, 1875 (Crustacea: Amphipoda), including its redescription

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ABSTRACT

Amathillopsis spinigera Heller, 1875, is an enigmatic peracarid crustacean species found in the Arctic Ocean. During the summer of 2024, it was recorded in the HAUSGARTEN observatory for the first time, following 25 years of regular sampling as part of the Fram Strait Long-Term Ecological Research observatory. This study significantly broadens the known geographic and bathymetric range of *A. spinigera*, with a total of 46 specimens collected from HAUSGARTEN (HG) and cold seeps at Svyatogor Ridge, during two expeditions conducted in 2024. Further, our review of all publicly available database (historical) records for *A. spinigera* leads to an expansion of its depth range from 186 – 1972 m to 11 – 3182 m. Recent observations using remotely operated vehicles (ROVs) have confirmed their clinging behavior on organic structures such as worm tubes, likely elevating the species within the water column to facilitate food capture. Females at various life stages, including egg-bearing individuals, were observed alongside juveniles and males of different sizes, enabling a redescription of the species based on an integrative taxonomy approach that incorporates both molecular and morphological data. The study also highlights biogeographic patterns, with a notable preference for eastern occurrences along the Arctic continental slope. While gaps in data from Greenland and Canadian regions, coupled with minimal sampling in the Central Arctic Ocean, suggest potential sampling bias, circumarctic connectivity appears plausible. This inference is supported by high genetic similarity in barcode data from individuals found across distant geographic locations.

1. Introduction

Our understanding of deep benthic ecosystems in the Arctic is rapidly increasing with technological advances, improved accessibility, and methods for recording and collecting specimens (Ramirez-Llodra et al., 2024). In contrast to a lifeless, monotonous biome once described by

early explorers (Anderson and Rice, 2006), the Arctic Ocean's deep-sea floor contains many habitats, including canyons, rocky reefs, cold seeps, and dropstones (e.g., Bluhm et al., 2011; Buhl-Mortensen et al., 2010; Meyer et al., 2016; Ramirez-Llodra et al., 2024). Each habitat provides a foundation for benthic communities to emerge. An important component of benthic communities is the occurrence of three-dimensional

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structures formed by benthic organisms, such as polychaete tubes on soft sediment and corals on hard substrate. These biotic structures provide vital habitats and bases where invertebrates can take hold, gaining greater access to food resources, shelter, and nurse juveniles (Burgos et al., 2020; Roberts et al., 2006; Morganti et al., 2021). Although considerable research has focused on deep-water corals and their associated fauna (Hartmann et al., 2024; Roberts et al., 2006; Schwentner and Lörz, 2021), there is a limited understanding of the fauna linked to non-coral habitats (Beazley et al., 2013; Meyer et al., 2019).

The HAUSGARTEN (HG) observatory, part of the German Long-Term Ecological Research observatory established in 1999 (Soltwedel et al., 2005), is situated within a relatively compact area in the Fram Strait. This region holds critical importance as the only deep-water link connecting the landlocked Central Arctic Ocean to the world's oceans. Serving as a gateway to the Arctic Ocean, it may play a pivotal role in enabling potential shifts in the geographic ranges of boreal and Arctic species.

With growing use of high-resolution imaging technology and remotely operated vehicles (ROVs) in bathyal and abyssal zones, more associated fauna is being discovered and confirmed to show a substrate-clinging lifestyle (Lörz and Horton, 2021). One such group is the amphipod genus *Amathillopsis* Heller, 1875. The 16 species described are enigmatic and large predators (or micro-predators), ranging from 20 to 70 mm in total body length (Coleman, 1998; Coleman and Coleman, 2008; Varela et al., 2023). They are visually striking for their spine-like dorsal projections and raptorial gnathopods. *Amathillopsis* is found in all oceans and ranges from bathyal to abyssal depths, with the deepest observed morphotype being from 5559 m in the southeast Pacific (Lörz and Horton, 2021). Two species are known from the Arctic Ocean: *Amathillopsis spinigera* Heller, 1875 and *Amathillopsis affinis* Miers (1881).

Members of the genus *Amathillopsis* exhibit a clinging lifestyle, as functionally inferred by the strongly curved dactylus of pereopods 3 and 4 and the pereopods being flexed backward, which allows them to attach to objects for stability and feeding (McCloske, 1970; Lörz and Horton, 2021). However, most *Amathillopsis* species are collected using towed gear, leaving their *in-situ* conditions unknown. This clinging behavior has only recently been confirmed through ROV imagery, with individuals observed clinging to various organic structures, including polychaete worm tubes, sponges, and corals (Lörz and Horton, 2021). It is hypothesized that any object they cling to is a means of elevating them higher in the water column for feeding (Lörz and Horton, 2021; Varela et al., 2023). They likely used the raptorial structure of the mouthparts and gnathopods to capture their prey, such as zooplankton or small supra-benthic crustaceans from the water column (Lörz and Horton, 2021).

We provide new records of *A. spinigera* present within the Fram Strait in the HG and at cold seeps of the Svyatogor Ridge (Soltwedel et al., 2005; Linse), and new behavioral information as *in-situ* observed specimens were clinging to primary (natural) and secondary (anthropogenic) structures in 1522 m–1935 m depth. With the ROVs *KIEL 6000* and *Aurora*, in total 46 individuals, including ovigerous females, were brought to the surface. With this rich sample set, we used an integrative taxonomic approach to redescribe the species, provide insights into its ecology, and collate historical records to offer biogeographic context for its broad geographic and bathymetric distribution across the Arctic benthos. This study provides holistic information on this species' geographic and bathymetric distribution, which is critical in the context of accelerated climate change and biodiversity loss.

2. Material and methods

2.1. Collection of material

During the PS143/1 expedition in June 2024 aboard this RV *Polarstern* (Wenzhöfer, 2024), one morphotype of an amathillopsid amphipod

was seen on both, primary and secondary structures during two of the ROV *KIEL 6000* dives (Fig. 1A–D; Table 1). Specimens were collected with a variety of methods, including a net, the suction sampler, and still attached to retrieved gear. They were clinging to the frames of the experiments recovered during Dive 1 (PS143/1_24-1) to the ArcForce Lander near HG-II at 1,522m throughout the whole ROV action and surfacing. On deck, the specimens were manually removed from the experiment frames and transferred into seawater for further processing. A single individual was seen on a stick-like structure (Fig. 1A) and was collected with a net. Dive 2 (PS143/1_26-1) focused on recovering gear related to Larval Experiments from the vicinity of the Senke station, near HG-III at ~1771 m. The Larval experiments included five types of gear: one marker, one beacon, four frames, three tube traps, and three predator-exclusion cages. Similar to Dive 1, specimens remained clinging to the retrieved experiments during surfacing. Once the ROV *KIEL 6000* returned to the deck, specimens were placed into buckets with cold-filtered seawater. Each specimen was photographed in a cold container and preserved in individual containers with 96 % ethanol to allow future molecular studies (DNA extraction). Males were identified by the presence of penile papillae, and females were identified by the presence of oostegites. Juveniles were classified by the visual absence of oostegites and penile papillae (Eustace et al., 2016; Ingram and Hessler, 1987). Specimens were photographed with a Canon EOS 5D Mark IV and a mounted compact macro-objective EF50mm f/2.5. Specimens from the PS143/1 expedition are curated at the German Center for Marine Biodiversity Research (DZMB), Senckenberg am Meer, in Hamburg, Germany. Final museum storage for the HAUSGARTEN specimens will take place at the Senckenberg crustacean collection in Frankfurt and the Leibniz Institute for the Analysis of Biodiversity Change (LiB) collection in Hamburg. Museum numbers are provided in the Barcode of Life Database (BOLD, Ratnasingham and Hebert, 2007) dataset (dx.doi.org/10.5883/DS-HG5C - Project: HGMS Barcoding of benthic marine invertebrates found within the Fram Strait methane seep) (see Table 2).

The Ocean Census Arctic Deep (OCAD) expedition took place in May 2024 aboard the RV *Kronprins Haakon*, with the objective of documenting the biodiversity of the northernmost part of the Mid-Atlantic Ridge. The *Amathillopsis* specimens were retrieved during one of the dives of the ROV *Aurora* at seep sites of the Svyatogor Ridge (dive 16, OCAD9_24). Dense patches of siboglinid tubeworms were found with other associated fauna, including clinging amathillopsid amphipods observed with the cameras (Fig. 1E–H). These patches were sampled with the ROV arm and suction sampler. Once ROV *Aurora* was back on deck, faunal specimens were placed in buckets filled with cold (4 °C) filtered seawater, sorted by morphospecies, and photographed with a Nikon D6 and a mounted Sigma 50 mm f/1,2 DG DN Art L-mount lens. The specimens were kept in vials with 95 % ethanol and stored onboard at –20 °C, and at room temperature after. One to three legs of selected specimens were dissected for DNA barcoding. Specimens from the OCAD Expedition are curated at the Arctic University Museum of Norway (UiT).

