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ORIGINAL PAPER

The first deep-sea ctenostome bryozoan from the Indian Ocean: *Aethozoon flavum* sp. nov.

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Abstract

Aethozoid ctenostome bryozoans are an unusual, small group of solitary ctenostome bryozoans, occurring almost exclusively in deep-sea habitats. Currently, there are only five species belonging to four, still insufficiently known genera, which have been reported from the Atlantic and Pacific Oceans. Recent examination of sediment core samples from an active volcanic area near Mayotte revealed a high abundance of aethozoids, recorded for the first time in the Indian Ocean. A comparative approach identified the specimens as belonging to a new species, *Aethozoon flavum* sp. nov. There are particular characters diagnostic of this new species, such as basally oriented duplicature bands, a highly denticulate proximal vestibular wall, and a highly elongated anal tube terminating in an almost vestibular anus. This species is the first ctenostome observed at depths of over 3.000 m in the Indian Ocean. Morphological characters are compared among all aethozoids, but still require more detailed analyses in most species. Aethozoids appear to be globally distributed and often occur in high numbers, which indicates that additional efforts will increase their distribution and species range. Ultimately, additional studies will be able to show the ecological importance of these bryozoans and molecular studies should reveal more about their diversity and phylogenetic affinities.

Keywords Solitary Bryozoa · Aethozoidae · Mayotte · Sediment cores · Marine volcano

Introduction

Bryozoa is a moderately large phylum of lophotrochozoans comprising mostly colonial, suspension feeders (Ryland 1970, 2005). Colonies consist of iterated modules or individuals termed zooids. Each regular or feeding zooid (known as an autozooid) carries a ciliated tentacle crown or lophophore, which is used for feeding among other functions, and an associated U-shaped digestive tract (Mukai et al. 1997). Along with associated neuro-muscular tissue, these structures are traditionally termed the 'polypide' in bryozoans, whereas the body wall is termed as cystid. The latter can be unmineralized or mineralized in form of calcium carbonate, depending on the taxonomic clade. Besides coloniality, the second characteristic of all bryozoans is the retractability of the polypide inside the body wall (Schwaha et al. 2020).

Two large clades are distinguished among bryozoans, Phylactolaemata and Myolaemata (Schwaha et al. 2020). Whereas the former comprises a small group of freshwater bryozoans, the latter represents the bulk of over 6.000 extant, mostly marine, species (Bock and Gordon 2013). Myolaemata is divided into Stenolaemata (Cyclostomata) and Gymnolaemata, with the latter comprising ctenostomes and cheilostomes. Ctenostome bryozoans are an assemblage of unmineralized gymnolaemates which are paraphyletic and gave rise to the monophyletic Cheilostomata, which have mineralized skeletons (Todd 2000; Waeschenbach et al. 2012; Taylor and Waeschenbach 2015).

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Bryozoans occur globally in all aquatic systems from freshwater lakes or rivers, intertidal and subtidal areas and even deep-sea habitats. The term 'deep sea' is generally used to describe environments that extend beyond the continental shelf, typically from a depth of approximately 200 m downwards. This begins with the bathyal zone, followed by the abyssal and hadal zones, with the latter representing depths exceeding the abyssal plain at ~ 6000 m (Tyler 2003). Research on deep-sea bryozoans mostly resulted from numerous voyages or cruises starting from the late nineteenth century until recent times (see Grischenko et al. 2019 for a summary). Initially, ctenostome and cyclostome bryozoans were not reported from areas beyond 3000 m (Schopf 1969), but later studies revealed a cryptic fauna of ctenostome bryozoans (d'Hondt 1976) that required careful sorting or specific collection techniques (Hayward 1981).

A recent series of surveys off eastern Mayotte (North Mozambique Channel, Indian Ocean) revealed the presence of a new very active volcanic edifice named Fani Maoré at 3500 m depth (Feuillet et al. 2021). The first visual survey of Fani Maoré and surrounding sediments did not reveal observable macro- or megafauna (Zeppilli and Pernet 2021). However, a rich meiofaunal community was recovered from sediments around this edifice, including the presence of numerous solitary bryozoans, which were preliminarily identified as aethozoids. Aethozoidae is a little-known family of ctenostome bryozoans with five species in four genera (Schwaha 2020a). Most records are from deep-sea habitats, but shallower specimens have also been encountered (Schwaha et al. 2019). In this study we provide a detailed analysis of the Indian Ocean specimens, and describe a new species of aethozoid bryozoans, which is also the first report of this group for the Indian Ocean.

Material and methods

Material and sampling location

Samples were collected near the Fani Maoré volcanic edifice in the east insular slope of Mayotte (Comoros Archipelago, southwestern Indian Ocean) during the oceanographic campaign '*GeoFLAMME*' on board the *R/V Pourquoi pas?* on 14–26 May 2021. Fani Maoré was discovered in May 2018 on the distal part of the volcanic ridge that runs off the eastern flank of Mayotte. This pyramidal, volcanic edifice is 820-m tall and has numerous radial ridges of coalesced pillow-lava mounds intercalated with flatter areas of channelized lava or sheet flows emplaced at high effusion rates (Clague et al. 2018, Chadwick et al. 2019).

Samples of accumulated sediment were taken by an Oktopus multi-corer at five different sites across the newly formed volcanic substrate (Table 1). On each deployment, three half-cores of 34.6 cm^2 surface were dedicated to meiofaunal taxonomic studies. Each sample was subsequently sliced in horizontal layers as follows: first layer at 0–1 cm, second layer at 1–3 cm, third layer at 3–5 cm, fourth layer at 5–10 cm, fifth layer at 10–15 cm. All sediment layers were fixed in 4% neutralised formalin.

Methods

Each sediment layer was profusely washed with 32 µm of filtered tap water to remove formalin remnants prior to meiofauna extraction. For this process, the sediment was passed through a 1-mm sieve (for possible separation of possible macrofauna and large particles) and a 32-µm sieve (for meiofauna isolation). Meiofauna was extracted with LUDOX® colloidal silica centrifugation (Burgess 2001), then preserved in 4% neutralised formalin and dyed with Phloxine B (80 mg/l in formalin). Meiofaunal samples were examined with a stereomicroscope at the Centre National de Tri d'Océanographie Biologique (CENTOB, Ifremer, France). Specimens were classified per metazoan phylum and counted, including the studied Bryozoa.

Fixed bryozoan specimens were documented and analysed with a Nikon SMZ25 stereomicroscope equipped with a DsRi2 microscope camera (Nikon, Tokyo, Japan). Zooidal dimensions were measured with the software FIJI (Schindelin et al. 2012). Selected zooids were transferred into glycerol and mounted on standard microscope slides and sealed afterwards with nail polish. Mounted samples were documented and analysed with a Nikon NiU compound microscope equipped with the same camera mentioned earlier.

