



A new species of *Fissidentalium* (Scaphopoda: Dentaliidae) in association with an actinostolid anemone from the abyssal Labrador Sea

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Received: 19 April 2024 / Revised: 5 September 2024 / Accepted: 1 October 2024
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Abstract

The benthic biodiversity of the abyssal Labrador Sea was investigated using Agassiz trawl and in situ imagery. A megafaunal scaphopod associated with an epizoic anemone was recovered from soft sediments. Morphological and molecular investigations revealed the scaphopod to be an undescribed species in the dentaliid genus *Fissidentalium* P. Fischer, 1885. The new scaphopod species is characterised by a large size for the genus, is moderately curved, with numerous narrow, longitudinal ribs (60 ribs at 11 mm diameter ventral aperture), a dentaliid radula, and is described herein as *Fissidentalium aurae* sp. nov. The new species shows a close genetic relationship to congeners of *Fissidentalium* and separates from the sister genera *Dentalium* Linnaeus, 1758 and *Antalis* H. Adams & A. Adams, 1854. Genetic COI barcoding of the epizoic anemone suggests the species is a member of the family Actinostolidae Carlgren, 1932. The discovered association of a burrowing scaphopod with an epifaunal anemone at abyssal depth is a new record for the region and is indicative of how little is known about symbioses in the deep sea.

Keywords Species-pair-associations · Ocean seafloor observation system · Abyssal plain · Taxonomy · Lebensspuren

Introduction

The marine realm is a challenging environment, and many organisms have developed a type of living together to benefit from each other's presence, in symbiosis, as defined by de Bary (1879). Symbiotic relationships are divided into the four different interaction types mutualism, commensalism, parasitism and amensalism, split into obligate and facultative dependencies, and by types of physical association (van Beneden 1873; Apprill 2020). Symbiotic associations can be found from shallow, nearshore waters to the deep sea.

Well known are the shallow water associations of stone corals with algae, of damselfish with anemones and of hermit crabs, using gastropod shells as a cover for their soft body parts, with sea anemones covering the gastropod shells (e.g. Vafeiadou et al. 2012; Roux et al. 2020; van Oppen and Medina 2020). Chemosynthetic symbioses are especially known from deep-sea habitats like hydrothermal vents, methane seeps and whale falls, where hydrothermal vent clams or gastropods profit from chemosynthetic endosymbionts (e.g. Dubilier et al. 2008; Treude et al. 2009; Chen et al. 2018). Lesser known are associations from non-chemosynthetic, deep-sea habitats, for example from mesophotic deep-water corals or bathyal and abyssal habitats (White et al. 1999; Buhl-Mortensen and Mortensen 2004; Girard et al. 2016).

Reynolds (2002) reviewed symbioses in Scaphopoda, dividing upon commensalism, parasitism and mutualism in species-pair associations. Commensalism is reported for ciliates living in the mantle cavities of scaphopods (Reynolds 1990). Parasitic relationships comprise ciliates and platyhelminth larvae in the scaphopod bloods (Bois-sevain 1904; Arvy and Gabe 1951), cercariae in gonads (Arvy 1949; Cribb et al. 2001), ectoparasitic copepods in the mantle cavity and endoparasitic nematodes (Davies

Communicated by B. A. Bluhm

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1987). The most distinct symbioses are mutualistic relationships in which sessile taxa like anemones, corals and barnacles live epizoic on the shell of the scaphopod, which can be found from shallow, nearshore waters to abyssal depths (e.g. Kozloff 1990; Zibrowius 1998; White et al. 1999). The benefits of these associations are suggested to be commensal or mutualistic. The epibiont has the benefit of being carried around, gaining access to resuspended organic particles, whilst the scaphopod might gain protection from predation (Reynolds 2002). These species-pair associations have mostly been reported from dentaliid scaphopods, especially of the genus *Fissidentalium* (Riemann-Zürneck 1973; Shimek and Moreno 1996; Shimek 1997; Zibrowius 1998; White et al. 1999; Reynolds 2002).

The genus *Fissidentalium* in the family Dentaliidae Children, 1834 comprises 61 nominal species. They are distributed in all oceans and from shallow continental shelves to abyssal depths, with 12 species reported from the abyss (Steiner and Kabat 2004; WoRMS Editorial Board 2024). Most species occur in the West Pacific, Indo-West-Pacific and Indian Ocean. Four species are known from the East Pacific whilst five and four species are known from the East and West Atlantic, respectively. The Southern Ocean only hosts two species of *Fissidentalium*. In his analysis of the inhabited depth of western Atlantic and Indo-Pacific scaphopods, Scarabino (1979, 1995) noted that *Fissidentalium* were preferentially distributed in bathyal and abyssal depths. Regarding eurybathy in *Fissidentalium* species, several species are only known from their type locality, 20 species have an eurybathic range of less than 200 m, and seven species show extended eurybathy (Brey et al. 1996), with depth distributions ranging of over 1000 m (Steiner and Kabat 2004). These latter species include the trans-Atlantic species *F. candidum* (Jeffreys, 1877) and *F. capillosum* (Jeffreys, 1877), both reported from the continental shelf and upper slope to abyssal depths. At present, five nominal species of *Fissidentalium* are listed as accepted in WoRMS (WoRMS Editorial Board 2024) with bathyal and abyssal type localities in the North Atlantic. *F. candidum* from West Greenland, *F. capillosum* from East Greenland, *F. paucicostatum* from West European basin, *F. semives-titum* from off West Sahara and *F. concinnum* off Guinea. Only *F. candidum* and *F. capillosum* are reported from sub-polar North Atlantic waters.

The aim of this study is to describe the encountered species-pair-association of a dentaliid scaphopod with an actinostolid anthozoan from abyssal depth of the sub-polar Labrador Sea. The description is supported by in situ imagery of an ocean seafloor observation system and bar-coding analyses of scaphopod and anemone. Based on the results, we describe a new species of *Fissidentalium* from the Labrador Sea.

Materials and methods

Study site

The Labrador Sea, situated between the north-eastern coast of Canada and western Greenland, is the coldest and freshest basin of the North Atlantic and susceptible to climate change (Yashayaev 2007; Yashayaev and Loder 2017). Its boundary to the North is the Davis Sea and is flanked by Greenland to the South-East, and Labrador and Newfoundland to the South-West. The bathymetry of the Labrador Sea can be subdivided into the wide continental shelf and relatively gentle continental slope on its western side and a narrow shelf and steep continental slope on the eastern side, with the abyssal Labrador Basin in-between (Chalmers and Pulvertaft 2001; Coté et al. 2019).

The Labrador Sea hydrography is of continuous scientific interest as it is an area of dynamic warm Atlantic to cold sub-Arctic water conversions (e.g. Lazier 1980; McCartney and Talley 1982; Straneo 2006). Increased sea ice melt has affected freshening inflow which might affect deep mixing of water masses and impact phytoplankton blooms and the benthic communities below (Zhai et al. 2013; Yashayaev et al. 2015).

Data collection

During the IceDivA2 expedition on RV Sonne (SO286) in November 2021, pelagic and benthic habitats were investigated in international waters of the Labrador Sea around 58°N and 054°W (Brix et al. 2023). Megabenthic fauna (> 1 cm in size) was collected by Agassiz trawl (AGT) and visually explored by an Ocean Floor Observation System (OFOS) in the Labrador Sea Basin at abyssal depths of 3380 to 3390 m (Fig. 1).

An AGT with an opening frame of 3.5 m width, 0.7 m height and 8.7 m long net of 1 cm mesh size was deployed to collect benthic megafauna and trawled for 20 min at 1 km along the seafloor. At arrival on deck, the catch was sieved over staggered sieves of 1 cm, 1 mm and 0.5 mm mesh size and visible fauna was removed for taxon identification, live photography, tissue sampling and fixation.

Live collected scaphopod specimens for taxonomic studies were fixed in 96% pre-cooled ethanol for molecular and morphological analysis. Most live collected scaphopods had an epizoic anthozoan attached, which were not removed to facilitate the description of the anemone. Further collected shell debris, which had no anemones attached, was preliminary fixed in 96% ethanol and then air dried.