2.2. DNA barcoding

Nine individuals from PS143/1 were selected for DNA barcoding. These individuals included three juveniles (HG500–502), three females (HG506–508), and three males (HG515–516, 518) (Table 1). DNA extractions were performed within 24 h after specimen fixation onboard the RV *Polarstern*. DNA was extracted from pleopod 1, thus avoiding damage to structures critical for potential morphological species identification. DNA was extracted using the NucleoSpin™ Tissue Kit (Macherey-Nagel), following the manufacturer's protocol with an overnight incubation (~12 h) and using the “high yield and high concentration” elution procedure. Following extraction, the obtained DNA was stored at –80 °C. Upon the RV *Polarstern*'s return to shore, the extracted DNA was transferred to the DZMB, where it was stored at –20 °C.

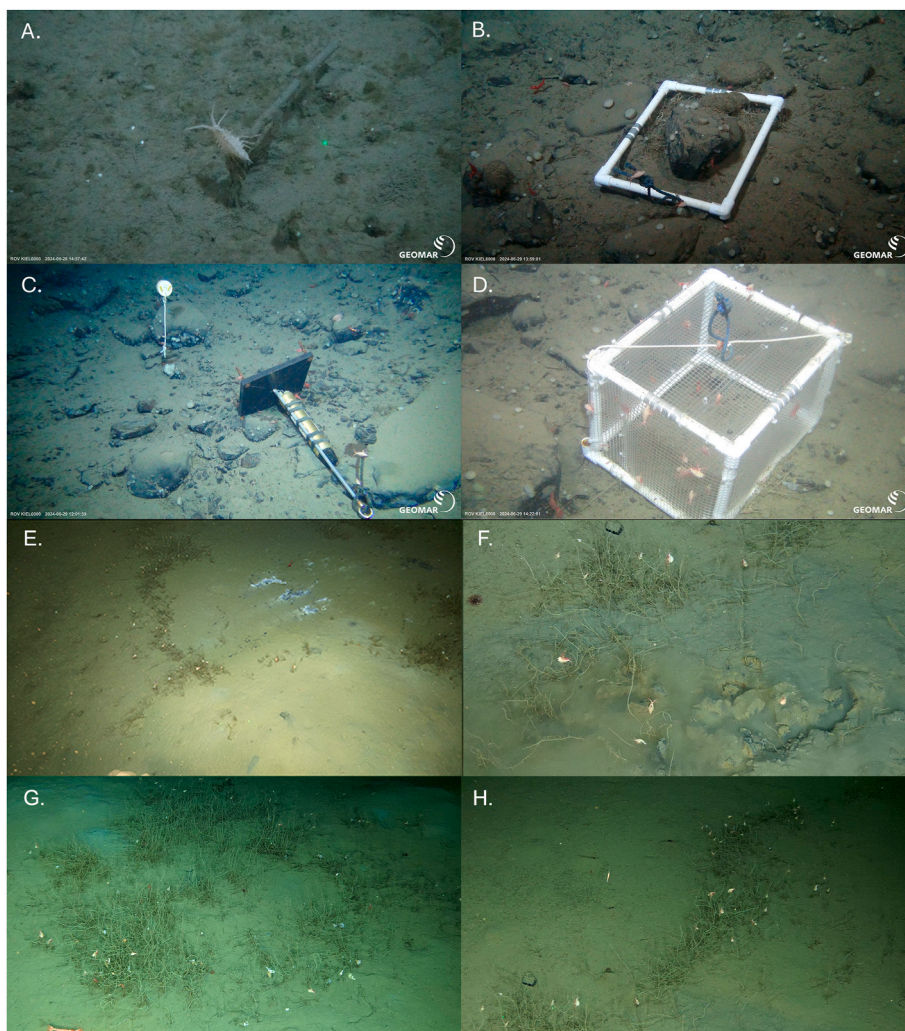


Fig. 1. Observations of *Amathillopsis spinigera* by the ROV KIEL 6000 during PS143-1. (A.) Single individual on a stick (primary structure) at HG-II Station. (B.-C.) Pairs seen on the site marker, beacon, and frame and (D.) multiples on cages associated with the Larval Experiments (secondary structures) near Senke/HG-III Station. Copyright: ROV KIEL 6000 Team / GEOMAR, Kiel. (E.-H.) Multiple individuals observed on worm tubes at seep sites of the Svygator Ridge during the Ocean Census Arctic Deep (OCAD) expedition in May 2024 during one of the dives of the ROV Aurora (dive 16, OCAD9_24). Copyright Ocean Census.

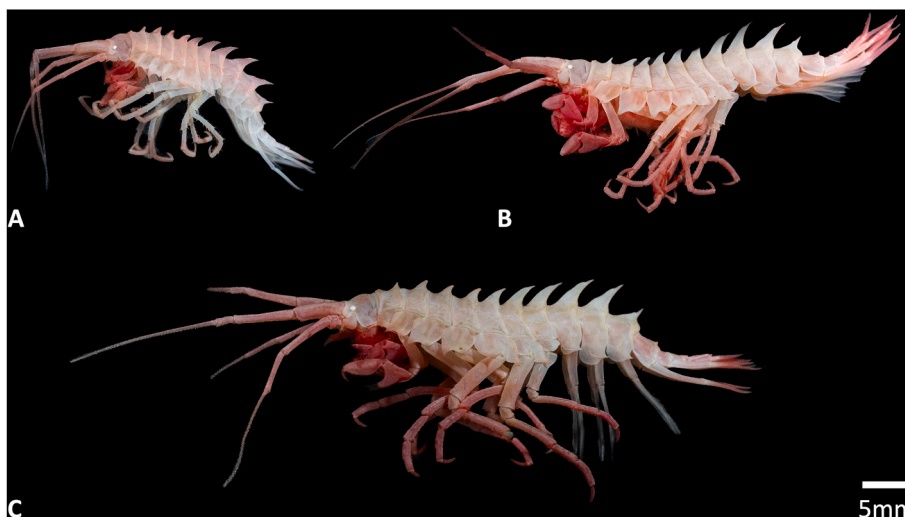


Fig. 2. Representative Specimens of *A. spinigera* collected during the PS143/1 expedition. All pictures refer to the 5 mm scale bar. A) Juvenile *A. spinigera* (HG501; total body length: 25.6 mm). B) Female *A. spinigera* (HG506; total body length: 29.6 mm). C) Male *A. spinigera* (HG515; total body length: 43.3 mm).

Table 1

Details of *Amathillopsis spinigera* investigated in this study. Most recent specimens were observed and collected by the ROV *Aurora* during the Ocean Census Arctic Deep (OCAD) expedition and ROV *KIEL 6000* during the PS143-1 expedition. The data source contains the abbreviations of Ocean Census Workshop (OCW), Tromsø Norges arktiske universitetsmuseum (TMU) or German Centre for Marine Biodiversity Research (DZMB). Except for the BOLD records included in the COI inferred phylogeny (highlighted in grey), all listed specimens were morphologically investigated by the authors. The currently accepted depth in meters was determined by matching the coordinates to IBCAO v5.

Process ID	Field ID	Cruise	Station	Station date	decLat	decLon	IBCAO v5 Depth [m]	Region	No. Indiv.	Source	DNA Barcode	Photo/ Drawing	Sex
AS188		OCAD24	ROV42-16-05	2024-05-17	78.39210	5.08550	−1972	Svyatogor ridge	2	OCW	no		NA
AS455		OCAD24	ROV42-16-05	2024-05-17	78.39210	5.08550	−1972	Svyatogor ridge	1	OCW	yes (Ocean Census specimen)		NA
AS457		OCAD24	ROV42-16-05	2024-05-17	78.39210	5.08550	−1972	Svyatogor ridge	2	OCW	yes (Ocean Census specimen)		NA
AS505		OCAD24	ROV42-16-04	2024-05-17	78.39210	5.08550	−1972	Svyatogor ridge	10	OCW	yes (Ocean Census specimen)		NA
Cr-10136	3306449361			1994-07-20	75.00440	−12.63780	−785	Grønlandshavet	1	TMU	no		NA
Cr-10179	3306449570			1995-07-01	73.71670	13.26670	−1676	Norskehavet	3	TMU	no		NA
Cr-10401	3306449017			1997-09-08	80.81670	13.88330	−1119	Questrenna	1	TMU	no		NA
Cr-10419	3306448936			1997-09-08	80.79830	13.86000	−1061	Questrenna, Svalbard N	1	TMU	no		NA
Cr-10775	3306450950			1981-08-29	68.60000	11.76670	−1200	Røstbanken	1	TMU	no		NA
Cr-10799	3306451162			1981-08-30	68.56670	11.78330	−1035	Røstbanken	3	TMU	no		NA
Cr-12028	3306455880			1979-08-19	70.83330	16.21670	−1682	Norskehavet	100	TMU	no		NA
Cr-12790	3306449386			1994-09-20	64.17330	−27.73000	−1051	Island W	1	TMU	no		NA
Cr-14321	3306461794			2005-09-07	80.65220	12.60390	−1156	Questrenna	1	TMU	no		NA
Cr-14920	3306457630			1980-05-31	69.83330	16.39170	−1700	Brottan, Andenes N	2	TMU	no		NA
Cr-14926	3306457629			1979-08-20	69.77500	16.25000	−1630	Norskehavet	1	TMU	no		NA
Cr-15038	3306460425			1981-03-22	63.28500	4.41330	NA	Norskehavet	1	TMU	no		NA
Cr-15208	3306459242			1980-05-31	69.83330	16.39170	−1700	Brottan, Andenes N	2	TMU	no		NA
DZMB-2-HH-20224	HG 477	PS143-1	24	2024-06-28	79.13548	4.87403	−1506	HG-II, Fram Strait	1	DZMB	no	Photo	NA
DZMB-2-HH-20240	HG 493	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20241	HG 494	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	RNA later	Photo	female, oostegites with setae
DZMB-2-HH-20242	HG 495	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	RNA later	Photo	male
DZMB-2-HH-20243	HG 496	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, immature
DZMB-2-HH-20244	HG 497	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	male
DZMB-2-HH-20245	HG 498	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20246	HG 499	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	male

