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# On the gonotheca of *Egmundella producta* (G.O. Sars, 1874) n. comb. (Cnidaria, Hydrozoa)

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**Abstract:** *Egmundella producta* n. comb., commonly used so far in the combination *Lovenella producta,* is re-described based on the type specimens, as well as new material from the NW Atlantic. The gonothecae are large, fan-shaped structures, and the gonophore could be either a medusoid or a medusa. The re-examination of the type material confirmed that it possesses stolonal nematophores and nematothecae. Applying currently used generic diagnoses, it becomes necessary to transfer the species to the genus *Egmundella*.

**Keywords**: Campanulinidae - Leptothecata - gonosome - nematothecae - nematophores - type material.

## INTRODUCTION

In 1874, G.O. Sars described a new species of campanulinid hydroid which he named *Calycella producta.* It is a small hydroid, but it was subsequently also found at other places, mostly in deep waters of the North Atlantic and North Pacific Oceans. Although it has been found and described several times, its gonothecae and the sexual reproduction remain inadequately known. Gonothecae were summarily described by Storm (1882) in material from Norway ["... on the stolon, smooth, circular, somewhat compressed at the sides, with a short aperture", translation from Bonnevie (1899: 76)]. Vervoort (1985) described putative gonothecae as being sac-shaped structures arising from the hydrorhiza, but he was not sure about his identification of the species.

Additionally, the correct genus for this species has also been controversial for almost a century (Stechow, 1922). The combination *Lovenella producta,* introduced by Hincks (1874a), has been used most frequently, and is the currently accepted combination of most contemporary authors (see synonymy below). This was, however, a temporary solution because the reproduction was unknown and the presence of nematothecae in the type material had not been noted before. As argued below, the binomen *Egmundella producta* seems more appropriate for a campanulinid with stolonal nematothecae.

## MATERIAL AND METHODS

The new sample from near Bergen was collected by dredging. Material for the museum collection was preserved initially in 4% formaldehyde and subsequently transferred to 70% ethanol. Polyps for DNA extraction were preserved in absolute ethanol. For morphological examination techniques and terms see Cornelius (1995a, b) and Schuchert (2012). Microslide preparations were made as follows: the specimen was stained with Fast Green (20 mg/100 ml 90% ethanol), dehydrated with absolute alcohol, transferred to xylene, and mounted in Eukitt® resin (Sigma-Aldrich Co.). Measurements were made on rehydrated ethanol preserved material.

DNA extraction and sequencing of part of the 16S mitochondrial RNA gene were done as described in Schuchert (2005, 2014).

**Museum acronym abbreviations:**

| | |
|---|---|
| MHNG | Muséum d'histoire naturelle, Genève, Switzerland |
| ZMUC | Zoological Museum of the University of Copenhagen, Denmark (loan obtained in 2002) |
| UZMO | Zoological Museum of the University of Oslo, Norway |

## TAXONOMY

Order Leptothecata Cornelius, 1992
Family Campanulinidae Hincks, 1868

### *Egmundella producta* (G.O. Sars, 1874)

Figs 1A-D, 2A-C, 3A-F

*Calycella producta* G.O. Sars, 1874: 118, pl. 5 figs 6-8. – Hincks, 1874a: 134. – Verrill, 1879: 17. – Storm, 1879: 26. – Broch, 1907: 7.

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*Lovenella producta*. – Segerstedt, 1889: 12. – Jäderholm, 1909: 79. – Kramp, 1935: 140, fig. 57E. – Fraser, 1937: 96, pl. 19 fig. 102. – Fraser, 1944: 175, pl. 31 fig 149. – Schuchert, 2000: 423. – Schuchert, 2001: 54, fig. 39. – Calder, 2012: 22, fig. 21.

*Campanulina producta*. – Bonnevie, 1899: 73. – Bonnevie, 1901:10. – Broch, 1903: table. – Stechow, 1922: 146.

not *Lovenella producta*. – Fraser, 1911: 44, pl. 3 figs 7-10. – Fraser, 1914: 159, pl. 18 fig. 64. [in part *Egmundella gracilis* Stechow, 1921]

? *Lovenella producta*. – Fraser, 1938: 40.

? not *Campanulina producta*. – Leloup, 1940: 8, pl. 1 fig. 4.

