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ORIGINAL ARTICLE

Endobacterial morphotypes in nudibranch cerata tips: a SEM analysis

Christian Schuett · Hilke Doepke

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Abstract The SEM investigation of nudibranch cerata material exhibits endobacterial morphotypes found in 12 out of 13 species tested: *Aeolidia papillosa, Berghia caerulescens, Coryphella brownii, Coryphella lineata, Coryphella verrucosa, Cuthona amoena, Facelina coronata, Flabellina pedata, Dendronotus frondosus, Doto coronata, Tritonia plebeia and Janolus cristatus*. Endobacteria could not be detected inside *Tritonia hombergi*. Endobacterial morphology found inside nudibranch species was compared to bacterial morphotypes detected earlier in tentacles of cnidarian species. SEM micrographs show endobacterial analogy among nudibranch species, but also similarity to cnidarian endobacteria investigated earlier. Of course, morphological data of microbes do not allow their identification. However, since most of these nudibranch species prey on cnidaria, it cannot be excluded that many of the endobacteria detected inside nudibranch species may originate from their cnidarian prey. Our previous data describing genetic affiliation of endobacteria from nudibranchian and cnidarian species support this assumption. Dominant coccoid endobacteria mostly exhibit smooth surface and are tightly packed as aggregates and/or wrapped in envelopes. Such bacterial aggregate type has been described previously in tentacles of the cnidarian species *Sagartia elegans*. Similar coccoid bacteria, lacking envelopes were also found in other nudibranch species. A different type of coccoid bacteria, characterized by a rough surface, was detected inside cerata of the nudibranch species *Berghia caerulescens,* and surprisingly, inside tentacles of the cnidarian species *Tubularia indivisa.* In contrast to cnidarian endobacteria, rod-shaped microorganisms are largely absent in nudibranch cerata.

Keywords SEM · Endobacterial morphotypes · Nudibranchia · Cerata · Cnidaria · Tentacles

Introduction

Microbial activity is present in a wide range of habitats and has even been found in extreme environments (Staley and Gosink 1999; Brinkmeyer et al. 2003; La Duc et al. 2007). Life often is made possible by symbiosis, usually between specialized bacteria and various eukaryotic partners, which demonstrates the prominent relevance of such interactions. Well known is the interaction between man and trillions of symbiotic bacteria inside the intestinal tract (Xu et al. 2007). Similarly established is the vital microbial role of cellulose fermentation inside the ruminant gut system harbouring many bacterial symbionts (Leschine 1995). Efficient N_2 fixation (nitrogenase production) generated by *Rhizobium* spp. provides legumes with the needed nitrogen (Fischer 1994). Fascinating microbial bioluminescence observed in eukaryotic marine organisms may make lanterns of anglerfish glowing and illuminates eye regions of octopus species (Case et al. 1977; Nealson and Hastings 1979; Ruby and McFall-Ngai 1992). The manifold helpful microbial activities emphasize the importance of symbiotic life strategies; only these wondrous abilities may allow for

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C. Schuett (✉)
Alfred-Wegener-Institut für Polar- and Meeresforschung, 27570 Bremerhaven, Germany
e-mail: cschuett@awi-bremerhaven.de

H. Doepke
Alfred-Wegener-Institut für Polar- and Meeresforschung, Biologische Anstalt Helgoland, 27498 Helgoland, Germany
e-mail: hdoepke@awi-bremerhaven.de

the survival of the eukaryotic partners. Unique and prominent is the symbiotic function in evolution such as mitochondrial ATP production, serving the entire eukaryotic world with essential endobacterial 'power units' (Cray et al. 1999; Dyall et al. 2004).

Certainly, literature provides various examples of symbiotic life inside marine organisms (Deming and Colwell 1982; Palincsar et al. 1989; Thuesen and Kogure 1989; Burnett and McKenzie 1997; Cary et al. 1997; Althoff et al. 1998; Ivanova et al. 2003; Kurahashi and Yokoto 2006). However, these observations are often too sketchy, and interaction mechanisms between prokaryotic and eukaryotic marine life are considered as black boxes. This particularly applies to the unknown physico-chemical conditions inside eukaryotic hosts and to endobacterial physiological activities (e.g. pathogenic traits, Schuett and Doepke 2010). Information on the structure and function of these endobacterial communities is mostly nonexistent. Moreover, realistic imagination of dimensions and spatial images of the detailed structures are unclear.

The present paper resumes previous reports on endobacteria in nudibranch and cnidarian species (Schuett et al. 2007; Schuett and Doepke 2010; Doepke et al. 2011) and provides a first comparative scanning microscopic study on symbiotic endobacterial morphotypes detected in the tentacles of cnidarian and in cerata of selected nudibranch species.