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Table 1 (continued)

Process ID	Field ID	Cruise	Station	Station date	decLat	decLon	IBCAO v5 Depth [m]	Region	No. Indiv.	Source	DNA Barcode	Photo/ Drawing	Sex
DZMB-2-HH-20247	HG 500	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	BOLD:AAR3656	Photo & Drawing	juvenile
DZMB-2-HH-20248	HG 501	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	BOLD:AAR3656	Photo	juvenile
DZMB-2-HH-20249	HG 502	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	BOLD:AAR3656	Photo	juvenile
DZMB-2-HH-20250	HG 503	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20251	HG 504	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20252	HG 505	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	RNA later	Photo	female, with eggs
DZMB-2-HH-20253	HG 506	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	BOLD:AAR3656	Photo & Drawing	female, with eggs
DZMB-2-HH-20254	HG 507	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	BOLD:AAR3656	Photo	female, with eggs
DZMB-2-HH-20255	HG 508	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	BOLD:AAR3656	Photo	female, with eggs
DZMB-2-HH-20256	HG 509	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20257	HG 510	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20258	HG 511	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20259	HG 512	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20260	HG 513	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	female, with eggs
DZMB-2-HH-20261	HG 514	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	RNA later	Photo	male
DZMB-2-HH-20262	HG 515	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	BOLD:AAR3656	Photo	male
DZMB-2-HH-20263	HG 516	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	BOLD:AAR3656	Photo & Drawing	male
DZMB-2-HH-20264	HG 517	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	male
DZMB-2-HH-20265	HG 518	PS143-1	26	2024-06-29	79.10100	4.52100	−1870	Senke, Fram Strait	1	BOLD	no	Photo	male
DZMB-2-HH-20266	HG 519	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	male
DZMB-2-HH-20267	HG 520	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	male
DZMB-2-HH-20268	HG 521	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	male
DZMB-2-HH-20269	HG 522	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	male
DZMB-2-HH-20270	HG 523	PS143-1	26	2024-06-29	79.09876	4.49962	−1889	Senke, Fram Strait	1	DZMB	no	Photo	male
HOLOTYPE	Type01			1873-06-23	79.15056	60.53583	−186	Franz Josef Land	1	Heller (1875)	no	Photo & Drawing	juvenile
AMPNB144-14		MAREANO			67.80500	9.68500	−833	Røstbanken	1	BOLD	BOLD:AAR3656		NA
AMPNB300-15		MAREANO			68.18800	10.35600	−878	Røstbanken	1	BOLD	BOLD:AAR3656		NA
BENTH631-11		RUSALCA09	GD7-ot-16	2009-09-21	76.70167	−163.99303	−671	Chukchi Sea	1	BOLD	BOLD:AAR3656		NA

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Table 1 (continued)

Process ID	Field ID	Cruise	Station	Station date	declat	declon	IBCAO v5 Depth [m]	Region	No. Indiv.	Source	DNA Barcode	Photo/ Drawing	Sex
BENTH632-11		RUSALCA09	GD7-ot-16	2009-09-21	76.70167	-163.99303	-671	Chukchi Sea	1	BOLD	BOLD:AAR3656		NA
WW003-07	CA162				70.63300	-123.16700	-497	Beaufort Sea	1	BOLD	BOLD:AAR3656		NA

A 658 bp fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene was analyzed for DNA barcoding. The amplification of this fragment was performed in an Eppendorf AG Mastercycler using the echinoderm-specific forward primer I: LCOech1aF1 (5'-TTTCTTCTAC-TAAACACAAGGATATTGG-3') (Layton et al., 2016) and the universal reverse primer II: HCO2198 (5'-TAAACTTCAGGGTGACCAAAA AATCA-3') (Folmer et al., 1994) following the protocol of Christodoulou et al. (2019). The PCR mastermix (1 × 12.5 µl) consisted of 6.25 µl Accu Start PCR mix (2 × PCR master mix, Quantabio), 4.75 µl molecular grade H₂O, 0.25 µl of each primer, and 1 µl DNA template. Negative controls were used in all runs.

Successful PCR products were purified using ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fischer Scientific™) and run on a thermal cycler (incubation: 37 °C, 15 min; enzyme inactivation: 80 °C, 15 min). Paired-end sequencing was carried out by the sequencing facilities MacroGen Europe Inc. (Amsterdam, Zuidoost, The Netherlands) and Eurofins Genomics Germany GmbH (Ebersberg, Germany) using ABI 3730xl sequencers. Sequences were assembled, and primer sequences were removed in Geneious Prime® (Version, 2022.1.1; Biomatters, Auckland, New Zealand; Kearse et al., 2012). Geneious was used to edit and assemble forward and reverse chromatograms and to check potential contaminations using the implemented NCBI BLAST search tool (Basic Local Alignment Search Tool; Altschul et al., 1990). The nucleotide sequences of COI were translated into amino acid sequences to check for the presence of stop codons.

The eight reported *A. spinigera* COI sequences were compared to seven *Amathillopsis* COI sequences from publicly available data on BOLD v4 and NCBI GenBank. These included two *A. spinigera* individuals from 604 m in the Chukchi Sea (BENTH631-11 and BENTH631-11), two from 823 to 890 m in the Norwegian Sea (AMPNB300-15 and AMPNB144-14), and one from 502 m in the Beaufort Sea (WW003-07). Comparative sequences also included representatives for *Amathillopsis lowry* Lörz & Peart, 2023 (ON644605 – Lörz and Peart, 2023) and *Amathillopsis inkenae* Lörz & Horton, 2021 (MW726208 – Lörz and Horton, 2021). For the outlier, a representative from *Cleonardopsis* K.H. Barnard, 1916 retrieved from BOLD (AMPIV082-17) and chosen as an outlier group as it is in the same family (Amathillopsidae) but a separate subfamily (*Cleonardopsinae* Lowry, 2006). Sequences were aligned with a ClustalW cost matrix (gap open cost: 15, gap extend cost: 6.66; Thompson et al., 1994) and trimmed for a final alignment of 586 bp. To assess phylogenetic relationships, a maximum likelihood phylogenetic tree was calculated using IQ-TREE (v. 1.6.12, Nguyen et al., 2015). Substitution model TPM2+F + I was chosen with ModelFinder (Kalyaanamoorthy et al., 2017), and bootstrap support for each split was assessed via 1000 iterations using UFBoot2 (Hoang et al., 2018). The resulting tree was visualized using FigTree (v. 1.4.4, Rambaut, 2018).

2.3. Morphological taxonomy and presence records

The holotype of *A. spinigera* (Inv. Nr. 7466, Fig. 3) was examined and photographed with a NIKON SMZ25 stereomicroscope at the Naturhistorisches Museum Wien Crustacean collection (Fig. 3). The camera Nikon DS-Ri2 worked on the PC with the software NIS Elements BR 5.02.03, including scale bars for the single pictures. Stacks were assembled out of a series of pictures directly, and plates were arranged using Adobe Photoshop.

The HAUSGARTEN *Amathillopsis* and the OCAD Expedition specimens were morphologically examined and compared with the *Amathillopsis spinigera* holotype. From the HAUSGARTEN material, three COI barcoded specimens were chosen for the drawings (Table 1).

Presence records for *A. spinigera* were collated from multiple sources — publications and records from the Ocean Biodiversity Information System (OBIS, accessed on January 29, 2025), Global Biodiversity Information Facility (GBIF, accessed on January 27, 2025; <https://doi.org/10.15468/dl.z24qpa>), and BOLD v4. A global map of presence records (Fig. 4) was produced using ArcGIS Pro 3.4.2 (Esri, 2025).