? *Egmundella grimaldii Leloup*, 1940: 7, pl. 1 fig. 3.

? not *Opercularella producta*. – Vervoort, 1966: 111, fig. 12a. – Verwoort, 1985: 279.

**Material examined:**

Syntypes, UZMO B1378, Sars collection, as *Calycella producta*; Norway, Bodø and Lofoten, 80-100 f (=146-183); identified by G. O. Sars, numerous hydranths, relatively well preserved.

MHNG-INVE-91796; Norway, North of Litlesotra Island, 60.4083°N 05.1167°W, 100 m depth, on tube of *Sabella pavonia*; collected 22.04.2015; with 3 gonothecae; part of this material processed to permanent microslide preparations; DNA isolate 1097 made from a few hydranths, 16S sequence **KU512889**; DNA isolate 1098 made from a gonotheca content, 16S sequence identical to KU512889.

MHNG-INVE-25136; Iceland, 64.842°N 24.217°W, 220 m depth, temperature 7.1°C; collection date 05.09.1990. ZMUC BIOFAR100; Faroe Islands, 61.5878°N 6.2847°W, 283 m depth, temperature 6.8°C; collected 24.07.1987; without gonothecae.

ZMUC BIOFAR165; Faroe Islands, 62.1844°N 4.9667°W, 184 m depth, temperature 7.9°C, on hydroids; collected 07.05.1988; without gonothecae.

ZMUC BIOFAR517; Faroe Islands, 60.6039°N 11.6364°W, 1099 m depth, temperature 5.6°C; collected 27.07.1989; without gonothecae.

ZMUC BIOFAR523; Faroe Islands, 60.7114°N 12.6075°W, 606 m depth, temperature 8.5°C, on polychaete tube made of sand grains; collected 28.07.1989; without gonothecae.

ZMUC BIOFAR524; Faroe Islands, 0.7364°N 12.6222°W, 702 m depth, temperature 7.9°C, on hydroid *Symplectoscyphus tricuspidatus*; collected 28.07.1989; without gonothecae.

**Description:** Colony stolonal, stolons tubular, diameter 90-140 µm, irregularly corrugated, ramified, creeping, forming a reticulated network. Stolons usually bear on upper surface a row of widely spaced nematothecae,