Table 1 Details of sampling sites, including a brief description of the places, geographic coordinates, depth, type of sediment and abundance of aethozoid bryozoans

Site code	Description	Geographic coordinates	Depth	Sediment	Abundance
MTB01	Reference site	12°42′13.244''S, 45°55′6.69''E	3.518 m	Fine mud with few tephra particles	6 individuals
MTB02	Deflation zone	12°49′23.725''S, 45°44′30.217' E	3.535 m	Sandy mud with thick tephra layer	180 individuals
MTB03	NE volcano	12°52′28.466''S, 45°45′44.719''E	3.511 m	Sandy mud	69 individuals
MTB04	NE volcano	12° 54′32.3''S, 45°48′4.3''E	3.530 m	Sandy mud	55 individuals
MTB05	E volcano	12°56′43.35''S, 45°51′51.80''E	3.531 m	Mud with few tephra particles	14 individuals

For histological analysis, zooids were dehydrated in a graded ethanol series, followed by infiltration and embedding into Agar Low Viscosity Resin (Agar Scientific, Stansted, UK). Cured resin blocks were serially sectioned with a Leica® UC6 ultramicrotome (Leica® Microsystems, Wetzlar, Germany) and a Diatome HistoJumbo diamond knife (Diatome, Switzerland) at a thickness of 1 µm. Section series were stained with toluidine blue and sealed in resin. Afterwards, series were documented with the aforementioned NiU microscope. Image stacks of zooids were processed with FIJI prior to their import into the reconstruction software Amira (2022.2) (ThermoFisher). Stacks were first aligned in Amira, segmented and afterwards visualized. Snapshots were taken with the Amira software.

Results

Taxonomic account

Class Gymnolaemata Allman, 1856

Clade *Ctenostomata* Busk, 1852

Family Aethozoidae d'Hondt, 1983 (sensu Reverter-Gil et al. 2016)

Genus *Aethozoon* Hayward, 1978

Aethozoon flavum sp. nov.

https://zoobank.org/03152A98-44F2-4484-99A9-31B220F2486A

Material examined: 'MTB02' (deflation zone): 12°49′23.725"S, 45°44′30.217"E, 3562 m depth, 'MTB03' (NE volcano): 12°52′28.466"S, 45°45′44.719"E, 3511 m depth, 'MTB04' (NE volcano): 12°54′32.35"S, 45°48′4.37"E, 3530 m depth. Types deposited in Muséum National d'Histoire Naturelle, Paris (France) under accession codes: holotype MNHN-IB-2017-723; paratypes MNHN-IB-2017-724 to MNHN-IB-2017-727.

Description: Solitary or pseudo-solitary bryozoans with elongated zooids. Zooid mainly consist of an elongated peristome (Figs. 1, 2, 3), measuring 1787–2996 µm in length (mean 2281 µm, $n = 8$), width 135–229 µm (mean 179 µm, $n = 8$), basal area slightly wider 295–392 µm (mean 257 µm, $n = 8$), containing gonads, digestive tract, retractor muscles and funicular system (Figs. 4, 5, 6). Kenozooidal cystid appendage (kca) on proximo-basal side of zooid and non-kenozooidal one (nca) opposite on distal side, attaching slightly more frontally (Figs. 2, 3, 4). Kca may be missing, sometimes two present (Fig. 2b). Both appendage types of variable length, nca 384–2119 µm (mean 896 µm, $n = 8$), kca 473–1244 µm (mean 821 µm, $n = 8$); when longer with terminal expansion carrying developing polypide bud (Fig. 2c). Kenozooidal appendage separated by pore-plate with approximately four special cells (Fig. 7). Frontal side of vestibular wall and often cystid appendages with distinct, strong yellow coloration, sometimes also observed in other areas including the gut (Figs. 1, 2). Intertentacular organ may be present at adneural tentacles (Fig. 7a). Zooids simultaneous hermaphrodites with spermatogenic tissue and ovaries with several small oligolecithal oocytes (Figs. 6b–c; 7b). Polypide with 14 or 15 tentacles (Fig. 7a) occupying middle third of retracted zooid. Foregut short, cardia highly elongated and thin tube expanding on a voluminous sac-shaped caecum directed basally (Figs. 3, 8). Intestine

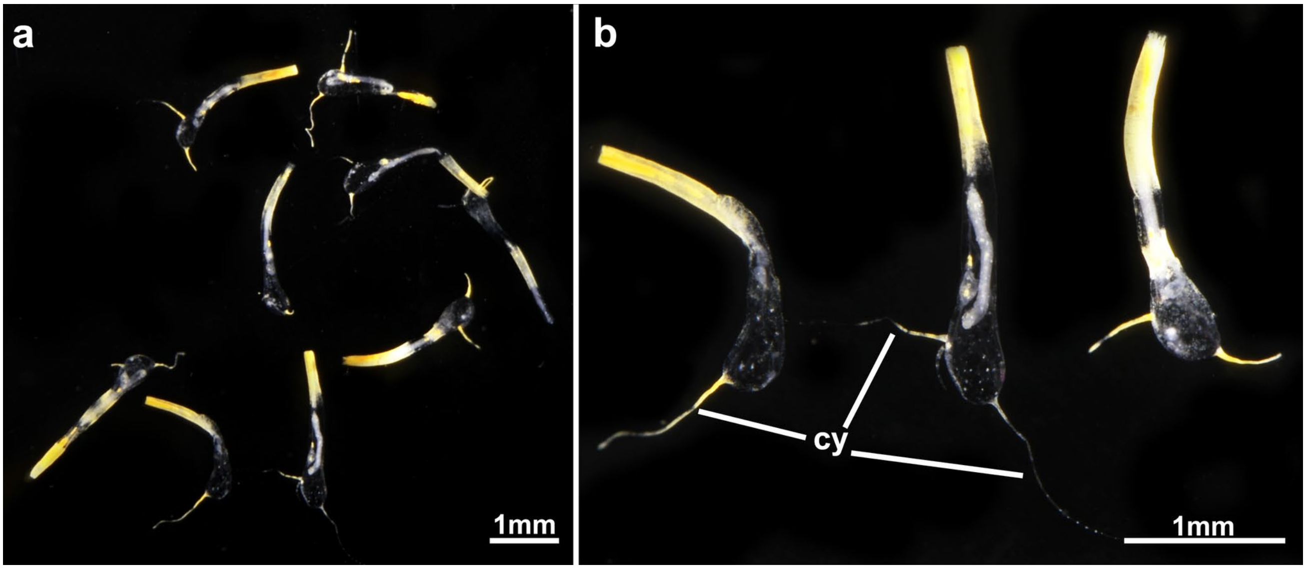


Fig. 1 *Aethozoon flavum* sp. nov. **a** General view of nine zooids; **b** Detail of three zooids showing elongated shape and cystid appendages. Note also the distinct yellow coloration of zooids. Abbreviation: cy = cystid appendage