Table 2
Pairwise distances between sequences specimens.

	HG500 _C \$	HG501 _C \$	HG502 _C \$	HG506 _C \$	HG507 _C \$	HG508 _C \$	HG515 _C \$	HG516 _C \$	AMPNB144 – 14	AMPNB300 – 15	BENTH631 – 11	BENTH632 – 11	WW003 – 07	MW726208.1	ON644605.1	Cleonardopsis _A MP1V082 – 17
HG500_CS																
HG501_CS	99.5															
HG502_CS	98.5	99														
HG506_CS	99.3	99.8	99.1													
HG507_CS	99.5	100	99	99.8												
HG508_CS	99.3	99.8	99.1	100	99.8											
HG515_CS	99.5	100	99	99.8	100	99.8										
HG516_CS	99.3	99.8	99.1	100	99.8	100	99.8									
AMPNB144-14	99.3	99.8	98.8	99.7	99.8	99.7	99.8	99.7								
AMPNB300-15	99.3	99.8	99.1	100	99.8	100	99.8	100	99.7							
BENTH631-11	99.3	99.8	99.1	100	99.8	100	99.8	100	99.7	100						
BENTH632-11	99.3	99.8	99.1	100	99.8	100	99.8	100	99.7	100	100					
WW003-07	99.1	99.7	99	99.8	99.7	99.8	99.7	99.8	99.5	99.8	99.8	99.8				
MW726208.1	80.3	80.7	80.4	80.9	80.7	80.9	80.7	80.9	80.9	80.9	80.9	80.9	81			
ON644605.1	76.3	76.7	76.5	76.8	76.7	76.8	76.7	76.8	76.7	76.8	76.8	76.8	77	78.4		
Cleonardopsis_AMPIV082-17	75.2	75.6	75.3	75.7	75.6	75.7	75.6	75.7	75.7	75.7	75.7	75.7	75.7	77.1	77	
Intraspecific average	99.6410256410256															
<i>A. spinigera</i> vs <i>A. inkenae</i> average	80.7769230769231															
<i>A. spinigera</i> vs <i>A. lowry</i> average	76.7230769230769															



Fig. 3. Photographs of Holotype. NMH Vienna Inv. Nr. 7466. Juvenile, 31.6 mm. A) habitus dorsal, B) habitus lateral, C) detailed view pleotelson dorsal, D) detailed view ventral Prn7: no papillae visible.

3. Results

3.1. Observation and collection of *Amathillopsis spinigera*

During the OCAD expedition, *Amathillopsis spinigera* were seen clinging to live siboglinid tubeworm cases at the Svyatogor Ridge cold seeps. A total of 14 individuals were collected from 1935 m (Table 1). These specimens were not sexed or categorized to life-stage.

During the PS143/1 expedition, we observed at least 72 and collected 32 *Amathillopsis spinigera* near two stations, HG-II and HG-III (Table 1). At the HG-II station (1522 m), a solitary individual was seen on what appeared to be a stick, and the individual was collected by a hand net of 1 mm mesh size (Fig. 1A).

At the HG-III station (1766–1780 m), the primary objective was to recover long-term Larval Experiments from 10 locations (Fig. 1B–D). A pair was observed and collected on the marker rope, and a pair was on the beacon base screws and beacon rope. One individual was seen on Larval Trap 7, five on the rope and weight of Larval Trap 1, and at least six on Larval Trap 6. Five were on the rope of Larval Frame 1, pairs on Larval Frame 2 and 3, and no amphipods on Larval Frame 4 (compare Fig. 1). More individuals were seen on the rope and cage sides of the Larval Cages, with at least 12 on Cage 2, 15 on Cage 3, and 16 on Cage 6. Thirteen individuals were collected with the suction sampler by “vacuuming” the sides of Larval Cages 3 and 6, and another 18 were opportunistically brought to the surface, either still clinging to the cage mesh or in the GeoBox of ROV KIEL 6000, as described above, showing

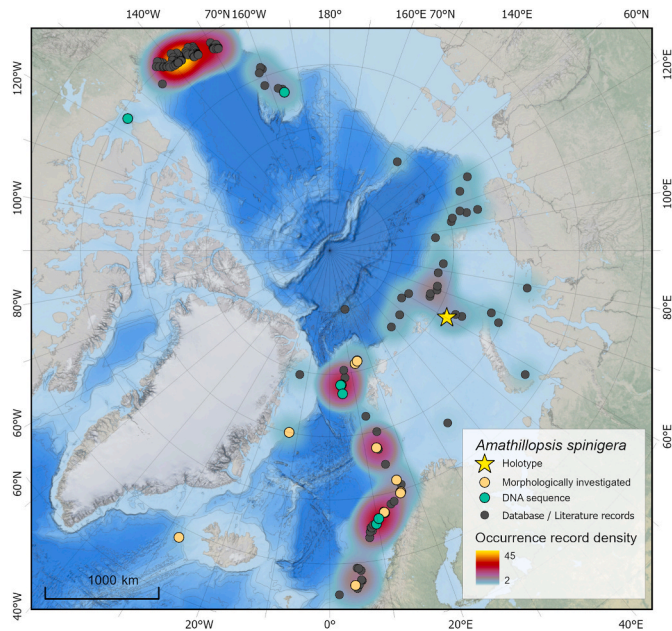


Fig. 4. Current distributional knowledge of *Amathillopsis spinigera* Heller, 1875, showing the type locality (star), publicly available occurrence records from databases and literature (GBIF, OBIS & Ramirez-Llodra et al. 2024; grey points), morphologically investigated specimens by the authors (orange) and specimens with additional genetic sequence data (cyan).

to be strongly attached to their substrate. The 32 HAUSGARTEN individuals spanned a range of genders and life stages. They consisted of three juveniles, 14 males, and 15 females. The females included one immature female (oostegites midway in development), one mature female (oostegites with setae), and 13 carrying eggs. The specimens also displayed a range of coloration—from all white to shades of pink, with the gnathopods and mouthparts being the darkest shade (Fig. 2). The total body length spanned between 23.5 mm and 43.3 mm.

3.2. Database records including DNA barcoding

Public records of *A. spinigera*, *A. affinis*, and other *Amathillopsis* species are present on OBIS, GBIF, Ramirez-Llodra et al. (2024), BOLD, and GenBank. *Amathillopsis affinis* has one collection record in BOLD, from a MAREANO beam trawl about 200–300 m depth in the Norwegian Sea (Hassel, 2014, Fig. 4, Supplementary Table 1). The material is stored at the Bergen Museum in Norway. A representative DNA barcode is absent on BOLD or GenBank for *A. affinis*. Considerably more records are available for *A. spinigera* in OBIS (187 records), Ramirez-Llodra et al. (2024) dataset (110 records), and GBIF (51 records; implemented in Fig. 4, all listed in Supplementary Table 1). The distribution records span the Norwegian Sea, one from the western Fram Strait (outside of the HAUSGARTEN), and multiple records in the Barents Sea, Kara Sea, Eastern Siberian Sea, and northern Canada. Unfortunately, some listed depths from database records were unreliable, with e.g. comma mistakes, hence, the realistic depth was determined by referencing the presented occurrence records to the latest IBCAO v5 GeoTiff (Jakobsson et al., 2024), resulting in a depth range between 186 and 1972 m of the investigated material and between 11 and 3182 m of public database records.

Five public records are available in BOLD for *A. spinigera*, including (1) two from the Norwegian Sea housed at the University of Bergen, Natural History Collections (AMPNG144-14, AMPNB300-15, 820–890 m), (2) two from the Chukchi Sea housed at the University of Fairbanks (BENTH631-11, BENTH631-11, 604 m), and one from the Beaufort Sea housed at Université du Québec a Rimouski (WW003-07, 502 m). Notably, two additional *A. spinigera* sequences are shown on the BOLD

map from the Fram Strait, but are not publicly available. Finally, two COI sequences for *A. inkenae* (MW726208) and *A. lowry* (ON644605) are available on GenBank, while no 16S sequences are available.

DNA barcoding of the six HAUSGARTEN specimens showed them to be a near-identical match to *A. spinigera* (Fig. 5). All individuals were placed in the *A. spinigera* BIN (BOLD: AAR3656). Percent sequence similarities ranged from 98.5 to 100 %, with a mean of 99.6 %. The phylogenetic tree had no apparent signals of phylogeographic structuring, with the six HAUSGARTEN specimens clustering with 100 % bootstrap support with the other available *A. spinigera* samples. *Amathillopsis spinigera* averaged 80.8 % sequence similarity to *A. inkenae* and 76.7 % to *A. lowry*.