In situ seafloor imagery

RV Sonne had a vessel owned OFOS with a tethered winch system of maximum 6000 m operating depth and was equipped with one high-definition serial digital interface

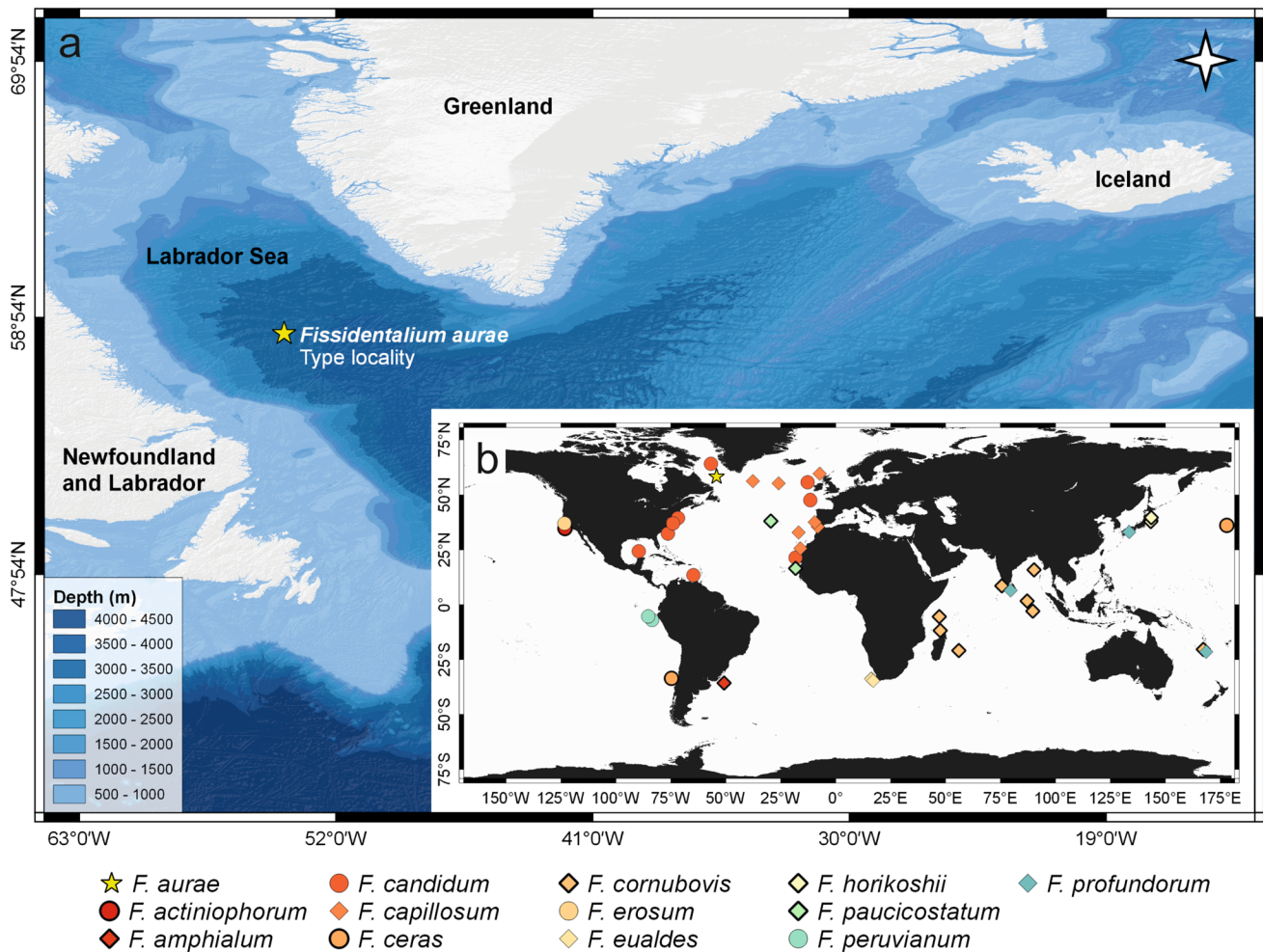


Fig. 1 Map of abyssal records of *Fissidentalium* species. **a** Type locality of *Fissidentalium aurae* sp. nov. in the Labrador Sea, 3387 m depth; **b** Global distribution of further 12 recent species of *Fissidentalium* with abyssal records

(HD-SDI)camera, one internet protocol (IP) video camera, one still camera (Canon EOS 5D Mark IV, 4096×2160 pixels, 4 K), two flashlights for still camera, four underwater lights, three red point lasers 18 cm apart and one altimeter. An ultra-short baseline system (USBL) Posidonia transponder was attached to the OFOS during the deployment, recording the positions and tow-speeds when the images were captured. The OFOS was deployed from the starboard side of the vessel and towed at a speed of 0.5 knots for 1.5 nautical miles at a minimum distance of 1.5 m above the seafloor. Still images were taken in a set 10 s photo interval along the transect line.

The OFOS still images were assessed to count selected taxon presences in four ways: (1) the presence of scaphopod shells visible on the substrate surface, (2) scaphopods carrying a light-coloured anemone and associated with a Lebensspur, (3) light-coloured anemones without a Lebensspur and (4) red-coloured anemones without a Lebensspur. The number of anemones without a Lebensspur was counted to assess

the abundance of anemones on scaphopods in the soft bottom habitat compared to those not attached to scaphopods. Lebensspuren, meaning traces of life, are biologically formed sedimentary structures (for classification see Miguez-Salas et al. 2024). To account for camera lens edge distortion effects, the images were split into 100 equal sized rectangles and the outer rectangle layer was excluded, leaving 64 rectangles for analysis, resembling a seafloor area of about ~0.5 m².

Specimen photography, energy dispersive spectroscopy morphometrics and repository

Live images of scaphopods were taken on board of RV Sonne with a digital Canon EOS 5D Mark IV SLR camera with macro lens and two linked flashes on a Kaiser RS copy stand. Smaller macrophotography was taken under a Leitz Stemi SV 6 stereomicroscope with an attached MU1803 USB camera and the AmScope software.

Scanning electron micrographs of shells and radula were made with a Hitachi TM3000 scanning electron microscope (SEM, Hitachi High-Technologies, Maidenhead, UK) at the British Antarctic Survey. Radulae were prepared by dissecting the radula sac, dissolving it in domestic bleach and cleaned for 15 s in an ultrasonic bath before SEM observation. Shells of one living individual and two debris pieces were hand-broken and investigated on the edge, inner and outer surfaces for microstructure surveys.

Energy Dispersive Spectroscopy (EDS) analysis for the elemental presence detection on radula and shells was performed with the Hitachi TM3000 SEM equipped with an Oxford Instrument INCA system and the Aztec software (Oxford Instruments, High Wycombe, UK). EDS maps for $\times 100$ (radula) and $\times 400$ (shell) magnified areas were acquired for five minutes, set to detect all elements, and quantified by the Aztec software. Elemental spectra of the bulk composition (% oxides) were displayed.

Shell morphometric measurements were taken from 19 individuals and shell debris using digital vernier calipers (0.01 mm). Shell length was measured as the longest length from the ventral aperture to the dorsal aperture (major axis) (Shimek and Moreno 1996), aperture width as the distance between the two widest anterior to posterior points, and aperture height as the distance between the two widest points perpendicular to the aperture width. Arc is the maximum distance to the shell from a chord running between the anterior edges of both apertures, lArc is the distance from the dorsal aperture to arc. As attached anthozoans were not removed from the scaphopods, arc and lArc measurements could not be taken in some specimens. Derived indices follow Shimek (1997) and Souza et al. (2020). Shell sizes were analysed in Microsoft Excel.

Specimens used in the present study, including type specimens, are deposited in the Senckenberg Research Institute and Museum Frankfurt, Germany (SMF) and the Natural History Museum, London (NHMUK, previous acronym BNHM). Museum numbers were given for the scaphopod specimens, if present, attached anthozoans were given collection numbers of German Centre for Marine Biodiversity Research (DZMB) for their Hamburg site (DZMB-2-HH). Museum numbers and shell morphometrics of collected scaphopod specimens are listed in Table 1.

DNA extraction, amplification and sequencing

DNA extractions were carried out using the Macherey–Nagel NucleoSpin Tissue Kit (Macherey–Nagel, Düren, Germany), following the manufacturer's instructions. Tissue was left for digestion overnight in a shaking bath at 56 °C/350 rpm. For all isolates, elution was carried out in two steps, using 50 μ l

pre-heated (70 °C) elution buffer each turn. DNA aliquots are stored at -80 °C at the German Centre for Marine Biodiversity Research (DZMB), Hamburg. The mitochondrial marker cytochrome *c* oxidase subunit I (COI) and the ribosomal marker 18S rRNA (18S) were selected for species delimitation analyses (Table 2). Polymerase chain reaction (PCR) was carried out using PCR-Beads, illustra™ PuReTaq Ready-To-Go™ (Avantor®; VWR Int. GmbH, Darmstadt, Germany) with a total reaction volume of 25 μ l per sample. In order to generate 18S sequences, PCRs were duplicated to gain a total of 50 μ l of product. Final primer concentrations were 10 μ mol and the amount of template DNA used was 2 μ l for COI and 3 μ l for 18S. Thermal cycling conditions were as follows: initial denaturation: 95 °C, 5 min; denaturation: 38 cycles, 95 °C, 45 s; annealing: 45 °C (COI), 50 °C (18S), 50 s; elongation: 72 °C, 1 min (COI), 3:20 min (18S); final elongation: 72 °C, 5 min (COI), 10 min (18S); cooling at 10 °C. Quality and quantity of amplified product was assessed by gel electrophoresis using 1.5% agarose gels. 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). Double stranded sequencing was carried out by the sequencing facilities Macrogen Europe Inc. (Amsterdam, Zuidooost, The Netherlands) and Eurofins Genomics Germany GmbH (Ebersberg, Germany) using ABI 3730xl sequencers.