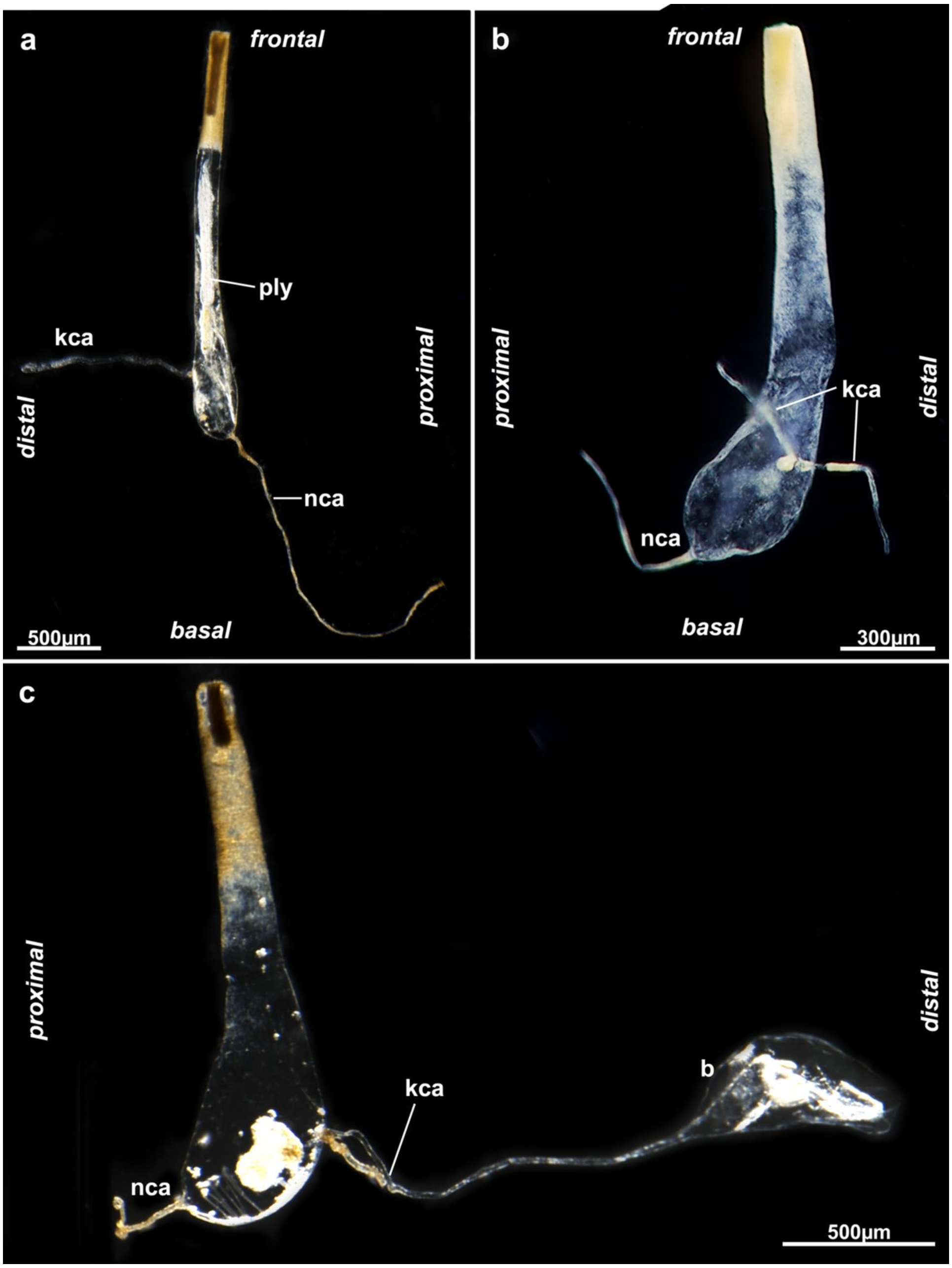


Fig. 2 Details of single zooids of *Aethozoon flavum* sp. nov. **a** Holotype (MNHN-IB-2017-723) showing long, non-kenozooidal cystid appendages; **b** Paratype (MNHN-IB-724) showing shorter cystid appendages including two shorter kenozooidal ones; **c** Paratype (MNHN-IB-725) showing zooid devoid of polypide and kenzooidal cystid appendage with distal bud. Abbreviations: b = bud; kca = kenozooidal cystid appendage; nca = non-kenozooidal cystid appendage; ply = polypide

elongated with very long anal tube terminating almost in vestibular area (Figs. 3c, d; 8d, e). Vestibular wall highly elongated occupying top third of retracted zooid (Figs. 1–3, 9). Distal vestibular area quadrangular (Fig. 9b) and usually wide with distinct yellow coloration (Figs. 1, 2, 9a), more proximally with strongly denticulate, dense cuticle (Fig. 9c). Short, vestigial diaphragmatic collar (Fig. 9d). Diaphragm inconspicuous with indistinct sphincter (Fig. 9e). Four sets of parieto-vestibular muscles, bilaterally arranged (Figs. 3, 4a, b). Four duplicature bands – two projecting frontally, two basally (Figs. 3, 4b, c, e, f). Funicular system single or branched, from caecal tip to pore-plate and basal body wall (Figs. 3, 4, 5).

Etymology: The specific Latin epithet of the new species, *flavum*, means yellow and alludes to the distinct yellow coloration of the specimens.

Type locality: Western Indian Ocean, Fani Maoré volcanic edifice.

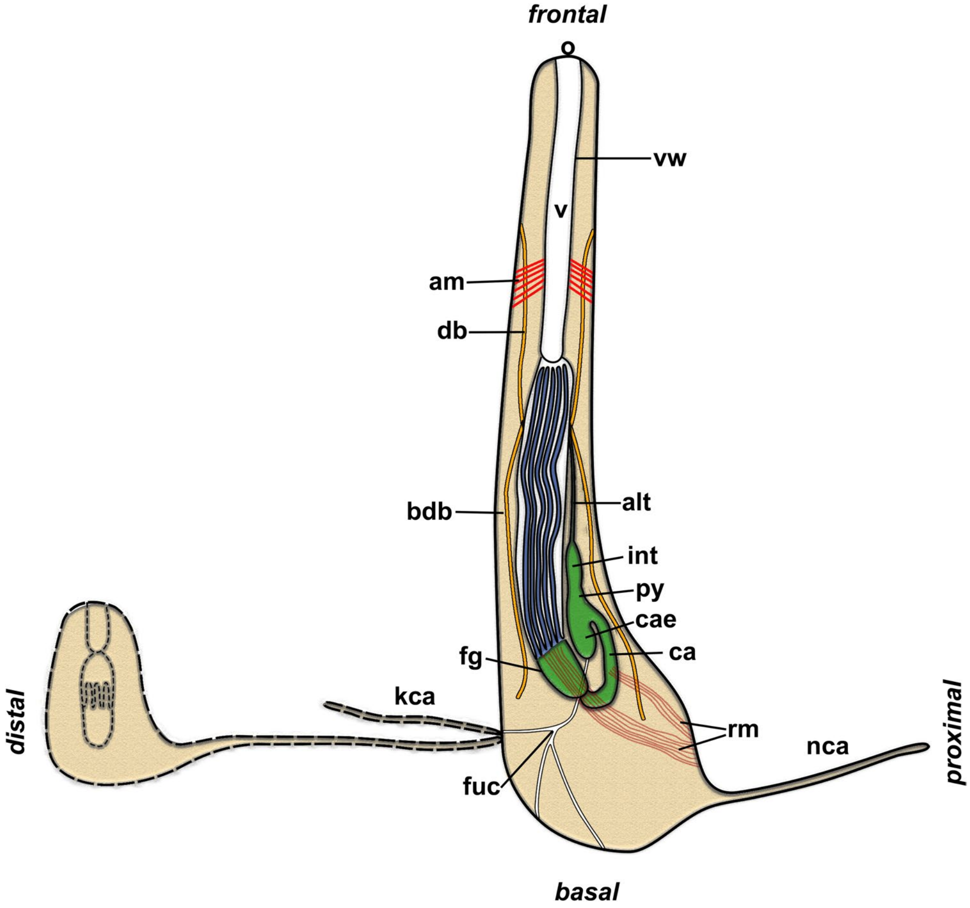


Fig. 3 Schematic drawing of *Aethozoon flavum* sp. nov. Abbreviations: alt = anal tube; am = apertural muscles; bdb = basal duplicature band; ca = cardia; cae = caecum; db = duplicature band; fg = foregut; fuc = funicular cords; kca = kenozooidal cystid appendage; int = intestine; nca = non-kenozooidal cystid appendage; py = pylorus; o = orifice; rm = retractor muscles; v = vestibulum; vw = vestibular wall

Discussion

Morphological characters and diversity of aethozoids

The general morphology of *Aethozoon flavum* sp. nov. conforms well to other aethozoids, as it bears elongated zooids and various appendages (Reverter-Gil et al. 2016; Schwaha et al. 2019; Schwaha 2020a; Schwaha and Ott 2020). Its size range accords more with those of *Franzenella limicola* (Franzén, 1960) (length 1–2.5 mm) and *Aethozooides uraniae* (Schwaha et al. 2019) (length 1–3 mm), but cystid appendages and gut morphology are most similar to those of *Aethozoon pellucidum* Hayward, 1978.