3.3. Taxonomy

3.3.1. *Amathillopsis* Heller, 1875

Amathillopsis Heller, 1875: 35.—Stebbing, 1906: 384.—Gurjanova, 1955: 209 (key).—J. L. Barnard, 1969: 394.—J. L. Barnard and Karaman (1991): 390.

Acanthopleustes Holmes, 1908: 533 (type species *Acanthopleustes annectens* Holmes, 1908, by original designation).

3.3.2. Type species. *Amathillopsis spinigera* Heller (1875) (by original designation) Diagnosis (after Lowry, 2006)

Head. Deeper than long; lateral cephalic lobe subquadrate, truncated apically; anteroventral margin straight, anteroventral margin moderately recessed, anteroventral margin moderately excavate; rostrum short or moderate length; eyes present (round or ovoid) or absent. Body smooth, or dorsally carinate. Antenna 1 subequal in length or longer than antenna 2; peduncle with sparse slender setae; peduncular article 1 shorter than or subequal to article 2; article 2 longer than article 3; article 3 shorter than article 1; accessory flagellum short or minute, 1- or 2-articulate; calceoli present. Antenna 2 medium length; peduncle with sparse slender setae or none; flagellum shorter than or as long as peduncle.

Pereon. Coxae 1–4 longer than broad, overlapping, coxae 1–3 or coxae 1–4 ventrally acute. Coxae 1–3 similar in size or progressively larger. Gnathopod 1 subchelate; carpus shorter than or subequal to propodus; propodus with or without peg-like robust setae along palmar margin. Gnathopod 2 subchelate; coxa smaller than but not hidden by coxa 3 or subequal to but not hidden by coxa 3; carpus short, shorter than propodus. Pereopods: some or none prehensile. Pereopod 4 coxa ventrally acute, with or without small posteroventral lobe. Pereopod 5 coxa equilobate, with posteroventral lobe or with acute posterodistal lobe; basis slightly expanded or linear. Pereopod 6 subequal in length to, or longer than pereopod 7; basis slightly expanded or linear. Pereopod 7 shorter than or subequal in length to pereopod 5; basis slightly expanded or linear.

Pleon. Urosomite 1 carinate, urosomites 1–2 carinate or urosomites not carinate. Uropods 1–2 apices of rami without robust setae. Telson notched, emarginate or entire; dorsal or lateral robust setae absent; apical robust setae absent.

Species (17). *Amathillopsis affinis* Miers, 1881, *A. annectens* (Holmes, 1908), *A. atlantica* Chevreux, 1908, *A. australis* Stebbing, 1883, *Amathillopsis charlottae* Coleman, 1998, *A. comorensis* Ledoyer, 1986, *Amathillopsis grevei* J.L. Barnard, 1961, *Amathillopsis inkenae* Lörz & Horton, 2021, *Amathillopsis lowry* Lörz & Peart, 2023, *A. pacifica* Gurjanova, 1955, *Amathillopsis pacifica margo* J.L. Barnard, 1967, *Amathillopsis roroi* Coleman & Coleman, 2008, *A. septemdentata* Ledoyer, 1978, *Amathillopsis spinigera* Heller, 1875, *A. takahashiae* Tomikawa and Mawatari, 2006.

3.3.3. Redescription of *Amathillopsis spinigera* Heller, 1875

Holotype (Fig. 3; Fig. 6A and B). Inv. Nr. 7466. Juvenile, 31.6 mm.

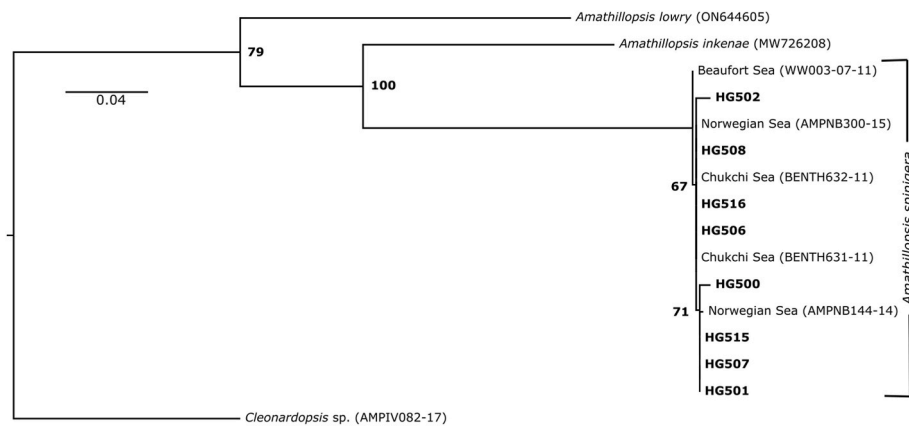


Fig. 5. Maximum-likelihood inferred phylogeny of *Amathillopsis spinigera* based on COI (586 bp). Study-generated sequences are in bold. Branch nodes show bootstrap values > 60.

Head slightly longer than pereonites 1, rostrum very short, lateral cephalic lobe rounded, eyes present, pigmented. Pereonites 1–7 with mid-dorsal processes increasing in size, Pleonites 1–3 each with a long dorsal upright-pointing process. Epimeral plates 1–3 with ventral margin curved and posteroventral corner produced into an acute tooth. Urosomite 1 with distinct dorsal process, urosomites 2–3 dorsally smooth (see Fig. 7).

3.3.3.1. Mouthparts. Missing from holotype. Pereon. Coxa 1 square shaped, coxae 2, 3 and 4 bilobed with the anterior lobe pointed, acute processes projecting anteroventrally. Coxae 5, 6 and 7 wider than long, bilobate, posterior lobe pointed posteriorly. Gnathopod 1 subchelate, basis posterior margin with row of robust setae, posterodistal lobe absent; ischium and merus short; carpus as long as propodus, ventral lobe broad, concave, allowing propodus to retract; propodus stout, tapering distally, palmar margin with long and short robust setae; dactylus 0.9 time as long as palmar margin. Gnathopod 2 subchelate, basis with posterodistal lobe present; carpus as long as propodus, ventral lobe broad, concave, allowing propodus to retract; propodus stout, dactylus as long as palmar margin. Pereopod 3 basis longer than merus, ischium short, as long as wide; merus margins subparallel with slight anterior curvature. Pereopod 4 is similar to pereopod 3. Pereopods 5–7 anterior and posterior margins of basis sub-parallel, linear, posterior lobe lacking; ischium short, as long as wide; merus margins subparallel with slight anterior curvature. Carpus, propodus and dactylus missing from pereopods 4–7.

Uropods. Uropod 1 long, peduncle length 1.5 times inner ramus; medial margin of peduncle with robust setae, inner ramus, lateral and medial margins with robust setae, outer ramus 0.9 times as long as inner, lateral and medial margins with robust setae. Uropod 2 with peduncle length 0.9 times inner ramus, lateral margin with robust setae, dorso-medial margin with robust seta distally; inner ramus, lateral and medial margins with robust setae; outer ramus subequal to inner, lateral and medial margins with robust setae. Uropod 3 peduncle length 0.7 times inner ramus; dorso-medial margin of peduncle with 1 robust setae distally; inner ramus with lateral and medial margins bearing robust setae, outer ramus 0.8 times as long as inner, lateral and medial margins with robust setae. Telson hourglass-shaped and distally bilobate; length 1.4 times width at the widest point and 1.75 times at the narrowest points, cleft 8.6 %. Each lobe smooth, no terminal setae.

HAUSGARTEN female (HG506, Fig. 7, Fig. 8, Fig. 9, Fig. 10), 29.6 mm total length, Cruise: PS143-1, Station: 26, Date: 2024-06-26, Latitude: 79.10100, Longitude: 4.52100, Depth: 1870 m.

Mouthparts (Fig. 8). Drawn from adult female: Upper lip with weakly convex apical margin, bearing two groups of setae. Lower lip with outer lobes broad, setulose; inner lobes indistinct, fused. Mandibles with left incisors bearing teeth, left *lacinia mobilis* with six teeth; accessory setal

row with distinct setae, some bearing a row of minute protuberances. Molar developed, tritulative. Palp articles 1, 2, and 3 in length ratio of 0.27: 0.8: 1, article 1 lacking setae, article 2 with marginal and sub-marginal setae, and article 3 with marginal and three terminal setae. Maxilla 1 with inner plate ovate and bearing plumose setae; outer plate with 9 serrate, robust setae; palp two-articulate, longer than outer plate, terminally with long robust setae. Maxilla 2 inner plate slightly broader than outer plate, bearing row of long plumose setae. Maxilliped, inner plate reaching base of palp, with three robust nodular setae on the distomedial margin, distolateral margin with apical robust setae; outer plate exceeding distal margin of palp article 1. Maxillipedal palp long, raptorial, four-articulate; article 2 and 3 heavily setose and widened medially; dactylus as long as article 3.

