Identification of coronate polyps from the Arctic Ocean: *Nausithoe werneri* Jarms, 1990 (Cnidaria, Scyphozoa, Coronatae), with notes on its biology

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Steenstrupia

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Nausithoe werneri, a solitary scyphozoan coronate polyp, was found and described from different localities in the Arctic Ocean (Canada Basin, Laptev Sea, and Greenland). The species was previously reported only from the type locality (Northeastern Atlantic Ocean, Moroccan coast, and the Mediterranean). Although only preserved material was available for this study, the number and morphology of the internal cusps enables precise identification of the species, distinguishing it from the other known solitary Nausithoidae polyps. An unusual growth pattern of the species is described. Comments on the polyp stage of the species *Atolla tenella* Hartlaub, 1909 are also made.

Keywords: scyphozoan, scyphistoma, *Atolla tenella*, Naumov, Nausithoidae, *Nausithoe werneri, Formquotient*, *Stephanoscyphistoma*

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INTRODUCTION

The number of studies dealing with coronate scyphozoans (Coronatae, Scyphozoa, Cnidaria) are increasing recently due to the development of new approaches for studying polyps and medusae. The life cycles and biology of several species have been described and investigated (*e.g.* Silveira & Morandini 1997; Jarms *et al*. 1999; Sötje & Jarms 1999; Morandini & Silveira 2001; Stampar *et al*. 2008), different reproduction strategies were noticed and described (Jarms, 1997; Silveira & Morandini 1998a, b; Silveira *et al*. 2003), inspection of museum collections revealed new species and rearranged others (Jarms *et al*. 2003; Morandini & Jarms 2005), and morphological and molecular analysis as well as developmental studies gave new insights on the evolution of characters within the group (Eggers & Jarms 2007; Hingston *et al*. 2007). But there are still unsolved problems pertinent to preserved material of museum collections.

In this paper we identify and describe solitary Arctic coronate polyps based on museum specimens. We also describe an unusual growth pattern observed first in preserved material but confirmed in living specimens. In addition, comments on the status of the polyp stage of the species *Atolla tenella* Hartlaub, 1909 described in Naumov (1961) are made.

MATERIAL AND METHODS

Solitary coronate polyps were obtained from the Cnidaria collection of the Zoological Museum, University of Copenhagen (ZMUC), collected during different expeditions to North Greenland

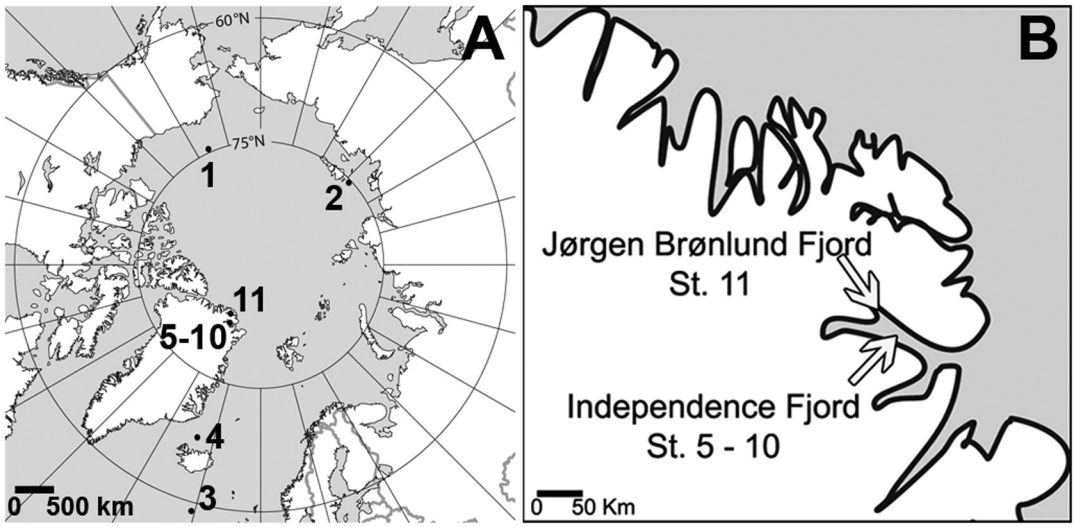

Fig. 1. Distribution of *Nausithoe werneri* Jarms, 1990 in Arctic waters. – A. World map (centered on North Pole), showing the Arctic Ocean and the stations from which coronate polyps were collected. – B. Detailed map of Greenland showing the stations collected at Independence Fjord and Jørgen Brønlund Fjord.

and the Faroe Islands. More polyp samples were sent to one of the authors (GJ) from the Canada Basin and from expeditions of the research vessel *Polarstern* to the Laptev Sea (Fig. 1A, B). Some specimens from ZMUC were deposited in the Cnidaria collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP). Collecting data are presented in Tab. 1.