Sequence editing, alignment and genetic analyses

Geneious Prime® (Version 2022.1.1; Biomatters, Auckland, New Zealand; Kearse et al. 2012) was used to edit and assemble forward and reverse chromatograms as well as to check for potential contamination using the implemented NCBI BLAST search tool (Basic Local Alignment Search Tool; Altschul et al. 1990). Assembled sequences were aligned using MUSCLE (Edgar 2004), implemented in Geneious Prime® with default settings. The software jModelTest 2 (Guindon and Gascuel 2003; Darriba et al. 2012) was used to estimate best-fit models of evolution applying the Akaike Information Criterion (AIC; Sakamoto et al. 1986). Phylogenetic analyses of single-gene alignments were performed using MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001), with three parallel runs of 5 million generations, sampling every 1000 generations. Convergence of independent runs was examined in Tracer 1.7.2 (Rambaut et al. 2018) with a burn-in of 10%. Trees were reconstructed using Bayesian Inference (BI), assessing branch support by posterior probability (PP) with values ≥ 0.95 considered as highly supported (Felsenstein 1985; Huelsenbeck et al. 2001). Tree editing was performed in FigTree 1.4.4 (Rambaut 2009) and Affinity Photo 1.10.5 (Serif Ltd., Europe).

Table 1 Museum numbers and shell morphometrics of collected scaphopod specimens

Museum number	Anemone present	Shell length (mm)	VAp width (mm)	VAp height (mm)	DAP width (mm)	DAP height (mm)	lArc (mm)	Arc (mm)	VAp ratio w/h	lnLTot	lnVApw1	lnAph1
SMF 366428	* Y*	61.91	11.34	11.28	2.36	1.99	19.0	4.22	1.01	4.13	2.43	2.42
SMF 366429	Y	45.8	8.73	8.6	1.47	1.6	11.8	1.06	1.02	3.82	2.17	2.15
NHMUK 2023932	* Y*	56.07	10.5	10.77	2.1	2.16	15.1	2.25	0.97	4.03	2.35	2.38
NHMUK 2023933	† N	15.52	3.1		1.1					2.74	1.13	
NHMUK 2023934	N	23.28	6.4		2.88					3.15	1.86	
SMF 366430	* Y*	63.63	10.9	10.6	2.02	2	23.9	2.84	1.03	4.15	2.39	2.36
SMF 366431	* Y*	50.15	9.27	10.2	1.93	1.75	15.2	2.89	0.91	3.92	2.23	2.32
SMF 366432	* Y*	40.35	7.76	7.55	1.26	1.23	11.8	1.42	1.03	3.70	2.05	2.02
SMF 366433	* Y	30.98	5.49	5.42	1.35	1.41	7.2	0.54	1.01	3.43	1.70	1.69
SMF 366434	* Y*	40.58	7.5	7.09	1.4	1.36	8.1	1.20	1.06	3.70	2.01	1.96
SMF 366435	* Y*	38.99	7.6	7.26	1.26	1.37			1.05	3.66	2.03	1.98
SMF 366436	* Y*	32.71	6.53	6.68	1.61	1.72	20.0	1.50	0.98	3.49	1.88	1.90
SMF 366437	Y	51.16	10.32	10.11	2.42	2.01	17.5	2.88	1.02	3.93	2.33	2.31
SMF 366438	Y	50.34	9.98	9.61	2.19	2.14	25.4	1.84	1.04	3.92	2.30	2.26
SMF 366439	Y	56.68	11.12	10.77	2.25	2.13	16.4	4.52	1.03	4.04	2.41	2.38
SMF 366440	Y	41.77	7.98	8.18	1.88	1.72	13.2	1.68	0.98	3.73	2.08	2.10
SMF 366441	Y	46.19	8.44	8.62	1.73	1.8	20.6	2.29	0.98	3.83	2.13	2.15
SMF 366442	Y	42.67	7.35	7.54	1.28	1.18	17.3	2.40	0.97	3.75	1.99	2.02
SMF 366443	Y	36.76	7.51	7.44	1.43	1.52	21.4	1.94	1.01	3.60	2.02	2.01
NHMUK 2023935	Y	41.78	7.98	7.35	1.91	1.7	10.0	1.80	1.09	3.73	2.08	1.99

*Barcoded specimen; †dry shells; bold, specimen designated as holotype; Arc, maximum distance to the shell from a chord running between the anterior edges of both apertures; DAp, dorsal aperture; N, No; lArc, distance from the dorsal aperture to arc; lnLTot, natural logarithm of shell length; lnVApw1, natural logarithm of ((VAp height)+1); lnAph1, natural logarithm of ((VAp width)+1); VAp, ventral aperture; Y, Yes

Table 2 Primers used for PCR and sequencing of COI and 18S

Primer	Sequence (5' to 3')	Reference
COI		
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
HCO2198	TAAACTTCAGGGTGACCAAAAATCA	Folmer et al. 1994
18S		
R-563	ACCAGACTTGCCCTCC	Díez et al. 2001
1155R	CCGTCAATTCCTTTAAGTTTCAG	Dreyer and Wägele (2001)
18A1mod	CTGGTTGATCCTGCCAGTCATATGC	Raupach et al. 2009
400F	ACGGGTAACGGGGAATCAGGG	Dreyer and Wägele (2001)
1800mod	GATCCTTCCGCAGGTTACCTACG	Raupach et al. 2009
1250FNmod	GGCCGTTCTTAGTTGGTGGAG	Raupach et al. 2009

Results

In the Labrador Sea Basin, the AGT was deployed at station SO286_19-1 on 21 November 2021 and OFOS on 22 November 2021. The AGT trawl collected 19 live scaphopods of which 18 were associated with an anemone, as well as shell debris (Fig. 2, Table 1).

The OFOS dive yielded 917 images, showing a soft sediment seafloor with Lebensspuren as traces of epifaunal and infaunal taxa, occasional megafauna and infrequent hard substrate (drop stones) (Neuhaus et al. 2024). The occasional epifaunal taxa comprised cnidarians (anthozoans), irregular sea urchins, comatulid crinoids, ophiuroids, asteroids, holothurians and porifera, whilst fish and decapods were rare with three rattail and a single squat lobster sighting. On a total of 62 images (6.7%) scaphopod shells, with or without Lebensspur were visible on the sediment surface, with no confirmation of their species affinity, if these were living specimens, or only shell debris (Fig. 2a). Anemones without Lebensspur, indicating either a burrowing species or a species attached to hard substrate, were seen on 67 (7.3%) images, 60 of them showing a red-coloured anemone and 7 of them a light-coloured anemone. In 31 images white-coloured anemones with Lebensspuren behind them were seen, indicating active movement on a scaphopod through the soft sediment surface (Fig. 2b). Based on these occurrences, the abundance of anemone-carrying scaphopods (Fig. 2c) is estimated as one per 15 m² along the OFOS track.

Molecular analysis

DNA was successfully amplified for nine scaphopods, yielding 11 novel sequences for two markers (COI: 9 sequences, 687 bp; 18S: 2 sequences, 1821 bp). The NCBI BLAST of the COI consensus sequences resulted in a pairwise identity of 98.1% with the Pacific specimen *Fissidentalium* sp. NHM_261 (MF157511), showing 13 mutational steps across 677 bp. The subsequent hit resulted in less than 90% coverage with the species *Antalis pilsbryi* (Rehder, 1942) (AF120639) and more than 100 unequal sites. The 18S sequence BLAST

results showed pairwise identities between 99.6–100% with *F. capillosum* (AF490596), *Fissidentalium* sp. NH_003 (ON257247), *F. candidum* (AF490595) and *Fissidentalium* sp. NHM_261 (MF157489), with zero to five mutational steps across 1659–1812 bp, respectively. In addition, several dentaliid species of the genera *Antalis* H. Adams & A. Adams, 1854 and *Dentalium* Linnaeus, 1758 yielded identical numbers of unequal sites and pairwise identities of up to 99.8%. To aid the species delimitation analysis and visualise the BLAST results based on Bayesian statistics, 13 COI and 25 18S sequences from the NCBI GenBank were included in the final alignments and species delimitation analyses (Figs. 3, 4). Both the COI and 18S phylogram place *Fissidentalium aurae* sp. nov. within the family Dentaliidae and separate the cluster from given sister species of *Fissidentalium*. This separation stands with a high support in the COI hypothesis (PP=0.98). Despite a low support for the clustering within the species of *Fissidentalium* in the 18S hypothesis (PP=0.19), the two Atlantic species *F. capillosum* and *F. candidum* separate from our abyssal species *F. aurae* sp. nov. with a posterior probability of 0.95. Both phylograms depict a close genetic relationship to the Pacific specimen *Fissidentalium* sp. NHM_261, however, clearly distinguish between this specimen and our new species—with full support for the COI genetic marker (PP=100; Fig. 3).