Franzenella limicola occurs in shallow habitats and has a high number of occasionally branching cystid appendages, supposedly supported by musculature (Franzén 1960; Berge et al. 1985). *Aethozooides uraniae* has two basal cystid appendages, more or less opposite to each other, plus mid-peristomial to rare frontal appendages (Schwaha et al. 2019). Like *A. pellucidum*, *A. flavum* sp. nov. has up to two distal, kenozooidal appendages, but below a mid-peristomial position. The lack of the characteristical pair of basal appendages supports the assignment of *A. flavum* to the genus *Aethozoon*.

The tentacle number of 14 in *A. flavum* sp. nov. differs from the 10 in *A. uraniae* (Schwaha et al. 2019) and is more similar to the 12–14 of *F. limicola* (Franzén 1960). The tentacle number in *A. pellucidum* is elusive and has previously been guessed at 30 (Hayward 1978) or could not be estimated in later studies (Hayward and Erseus 1980). Although *A. pellucidum* represents the largest of all aethozoids (~ 6–9 mm), tentacle numbers rarely exceed over 20 in ctenostomes (Schwaha 2020a).

The gut morphology is best known in *Aethozooides uraniae*, which is rather short and straight compared to *A. flavum* sp. nov. (Schwaha et al. 2019). The latter corresponds better to the situation in *A. pellucidum* (Hayward 1978; Hayward and Erséus 1980), but also in *F. limicola* (Franzén 1960) with elongated cardiac portions and a more frontal position of

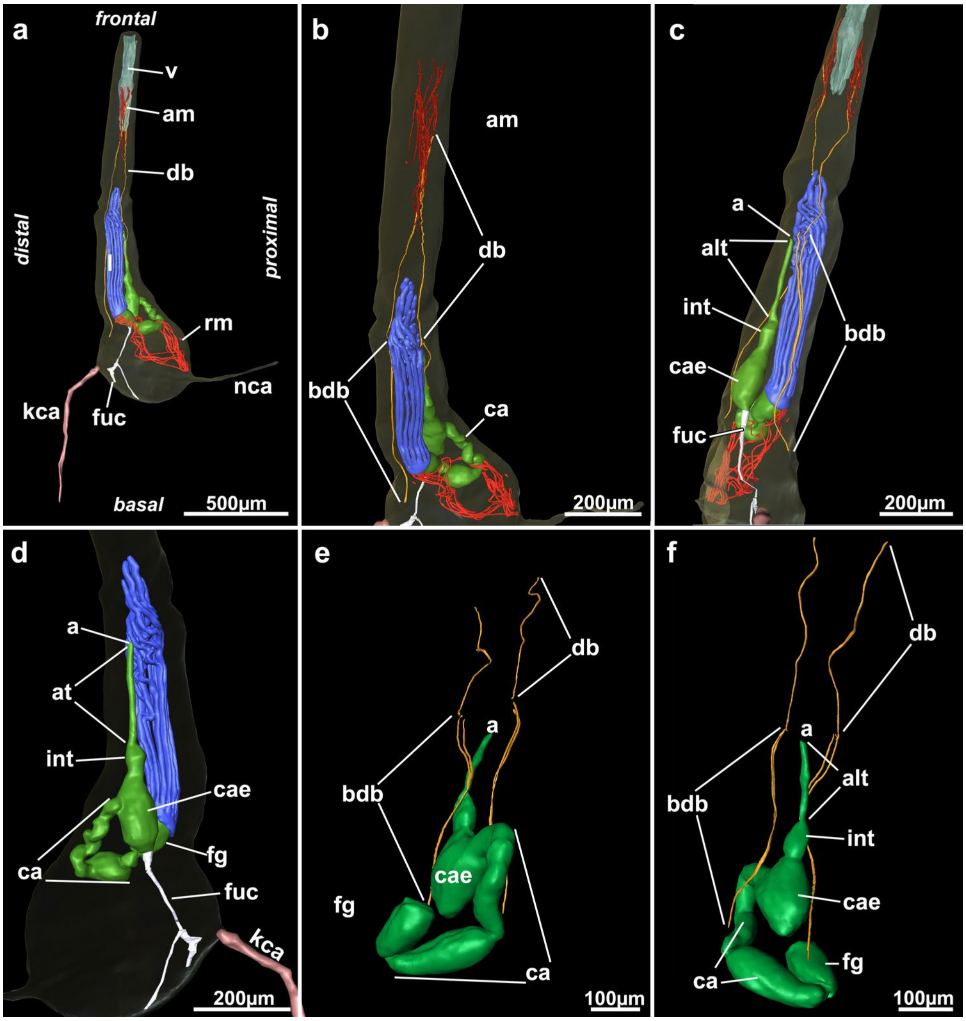


Fig. 4 3D-reconstructions based on serial histological sections of *Aethozoon flavum* sp. nov.. **a**–**d** Reconstruction of one zooid; a Lateral view showing general structure; **b** Detail of frontal area; **c** Detail of basal duplicature bands; **d** Detail of the lophophore and digestive tract; **e**, **f** Another zooid. Digestive tract and duplicature bands in two opposing lateral views. Abbreviations: a = anus; alt = anal tube; am = apertural muscles; bdb = basal duplicature band; ca = cardia; cae = caecum; db = duplicature band; fg = foregut; fux = funicular cords; kca = kenozooidal cystid appendage; int = intestine; nca = non-kenozooidal cystid appendage; rm = retractor muscles; v = vestibulum

the caecum in retracted zooids. A highly elongated anal tube has also been indicated in *A. pellucidum* and *F. limicola* and is also weakly present in *A. uraniae*. In the latter three species, however, it usually terminates via a lophophoral anus, whereas *A. flavum* sp. nov. shows the most elongated anal tube observed and has a more vestibular anus (see Schwaha 2020b for differentiation of ctenostome anuses).