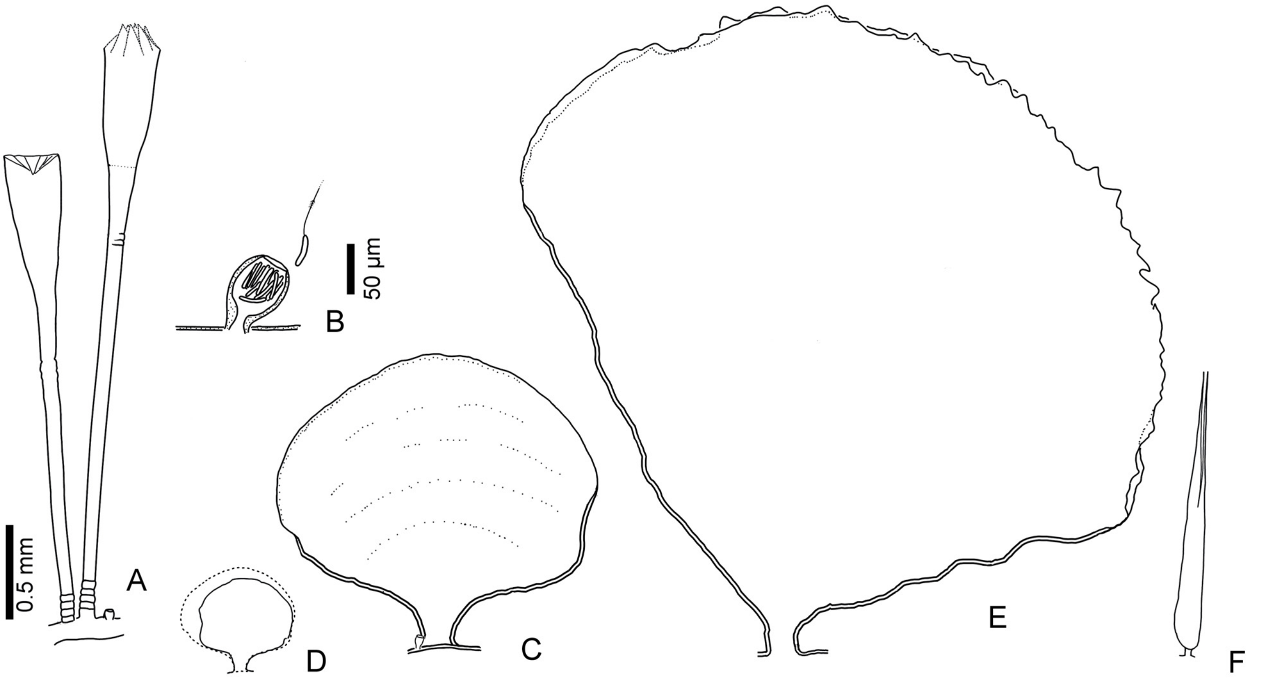

Fig. 1. *Egmundella producta* (G.O. Sars, 1874), line drawings of MHNG-INVE-91796, rehydrated alcohol material. (A) Two hydrothecae, left one with inverted operculum. (B) Nematotheca on stolon with bundle of large haplonemes. (C) Smallest gonotheca seen from broad side, same scale as A. (D) Shrinkage of the gonotheca shown in C, dotted line shows its outline after alcohol fixation, solid line after staining and embedding for a permanent microscopic slide preparation. (E) Largest of the three gonothecae seen from broad side, same scale as A. (F) Gonotheca shown in E seen from narrow side, not the same scale as E.

number variable between colonies, nematothecae about 60-100 µm high, on short pedicels, bodies egg-shaped, distally truncate, lumen filled with large haplonemes (Fig. 1B). The hydrothecae are not evenly distributed and tend to arise in clusters of 3-6, total height of hydrotheca and pedicel very variable 3-6 mm (Fig. 1A), diameters of pedicels 80-90 µm. Pedicels straight, smooth for the most part but regularly some short, annulated stretches present, this especially at base. Hydrotheca elongate, height 0.5-0.8 mm from diaphragm to operculum tip, walls thin, widest at base of operculum (diameter 0.28-0.32 mm), tapering towards below, and basally merging imperceptibly into pedicel, with no node at base of hydrotheca. Operculum low, conical, formed by about 10-12 triangular flaps. In fresh and alcohol preserved material, the operculum is not delimited from the hydrothecal wall by a crease line. A crease line can appear when the operculum is inwardly folded into the hydrotheca (Fig. 1A). Towards base of hydrotheca a very fine, membranous, funnel-shaped diaphragm, which is only discernible while there is a living polyp in the hydrotheca.

Gonothecae arise directly from stolons (Fig. 1C, E), fan-shaped, strongly flattened (Fig. 1F), the thickness of the