Materials and methods

Nudibranch cerata and cnidarian tentacles were collected in July 2008 and 2009 by divers from waters around the Orkney Islands and the Outer Hebrides. Cnidarian tentacles and nudibranch cerata material were fixed in glutaraldehyde. Ethanol replaced sea water, which was exchanged later by amyl acetate. After critical point drying in liquid CO_2, sample material was mounted on SEM stabs. A first Au-coating (sputter) and the clipping off cerata or tentacle tip regions were followed by a second Au-coating. This procedure allowed an insight into the inner tissue structure and their endobacteria. Micrograph documentation of epidermis regions was conducted by using SEM Hitachi S-800. Complete details are given in Doepke et al. (2011).

Results

This first scanning microscopic documentation shows a wide distribution of different characteristic endobacterial morphotypes in nudibranch cerata (Table 1). The data do not claim for completeness; however, the investigation enables a tentative overview of the morphological diversity of endobacteria in nudibranch cerata tips. These results were compared to those on endobacterial aggregates and dispersed bacteria previously detected in tentacle material of the cnidarians *Metridium senile, Sagartia elegans* and *Tubularia indivisa* (Table 2) collected from Scottish diving locations (Schuett et al. 2007; Schuett and Doepke 2010; Doepke et al. 2011).

Endobacteria

Twelve of 13 nudibranch species examined harboured endobacteria inside the cerata epidermis, which corresponds to earlier findings of Doepke et al. (2011). No endobacteria could be detected inside of *Tritonia hombergi*. A characteristic spectrum of streptococcus-like bacteria with smooth surface represented the majority of the endobacteria found.

Oval-shaped bacteria were less frequent. These microorganisms occurred as two types of tightly packed bacterial aggregates. The first type was covered by envelopes (*Janolus cristatus*)and the second exhibited no sheath (*Janolus cristatus, Berghia caerulescens*). Distinct similarities but also differences between endobacteria in nudibranch cerata and cnidarian tentacles were noticed.

Bacterial aggregates

Aggregates with envelopes harboured two bacterial types of mainly coccoid forms with smooth surface and oval forms. The streptococcus-like bacteria display a wide range of diameters between 0.5 and 1.5 µm, which may account for bacterial division and growing stages inside the envelopes. The envelopes are extremely thin, and the spherical shapes of the tightly packed endobacteria are visible through the envelopes (Fig. 1). These characteristic aggregates were detected in most of the nudibranch species studied (*Aeolidia papillosa, Berghia caerulescens, Coryphella brownii* (Fig. 2)*, Coryphella verrucosa, Facelina coronata* (Fig. 3), *Flabellina pedata, Janolus cristatus*). Interestingly, this type of aggregate containing the typical coccoid endobacteria was also found in tentacles of the cnidarian species *Sagartia elegans* (Fig. 4). Uncommon large coccoid bacteria of 2–4 µm were detected exclusively in *Coryphella brownii* and *Dendronotus frondosus.*

Only *Janolus cristatus* carried a type of oval bacteria covered by envelopes (Fig. 5). This particular shape has been observed in cerata sample material collected in 2008. The image shows additional coccoid bacteria with smooth surface, tightly packed in aggregates and covered by envelopes as described above.

Apart from the coccoid bacterial majority with smooth surface, *Berghia caerulescens* moreover harboured spherical bacterial aggregates containing coccoid-shaped forms with rough surface (Fig. 6). Similar organisms with rough

Table 1 Overview of endobiotic bacteria and their aggregates within the epidermic tip region of cerata from 12 nudibranch species

Nudibranch groups	Aeolidiacea								Dendronotacea			Arminiaceae
Species	*Aeolidia papillosa*	*Berghia caerulescens*	*Coryphella brownii*	*Coryphella lineata*	*Coryphella verrucosa*	*Cuthona amoena*	*Facelina coronata*	*Flabellina pedata*	*Dendronotus frondosus*	*Doto coronata*	*Tritonia plebeia*	*Janolus cristatus*
Aggregates and endobacterial morphology												
Bacterial aggregates with envelope												
Coccoid shaped bacteria (μm)	10/1.4[a]	6/0.8	25/2.5		15/1.7		5/0.5	6/0.6				6/1.0
	4/0.5	13/0.9 r										
		ne/1.3 po										
Oval-shaped bacteria (μm)		5/0.8 × 1.3										4/0.8 × 1.6
		No envelope										Envelope
												7/0.8 × 1.5
												No envelope
Coccoid bacteria and aggregates without envelope (μm)				0.5								0.9
				0.5 × 0.9 sp								
Dispersed coccoid endobionts (μm)	0.8	0.9	1.2			1.4	1.0	0.7	ca 2-4 μm	1.5	1.0	
Endobionts located closely to cnidocysts	+	+	+	+	+	nd.	+	+	nd	+	+	nd