All specimens were already presorted, thus detailed information on the substrate is unavailable, but some stephanoscyphistomae specimens were still attached to small calcareous debris (pieces of corals or mollusc shells).

Measurements of the periderm tubes were performed to the nearest 0.01 mm using a stereomicroscope with an eyepiece grid. Tube structures and internal cusps were examined by scanning electron microscopy (SEM) using a Cambridge S4 Stereoscan microscope as described in Jarms (1990) and Jarms *et al*. (2002a, b). The periderm tubes maintained in 70% ethanol were transferred to 100% ethanol, and preparations were made cutting the tubes into pieces just above the internal cusps; pieces were then fixed on stubs, dried at room temperature and sputtered with gold.

Observations of living animals were performed in polyps kept in cultures descending from the original polyps collected off the Moroccan coast (see details in Jarms 1990) and specimens from the Mediterranean (unpublished data).

TAXONOMY

Class **Scyphozoa Goette, 1887**

Order **Coronatae Vanhöffen, 1892**

Family **Nausithoidae Haeckel, 1880**

***Nausithoe* Kölliker, 1853**

***Nausithoe werneri* Jarms, 1990**
Figs 2–3

Stephanoscyphus sp. – Naumov 1959: 904 (brief description), figs 1b, b‘.
Stephanoscyphus sp., Nº 1. – Naumov 1961: 57 (brief description), fig. 36 [Polar Basin, Arctic Ocean].
Atolla tenella. – Naumov 1961: 57 (mention).
Stephanoscyphistoma Nº 1. – Jarms 1990: 11 (mention).
Nausithoe werneri Jarms, 1990: 12–17, figs 1–2 (cusps whorl), figs 3–5 (ephyra), figs 6–7 (adult medusa), pls I–II (cusps and tube morphology), pl. III (strobilation) [Moroccan coast, North Atlantic Ocean].
Not *Atolla tenella* Hartlaub, 1909.