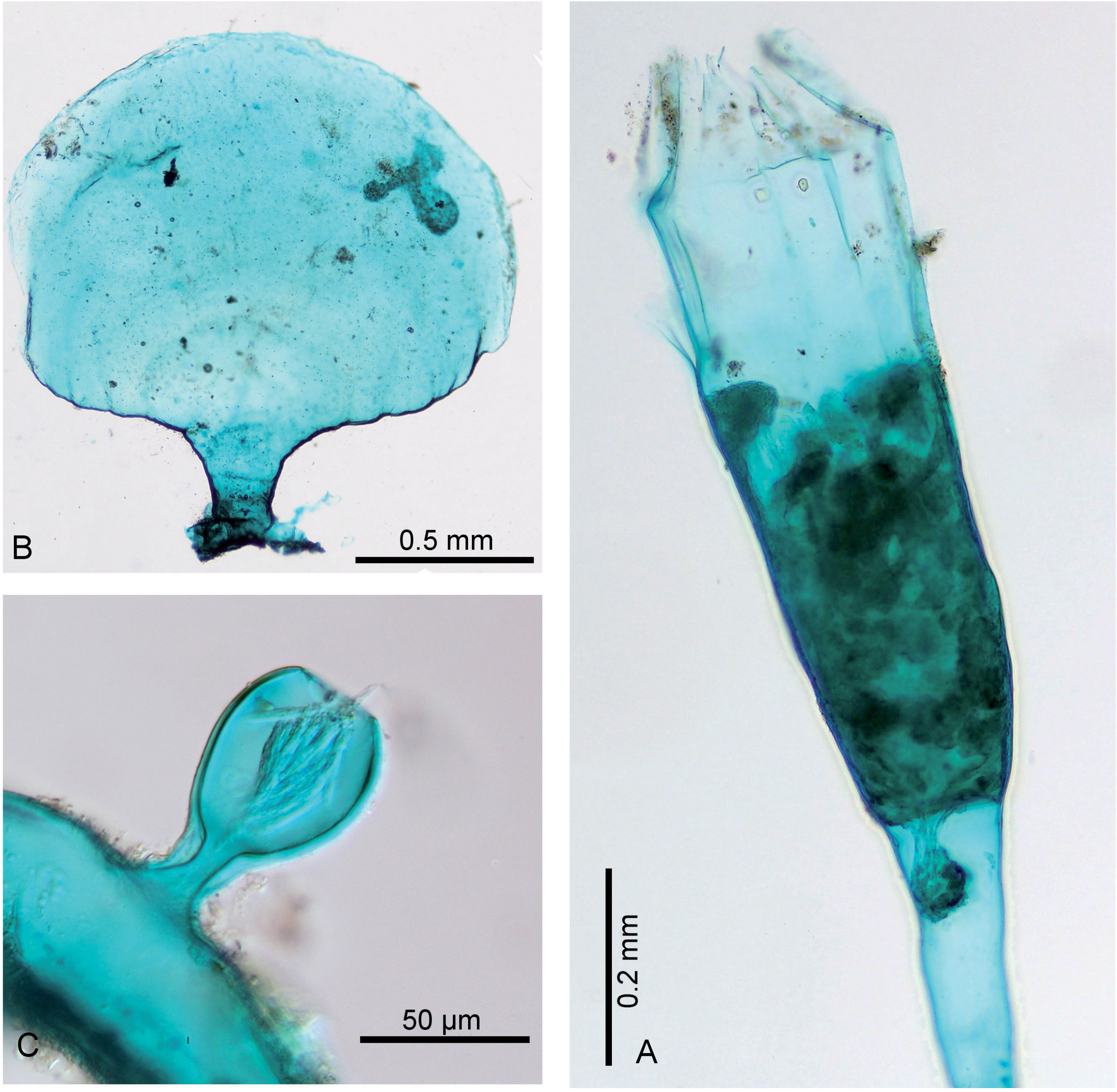

Fig. 2. *Egmundella producta* (G.O. Sars, 1874), photomicrograph of permanent slide preparation MHNG-INVE-91796. (A) Hydrotheca, note that the crease line delimiting the operculum at its base is a preparation artefact which appeared during the slide preparation. (B) Gonotheca. (C) Nematotheca.

gonotheca in the proximal part is about 1/8 to 1/10 of the height, thinning out towards the periphery, with a large opening spanning from one side to the other (Fig. 1E-F), margin of opening irregularly serrated, possibly resulting from rupture of perisarc at maturity, lower walls of gonotheca undulated, pedicel short. Size of gonotheca variable, observed range (n=3, newly collected material) was 1.5 x 1.7 mm to 4.4 x 4.6 mm (height x maximal width). Only largest gonotheca contained soft tissue, represented by a very young and an advanced gonophore, gonophore a medusoid or a medusa.
Nematocysts:

- large merotrichous and atrichous haplonemes (Fig. 3A-B, E-F), concentrated in nematothecae but also present in hydranths, stolons and gonophores, (31-35) x (3.5-4) µm, straight or curved, thread of discharged capsules thin, tapering inconspicuously, some capsules without barbs (Fig. 3F), some with a stretch of about 30 µm beset with strong barbs, about 40 µm away from capsule (Fig. 3E).
- spindle shaped isorhizas (Fig. 3C), concentrated in tentacles, but also elsewhere, (7.5-9) x (1.5-2) µm, in light microscopy lacking visible spines.
- rare, small, unidentifiable capsules (Fig. 3D), (4-5) x (1-1.5) µm, may be developmental stages.

**Biology:** Grows on a variety of substrates like other hydroids (especially *Tubularia indivisa*), tubes of polychaetes, and ascidians. Depth range of reliably-identified material 6-750 m, usually below 80 m in boreal regions.