Nudibranch species selected prey on cnidarian diet (exception *Janolus cristatus* usually feeds on bryozoan *Bugula* sp.). Aggregate and bacterial sizes are approximate values

nd not detected, *ne* not estimable, *r* rough surface, *po* polymorphic, *sp* spindle shaped

[a] First number gives aggregate diameter and second refers to bacterial size, + detected

Table 2 Similarity of bacterial shapes detected in cnidarian tentacles and in cerata of nudibranch predators

Predators and hosts	Nudibranchia hosting bacteria	Cnidaria hosting bacteria
Aggregates and bacterial morphology		
Coccoid shapes	*Aeolidia papillosa*	*Sagartia elegans*
(smooth surface, Ø ca. 1.2 µm)	*Berghia caerulescens*	
	Coryphella brownii	
	Facelina coronata	
	Flabellina pedata	
	Janolus cristatus	
65 Coccoid shapes	*Berghia caerulescens*	*Tubularia indivisa*
(rough surface, Ø ca. 1.0 µm)		
Oval shapes	*Berghia caerulescens*	*Tubularia indivisa*
(Ø ca. 0.7 × 1.7 µm)	*Coryphella lineata*	
	Janolus cristatus	

Aggregates inside cnidarian tentacles are usually larger than those found in nudibranch cerata

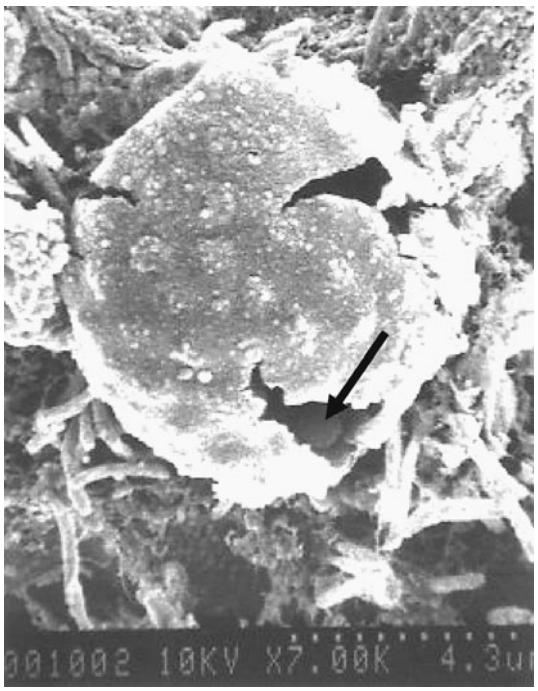

Fig. 1 Thin envelope of aggregate from *Berghia caerulescens*; single coccoid bacterium visible (*arrow*)

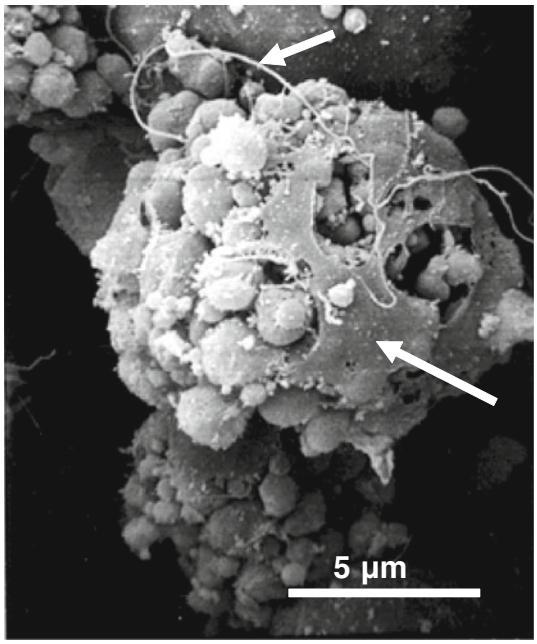

Fig. 2 Aggregate (Ø ca. 23 µm) with envelope (*arrow*) originating from cerata of nudibranch *Coryphella brownii* containing streptococcus-like bacteria (Ø ca. 0.5–2.5 µm) with smooth surface. Thread may derive from fired cnidocyst (*arrow*)

coccoid appearance have been detected earlier in *Tubularia indivisa;* however, these structures were lacking envelopes (Doepke et al. 2011). It cannot be excluded that envelopes were lost during preparation.

Bacterial aggregate sizes and numbers

Each of the cerata was found to harbour approximately 5–20 aggregates. Sizes of the mainly egg-shaped aggregates ranged between 4 and 25 µm. Aggregates may be hidden in caverns (*Facelina coronata*, Fig. 7). The number of bacteria inside a single envelope was between fifty and some hundreds. In comparison, cnidarian tentacles carry significantly higher numbers of aggregates and endobacteria than those found in the certata of nudibranchia.