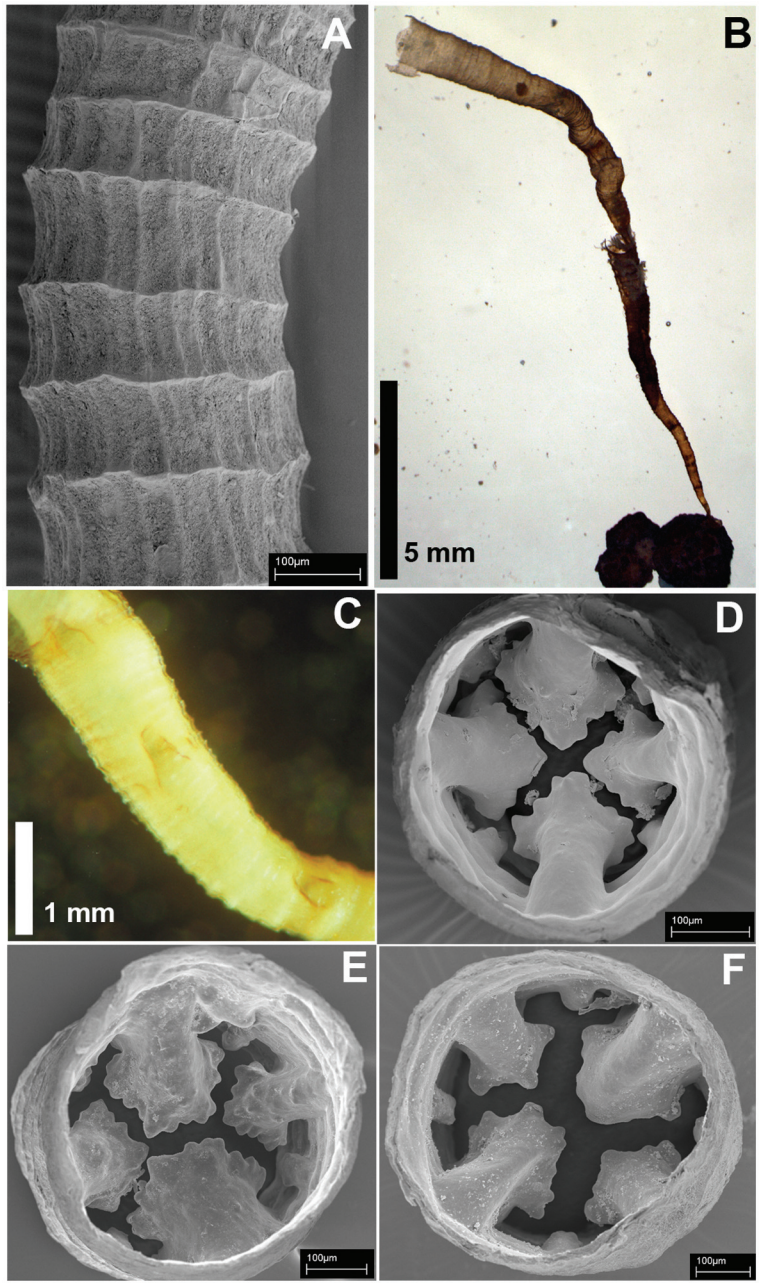

Fig. 2. *Nausithoe werneri* Jarms, 1990 from Arctic waters. – A. Scanning electron micrograph of the outer structure of the periderm tube of polyp collected by the R.V. *Polarstern* at 78º10.5' N, 133º25.26' E. – B. Overview of polyp collected at Independence Fjord (82º05.7' N, 29º52' W, Greenland). – C. Detailed view of polyp in B, showing cusps outline (higher than broader). – D. Scanning electron micrograph of the 5th circle of cusps of the periderm tube of polyp collected by the R.V. *Polarstern* in the Laptev Sea. – E. Scanning electron micrograph of the 7th circle of cusps of the periderm tube of polyp collected at Independence Fjord (82º06.52' N, 29º55' W, Greenland). – F. Scanning electron micrograph of the 4th circle of cusps of the periderm tube of polyp in B. – Scale bars: A, D–F = 100 µm, B = 5 mm, C = 1 mm.

Voucher specimens:
MZUSP 987: 2 Aug 1995, Independence Fjord (st. 26), 82°05.7' N, 29°52' W, 185–200 m, 70% ethanol; **MZUSP 988**: 30 Jul 1995, Independence Fjord (st. 19), 82°06.52' N, 29°55' W, 100–120 m, 70% ethanol; **MZUSP 989**: 29 Jul 1995, Independence Fjord (st. 14), 82°06.5' N, 29°55' W, 95–110 m, 70% ethanol; **ZMUC**: several specimens from different stations, without collection numbers, see Table 1 for collection data.

Diagnosis

Solitary Nausithoidae coronate polyp; periderm tube with eight cusps per circle; secondary cusps scattered over surface of primary cusps.

Description of periderm tubes

The outer structure of the periderm tube is typical for solitary coronate polyps within the family Nausithoidae (Fig. 2A); but with the transverse ridges pointed compared to other coronates. The colour of the tube is yellowish-brown, becoming darker and less transparent towards the basal part. The total length of the tube varies from 2.6–33 mm, basal disc for attachment 0.2–1.28 mm in diameter, diameter of the tube just above the basal disc varies from 0.32–1.42 mm, and diameter of the opercular aperture varies from 0.32–1.4 mm (Fig. 2B). The *Formquotient* (see Tab. 2 for definition) at 2 mm varies from 0.1–0.65, at 5 mm varies from 0.07–0.22, and at the aperture varies from 0.02–0.44. The tubes present 1 to 12 circles of internal cusps (see measurements in Table 2). Each circle comprises eight cusps. The outline of the internal cusps is higher than broad (Fig. 2C), with the four perradial cusps being larger than the others; the outline of the larger cusps resemble a "fat 8", sometimes with the upper

Table 1. Collecting data of the specimens of *Nausithoe werneri* Jarms, 1990 from the Arctic Ocean and surroundings.