**Distribution:** In cool temperate to cold waters of the North Atlantic, rarely reported from the high Arctic: Norway (Sars, 1874; Storm, 1879; Bonnevie, 1899, 1901), Sweden (Segerstedt, 1889), Denmark (Kramp, 1935), North Sea (Broch, 1903), Iceland (Schuchert, 2000, 2001), North-western Atlantic (Verrill, 1879; Fraser, 1944).
The identities of records from deep waters of the Gulf of Gascogne and the Azores (Leloup, 1940; Vervoort, 1985) are uncertain.
Not reported so far from the Russian Arctic Sea (Antsulevich, 2015) or other high arctic waters (Ronowicz *et al.*, 2015), except for one record by Broch (1907) from the Jones Sound (south of Ellesmere Island, Canada).
Type localities: Norway, Nordland county, Bodø and Lofoten Islands, 146-366 m depth, on *Tubularia indivisa* and a serpulid tube.

**Remarks:** The presence or absence of nematothecae in campanulinid hydroids is usually considered to be a genus level difference (Levinsen, 1893; Jäderholm, 1909; Stechow, 1921; Bouillon *et al.,* 2006). The genus *Lovenella* Hincks, 1868 has as type species *Campanularia clausa* Lovén, 1836 by monotypy, a species with no stolonal nematothecae.
Contemporary authors (e. g. Cornelius, 1995a; Schuchert, 2001; Calder, 2012) did nevertheless not apply this and continued to use the combination *Lovenella producta* (G.O. Sars, 1874), despite the fact that nematothecae were always found. The reason for doing so was because the species remained incompletely described and it was assumed that the type material does not have stolonal nematothecae as these were not mentioned by Sars (1874). However, the re-examination of the syntypes showed that stolonal nematothecae are present in both of them. According to Bouillon *et al.* (2006) – currently the most comprehensive and widely accepted taxonomic system of the Hydrozoa – the species must thus be placed in the genus *Egmundella* Stechow, 1921 (Stechow, 1921: 225; type species *Egmundella gracilis* Stechow, 1921 by original designation).
A comparison with the syntype specimens made it evident that the new material from Norway is indistinguishable from them, the hydrothecae being only slightly shorter. The syntype material, as already stated by Sars (1874), is composed of specimens from at least two localities (Bodø and Lofoten Islands), each attached to a different substrate (*Tubularia indivisa* stem fragments and a serpulid tube fragment, respectively). The material is relatively well preserved, though most hydrothecae are damaged. The stolons bear numerous nematothecae, although their local density is variable. Since they were not mentioned by Sars (1874), it is assumed that he must have overlooked them. Considering the quality of the optical instruments available at his time, this is not surprising, as they are inconspicuous structures that need a careful examination to be discovered.
Sars (1874) stated that the type material had no gonothecae. However, I found one small (1 mm), developing gonotheca on the colony growing on the serpulid tube. The gonotheca is comparatively smaller, but otherwise morphologically similar to those observed in the new material (Fig. 1C, 2C). The gonotheca in the type material seems to be a younger stage than the one depicted in Fig. 1C and apparently there is no opening yet. There is a visible gonophore inside it, but no internal structures could be identified.
Unfortunately, the content of the gonotheca in the new material could not be identified with sufficient precision. The material had to be preserved immediately because the tissues started to deteriorate due to damage suffered during the collecting process. Only the largest gonotheca contained soft tissue, represented by one advanced gonophore and a very young one. The gonophore was provisionally identified as a medusoid with developed gonads, but it is not excluded that it could further develop into a medusa with tentacles. New observations based on living colonies are needed.
The shape of the gonothecae observed in the material of the present study matches only partially Storm's (1879) description. Storm mentions a short aperture, while in the present material there is a wide distal opening. Without any illustration of Storm's material it is difficult