Specially shaped endobacteria

Coryphella lineata exclusively carried spindle-like bacteria (Fig. 8). *Berghia caerulescens* showed unusual polymorphic organisms (Fig. 9). These bacterial structures have not been found inside cnidarian tentacle material.

Fig. 3 Aggregate (Ø ca. 5 µm) with envelope collected from cerata of nudibranch *Facelina coronata* harbouring coccoid bacteria with smooth surface of ca. 0.5 µm diameter

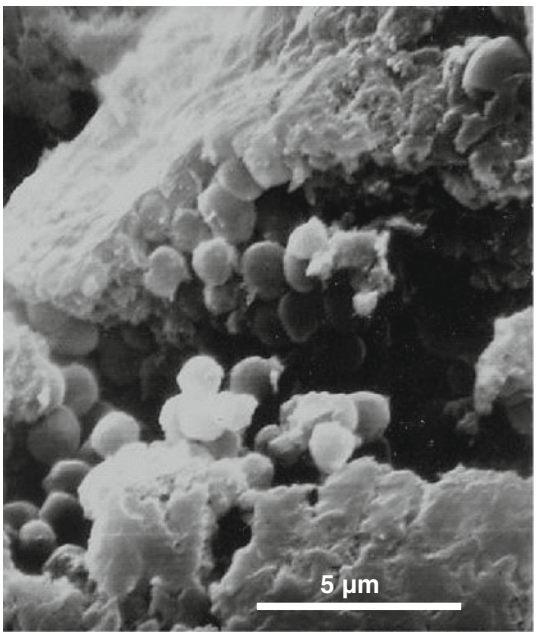

Fig. 4 Streptococcus-like bacteria (Ø ca. 1.3 µm) inside tentacle of cnidarian species *Sagartia elegans,* located in a cavern, no envelope

Filaments

Extremely fine fabric structures interconnecting endobacteria have been detected inside cerata material of *Coryphella brownii*, *Coryphella lineata* and *Flabellina pedata* (Fig. 10). Similar structures were detected earlier

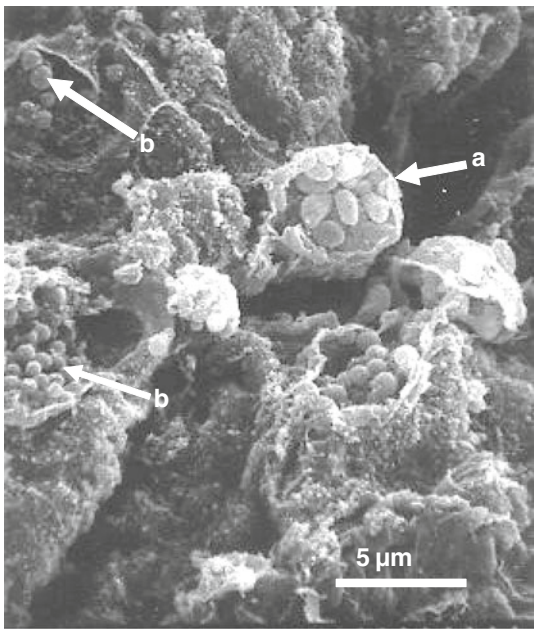

Fig. 5 Two different types of aggregates were found in cerata of nudibranch *Janolus cristatus.* **a** Aggregate covered with envelope (Ø ca. 5 µm) containing oval microorganisms (Ø ca. 0.8 × 1.6 µm); **b** aggregates in envelopes (Ø ca. 6 µm) harbouring streptococcus-like bacteria (Ø ca. 1.0 µm)

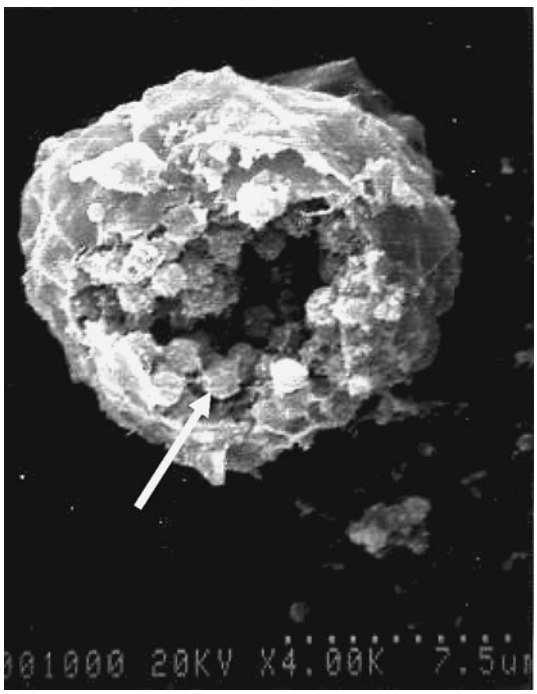

Fig. 6 Aggregate (Ø ca. 13 µm) in envelope with tightly packed bacteria (Ø ca. 0.9 µm) with rough surface (*arrow*), detected in nudibranch cerata of *Berghia caeruslescens*

in tentacles of the cnidarian species *Metridium senile* (Schuett et al. 2007) and *Tubularia indivisa* (Doepke et al. 2011).