In addition to the scaphopods, DNA was amplified for each of the associated epizoic anemones, yielding eight novel sequences for the COI marker (696 bp) and one novel sequence of the 18S marker (1768 bp). The NCBI BLAST search of the anthozoan sequences resulted in a pairwise identity of 98.3–99.4% with published sequences of *Maractis* sp. (MW323564, KJ566948) and *Actinostolidae* sp. (OK267405, OK267413), resulting in three to seven mutational steps across 618–676 bp. As further taxonomic identification of this species is not part of this manuscript, we refer to the epizoic anthozoan as actinostolid anemone. All sequence data can be found in the Barcode Of Life Database (BOLD) dataset dx.doi.org/https://doi.org/10.5883/DS-FISSI as well as on the NCBI GenBank via the accession numbers PP464856–PP464864 (*F. aurae* sp. nov.) and PP464848–PP464855 (actinostolid anemone) (Table 3).



Fig. 2 In situ and life images of scaphopod-actinostolid symbiosis; **a** Scaphopod (black arrow) hosting anemone with retracted tentacles and its Lebensspur (grey arrows).; **b** Anemone with extended tenta-

cles (white arrow) and scaphoid created Lebensspur (grey arrow); **c** Scaphopod (Paratype 1 SMF 366429) with an epizoic actinostolid anemone

Class Scaphopoda Bronn, 1862

Order Dentaliida Starobogatov, 1974

Family Dentaliidae Children, 1834

Genus Fissidentalium P. Fischer, 1885

Type species *Dentalium ergasticum* P. Fischer, 1883: 275–277; accepted as *Fissidentalium capillosum* (Jeffreys, 1877) type by monotypy.

Fissidentalium aurae sp. nov.

(Figs. 2c, 5, 6, 7)

<https://zoobank.org/BE3E3500-193E-43B1-B2FE-4701C5222BE6>

Diagnosis: A large-sized, over 60 mm in length and 10 mm in ventral aperture width, *Fissidentalium* with numerous regular, fine longitudinal ribs. The white shells are robust and no posterior slit on the dorsal aperture was observed in the examined specimens. Most live specimens with shell lengths of 32–63 mm have a sea anemone attached to the concave, anterior surface of the shell. The ventral and

Table 3 Museum numbers for scaphopod specimens with their respective associated epizoic anemone (each given a DZMB number). COI and 18S loci GenBank accession numbers are given where applicable

Scaphopod museum number	Anemone		DZMB number	COI	18S
	COI	18S			
SMF 366428	PP464863	PP464630	DZMB-2-HH-7142	PP464854	PP464627
NHMUK 2023932	PP464861	PP464629	DZMB-2-HH-7144	PP464852	
SMF 366430	PP464864		DZMB-2-HH-7141	PP464855	
SMF 366431	PP464862		DZMB-2-HH-7143	PP464853	
SMF 366432	PP464860		DZMB-2-HH-7145	PP464851	
SMF 366433	PP464859		DZMB-2-HH-7146		
SMF 366434	PP464858		DZMB-2-HH-7147	PP464850	
SMF 366435	PP464857		DZMB-2-HH-7148	PP464849	
SMF 366436	PP464856		DZMB-2-HH-7149	PP464848	

Bold, specimen designated as holotype

dorsal apertures are slightly wider than high. Preserved, unrelaxed soft body dividable into a ventral buccal, a middle gut and a dorsal gonad region (following Shimek and Moreno 1996) and is about 2/3 of total shell lengths. Buccal and gonadal regions are of similar size and each about 3 times longer than the gut region.

Type material: Holotype SMF 366428, Fig. 5a–b, Labrador Sea, 58° 12.289' N 054° 13.409' W, 3387 m depth, AGT SO286_19-1, RV Sonne SO286, 21.11.2021, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7142. In ethanol; DNA extracted from scaphopod and anemone.

Paratype 1 SMF 366429, Fig. 1c, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone. In ethanol.

Paratype 2 NHMUK 20230932, Fig. 5c–d, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7144. In ethanol; DNA extracted from scaphopod and anemone.

Paratype 3 NHMUK 20230933, Figs. 5e, 7, type locality, leg. Katrin Linse. Dry empty shell.

Paratype 4 NHMUK 20230934, type locality, leg. Katrin Linse. Shell and remaining soft part in ethanol. Radula on SEM stub.

Paratype 5 SMF 366430, type locality, AGT SO286_19-1, RV Sonne SO286, 21.11.2021, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB7141. In ethanol; DNA extracted from scaphopod and anemone.

Paratype 6 SMF 366431, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7143. In ethanol; DNA extracted from scaphopod and anemone.

Paratype 7 SMF 366432, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7145. In ethanol; DNA extracted from scaphopod and anemone.

Paratype 8 SMF 366433, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7146. In ethanol; DNA extracted from scaphopod. Paratype 9 SMF 366434, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7147. In ethanol; DNA extracted from scaphopod and anemone.

Paratype 10 SMF 366435, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7148. In ethanol; DNA extracted from scaphopod and anemone.

Paratype 11 SMF 366436, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7149. In ethanol; DNA extracted from scaphopod and anemone.

Paratypes 12–18 SMF 366437–366443, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemones. In ethanol.

Paratype 19 NHMUK 20230935, Fig. 6b–d, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone. In ethanol. Shell fragments on SEM stub.

Additional material examined: Shell debris, (NHMUK 20230936), Fig. 6a, type locality, leg. Katrin Linse. Dry empty shells. Shell fragments on SEM stub.

Etymology: “aura” means breeze in Latin and used in genitive case. This name refers to the windy conditions during SO286 as well as to the shipping company Briese Research operating RV Sonne.

Type locality: Sedimented abyssal plain in the Labrador Sea, 58° 12.289' N 054° 13.409' W, 3380–3390 m depth.

Distribution: Known only from the area around the type locality in the Labrador Sea in 3380–3390 m depth.

Description: Shell length to 63.63 mm; Holotype 61.90 mm, ventral aperture diameter 11.34 × 11.28 mm, dorsal aperture 2.36 × 1.99 diameter; thick, moderately curved, more towards the dorsal aperture (Fig. 5). Sculpture

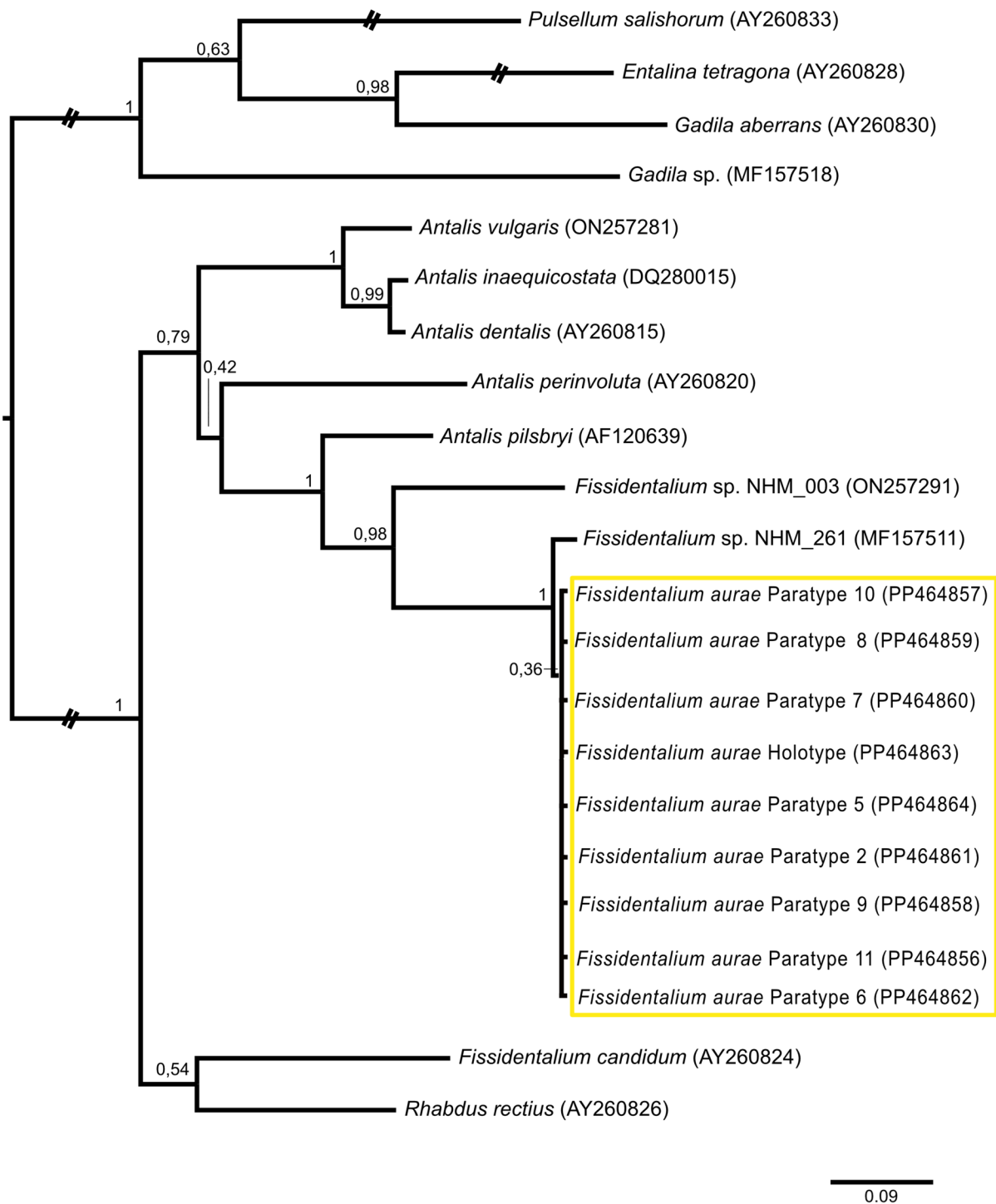


Fig. 3 COI Bayesian phylogram with posterior probabilities depicted on the nodes. The tree is rooted with four representatives of the order Gadilida Starobogatov, 1974 which stands monophyletic and sister to

the Dentaliida. GenBank accession numbers are displayed in brackets. Node values are posterior probabilities

of 30 ribs at the dorsal aperture, intercalating to 60 narrow, longitudinal ribs at the ventral aperture; interstice wide, concave; ribs and interstices crossed by fine transverse growth lines. Aperture slightly ovate, being slightly higher

anterior-posteriorly; protoconch unknown; ribs towards dorsal aperture often eroded. Colour opaque white near ventral aperture, white near dorsal aperture. Shell with three layers: a thin outer layer, a thicker middle layer of vertically