No. on Fig. 1A	Source	Locality	Date	Depth (m)	No. of spec.
1	Canada Basin	75º58.97' N, 156º07.6' W	Sept 2002	800	6
2	Polarstern	78º10.5' N, 133º25.26' E	5 Sept 1993	1039	8
–	Polarstern	Laptev Sea 36/062, st. 64a	29–30 Aug 1995	–	16
3	ZMUC	60º36.74' N, 11º37.71' W Faroe Islands, BIOFAR st. 517	27 Jul 1989	1099	1
4	ZMUC	67º59.86' N, 19º26.29' W Faroe Islands, BIOFAR st. 2102	6 Jul 1992	1146	5
5	ZMUC	82º07' N, 29º48' W Independence Fjord st. 7	20 Jul 1995	68	2
6	ZMUC	82º06.15' N, 29º55' W Independence Fjord st. 11	28 Jul 1995	160–170	7
7	ZMUC MZUSP 989	82º06.5' N, 29º55' W Independence Fjord st. 14	29 Jul 1995	95–110	10
8	ZMUC	82º06' N, 29º54' W Independence Fjord st. 15	30 Jul 1995	170–185	10
9	ZMUC MZUSP 988	82º06.52' N, 29º55' W Independence Fjord st. 19	30 Jul 1995	100–120	9
10	ZMUC MZUSP 987	82º05.7' N, 29º52' W Independence Fjord st. 26	2 Aug 1995	185–200	10
11	ZMUC	82°10'60 N, 30°45'0 W Jørgen Brønlund Fjord st. 52	29 Jul 1966	160–200	11

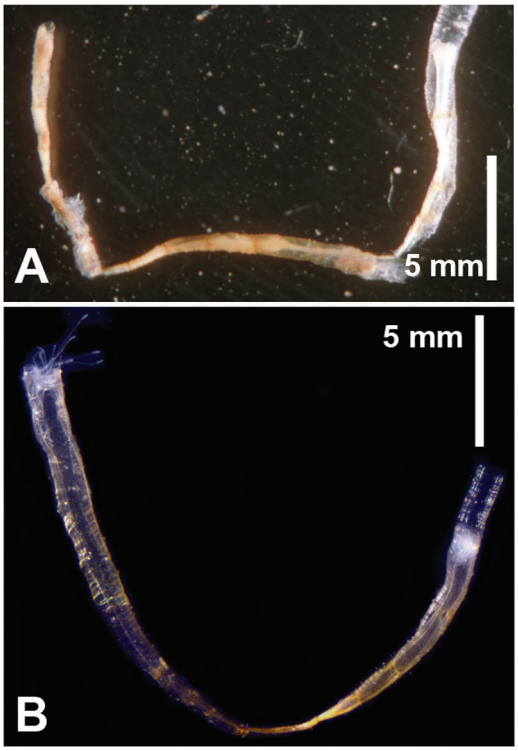

Fig. 3. *Nausithoe werneri* Jarms, 1990. Polyps with two oral discs. – A. Overview of a preserved polyp, collected at Independence Fjord (82º05.7' N, 29º52' W, Greenland). Note growing structure of the tube. – B. Overview of a living polyp, collected in the Mediterranean. Note the polyp growing to both sides of the tube. – Scale bars = 5 mm.

part smaller than the lower one (see Fig. 2C). The morphology of the cusps is somewhat similar to other Nausithoidae, but the eight main cusps bear secondary cusps over their surface (Fig. 2D–F). These secondary cusps are rounded, and increase in number beneath the third circle (from aperture to the base).

Comments

Much work has to be done in the systematics of coronates, mainly regarding the medusae for which further information on the biology is lacking, especially concerning the life cycle (Jarms *et al*. 2003). It is rather unsatisfactory investigating only preserved material, or nominal species described by earlier researchers based on a few or only one museum specimens, *e.g. Atorella sibogae* (Leloup, 1937) and *Nausithoe striata* (Vanhöffen, 1910) (Morandini & Jarms 2005).

Literature on Coronatae (*e.g.* Jarms 1997) emphasizes that life cycle studies would be the most appropriate tool in solving systematic and taxonomic problems within the group. Despite this, as dealing with specimens showing an extremely different morphology, a new species has recently been described (Jarms *et al.* 2003) and new combinations have been established based solely on preserved animals (Morandini & Jarms 2005).

Naumov (1959, 1961) studied three different coronate polyps just numbering them (1, 2 and 3). He also stated that the structure and arrangement of the internal cusps were constant and thereby he was able to differentiate three putative species in his material (see below).

Within the coronates, 22 nominal species present a polyp stage (Jarms 1997; Morandini & Jarms 2005). The outer structure of the periderm tube (ring pattern and *Formquotient*) permits to attribute the present specimens to the genus *Nausithoe*, and excluding clearly the genera *Atorella* (narrow ring pattern), *Linuche* (colonial, isodiametric tubes), and *Thecoscyphus* (short horn-like tubes).