Antennae. Antenna 1 long, as long as body length, with peduncular articles 1, 2, and 3 in length ratio of 1.0: 1.0: 0.25. Article 1 longer than head length; accessory flagellum present; primary flagellum consisting of 50+ articles. Antenna 2 slightly longer than antenna 1; peduncular article 3 reaching to mid-length of peduncular article 2 of antenna 1, flagellum about the same length, as long as peduncle, 35+ articles.

3.3.4. Remarks

Sexual dimorphism. Sexual dimorphism beyond size differences is not apparent. This made the sex identification of the holotype difficult, and all visible structures indicate that the holotype is a juvenile specimen. Males seem to have a larger body size than females (Fig. 2). Total body length did vary among the developmental stages and sexes, with juveniles spanning 23.3–28.3 mm, females 28.3–34.6 mm, and males 40.8–43.3 mm.

Morphological variation amongst known material. Based on an illustration in [Barnard and Karaman \(1991\)](#) and photos of the new specimen, some potential differences were observed between the HAUSGARTEN specimens and the original description. These differences included: (1) the number of articles on the accessory flagellum (*A. spinigera* is biarticulate versus unarticulate); (2) the mandible palp article 3 to article 2 ratio (*A. spinigera* is 0.9 versus 1.1); (3) the ratio of antenna 1 article 3: 2: 1 (1: 3.1: 2.1 in *A. spinigera* versus 1: 1.6: 1.2); (4) the shape of the anterior lobe of coxa 5 (rounded in *A. spinigera* versus coming to a strong point); (6) the shape of the cephalic lobe (rounded in *A. spinigera* versus straight/subquadrate); (7) degree of separation between the carpus lobe and propodus; (8) degree of expansion of the pereopod 7 basis dorsal posterior lobe; (9) degree of spininess of the posteroventral corners on the epimeron 1–3; (10) degree of pointedness and angle of the pereon dorsal projections; and (11) degree of pointiness of the urosome 1 dorsal projection. However, genetic evidence clearly points to low genetic divergences in this group, and these have to be considered at the intraspecific level of variability for now. Additionally, the BoLD photo of *A. spinigera* from the University of Bergen does appear

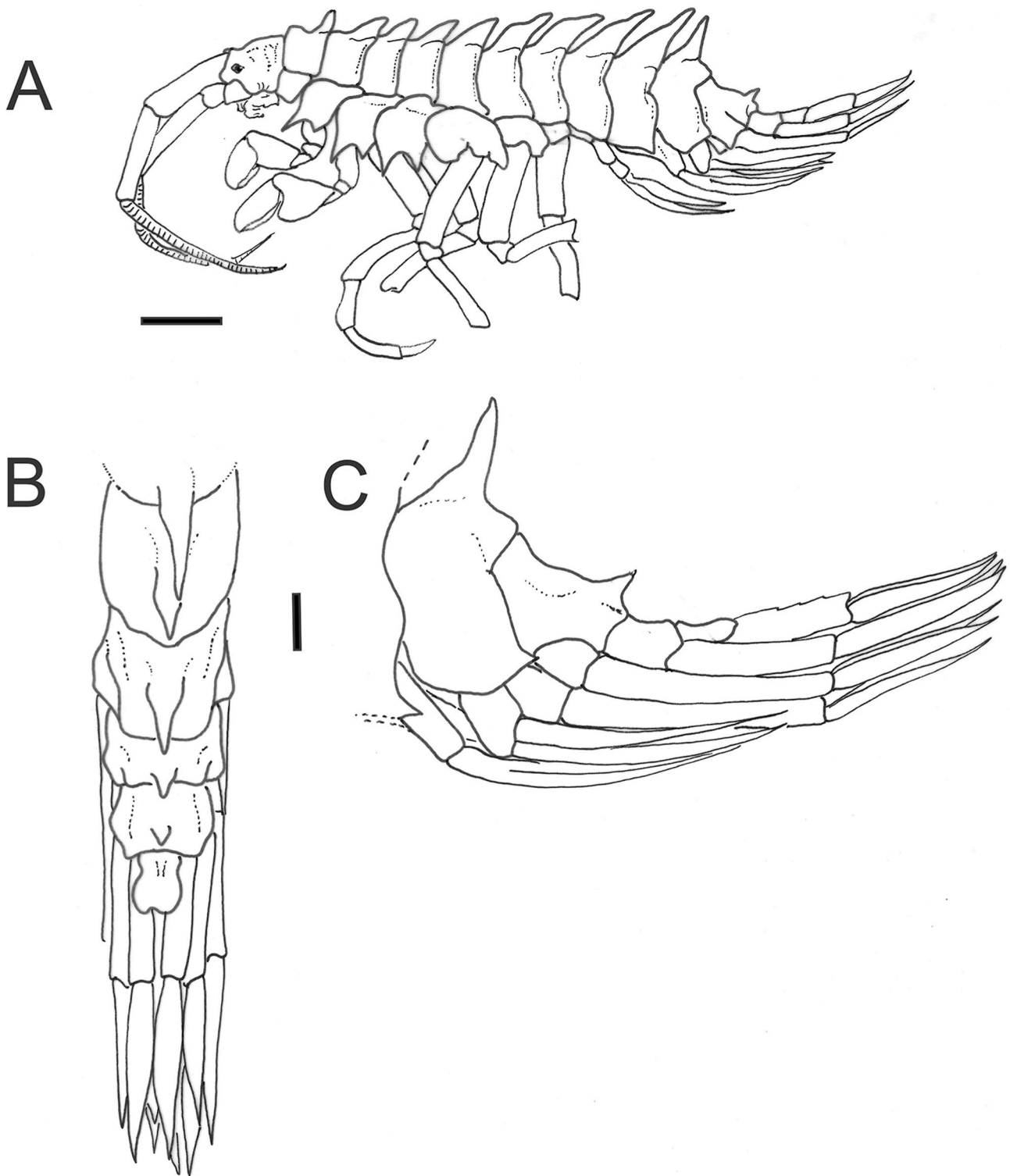


Fig. 6. A lateral drawing of holotype (Scale bar 5mm), B dorsal view of telson and spination from holotype, C lateral drawing of telson from holotype, B & C: Scale bar 1mm.

to share some morphological features with the *A. spinigera* illustration, namely the antenna 1 article ratios, the shape of coxa 5, and the general shape of the dorsal projections.

4. Discussion

The numerous specimens of *Amathillopsis spinigera* collected in

HAUSGARTEN, combined with those from the Ocean Census, offer a unique opportunity to comprehensively analyze this species and its distribution (Fig. 4). The concept of morphotype identification, supported by DNA barcoding, has facilitated the redescription of *A. spinigera* within a biogeographic framework. This species demonstrates a broad vertical distribution, ranging from the shelf to bathyal depths highlighting that the bathymetric range of *A. spinigera* extends deeper than