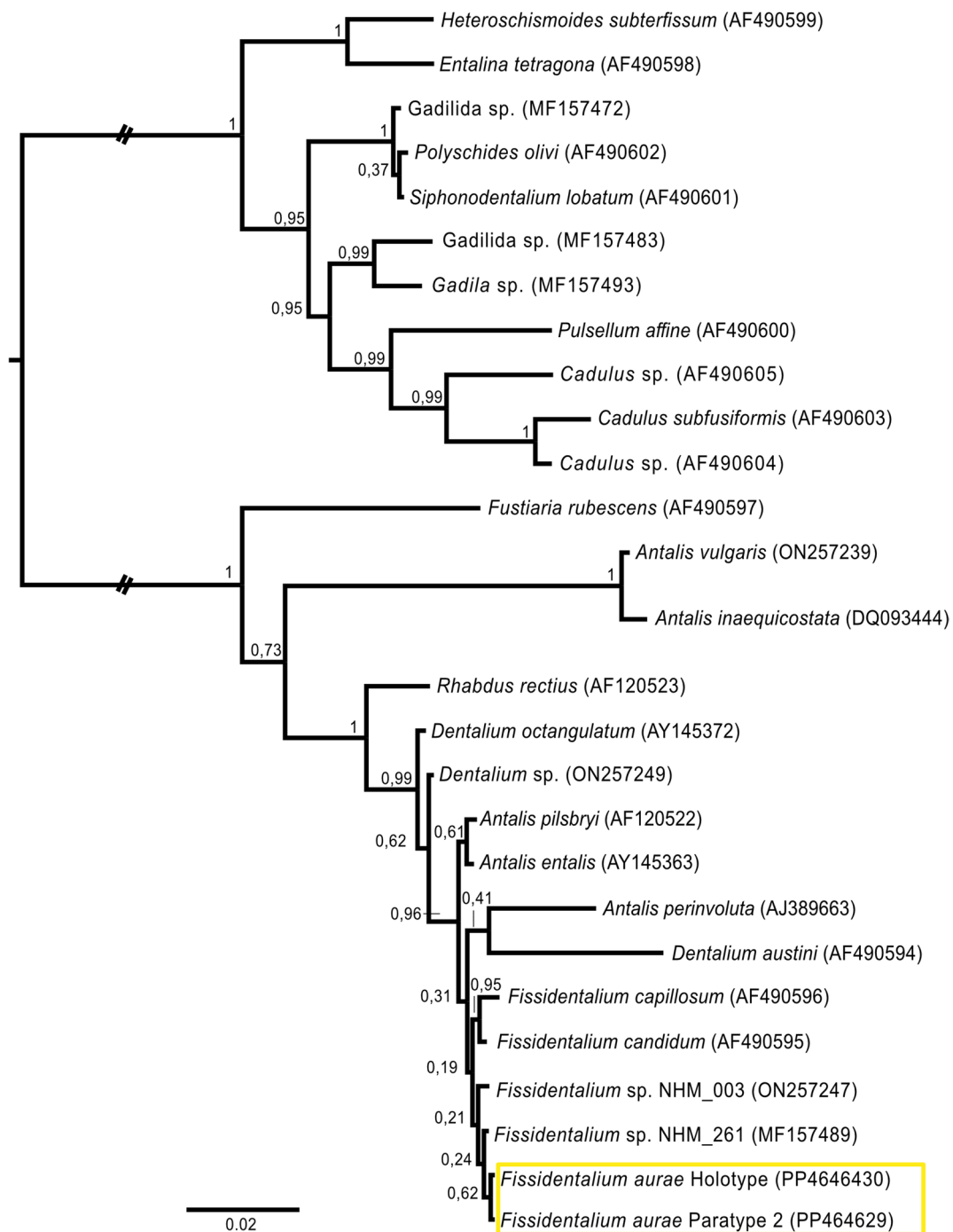


Fig. 4 18S Bayesian phylogram with posterior probabilities depicted on the nodes. The tree is rooted with 11 representatives of the order Gadilida which stands monophyletic and sister to the Dentaliida.

GenBank accession numbers are displayed in brackets. Node values are posterior probabilities

orientated tablets and an inner layer of cross-lamellar aragonite tablets (Fig. 6). The overall thickness ranged from 190 to 497 μm in interstice areas and 265 to 542 μm in rib areas with the thickness of the vertically orientated prisms ranging from 15 to 98 μm and the cross-lamellar layer from 165

to 480 μm . EDS analysis of the shell confirmed calcium carbonate as the compound with no traces of Mg calcite. Individual shell measurements and derived indices of the holotype and paratypes are given in Table 1.

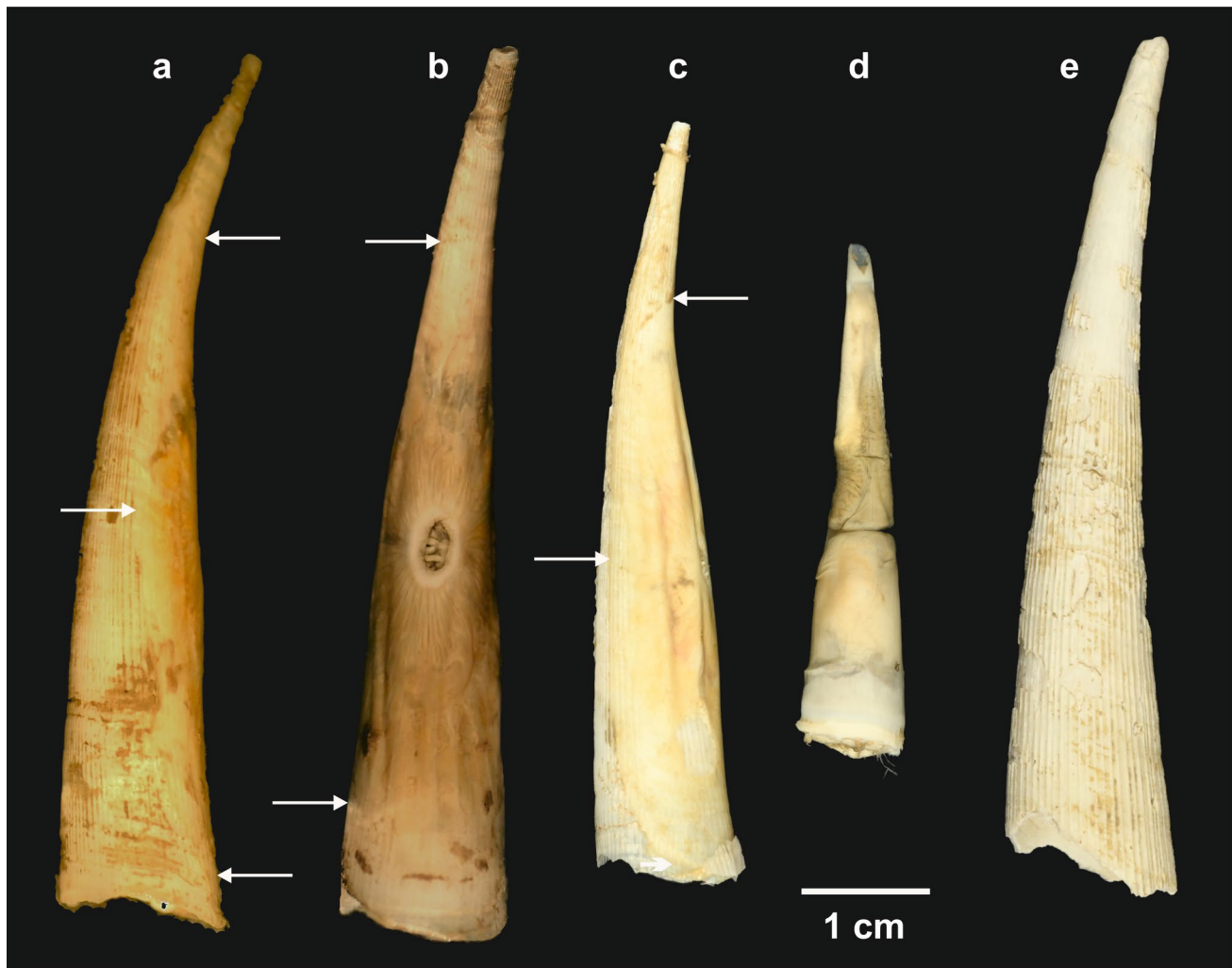


Fig. 5 *Fissidentalium aurae* sp. nov.; **a–b** Holotype SMF 366428, side and anterior view of shell and associated anemone; **c–d** Paratype 2 NHMUK 20230932, side view of shell and anemone and soft parts;

e Paratype 3 NHMUK 20230933, side view of dead shell. Arrows indicate delineation of the anemones

External anatomy: Length of ethanol preserved soft-body-part was 38.65 mm in Paratype 2 with 56.07 mm shell length (Fig. 5).