The apertural area of *A. flavum* sp. nov. has two remarkable features. First, duplicature bands that project basally (in comparison, proximally to other bryozoans) have never been observed in any other bryozoan (Schwaha et al. 2011, 2020; Schwaha 2020c). Four duplicature bands are common, but usually all of them project in the same direction and not in opposite directions. *Aethozooides uraniae* has four, short duplicature bands extended frontally from the tentacle sheath (Schwaha et al. 2019). Second, the proximal vestibular wall shows a thick, denticulate cuticle obstructing the vestibulum. Thick vestibular walls are common among ctenostome bryozoans (Decker et al. 2021; Schwaha 2021), but a denticulate structure is unusual and probably only previously reported in *Harmeriella terebrans* Borg, 1940, which supposedly uses these structures as a boring apparatus into other bryozoans (Borg 1940), a function not feasible for solitary bryozoans such as aethozoids. At least in *A. uraniae* such a denticulate structure is not present, however, none of the other species or genera of aethozoids have been analysed in this respect with comparable histological methods.

A collar, as an acellular defensive structure projecting from the diaphragm into the vestibulum, is present in the apertural area of most ctenostome bryozoans (Schwaha 2020a). Among aethozoids, it is short in *F. limicola*, *A. uraniae* (Schwaha et al. 2019) and *A. flavum* sp. nov. (this study), whereas it is highly elongated in *A. pellucidum* (Hayward 1978; Grischenko et al. 2019). The highly denticulate vestibular wall of *A. flavum* sp. nov. probably renders a long collar superfluous as it obstructs the passage of the vestibulum, which is otherwise achieved via the collar.

The funicular cord or system is a thin peritoneal tissue strand with musculature that generally projects from the proximal end of the caecum to the body wall (Schwaha 2020c). In several ctenostomes, it forms a colonial system of integration by creating a network of tissue strands in

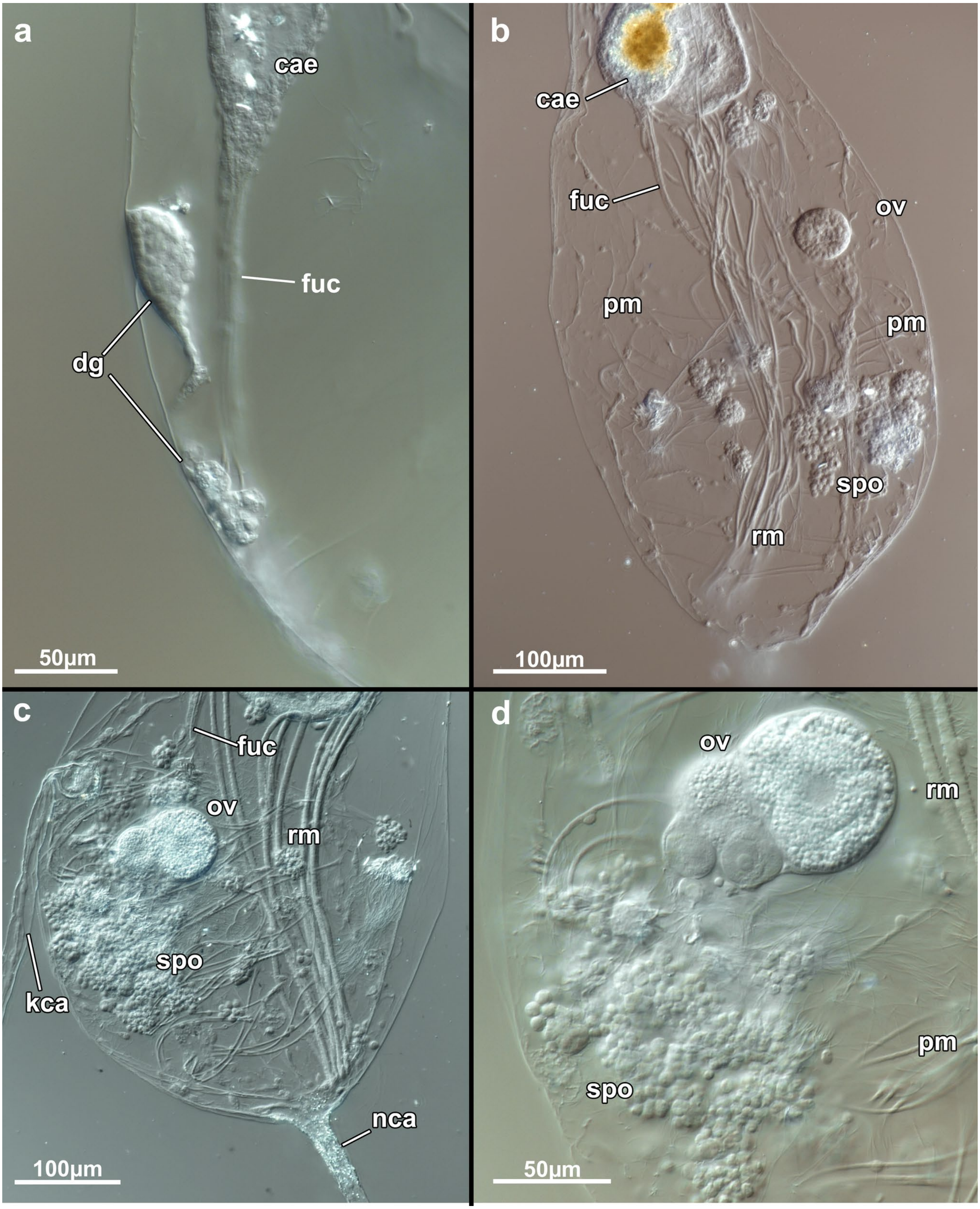


Fig. 5 Reproductive organs, whole mounts of *Aethozoon flavum* sp. nov. **a** Basal area of zooid with developing gonads; **b** Basal area with ripe gonads showing particular association of the spermatogenic tissue with funicular cords; **c** General view of basal area; **d** Detail of c showing developing oocytes and spermatogenic tissue. Abbreviations: cae = caecum; dg = developing gonad; fuc = funicular cord; kca = kenozooidal cystid appendage; nca = non-kenozooidal cystid appendage; ov = ovary; pm = parietal muscles; rm = retractor muscles; spt = spermatogenic tissue