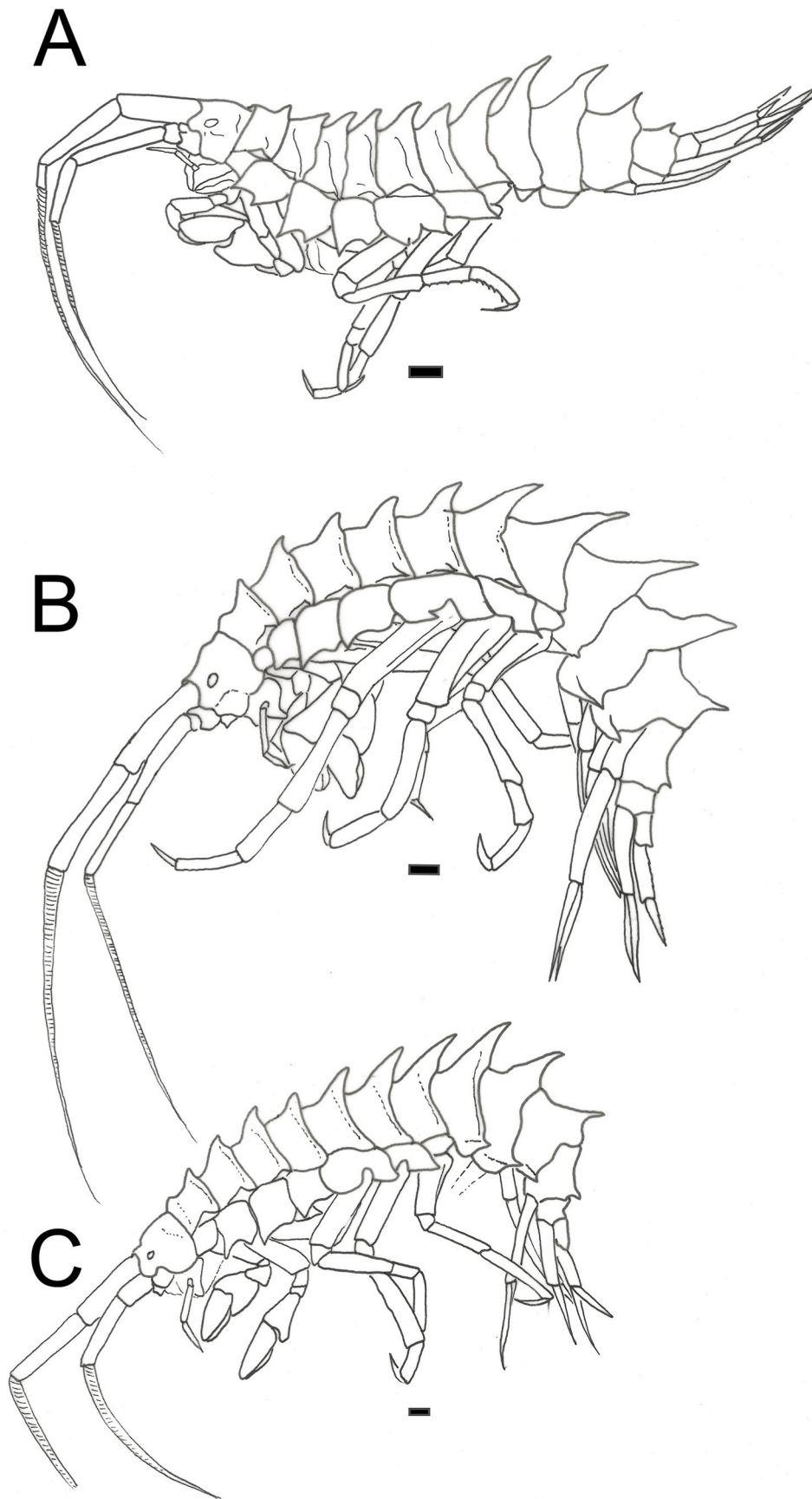


Fig. 7. A lateral drawing of female oov. (HG506), B lateral drawing of male (HG516), C lateral drawing of juvenile (HG500), Scale bar 1mm.

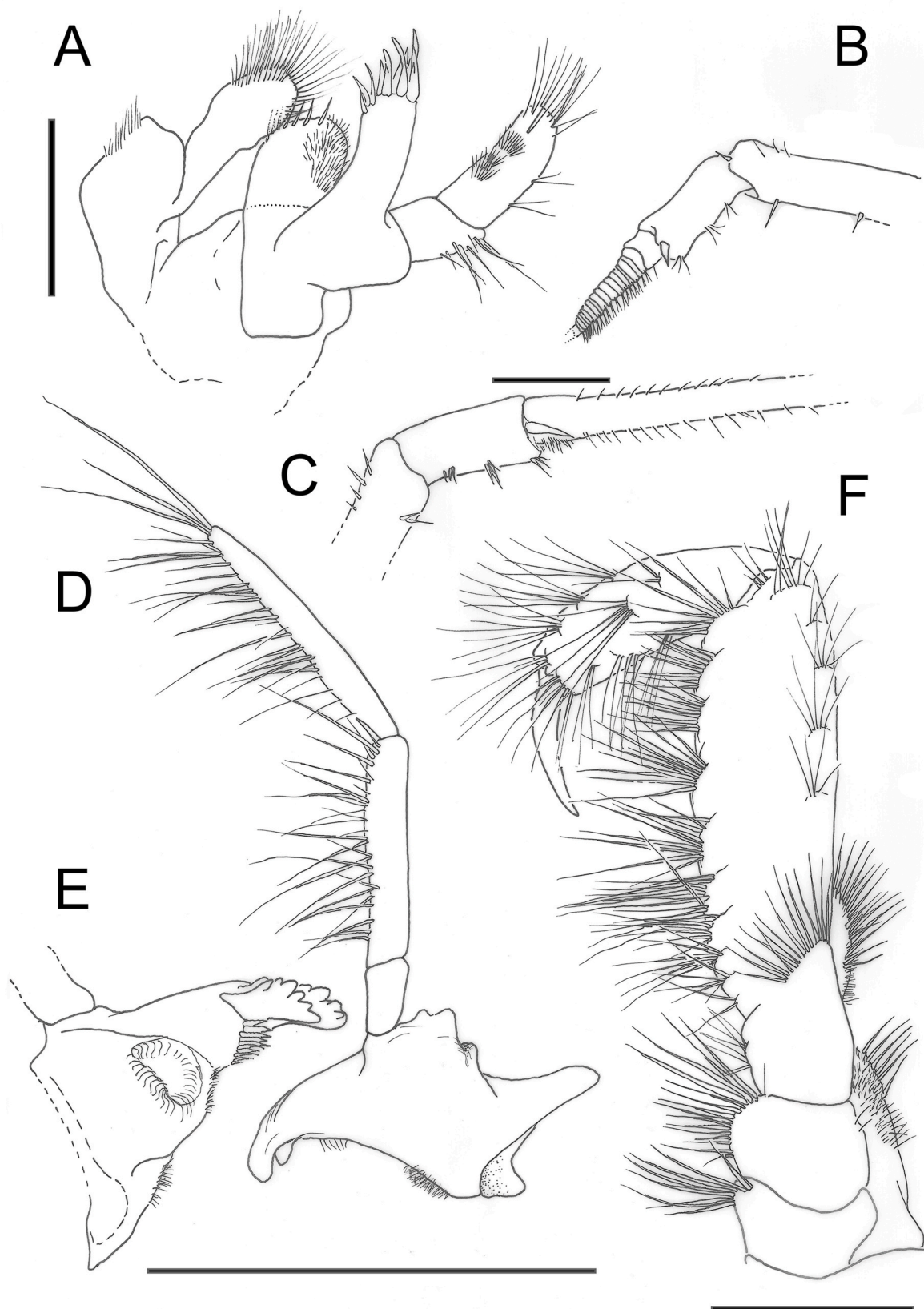


Fig. 8. Mouthparts and Antenna. A maxille 1,2 as dissected together of female (HG506), B antenna of female inner view (HG506), C antenna of male (HG516), D left mandible of female (HG506) outer view, E left mandible of female (HG506) inner view, F maxilliped of female (HG506).

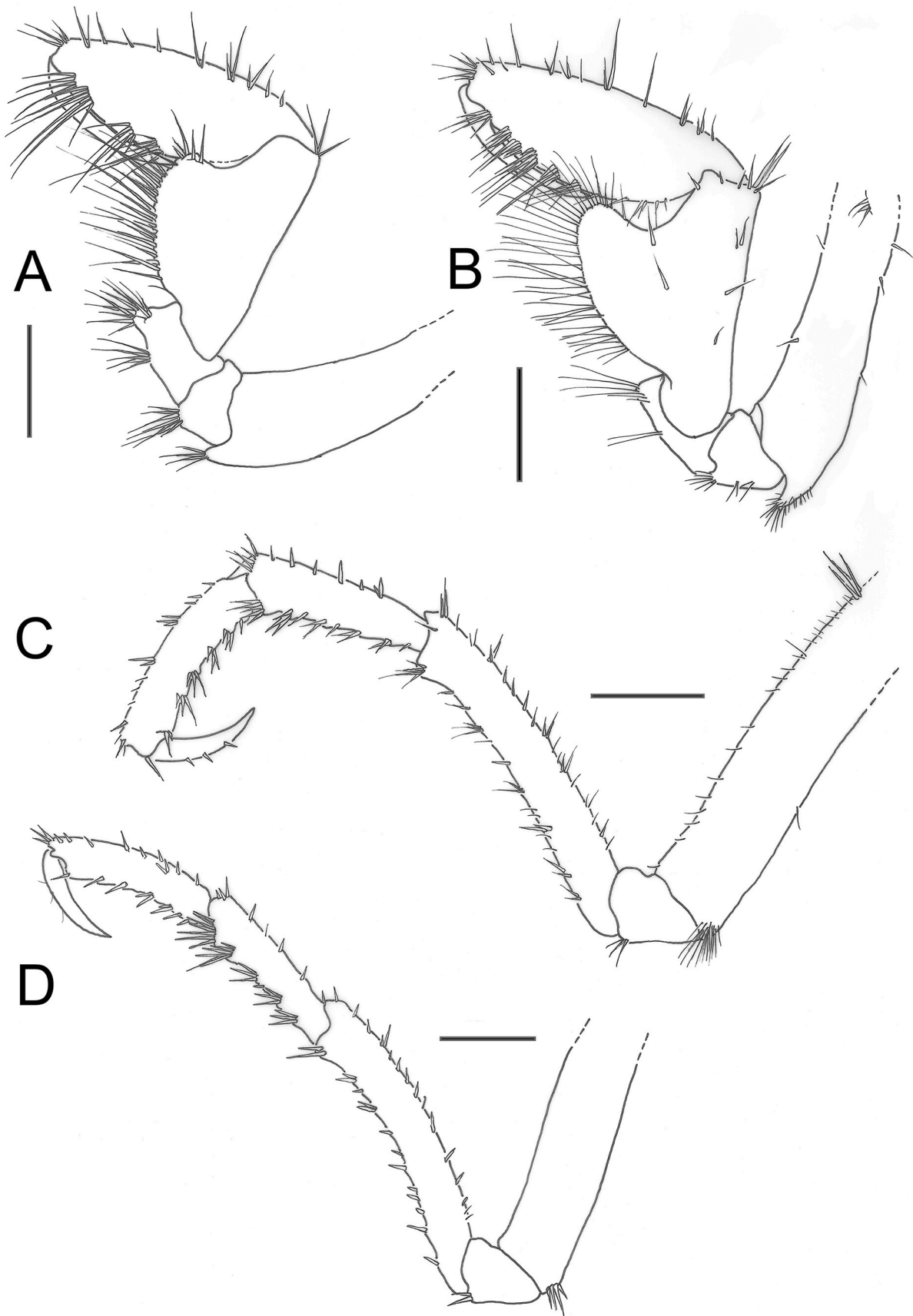


Fig. 9. Anterior legs of female (HG506). A Gnathopod 1, B Gnathopod 2, C PIII, D PIV. Scale bar 1 mm.