Radula: The radula has five teeth per row and is composed of a rachidian tooth, which is flanked by one lateral and one marginal tooth on each side (Fig. 7). On the oldest teeth, iron is visible as a high quantity mineral component of the radula (Fig. 7a, b), as confirmed by EDS. The rachidian tooth is wider than high, concave dorsally and about twice as wide as the lateral tooth. The lateral teeth are convex anteriorly and concave posteriorly with sharply pointed forward projections bent and solid build. The marginal teeth are thin, wide and end at the lower flank of the lateral teeth.

The imaged radula was extracted from an individual of 23.28 mm shell length, ~2.6 mm in length (rachidian teeth measured), ~1.2 mm in width and had ~14 rows (15

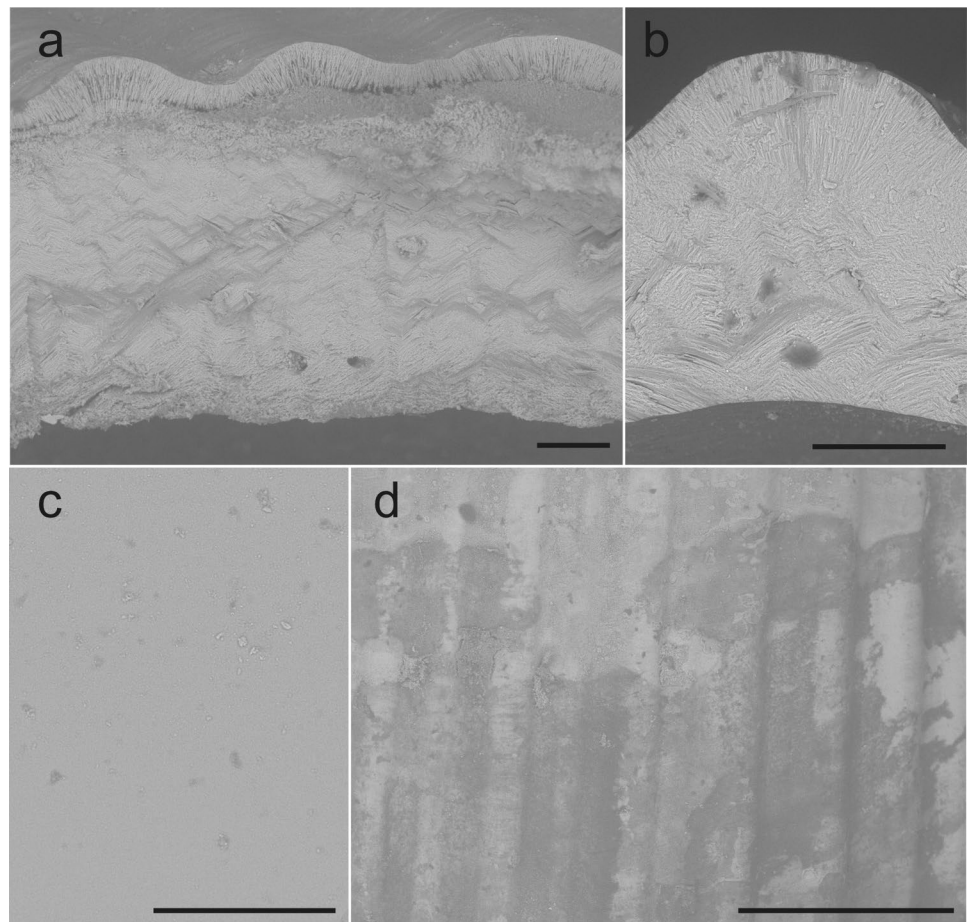
lateral teeth present on the left and 13 on the right side after dissection).

Molecular barcoding: Nine partial sequences of the COI barcoding region and two 18S sequences were amplified from *Fissidentalium aurae* sp. nov. and compared with previously published sequences of congeneric species (Figs. 3, 4, Table 3).

Remarks: Based on their morphology, the investigated scaphopod specimens are recognisable as belonging to the genus *Fissidentalium* (Shimek and Moreno 1996; Lamprell and Healy 1998).

The shell of *F. aurae* sp. nov. is with 190 to 542 µm similar in thickness to *F. actiniophorum* Shimek, 1997 (189 to 479 µm; White et al. 1999) which Shimek (1997) described as thin compared to *F. megathyris* (Dall, 1890) and *F. erosum* Shimek & G. Moreno, 1996.

Fig. 6 Shell microstructure of *Fissidentalium aurae* sp. nov.; **a** Shell layers of shell debris at ventral aperture with 12.1 mm width; **b–d** Paratype 19 NHMUK 20230935 shell layers; **b** Ventral aperture with 7.98 mm width.; **c** Inner surface; **d** Outer surface. Scale bars: A–C: 100 μ m, D: 1 mm



The only other *Fissidentalium* species with subpolar North Atlantic distributions are *F. candidum* and *F. capillosum*, with *F. candidum* being recorded from the west of Greenland in the Labrador Sea from 748–2464 m depth and *F. capillosum* from the east of Greenland in 1259–3528 m depths (Steiner and Kabat 2004).

Specimens of *F. aurae* sp. nov. were morphologically compared with two syntypes of *F. candidum* (BNHM 1885.11.5.1239, BNHM 1885.11.5.1240) and two syntypes of *F. capillosum* (BNHM 1885.11.5.1336, BNHM 1887.2.9.4.6) at the Natural History Museum in London. The shell morphology of *F. aurae* sp. nov. can be differentiated from *F. candidum* by not having a dorsal aperture slit and being wider towards the ventral aperture, whilst having for similar numbers of longitudinal ribs at similar diameter. The foot of *Fissidentalium candidum* is described as conical (Jeffreys 1877), whilst it is not conical in *F. aurae* sp. nov. In the COI barcode region, a difference of 23% across 687 bp discloses the presence of two species. Across 1811 base pairs of the 18S region, a difference of mere five nucleotides (0.3%) is resolved between the species.

Shells of *F. aurae* sp. nov. can be morphologically distinguished from *F. capillosum* by missing the dorsal slit, having a wider ventral aperture at similar shell length (Jeffreys 1877), and having wider ribs and narrower interspaces. As there is no COI sequence of *F. capillosum* publicly available, the genetic difference to *F. aurae* sp. nov. can solely be examined across the 1812 bp of the 18S region, yielding eight different nucleotides (0.3%).

Specimens of *Fissidentalium aurae* sp. nov. were morphometrically compared to two abyssal species found off California and Portland in the East Pacific, namely *F. erosum* Shimek & G. Moreno, 1996 and *F. actiniophorum* Shimek, 1997. Whereas *F. erosum* has never been found associated with an anemone, the latter species was described as an anemone-carrying scaphopod (Shimek 1997), whereupon White et al. (1999) designated the anemone to their newly described species *Anthosactis nomados*. *Fissidentalium aurae* sp. nov. shows differences in ventral aperture width and height at similar shell length, having a wide and higher dorsal aperture compared to its sister species. Three paratypes of *F. actiniophorum* (BNHM 19962120 (1), BNHM 19962121 (2)) were directly compared at the