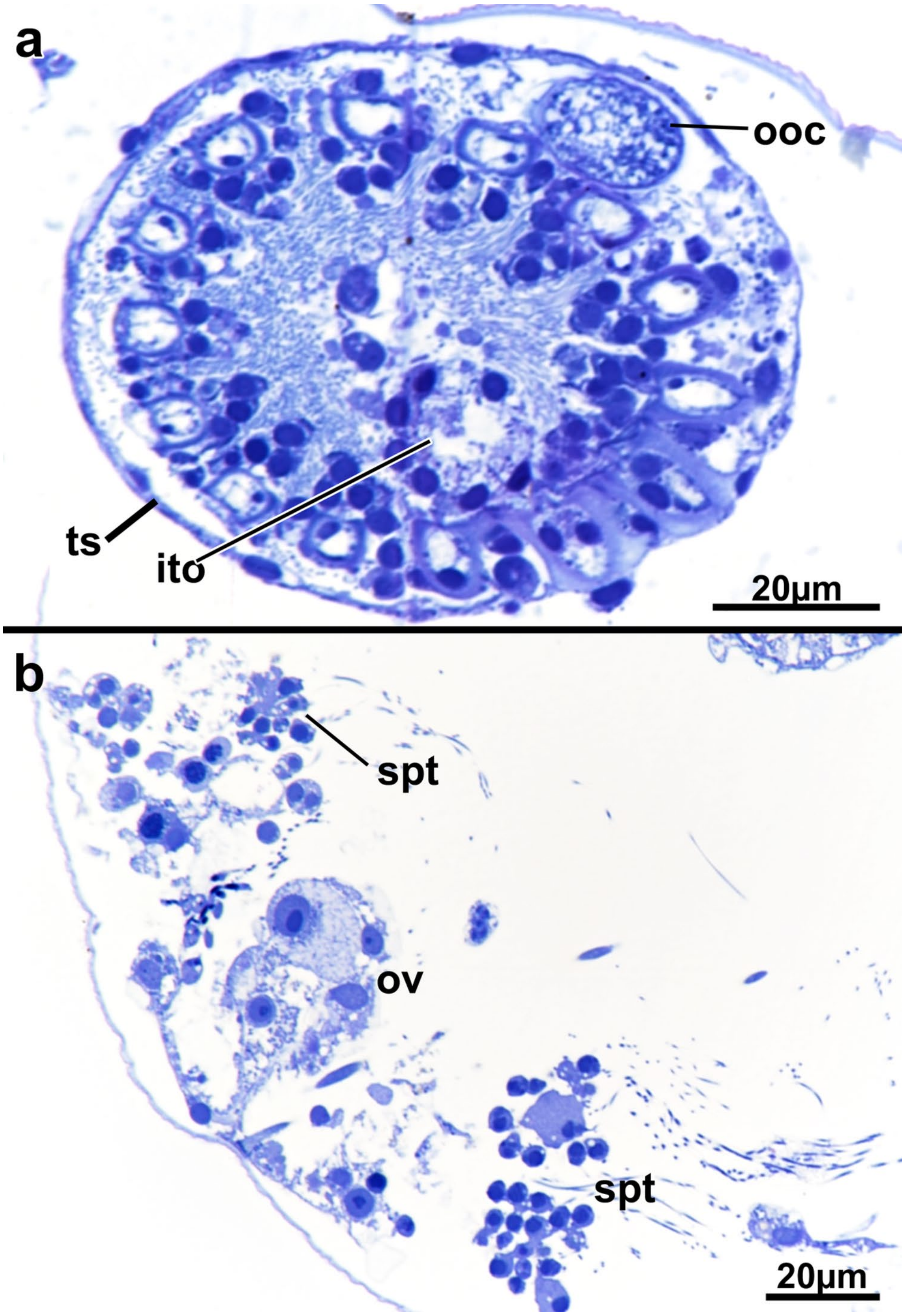


Fig. 6 Histological sections of reproductive organs of *Aethozoon flavum* sp. nov. **a** Cross-section of lophophoral base with intertentacular organ; **b** Section of basal region showing gonads. Abbreviations: ito = intertentacular organ; ooc = oocyte; ov = ovary; spt = spermatogenic tissue; ts = tentacle sheath

contact with interzooidal pore-plates (Schwaha et al. 2020). In aethozoids, it either is present as a simple cord not associated with the interzooidal pore-plate in *A. uraniae* (Schwaha et al. 2019) or projects basally from the caecum to branch into several strands, also associated with pore-plates, as found in *F. limicola* (Franzén 1960), and *A. flavum* sp. nov. of the present study. No data is available for *A. pellucidum*. Because studied specimens of *F. limicola* and *A. flavum* sp. nov. showed sexual reproduction, the extent of the funicular branching could correlate to gonad development.

Diversity and distribution of aethozoids

Aethozoon flavum sp. nov. is only the fifth species of Aethozoidae and the second of the genus *Aethozoon* (Schwaha et al. 2019). The type species, *A. pellucidum*, was originally

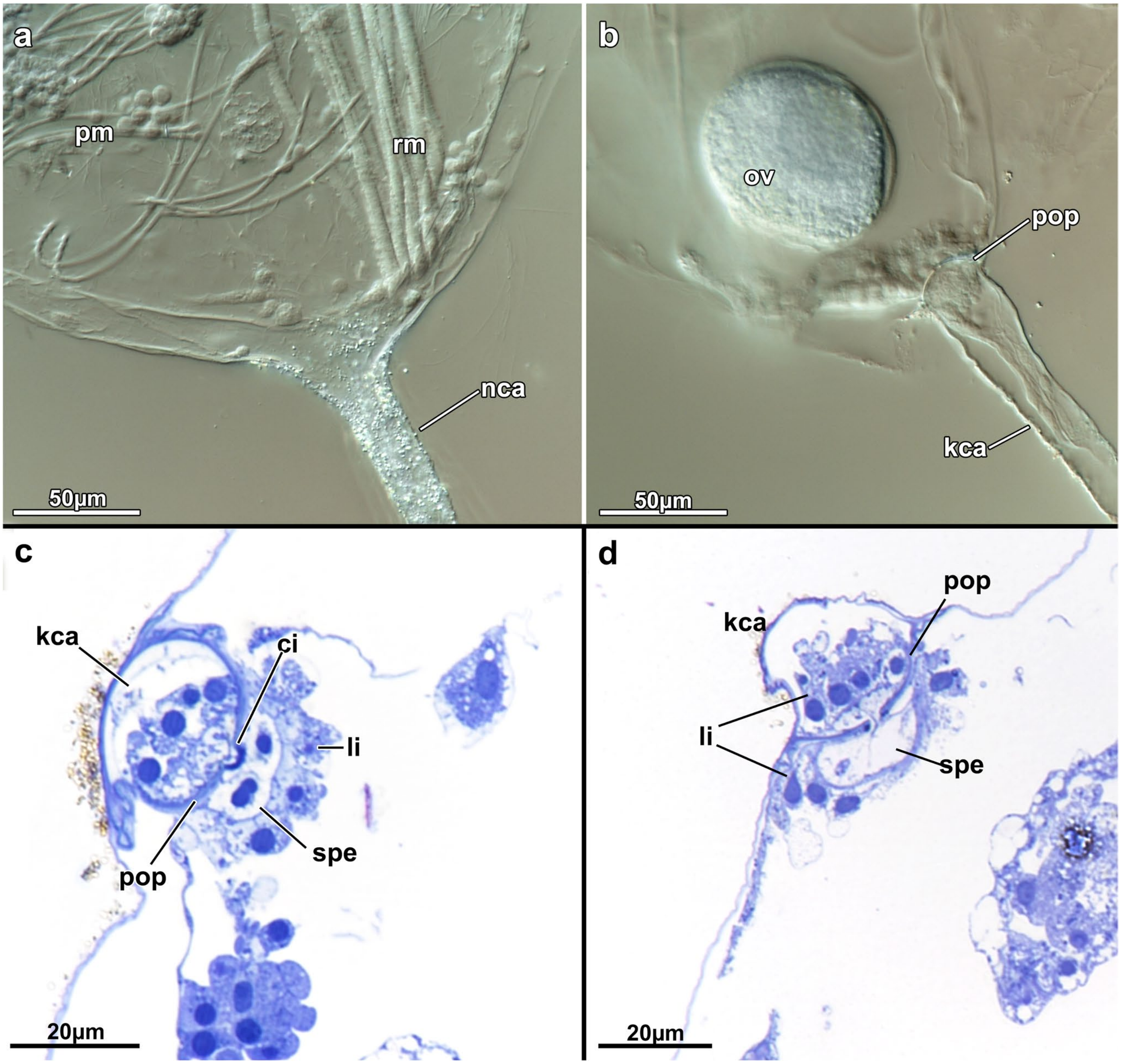


Fig. 7 Cystid appendages of *Aethozoon flavum* sp. nov. **a** Non-kenozooidal cystid appendage, whole mount; **b** Kenozooidal cystid appendage showing pore-plate; **c**, **d** Sections showing details of pore-plate and separation of kenozooidal cystid appendages with specialized cells. Abbreviations: ci = cincture cell; fuc = funicular cord; kca = kenozooidal cystid appendage; li = limiting cell; nca = non-kenozooidal cystid appendage; ov = ovary; pm = parietal muscles; pop = pore plate; rm = retractor muscles; spe = special cell