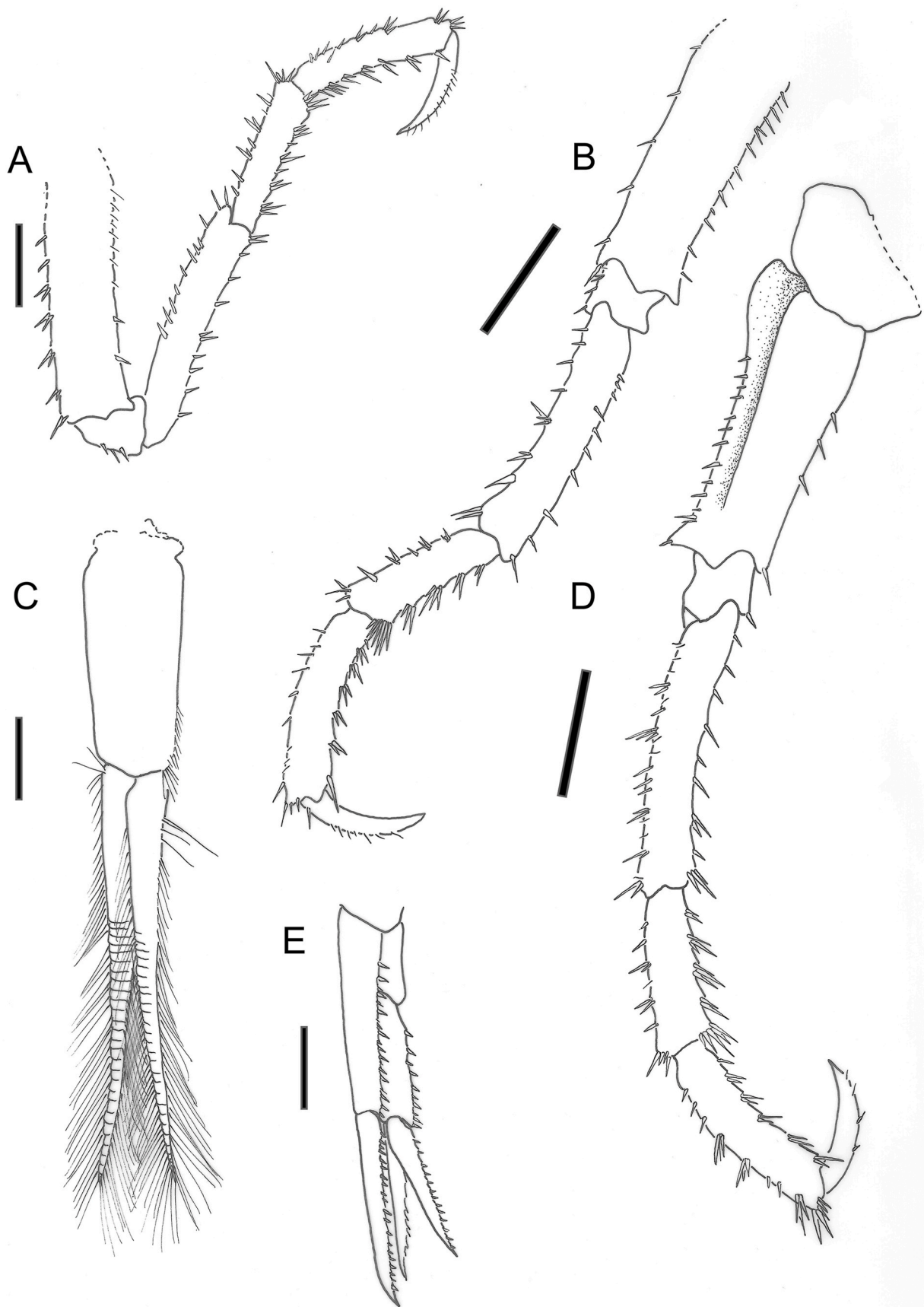


Fig. 10. Posterior legs and pleopods of female (HG506). A PV, B PVI, D PVII, C Plp2, E Urp. Scale bar 1 mm.

previously documented. Such eurybathic distribution is characteristic for Arctic peracarid crustaceans found in the Eurasian Arctic (Brandt et al., 1996; Uhlir et al., this issue). This species cannot be considered endemic specifically to the HAUSGARTEN region. In HG, specimens were collected at depths of 1199–1255 m near to the station HG-I, recognized as an active methane cold seepage area (Linse et al., this issue), indicating their occurrence in different habitats as long as structures to cling to are present.

An intriguing observation is that individuals of *Amathillopsis* species are often seen clinging in pairs or triplets (Lörz and Horton, 2021). During this study, over a dozen specimens were found at a single location. Fig. 1 highlights the occurrence of *A. spinigera* among methane seep-associated fauna located on the northwestern Vestnessa Ridge (Linse et al., this issue). Further exploration into their clinging behavior suggests a possible association with breeding pairs and structural elements. The larger size of males raises questions about potential competitive dynamics. Additionally, the dispersal range of juveniles may warrant further consideration. Bueno et al. (2019) investigated the dynamics of juvenile amphipods in algae of shallow waters that juvenile amphipods may have higher dispersal potential by colonizing more distant areas and/or patches with variable amounts of available substrate when compared to adults. Interestingly, database records reveal an eastern trend along the Arctic continental slope. However, is this pattern indicative of real distribution, or could it reflect sampling bias? If *Amathillopsis* had a presence in Greenlandic waters (East Greenland shelf), it would likely have been identified in previous sampling (Brandt et al., 1996) or BIOICE or IceAGE stations in the Denmark Strait (Brix et al., 2014). Notably, Ramirez-Llodra et al. (2024) did not report this species below 500 m. Given the cold waters flowing along East Greenland and the absence of specimens from HAUSGARTEN sites, this trend may reflect a true distribution pattern rather than sampling bias. The limited sampling due to ice cover and reduced research efforts in Greenland, combined with minimal Central Arctic sampling, suggests potential absence bias. The generally low taxa uniqueness in the Central Arctic Ocean (Ramirez-Llodra et al., 2024; Søhol, 2025) and the Fram Strait's role as the sole deep-water connection for species dispersing into the Arctic Ocean increase the likelihood of a circumarctic distribution of *A. spinigera* and a potential connectivity of the populations of *A. spinigera* surrounding the deeper parts of the Central Arctic Ocean. Future research should focus on understanding population connectivity across the Central Arctic Ocean, particularly in sampling hotspots (Fig. 4) like the Chukchi Sea and HAUSGARTEN in the Fram Strait.

CRedit authorship contribution statement

Saskia Brix: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Thea Sophie Elsig:** Writing – review & editing, Visualization, Methodology. **Patricia Esquete:** Writing – review & editing, Visualization, Validation, Investigation, Data curation, Conceptualization. **Áki Jarl Láruson:** Writing – review & editing, Visualization, Validation, Resources, Investigation, Formal analysis, Data curation. **Katrin Linse:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Data curation. **Elisabeth Schaal:** Writing – review & editing, Visualization, Methodology, Investigation. **Lydia Anastasia Schmidt:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Data curation. **Carolyn Uhlir:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **Johanna N.J. Weston:** Writing – review & editing, Writing – original draft, Validation, Methodology, Data curation, Conceptualization. **Anne-Nina Lörz:** Writing –

review & editing, Validation, Supervision, Methodology, Investigation, Formal analysis.

Data Availability

GenBank accession numbers and/or NoLD number for DNA sequences are provided via the BOLD project entitled **Barcoding of benthic marine invertebrates found within the Fram Strait methane seep**, project code HGMS (HausGarten Methane Seep).

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr2.2025.105552>.

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