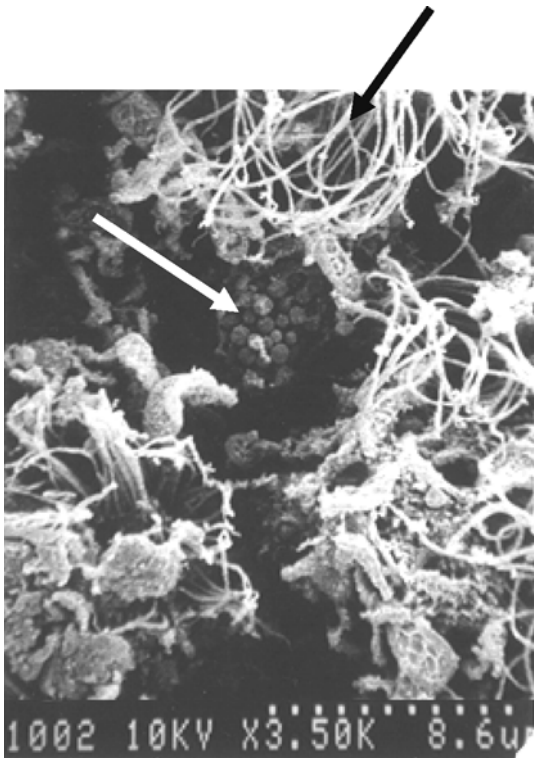

Fig. 7 Bunches of cnidocyst threads (*arrow*) in the vicinity of bacterial aggregates (envelopes cannot be identified). A cavern contains smooth surface streptococcus-like bacteria (Ø ca. 0.7 µm, *arrow*) detected in cerata of nudibranch *Facelina coronata*

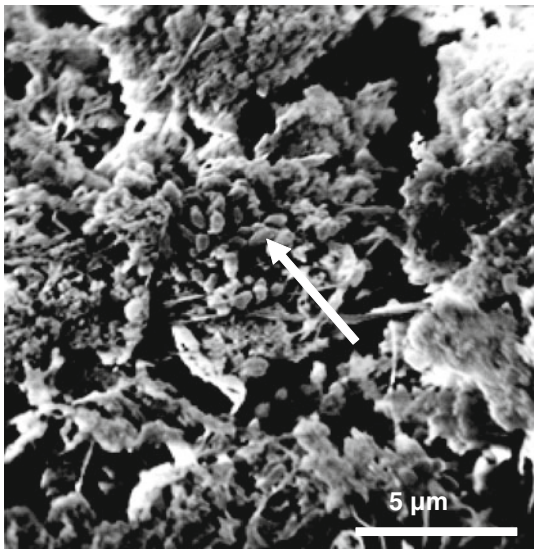

Fig. 8 Aggregates without envelope consisting of spindle-like bacteria (Ø ca. 0.5 × 0.9 µm; *arrow*); only found inside *Coryphella lineata* cerata

Kleptocnides

For nine out of 13 different cerata samples, the SEM micrographs demonstrated a close association between kleptocnides and endobacteria. Figure 11 shows typical

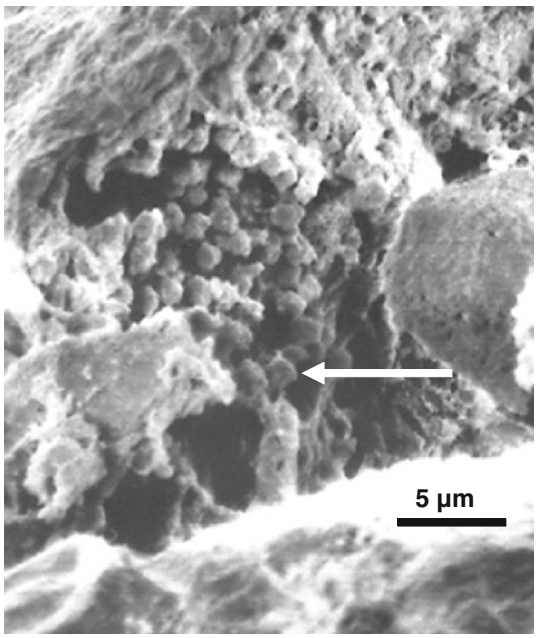

Fig. 9 Aggregate without envelope consisting of polymorphic bacteria (Ø ca. 1.3 µm, *arrow*) found in an epidermis cerata cavern of nudibranch *Berghia caerulescens*