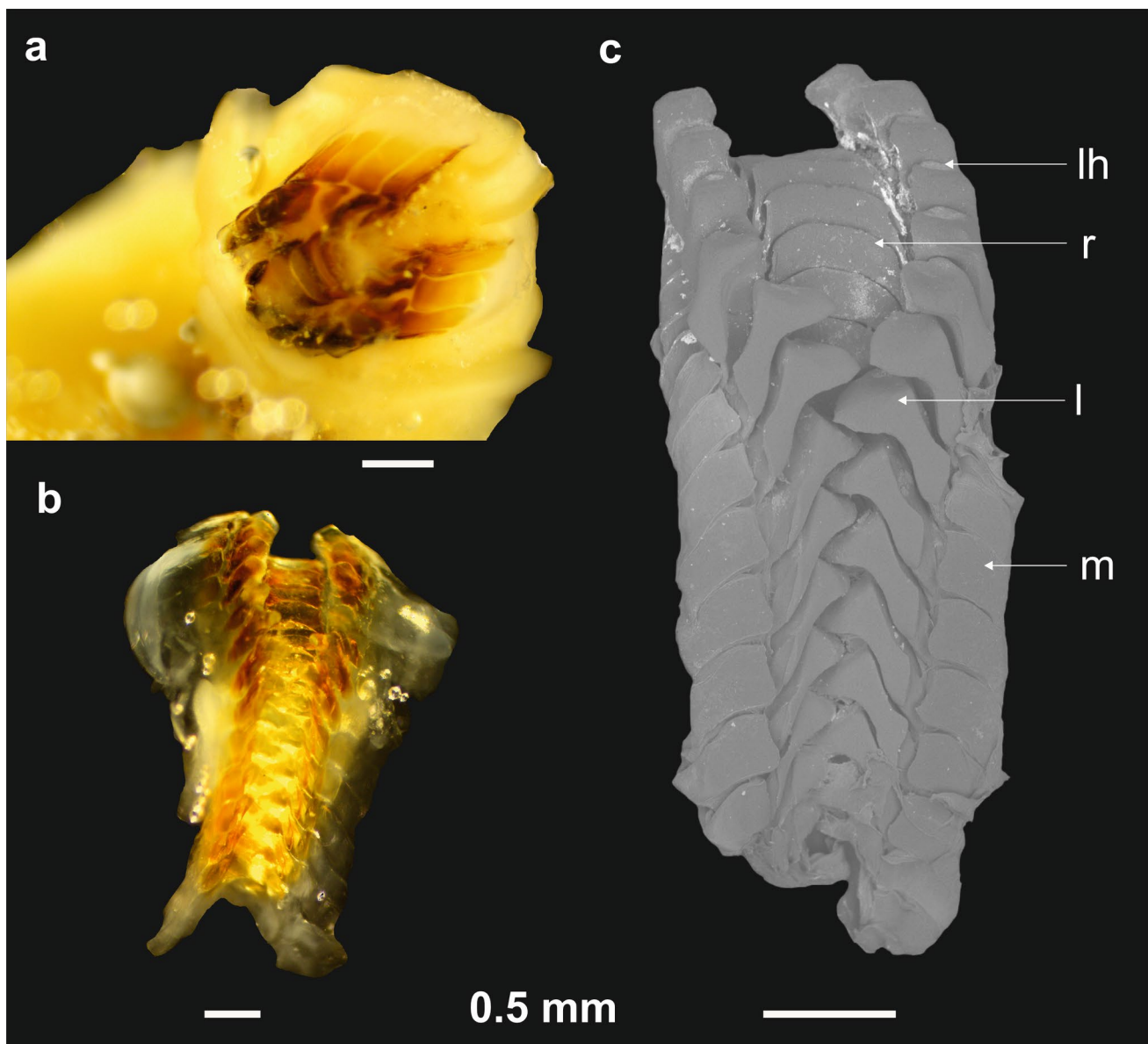


Fig. 7 Radula of *Fissidentalium aurae* sp. nov. Paratype 3 NHMUK 20230932; **a** Scaphopod sack showing radula under stereomicroscope; **b** Whole radula; **c** SEM of whole radula. Abbreviations: l, lateral tooth; lh, worn head of lateral tooth; m, marginal tooth; r, rachidian tooth

NHMUK, and next to confirming the morphometric differences, similarity of longitudinal rib and interspace structure was seen. However, at a comparable shell diameter of 3 mm, *F. actiniophorum* has about two-thirds the number of longitudinal ribs (30 ribs) compared to *F. aurae* sp. nov. with 47 longitudinal ribs. Unfortunately, the obtained tissue sample of one specimen of *F. actiniophorum* as well as the associated anemone did not yield viable DNA aliquot to amplify and use in the genetic analysis.

Of all specimens included in the molecular analysis, the individual designated as *Fissidentalium* sp. NHM_261, shows the closest genetic relation to *F. aurae* sp. nov.

However, the difference of 14 nucleotides across 667 bp of the COI gene region is sufficient to differentiate between species on the molecular level. This differentiation concurs with the geographic distance between these species, as *Fissidentalium* sp. NHM_261 was collected at 4076 m depth in the Pacific Clarion-Clipperton Zone (Wiklund et al. 2017). Morphologically, the number of longitudinal ribs at comparable shell height is lower in the Pacific species than in our new species from the Labrador Sea. Similar to the paratype *F. actiniophorum* BNHM 19962120 with 20 latitudinal ribs at 1.5 cm diameter, *Fissidentalium* sp. NHM_261 carries 19 latitudinal ribs at the same diameter.

Ecological observations: On in situ images, only living *F. aurae* sp. nov. associated with an actinostolid anemone as well as broken shell fragments were observed. These living scaphopods are noticeable by the Lebenspuren they left behind in the soft sediment, which resembled the width of a feeding anemone. Of the 19 live collected *F. aurae* sp. nov. specimens, 18 had an anemone attached to their shell. Thus, there seems to be an interest in anemones to find a hosting scaphopod. The in situ images did not show Lebensspuren traceable to a living *F. aurae* sp. nov. without an attached anemone. *Fissidentalium aurae* sp. nov. occurs sympatrically with at least two other scaphopod species. At the type locality of *F. aurae* sp. nov., four other scaphopod specimens were collected from the same AGT. Three specimens resemble the dentaliid genus *Antalis* and were identified as *Antalis agilis* (Sars, 1872), a species with a known distribution record from the Labrador and Norwegian seas to the Azores in 60–5000 m depth (Ivanov and Zarubina 2004; Steiner and Kabat 2004). The fourth specimen resembles the gadilid scaphopod genus *Siphonodentalium* M. Sars, 1859 and was identified as *Siphonodentalium lobatum* (Sowerby 1860). The species is recorded from the Arctic and North Atlantic Ocean, from shelf to bathyal depths (Ivanov and Zarubina 2004). According to Steiner and Kabat (2004), further three species are found in the deep North Atlantic basins, namely *Bathoxiphus ensiculus* (Jeffreys, 1877), *Cadulus gracilis* Jeffreys, 1877 and *Heteroschismoides subterfissus* (Jeffreys, 1877).

Discussion

During the expedition IceDivA2 (SO286), sampling in the abyssal Labrador Sea disclosed a new species of dentaliid scaphopod as well as a new association between the scaphopod and an actinostolid anemone.

Species richness in the genus *Fissidentalium*

The new dentaliid *Fissidentalium aurae* sp. nov. was described based on an integrative taxonomic approach, using shell morphology and morphometrics, radula and soft part measurements, and molecular barcoding analyses. The genus *Fissidentalium* is known for its paucity of shell morphological characters between species. Distinct characters are the presence or absence of the dorsal aperture slit, low numbers of latitudinal ribs (16–36) at the ventral aperture versus high numbers (50–90), or circular versus oval apertures (Shimek and Moreno 1996; Lamprell and Healy 1998). Lamprell and Healy (1998) acknowledged that the status and species composition of this genus requires comprehensive revision including anatomical and molecular comparisons next to detailed shell and radula morphology.

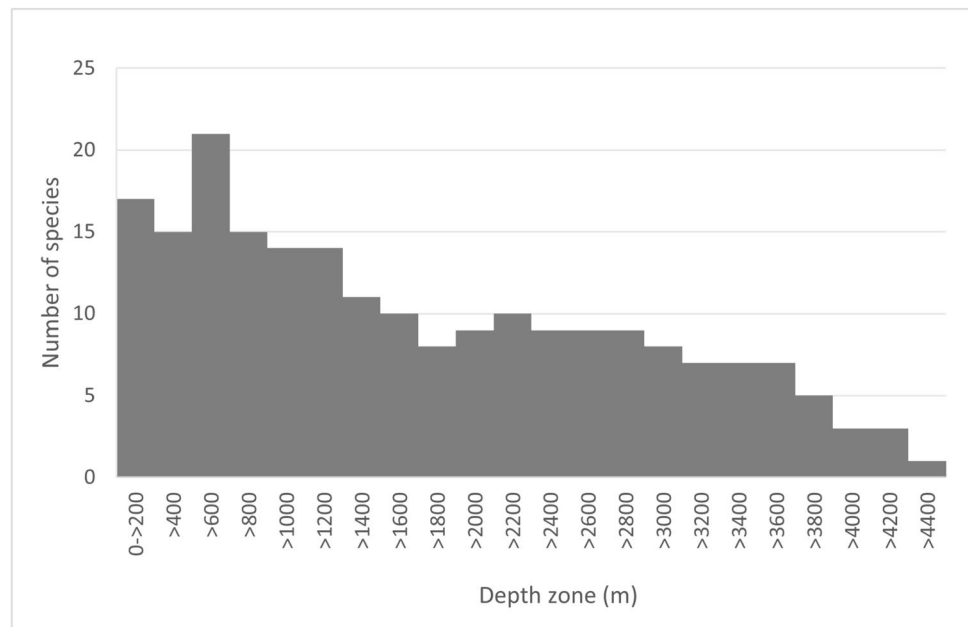
The genetic distinction of *F. aurae* sp. nov. from the Labrador Sea (58° 12' N 54° 13' W, 3387 m) to the sequenced *F. candidum* from Iceland (60° 05' N 20° 50' W, 2709 m) (Steiner and Dreyer 2003) with respective type localities west of Ireland and in the Bay of Biscay (Jeffreys 1877), together with the similarity of the shell morphology between the two species, is raising doubts for the correct species assignment for the Davis Strait records of *F. candidum* from the HMS *Valorous* expedition in 1875 (Steiner and Kabat 2004).