Within the genus *Nausithoe,* only three species present solitary polyps with just eight cusps per circle (*N. globifera* Broch 1913, *N. marginata* Kölliker, 1853, *N. werneri* Jarms, 1990). Among these three species, *N. werneri* is the only one showing cusps with secondary teeth. Additionally, specimens that were recently collected from the depth of the Mediterranean (Pec 2007, unpublished data) and specimens collected in the Arctic Ocean differ slightly from the original description (Jarms 1990).

The *Formquotient* from the original description and from the Arctic specimens are overlapping (see comparative table in Morandini & Jarms 2005). The species *Nausithoe werneri* was originally described from the North Atlantic (Moroccan coast) using specimens collected from 25º20.4'–34º59.5' N, 07º07.1'–16º14.7' W in two different cruises of the research vessel *Meteor* (1980 and 1982), varying in depth from 415–3093 m (Jarms 1990). The specimens described in this paper came from a distant area (Arctic Ocean), rather distant from the "previously known" dis-

Table 2. Measurements (in mm) of the periderm tube of different specimens of *Nausithoe werneri* Jarms, 1990 from the Arctic Ocean. Data are presented as the minimum and maximum values measured for the whole sample. For details of collecting data see Table 1. Symbols: - = no measurement; Db = diameter just above the basal disc; Dbd = diameter of the basal disc; Do = diameter of the distal aperture; D/L_{2mm} = diameter at 2 mm divided by 2; D/L_{5mm} = diameter at 5 mm divided by 5; D/L_{tot} = *Formquotient* = ratio between the diameter of the distal aperture (Do) and the total length (L_{tot}); L_{tot} = total length; *N. werneri* (1990) refers to the measurements of the original description by Jarms (1990); n = number of specimens; Nwt = total number of circle of cusps. Abbreviations according to Jarms (1991) and Jarms *et al*. (2002b), "–" broken just above basal disc.

Specimens from	n	L_{tot}	D_o	D_b	D_{bd}	D/L_{tot}	D/L_{2mm}	D/L_{5mm}	Nwt
Canada Basin	6	6.8–10	0.6–0.92	0.1–0.3	-	0.07–0.097	0.14–0.19	0.1–0.11	6–10
Laptev Sea	8	4.6–33	0.7–1.36	0.1–0.9	0.28–0.5	0.02–0.44	0.1–0.65	0.08–0.22	3–13
Laptev Sea	16	3–23.48	0.32–1.4	0.08–0.48	0.6–1.28	0.04–0.21	0.14–0.26	0.08–0.16	1–10
Faroe Islands st.517	1	7.8	0.66	0.12	-	0.08	0.15	0.072	8
Faroe Islands st.2102	5	2.6–10.6	0.4–1.12	0.12–0.26	-	0.08–0.3	0.17–0.29	0.1–0.17	3–6
Indep. Fjord st.7	2	8.16	0.78	0.12	0.6	0.09	0.13	0.096	3
Indep. Fjord st.11	7	3–16.8	0.6–1.42	0.1–0.14	0.2–0.6	0.07–0.28	0.11–0.22	0.09–0.13	6–9
Indep. Fjord st.14	10	12.8–19.8	0.9–1.5	0.08–0.2	0.3–0.6	0.05–0.1	0.15–0.2	0.1–0.12	4–12
Indep. Fjord st.15	10	7.3–14.3	0.6–1.2	0.06–0.12	0.3–0.66	0.08–0.12	0.12–0.18	0.09–0.13	5–12
Indep. Fjord st.19	9	4–22.2	0.8–1.5	0.1–0.3	0.3–0.4	0.06–0.2	0.15–0.3	0.09–0.16	4–11
Indep. Fjord st.26	10	5–16.3	0.5–1.2	0.08–0.14	0.3–0.5	0.06–0.1	0.15–0.22	0.1–0.13	4–8
Pearyland st.52	11	5.7–15.6	0.5–1.34	0.1–0.4	0.2–0.8	0.07–0.12	0.13–0.3	0.1–0.16	2–9
range Arctic	95	2.6–33	0.32–1.5	0.08–0.48	0.2–1.28	0.02–0.44	0.1–0.65	0.072–0.22	1–13
range Arctic >5mm	83	6–33	0.6–1.5	0.06–0.4	0.2–0.6	0.02–0.12	0.1–0.26	0.07–0.16	3–14
N. werneri (1990)	14	12.4–21.6	1–1.6	0.08–0.14	0.44–0.6	0.069–0.113	0.14–0.2	0.096–0.14	6–11

tribution. The depth distribution of the current specimens comprises lesser depths than originally described (68–1039 m).