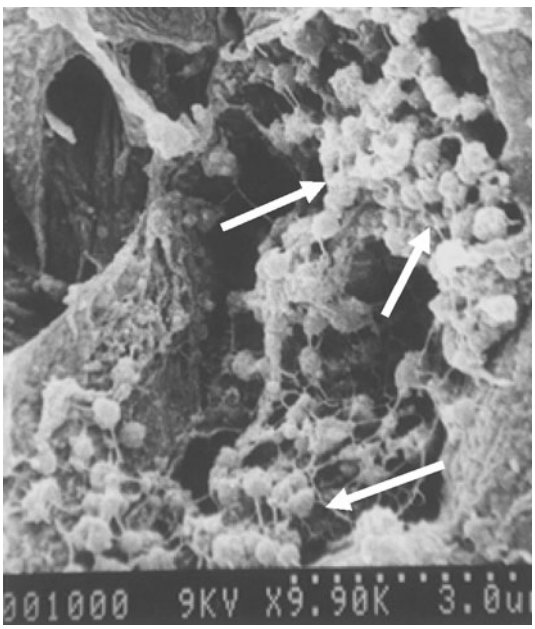

Fig. 10 Endobacteria detected inside cerata of nudibranch *Flabellina pedata* (*arrow*), connected by thin filaments (*arrows*)

kleptocnides inside of *Aeolidia papillosa*; these observations agree with earlier findings (Doepke et al. 2011).

Discussion

This paper provides a scanning electron microscopic survey of endobacterial morphotypes living inside cerata tip

Fig. 11 Cnidocysts (*arrows*) on the surface and/or within the epidermis region of the nudibranch *Aeolidida papillosa* cerata

regions of several nudibranch species. These findings are compared to those on endobacterial morphotypes found earlier in tentacles of different cnidarian species.

Similarities and differences between endobacteria of nudibranchia and cnidaria

There are considerable morphological analogies between endobacteria observed in cnidarian tentacle and nudibranch cerata material (Table 2). This particularly applies to the aggregates containing the many coccoid bacteria with smooth surface found in several nudibranch species but also inside *Sagartia elegans*. Further similarities include rough coccoid forms observed in *Berghia caerulescens* and *Tubularia indivisa*. Additional indication is provided by 16S rDNA sequencing data, which showed perplexing similarities of endobacterial species found in tentacles and cerata (Doepke et al. 2011).

However, there are also certain differences concerning aggregate sizes, number of bacteria per aggregate and the many rod-shaped bacterial forms inside cnidarian tentacles. Rod-shaped bacteria are largely absent inside the cerata of nudibranchia.

Aggregate envelopes

Besides, the remarkable analogies concerning aggregates and bacterial shapes substantial questions remain. It is unclear whether the cnidarian and nudibranch hosts or else the endobacterial tenants do produce the envelopes. There is no investigation concerning the chemical composition and origin of aggregate envelopes.

Furthermore, the origin of dispersed bacteria has to be elucidated yet. They may occur only as an artefact after opening of tentacle and cerata tips (clipping procedure and Au resputtering of the opened surface), resulting in aggregate breakage and the release of bacteria.

Filaments

Filaments interconnecting bacteria were termed 'nanowires' by Gorby et al. (2005). The striking findings by El Naggar et al. (2008, 2010) and Nealson (2010) showed that nanowires formed by *Shewanella oneidensis* MR-1 are communication devices. In biofilm experiments, electron transport along bacterial nanowires could be measured and has been interpreted as cooperative respiration within the bacterial community. It is open whether this is a general mechanism.

Nevertheless, the development of interconnecting filaments between bacteria often occurs in nature. Duchow and Douglas (1949) reported this morphological feature for the photoheterotrophic *Rhodomicrobium vaniellii*. Funke et al. (1997) described a coryneform bacterium with filaments. Kuhner et al. (2000) and Matthies et al. (2001) studied anaerobic clostridia from acidic forest bog locations and suggested these appendages to serve as electron transport system.

Our current and previous SEM data (Schuett et al. 2007; Doepke et al. 2011) showed endobacterial filaments in cnidarian tentacles and nudibranch cerata. However, cnidarian microorganisms developing filaments were rod-shaped, in contrast to nudibranch endobacteria with coccoid forms.