found in the Norwegian Sea, Atlantic Ocean (Hayward 1978; Hayward and Erseus 1980) and later reported from other areas in the Atlantic (see Reverter-Gil et al. 2016 for a summary). *Aethozooides uraniae* was recently described from the deep-sea hypersaline anoxic basins (DHAB) haloclines of the Mediterranean (Bernhard et al. 2015; Schwaha et al. 2019). *Aethozoon pellucidum* was recently found in the Pacific Ocean (Grischenko et al. 2019), from the Kuril-Kamchatka Trench at > 7000 m depth, comprising the deepest record of an aethozoid and of ctenostomes. Previously it was only recorded from New Caledonia in the Pacific Ocean (d'Hondt and Gordon 1996). The present study documents the first report of an aethozoid bryozoan from the Indian Ocean and supplements the general picture of a global distribution of the family both geographically and bathymetrically.

The high abundance of aethozoids in the analysed core samples is of particular interest. Although distributed in

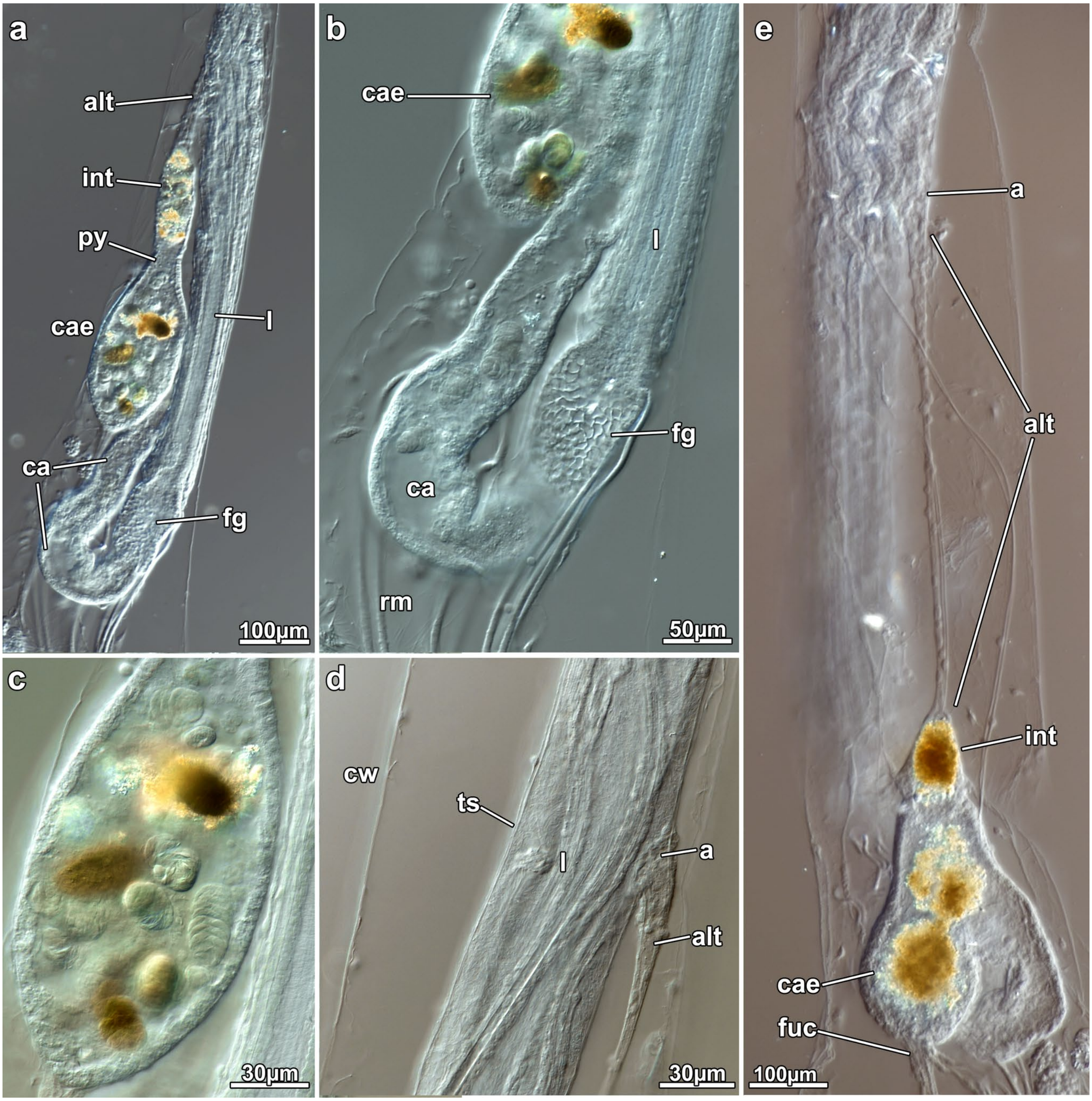
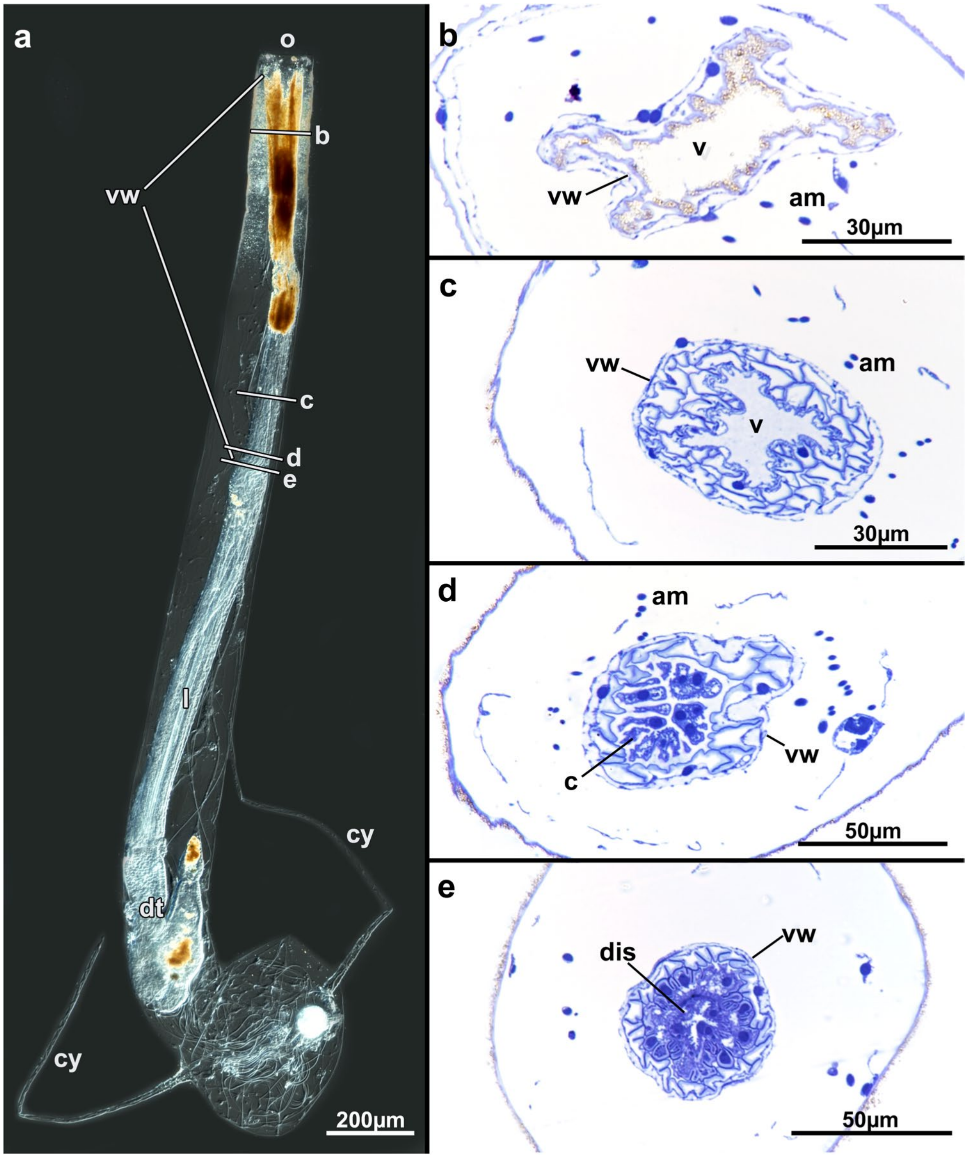