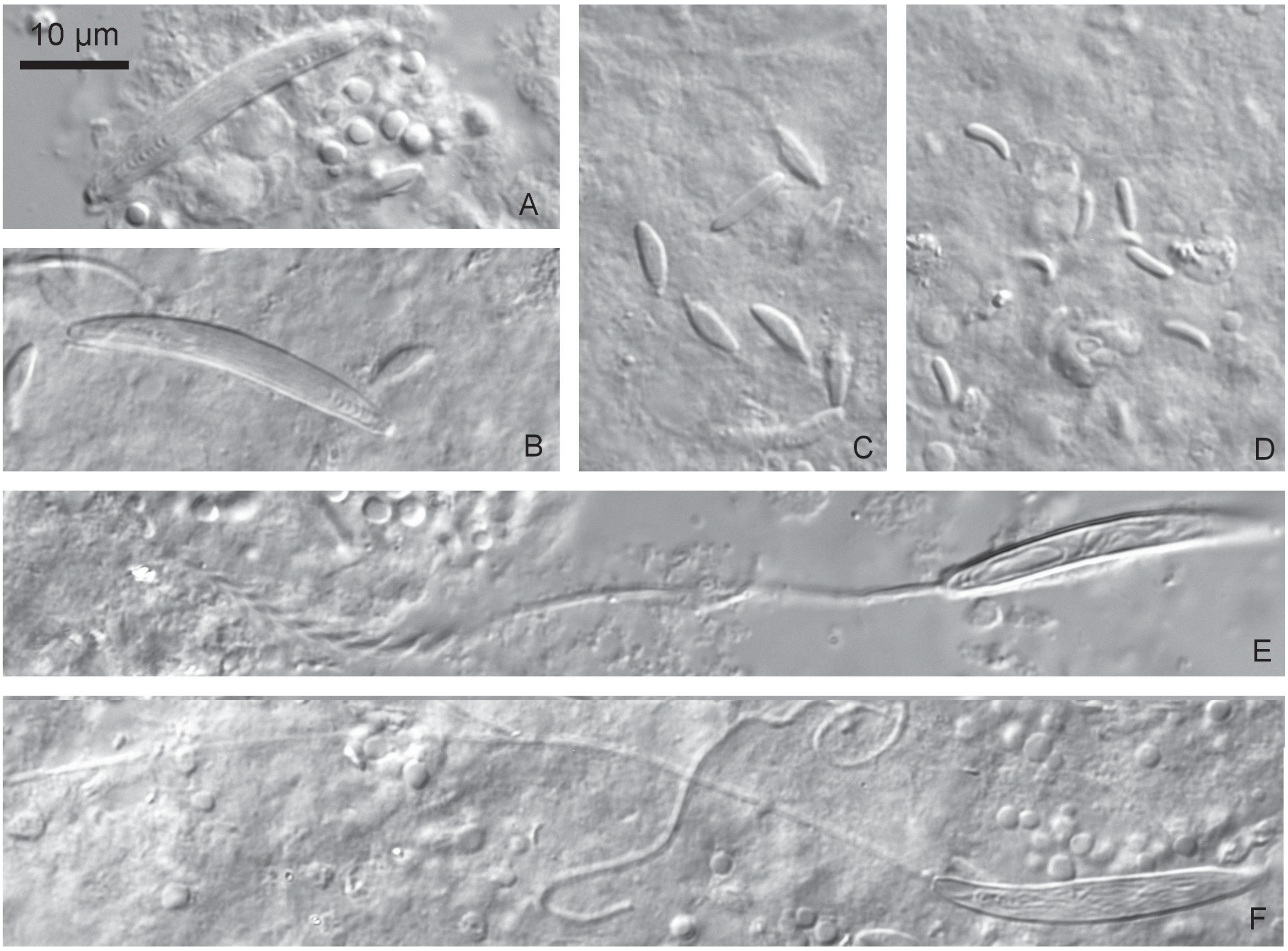

Fig. 3. Nematocysts of *Egmundella producta* (G.O. Sars, 1874), alcohol preserved material in 50% lactic acid, same scale for all images. (A-B) Undischarged large haplonemes. (C) Undischarged isorhiza capsules. (D) Unidentified small capsules. (E) Discharged large haploneme with barbs on thread. (F) Discharged large haploneme without apparent barbs on thread.

to assess its validity and significance. Also Vervoort (1985, as Verwoort) described gonothecae in material he tentatively identified as *L. producta*: "... hyaline, sac-shaped body, about as long as the hydrothecal pedicel and attached to the stolon by means of a very short collar-shaped pedicel. The lateral wall is slightly wrinkled; terminally it is open, with a slightly folded apical portion ...". Also this description does not match well the gonothecae found here, notably there is no mention of the gonothecae being flattened. Vervoort's material from deep waters of the Bay of Biscay originated from beyond the southern limit of the distribution of *E. producta* and it lacked nematothecae. I therefore think that Vervoort's hydroid was not *E. producta*, an opinion likely shared by Vervoort himself, because he added a question mark in front of the binomen.