DISCUSSION

Growth pattern

Several examined specimens revealed an uncommon growth pattern. From the 95 examined specimens, 12 (~13%) presented two apertures (Fig. 3A), suggesting that the living polyps were probably growing in opposite directions. Detailed observation of the tube sculpture and arrangement of the internal cusps confirmed this hypothesis.

The uncommon growth pattern revealed by the polyps of *Nausithoe werneri* from the Arctic Ocean was already observed in our cultures of Coronatae polyps. However, in the laboratory this bidirectional growth occurred as a response of the polyps to injuries or debris blocking the periderm tube. After some time, the polyp started to grow in the opposite direction. Furthermore, part of the soft body might repair and pass the injury, the debris might be engulfed or pushed out (see similar behaviour in Holst & Jarms 2006), and the polyp could continue to grow as initially, resulting in a polyp with two oral discs ("two heads", Fig. 3B). Another possible way is that the tube is torn off from the basal disc and the polyp residue regenerates an apical structure at the breaking point, thus replacing the original basal-oral polarity by an unusual, oral-oral polarity.

Specimens of *Nausithoe werneri* from the type locality and from the Mediterranean presented both growth patterns in laboratory cultures. We assume that polyps of *Nausithoe werneri* face the same problems with the tube under natural conditions (injuries, debris, and tear off). In order to deal with this problem, polyps could grow to the opposite side and eventually, once the debris are removed or engulfed, back again to the first direction, but interestingly retaining the unusual bi-headed organisation. The repair capacities and the growth of the periderm in Coronates has been studied by, *e.g.* Chapman & Werner (1972) and Werner (1970, 1973, 1979). The ability to develop deviant polarities and body organisation demonstrates again the great morphological plasticity and flexibility of the life-history observed in this group (Silveira *et al*. 2003; Holst & Jarms 2006).

Status of *Atolla tenella*

Naumov (1959, 1961) studied the tubes of coronate scyphozoans which he attributed to three different species of *Stephanoscyphus* (sp. nº 1, 2 and 3, note that *Stephanoscyphus* is a name that was earlier indiscriminately applied to any indeterminate coronate scyphozoan polyp). In 1961, he stated that *Stephanoscyphus* sp. nº 1 are likely the polyps of the medusa *Atolla tenella* Hartlaub, 1909. His conclusion derived from the distribution pattern of both species (*A. tenella* and *S.* sp. nº 1) in the Polar Basin, *A. tenella* being the only coronate medusa occurring in the same area where the polyps are found. Nowadays, life cycle studies are preferred to obtain a direct proof of this, but at his time it might have been an acceptable conclusion.

The figures of *Stephanoscyphus* sp. nº 1 presented by Naumov (1961: 58, fig. 36) lack somewhat the desirable precision, but one can observe at least four large cusps on the tube wall, with an outline of being higher than wide. In contrast, *Stephanoscyphus* sp. nº 2 (which had also four visible cusps) (Naumov 1961: 59, fig. 37) presents an outline that is wider than high (characteristic of the Atorellidae polyps). *Stephanoscyphus* sp. nº 3 (Naumov 1961, fig. 38) shows only two large cusps, rendering it clearly distinct from the two other morphotypes.

Based on the morphology of the cusps, and our findings that *N. werneri* is also common in the Arctic, we can conclude that Naumov's *Stephanoscyphus* sp. nº 1 from Arctic waters is better referred to *Nausithoe werneri* and not *Atolla tenella,* whose polyps remain unknown.

In his synopsis of the medusae of the world, Kramp (1961: 312) listed *Atolla tenella* Hartlaub, 1909 as a synonym of *A. wyvillei* Haeckel, 1880. However, Russell (1970: 38) doubted that they are conspecific due to the pairs of pigment spots around the margin the bell. The name *Atolla tenella* remains thus available for the moment, but its status must be re-evaluated in a comprehensive revision of the whole genus *Atolla*.

CONCLUSIONS

The distribution of *Nausithoe werneri* Jarms, 1990 also includes the Arctic Ocean (Canada Basin, Laptev Sea, North Greenland, and Faroe Islands). The species presents an unusual bidirectional growth pattern (with two "heads") derived from injuries, debris, and tear off of the tube evidencing great morphological plasticity in the life-history of coronates. *Stephanoscyphus* sp. nº 1 described by Naumov (1961) should be referred to *N. werneri* and not the medusa *Atolla tenella* Hartlaub, 1909.

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