Bacterial passage into the epidermis

An important question concerns the passage mechanism of bacteria to settle inside cerata or tentacles epidermis. Our previous examination showed that microbes displayed other pathogenic activities, notably necrotic traits which may allow for a microbial invasion (Schuett et al. 2007; Schuett and Doepke 2010; Doepke et al. 2011). *Vibrio* species with necrotic ability were detected in cnidarian species (*Metridium senile, Tubularia* indivisa) as well as in several nudibranch species (*Berghia caerulescens, Coryphella lineata, Coryphella grancilis, Dendronotus frondosus, Polycera faeruensis, Polycera quadrilineata*).

Do endobacteria of cerata originate from cnidarian tentacles?

The most exciting question concerns the origin of endobacteria inside nudibranchia, which predominantly prey on cnidarian species. Our observation favours the idea that bacteria inside cerata originate from cnidarian tentacles. Relevant indications like the absence of these microbes in the seawater (Schuett et al. 2007) support this assumption.

The observed difference in endobacteria may be due to variations in diet, for example the spindle-like bacteria in *Coryphella lineata* and the two different oval forms in *Berghia caerulescens* and in *Janolus cristatus*. For the latter, nudibranch species (member of the family Zephyrinidae) Cimino and Ghiselin (1999) reported a possible diet switch from sponges to cnidaria. Further, major evidence supports the probability of bacterial transfer from cnidaria to nudibranchia: the uptake of the many unfired kleptocnides and their path through the complex nudibranch gut system to cnidosacks, their final destination in the tip region of cerata. In all likelihood, cnidarian microorganisms follow the same track. It can be assumed that bacteria reproducing inside cerata will find a milieu, which resembles that inside cnidarian tentacles.

Future research

The elucidation of the complex aspects of symbiosis is a great challenge to future research. To decode the black box, it requires a wide scope of experimental approaches, comprising intensified attempts in the fields of ecology, molecular biology, physiology, cell biology, structural chemistry, and physics, but also in the use of imaging systems. A major bottle neck in the analysis of physiological traits is due to the limited culturability of endobacteria. In order to bypass culture problems, Markert et al.(2007) and Gardebrecht et al. (2012) suggest the approach of physiological proteomics. However, this procedure is still in its infant state. It requires detailed preparatory proteomic information of endobacterial activities before it can become a powerful tool to enlighten complex black physiological and biochemical boxes.

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References

Althoff K, Schuett C, Krasko A, Steffen R, Batel R, Müller WEG (1998) Evidence for symbiosis between bacteria of the genus *Rhodobacter* and the marine sponge *Halichondria panicea*: harbour also putatively-toxic bacteria? Mar Biol 130:529–536

Brinkmeyer R, Knittel K, Jürgens J, Weyland J, Amann R, Helmke E (2003) Diversity and structure of bacterial communities in arctic versus antarctic sea ice: a comparison. Appl Environ Microbiol 69:6610–6619

Burnett WJ, McKenzie JD (1997) Subcuticular bacteria from the brittle star *Ophiactis balli* (*Echinodermata, Ophiuroidea*) represent a new lineage of extracellular marine symbionts in the α-subdivision of the class proteobacteria. Appl Environ Microbiol 63:1721–1724

Cary SC, Cottrell MT, Stein JL, Camacho F, Desbueres D (1997) Molecular identification and location of filamentous symbiotic bacteria associated with hydrothermal vent annelid *Alvinella pompejana*. Appl Environ Microbiol 63:1124–1130

Case JF, Warner J, Barnes AT, Lowenstine M (1977) Bioluminescence of lantern fish (Mycotophidae) in response to changes in light intensity. Nature (London) 265:179–181

Cimino G, Ghiselin T (1999) Chemical defence and evolutionary trends in biosynthetic capacity among dorid nudibranchs (Mollusca: Opistobranchia). Chemoecology 9:187–207

Cray MW, Burger G, Lang F (1999) Mitochondrial evolution. Science 283:1476–1481

Deming J, Colwell RR (1982) Barophilic bacteria associated with digestive tracts of abyssal holothurians. Appl Environ Microbiol 44:1222–1230

Doepke H, Herrmann K, Schuett C (2011) Endobacteria in the tentacles of selected cnidarian species and in cerata of their nudibranch predators. Helgol Mar Res. doi:10.1007/s10152-011-0245-4

Duchow E, Douglas HC (1949) *Rhodomicrobium vaniellii*: a new photoheterotrophic bacterium. J Bact 58:409–416

Dyall SD, Brown MT, Johnson PJ (2004) Ancient invasions: from endosymbionts to organelles. Science 304:253–2657

El Naggar MY, Gorby YA, Xia W, Nealson KH (2008) The molecular density of states in bacterial nanowires. Biophys J 95:10–12