The depth zonation of *Fissidentalium* shows higher numbers of species at shelf and upper slope depth whilst numbers of species decrease with depth (Fig. 8). Eurybathy is not common in the genus. Twenty-one of the 62 known species have a known depth range of less than 200 m, 15 species of more than 200 but less than 1000 m and only seven species have known ranges of more than 1000 m depth. Only five species are known for extended eurybathic depth ranges of more than 2000 m, including *F. candidum* (403–3814 m) and *F. capillosum* (100–4088 m). Molecular analyses of specimens from several depths and locations of these eurybathic and often geographically wide-ranging species would confirm if these were wide-ranging species or species complexes.

Epizoic associations on Scaphopoda

The epizoic association of *Fissidentalium aurae* sp. nov. with an actinostolid anemone is not the first record of this kind for scaphopods or even species of *Fissidentalium*. Shimek and Moreno (1996) mentioned some records of the Pacific *F. megathyris* with attached anemones, later designated to *Anthosactis nomados* (White et al. 1999), suggesting a near sediment surface life style of the scaphopod enabling anemone attachment. The northeast Pacific species *Fissidentalium actiniophorum* was named after its anemone association as 90 of 133 live collected specimens carried an anemone (Shimek 1997). Like in the collection of *F. aurae* sp. nov., no dead collected shells of *F. actiniophorum* carried an anemone (Shimek 1997). The anemone was later described as *Anthosactis nomados* White et al. 1999. Specimens of a South Atlantic scaphopod identified as *Dentalium* sp. carried specimens of the anemone *Hormathia pectinata* (Hertwig, 1882) (Riemann-Zürneck 1973). More recently, a deep-sea scaphopod-anemone association was discovered during the “AleutBio” expedition SO293 to the eastern site of the Aleutian Trench, Alaska (Prof. Julia Sigwart, personal communication). A further scaphopod-cnidarian association was reported for *Pictodentalium venedei* (Sowerby 1860) and the solitary scleractinian *Heterocyathus japonicus* (Verrill, 1866) (Zibrowius 1998). Carlgren (1928) found the anemone *Paracalliactis stephensoni* Carlgren, 1928, on a

Fig. 8 Depth distribution patterns of *Fissidentalium* species in 200 m depth zones



large *Dentalium* shell inhabited by the hermit crab *Parapagurus pilosimanus* Smith, 1879, off the Irish coast.

In all these cases, the attached anemones and scleractinians were reported from the concave anterior side, which is reported to facing the sediment surface in *Fissidentalium* (Zibrowius 1998). The scleractinians were found attached near the dorsal aperture, whilst the anemones on *F. actinophurum* and *F. aurae* sp. nov. were covering most of the dorsal area from near the ventral aperture onwards (Shimek 1997; Zibrowius 1998; this study). To date, it is unclear what the mutual benefit for both partners of this association is and whilst Shimek (1997) mentions symbiosis, Reynolds (2002) suggests mutualism. The gain for the anemone is an attachment point in sedimented deep-sea areas, where hard substrates can be rare, and a transport medium to different feeding areas. The in situ images from the Labrador Sea show clear Lebensspuren from *F. aurae* sp. nov. with attached anemones, in some images with anemone tentacles reaching over the movement ridge created, potentially accessing food resources from there. White et al. (1999) inferred that the deep-sea scaphopods were protected from predators by their actinian symbionts, a symbiosis well accepted from shallow-water symbioses of gastropods and hermit crabs in gastropod shells with attached anemones (Williams and McDermott 2004). Potential predators of scaphopods are rattail fish and crabs (Reynolds 2002; Shimek 1989). During the OFOS dive in the abyssal Labrador Sea, potential motile predators such as rattails and squat lobsters were seen in the in situ images, but no records are available if these include *F. aurae* sp. nov. as their prey. White et al. (1999) additionally suggest that the anemone might protect the scaphopod shell from dissolution in calcium-carbonate undersaturated deep-sea habitats.

The two anemones associated with scaphopods, *Anthosactis nomados* and *Hormathia pectinata*, belong to the families Actinostolidae and Hormathiidae Carlgren, 1932 (WoRMS Editorial Board 2024). Barcode sequences obtained from eight specimens of the undescribed anemone attached to *F. aurae* sp. nov. revealed closest matches to *Maractis* sp. (MW323564, KJ566948) of the family Actinostolidae. Sanamyan et al. (2021) defined the new family Anthosactinidae, including the genera *Tealidium* Hertwig, 1882, *Hormosoma* Stephenson, 1918 and *Anthosactis* Danielsens, 1890 but stated on page 433 that they exclude *Anthosactis nomados* from the genus *Anthosactis*, but did not give a genus relationship for it. WoRMS still lists the species as *Anthosactis nomados* in the Actinostolidae (WoRMS Editorial Board 2024).

The type species of *Anthosactis*, *A. janmayeni* Danielsens, 1890, is an eurybathic (51–1073 m), circum-Arctic species, reported as rare and locally confined (Riemann-Zürneck 1997). The specimens in the latter redescription are with ~30–75 mm diameters significantly larger than the anemones on *F. aurae* sp. nov. and despite an overlap in geographic region, but not in depth, this species is considered as an unlikely match with the undescribed actinostolid species mentioned herein.

An integrative taxonomic approach for the identification of the actinostolid anemone attached to *F. aurae* sp. nov. is suggested as that would not only formally classify this species from the Labrador Sea but might also clarify the position of *Anthosactis nomados*.

The herein described association of a burrowing scaphopod with an epifaunal anemone in the abyss of the Labrador Sea has not only revealed a new species of Atlantic

scaphopod, but also shows how little is known about symbioses in the deep sea. Our study highlights the benefit of deep-sea imagery to support species descriptions with information on habitat and ecology. A future integrative taxonomy-based revision of the genus *Fissidentalium* would resolve phylogenetic relationships within the Dentaliida and clarify the status accepted nominal species and their current synonymies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12526-024-01481-1>.

Acknowledgements The authors thank Master Thilo Birnbaum, the crew of RV Sonne, SO286 chief scientist Saskia Brix, technical staff and fellow scientists on the expedition for their support. Angelina Eichsteller is thanked as scientific lead of AGT deployments and James Taylor for leading OFOS deployments. We are grateful to Malacology section curators Julia Sigwart (Senckenberg Research Institute and Museum) and Tom White (NHMUK) for access to their scaphopod collections and allowing tissue sampling. Nicole Gatzemeier (DZMB Hamburg) photographed the specimens for Figures 2 and 3, and Lucy Stephenson extracted deep-sea *Fissidentalium* records from OBIS for Figure 1. We thank three anonymous reviewers for their constructive comments which improved the earlier version of this publication.

Funding Katrin Linse is part of the British Antarctic Survey Polar Science for Planet Earth Programme funded by The Natural Environment Research Council (NERC) [NC-Science]. Fieldwork during expedition SO286 on RV Sonne was funded by the Federal Ministry of Education and Research (BMBF) through the IceDivA2 grant GPF 21-2_052 (SO286) given to Saskia Brix, Katrin Linse, Pedro Martínez Arbizu and Alexander Kieneke. Jenny Neuhaus was as well supported through grant GPF 21-2_052 as part of the IceDivA project. The IceDivA expeditions (SO280; SO286) are a contribution to the iAtlantic project, funded by EU/HORIZON 2020, Blue Growth (grant agreement No 818123). Jenny Neuhaus is currently supported by the iAtlantic project and owes gratitude to Prof. Colin Devey and associated working group at GEOMAR Helmholtz Centre for Ocean Research for their fundamental support.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics approval All applicable international, national, and/or institutional guidelines for animal testing, animal care and use of animals were followed by the authors. The scaphopod and anemone specimens have been treated and fixed under the marine invertebrate ethics policy of the British Antarctic Survey.

Sampling and field studies The field study was carried out in international waters in November 2021, requiring no sampling permits. The study is compliant with CBD and Nagoya protocols.

Data availability All datasets analysed and generated in this study e.g. OFOS imagery and morphometric data, are publicly archived in the UK Polar Data Centre at <https://www.bas.ac.uk/data/uk-pdc/> and available under <https://doi.org/https://doi.org/10.5285/C57A3261-F5F8-40E3-BCD3-C749733B3119>. Molecular data is available in the Barcode of Life Database [dx.doi.org/https://doi.org/10.5883/DS-FISSI](https://doi.org/https://doi.org/10.5883/DS-FISSI).

Author contribution KL and JN conceived and designed the research, wrote the manuscript and prepared figures and tables. KL analysed the

morphological data; JN analysed the molecular data. Both authors read and approved the manuscript.

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