*Egmundella grimaldii* Leloup, 1940, from deep waters of the Bay of Biscay, is rather similar to *E. producta*, but has very short hydranth pedicels. More material from this region is also needed to evaluate if it not just a mere growth variant of *E. producta*.

The reliability of the records of *E. producta* from the Pacific is also difficult to evaluate, and this is not only due to the infertile state of the known specimens. Fraser (1911, 1914) described *L. producta* colonies from British Columbia, but later Stechow (1921) re-examined part of this material and found nematothecae. Stechow attributed these samples with nematothecae to a new species, *Egmundella gracilis* Stechow, 1921. The colonies lacking nematothecae were left in *L. producta.* The NE Pacific *E. gracilis* differs from the Atlantic *E. producta* by the presence of nematothecae on the hydranth pedicels, a situation never met with in the latter species. I think that reproductive colonies of *E. gracilis* and *L. producta* sensu Fraser must be re-sampled in the Vancouver Island region before a reliable conclusion on their status can be made. In this context, also *Oplorhiza diaphragmata* Naumov, 1960 needs a re-evaluation. Although *O. diaphragmata* has been allocated to a different genus, I suspect that it is conspecific with *E. gracilis*.

There are about 12 species of either *Egmundella* Stechow, 1921 or *Oplorhiza* Allman, 1877 (Bouillon *et al.,* 2006), two genera which are hardly separable and it is a matter of personal opinion whether they should be kept distinct or not. For more details on how to distinguish these two genera and also other similar ones see Bouillon *et al.* (2006). For these 12 species of *Egmundella* or *Oplorhiza*, gonothecae are only known for *Egmundella humilis* Fraser, 1936, *E. polynema* Fraser, 1948, *E. sibogae* Billard, 1940, and *Oplorhiza diaphragmata* Naumov, 1960 (see Hirohito, 1995; Fraser, 1948; Billard, 1940; Naumov, 1969, respectively). The Japanese *E. humilis* produces a free medusa, but the adult is unknown. *Egmundella sibogae* is supposed to produce either a medusoid or a medusa. The gonothecae of both these species are more or less cylindrical and thus very unlike the ones observed for *E. producta*. The gonothecae of *O. diaphragmata* are shaped like high, narrow, inverted cones. These three species have thus gonothecae forms which are quite different from *E. producta* and they are certainly separate species.

Although I advocate here for a genus change to *Egmundella producta,* this may nevertheless be only a temporary solution. Molecular phylogenies will almost certainly make it necessary to revise the scope of many genera of the Campanulinidae (comp. Leclère *et al.*, 2009). In this context, not too much energy should therefore be wasted in discussions on the generic limits and subdivisions of the Campanulinidae based on morphological traits with very low complexity and high variability.

Much emphasis has been placed by some authors (e.g. Stechow, 1922; Miranda *et al*., 2013) on the presence of a crease line delimiting the operculum from the hydrotheca wall. In the present material of *E. producta,* no such crease line could be found in intact hydrothecae of living material or material kept in liquid fixative (including the type specimens). A crease line becomes visible once the operculum is tucked inside the hydrotheca (due to collecting process?), or it appeared after the material had been dehydrated for permanent microslide preparations [see also Cornelius (1995a: 168) for similar observations]. Thus, the presence of crease lines may, in some cases, be a mere preparation artefact. This should not be taken as a general invalidation of this character, but a cautionary note when using permanent slide preparations only. Some species, e. g. *Calycella syringa* (Linnaeus, 1767) or *Tetrapoma quadridentatum* (Hincks, 1874b) (see Schuchert, 2001 for descriptions), always have a distinct crease line delimiting the operculum base. In these cases, it is a stable and important taxonomic character that may not be neglected.

More generally, shrinkage artefacts in slide preparations can be quite dramatic as was observed for the gonothecae in the present material. The dimensions of the single gonotheca processed into a permanent slide preparation shrunk about 10-19%. Shrinkage was unequal for different regions and appeared most pronounced where the perisarc is very thin, but limited in the basal regions with comparatively thicker perisarc (Fig. 1D). Shrinkage takes certainly always place to some degree in all permanent microslide preparations and this compromises, to some extent, the precision and comparability of measurements.

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