El Naggar MY, Wanger G, Leung KM, Yuzvinsky TD, Sutham G, Yang J, Lau WM, Nealson KH, Gorby YA (2010) Electrical transport along bacterial nanowires from *Shewanella oneidensis* MR-1. PNAS 107:1817–18131

Fischer HM (1994) Genetic regulation of nitrogen fixation in rhizobia. Microbiol Rev 58:352–386

Funke G, Lawson PA, Collins MD (1997) *Corynebacterium mucifaciens* sp. nov., an unusual species from human clinical material. Int J Syst Bact 47:952–957

Gardebrecht A, Markert S, Sievert SM, Felbeck H, Thürmer A, Albrecht D, Wollherr A, Kabisch J, Le Bris N, Lehmann R, Daniel R, Liesegang H, Hecker M, Schweder T (2012) Physiological homogeneity among the endosymbionts of *Riftia pachyptila* and *Tevnia jerichonana* revealed by proteogenomics. ISME J 6:766776

Gorby YA, Yanina S, McLean JS, Rosso KM, Moyles D, Dohnalkova A, Beverridge TJ, Chang IS, Kim BH, Kim KS, Culley DE, Reed SB, Romine MF, Saffarini DA, Hill EA, Shi L, Elias DA, Kennedy DW, Pinchuk G, Watanabe K, Ishii S, Logan B, Nealson KH, Fredrickson K (2005) Electrically conductive bacterial nanowires produced by *Shewanella oneidensis* strain MR-1. PNAS 103:11358–11363

Ivanova EP, Nedashkowskaya OI, Zhukova NV, Nicolau DV, Christian R, Mikhailov VV (2003) *Shewanella waksmanii* sp. nov., isolated from spuncula (*Phascolosoma japonicum*). Int Syst Evol Microbiol 53:1471–1477

Kuhner CH, Matthies C, Acker G, Schmittroth M, Gößner ASDrake HL (2000) *Clostridium akagii* sp. nov. and *Clostridium acidisoli* sp. nov.: acid tolerant, N_2fixing clostridia isolated from acidic forest soil and litter. Int J Evol Microbiol 50:983881

Kurahashi M, Yokoto A (2006) *Endozoicimonas elysicola* gen. nov., sp. nov., a γ-proteobacterium isolated from the sea slug *Elysia ornata*. Syst Appl Microbiol 30:202–206

La Duc MT, Dekas A, Shariff O, Moisl C, Newcombe D, Venkateswaran K (2007) Isolation and characterization of bacteria capable of tolerating extreme conditions of clean room environments. Appl Environ Microbiol 73:2600–2611

Leschine SB (1995) Cellulose degradation in anaerobic environments. Annu Rev Microbiol 49:399–426

Markert S, Arndt C, Felbeck H, Becher D, Sievert SM, Hügler M, Albrecht D, Robidart J, Bensch S, Feldman RA, Hecker M,

Schweder T (2007) Physiological proteomics of the uncultured endosymbiont of *Riftia pachyptila*. Science 315:247–250

Matthies C, Kuhner C, Acker G, Drake HL (2001) *Clostridium uliginosum* sp. nov., a novel acid-tolerant, anaerobic bacterium with connecting filaments. Int J Evol Microbiol 51:1119–1125

Nealson KH (2010) Geomicrobiology: sediment reactions defy dogma. Nature 463:1033–1034

Nealson KH, Hastings JW (1979) Bacterial bioluminescence: its control and ecological significance. Microbiol Rev 43:496–518

Palincsar EE, Jones WR, Palincsar JS, Glogowski MA, Mastro JL (1989) Bacterial aggregates within the epidermis of the sea anemone *Aiptasia pallida*. Biol Bull 177:130–140

Ruby EG, McFall-Ngai MJ (1992) A squid that glows at the night: development of an animal-bacterial mutualism. J Bact 174:4865–4870

Schuett C, Doepke H (2010) Endobacteria and their pathogenic potential in cnidarian tentacles. Helgol Mar Res 64:205–212

Schuett C, Doepke H, Grathoff A, Gedde M (2007) Bacterial aggregates in the tentacles of the sea anemone *Metridium senile*. Helgol Mar Res 61:211–216

Staley JT, Gosink JJ (1999) Poles apart biodiversity and biogeography of sea ice bacteria. Annu Rev Microbiol 53:189–215

Thuesen EV, Kogure K (1989) Bacterial production of tetrodotoxin in four species of *Chaetognatha*. Biol Bull 176:191–194

Xu J, Mahowald MA, Ley RE, Lozupone CA, Hamady M, Minx P, Latreille P, Cordum H, Van Brunt A, Kim K, Fulton RS, Fulton LA, Clifton SW, Wilson RK, Kinght RD, Gordon JI (2007) Evolution of symbiotic bacteria in distal human intestine. PLoS Biol 5:1574–1586