Fig. 8 Digestive tract of *Aethozoon flavum* sp. nov. **a**–**c** Same specimen; **a** Overview; **b** Detail of the foregut and parts of the midgut; **c** Detail of the caecum contents; **d**, **e** Same specimen; **d** Detail of the vestibular anus; **e** Digestive tract showing highly elongated anal tube from the intestine to the anus. Abbreviations: a = anus; alt = anal tube; ca = cardia; cae = caecum; cw = cystid wall; fg = foregut; fuc = funicular cord; int = intestine; l = lophophore; py = pylorus; rm = retractor muscles; ts = tentacle sheath

patches, a mean of 252 individuals per/cm^2 was observed in samples of *Aethozooides uraniae* (Bernhard et al. 2015). Specimens of the current core samples of *A. flavum* sp. nov. also showed a high abundance of specimens in samples (mean 22 individuals per 34,6 cm^2 core diameter), being in some cases the second most abundant taxon in the sample, only after nematodes. In addition to deep-sea aethozoids, studies on the shallow-water inhabiting *F. limicola* showed abundant specimens (mean 27.5 individuals per 6 cm core diameter) in 6 out of 24 cores, with a total number of 662 individuals in seven months (Berge et al. 1985). Apparently, aethozoids can have an important role in soft-sediment

Fig. 9 Vestibular area of *Aethozoon flavum* sp. nov. **a** Overview of a zooid showing general proportions and large size of the vestibular area. Transparent section planes indicate approximate section area in; **b**–**e**; **b** Section of the distal vestibular area; **c** Section of the proximal vestibular area; **d** Section of the collar area of the vestibulum; **e** Section of the diaphragm. Abbreviations: am = apertural muscles; c = collar; cy = cystid appendage; dis = diaphragmatic sphincter; dt = digestive tract; l = lophophore; o = orifice; v = vestibulum; vw = vestibular wall



ecosystems, both in shallow and deeper environments. We have little knowledge on the ecological and trophic networks in such ecosystems, but we found probable retarian tests in the gut of *Aethozoon flavum* sp. nov. of the current study (Fig. 8), which gives a first indication of what aethozoids might feed on.

So far, sequence data for any aethozoid are still lacking. As previously indicated, it is currently unknown whether specimens identified as *A. pellucidum*, which show a wide geographical and bathymetric distribution, actually belong to the same species (Hayward and Erséus 1980; Grischenko et al. 2019). As advocated in previous ctenostome studies (Decker et al. 2021; Schwaha et al. 2022) and also shown for aethozoids (Schwaha et al. 2019), detailed soft-body morphological analyses are essential for species identification and distinction. For most species, however, detailed histological analyses are still missing. Likewise, the finding of *A. pellucidum* in the Pacific Ocean only concerned a single zooid (Grischenko et al. 2019), which restricted detailed morphological analyses. We conclude that a holistic methodology, combining both morphological and prospective molecular approach will yield insights into the species diversity of this unexplored group of bryozoans.

Reproductive aspects

Aethozoids are one of few examples of genuinely solitary bryozoans (Schwaha 2020a). While the presence of kenozooids, as true polymorphs, may provoke questions about the solitary nature of this clade, we argue that, on one hand, there is never more than one feeding autozooid present in such animals. On the other hand, there is strong indication that kenozooidal cystid appendages are actually asexual budding stages that will ultimately separate from the parent specimen. This was recently also indicated in *Aethozooides uraniae*, where evidently some of the kenozooidal appendages were buds, or at least part of them were buds (Schwaha et al. 2019). In the current study, we found similar evidence in *Aethozoon flavum* sp. nov. where the terminal end of one of the kenozooidal appendages showed an advanced budding stage (Fig. 2c). Consequently, the kenozooidal appendage of the mother zooid may represent the non-kenozooidal, caudate, cystid appendage of the bud. Elongated, proximal and tubular cystid parts are typical for other ctenostomes such as some nolellids or arachnidiids (Schwaha 2020a). Ultimately, we think that all kenozooidal appendages in *A. flavum* sp. nov. are various budding stages that ultimately will separate from the mother animal. Given the abundance encountered and the lack of anything showing more than two functional feeding zooids or often even traces of a polypide, we consider the entire budding and separation processes from the mother zooid as very fast. This is also supported by the few budding stages observed in samples.

Concerning sexual reproduction, we detected an intertentacular organ in *A. flavum* sp. nov., a character found in zygote-spawning species associated with numerous small oligolecithal eggs and planktotrophic larval development (Ostrovsky and Porter 2011; Ostrovsky 2020). As recently summarized, *Aethozooides uraniae* and *Franzenella limicola* have an intertentacular organ (Schwaha et al. 2019), whereas information on *A. pellucidum* and all species of *Solella* Schwaha et al. 2019 is still lacking. Suffice it to say, the observations on *A. flavum* sp. nov. confirm that aethozoids generally appear to have a reproductive mode with oligolecithal eggs and planktotrophic larvae. Although larvae have, not surprisingly, never been observed for aethozoids, it should favour a wider distribution of the species owing to the long-lived nature of planktotrophic larvae (Reed 1991; Gruhl 2020). Other, true colonial deep-sea ctenostome bryozoans have lecithotrophic larvae including brooding (Schwaha pers. observation), and also the other solitary form of bryozoan, the Monobryozoidae, probably show lecithotrophic development too (Ott 1972; Schwaha 2020a; Schwaha and Ott 2020). The consequence of these different sexual reproductive strategies remains unknown and requires additional studies.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability Data is available on reasonable request.

Author contribution DZ and DC designed the study. AG and DC sorted all material. TS performed all morphological analyses and wrote the manuscript draft, TS, AG, and DC analysed the data. All authors contributed to the writing of the manuscript and approved the final version of the manuscript.

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