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Nausithoe aurea n. sp. (Scyphozoa: Coronatae: Nausithoidae), a species with two pathways of reproduction after strobilation: sexual and asexual

Fábio Lang da Silveira & André Carrara Morandini
Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11461, 05422-970, SP, Brazil

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Abstract

Nausithoe aurea, a new species of scyphozoan Coronatae, is described from São Paulo State, Brazil. The solitary scyphistomae, with some zooxanthellae, strobilated producing planuloids and medusae; this represents an intermediate life cycle between that of metagenetic Nausithoidae and the submarine cave-dwelling, reduced medusa stage of *Nausithoe planulophora* (Werner, 1971). The periderm tube of the scyphistomae has 16 internal cusps in all whorls. The medusae present yellow pigment spots in most of their lappets. The early embryonic development is briefly described. Planuloid formation is hypothesized as explanation for polyp-stage philopatry.

Résumé

On décrit *Nausithoe aurea*, nouvelle espèce de Scyphozoaire (Coronatae) de l'Etat de São Paulo, Brésil. Les scyphistomae solitaires, contenant des zooxanthelles, produisent des planuloïdes et des méduses par strobilation; ceci représente un cycle vital intermédiaire entre celui des Nausithoidae métagénétiques et celui de *Nausithoe planulophora* (Werner, 1971) avec son stade méduse réduit habitant des grottes sous-marines. Le tube péridermique des scyphistomae présente 16 pointes internes dans chaque spire. Les méduses présentent des taches pigmentaires jaunes dans la plupart de leurs lobules. On donne une succincte description des phases initiales du développement embryonnaire. On émet l'hypothèse que c'est la formation de planuloïdes qui pourrait expliquer la philopatrie du stade polype.

Introduction

Coronatae have a polyp stage with a firm periderm tube enveloping the soft body, and a medusa stage with a coronal furrow in the exumbrella and, below, pedalia in equal numbers to the tentacles and rhopalia (Franc, 1993; Russell, 1970). The Coronatae are represented mostly by deep-sea medusae (Tardent, 1978) and only few species live in shallow waters (Larson, 1990). Therefore, their life cycles are still little known (Jarms, 1991). Some 40 species of coronate medusae are recognized and the metagenetic life cycles of 9 species are known (Jarms, pers. comm.). The life cycles of 4 additional species without free medusae are known (Jarms, 1990; 1991). Although they have a metagenetic life cycle, the polyps of all species of uncertain medusa genera are collectively grouped *Stephanoscyphistoma* (sensu Jarms, 1990; 1991). Several authors, e.g., Werner (1971a, b; 1983), Jarms (1990), and Meroz & Ilan (1995), have stressed the importance of life cycle studies for the correct identification of species.

The only coronate recorded from the Brazilian coast is the medusa stage of *Nausithoe punctata* Kölliker, 1853, from the north of Bahia State (Goy, 1979). Recently, Silveira & Morandini (in press) redescribed the scyphistoma of a coronate, *Stephanoscyphistoma corniformis* (Komai, 1936) from the Brazilian coast.

Material and methods

The solitary scyphistomae are sampled by SCUBA diving from calcareous debris, mainly the stony coral *Mussismilia hispida* (Verrill, 1902) (Scleractinia, Mussidae), in the São Sebastião Channel (23°50'S 45°25'W). We searched for the polyps on the calcareous substrata with the aid of a stereomicroscope. The

Table I. Locality data and variability of total periderm tube length of *Nausithoe aurea* n. sp. scyphistomae collected in the São Sebastião Channel. The collector initials stand for the authors of this paper.

Date of sample	Scyphistomae number	Total periderm cone length (mm)	Depth (m)	Collector (initials)
04/VII/1995	6	2.85–6.75	6	FLS/ACM
06/VII/1995	3	3.41–4.73	3	FLS/ACM
27/VII/1995	16	1.76–8.25	4	FLS/ACM
31/VIII/1995	28	1.35–9.18	6	FLS
08/I/1996	9	1.42–5.64	9	ACM
10/I/1996	6	1.89–8.10	6	ACM
11/I/1996	6	1.68–5.17	6	ACM

scyphistomae were reared in the Centro de Biologia Marinha da Universidade de São Paulo (CEBIMar USP), at São Sebastião, SP. They were transferred into and maintained in small petri dishes. The seawater was changed every day and the animals were fed every other day with homogenized gonad of the clam *Perna perna* (Linnaeus, 1767) (Bivalvia, Mytilidae). In mid-winter, from 8 to 27 July 1995, we made the first cultivation at room temperature (range 20.7°C–26°C) to establish the best rearing technique. In spring, from 31 August to 15 October 1995, we kept all specimens at room temperature (range 21°C–27.6°C) and from 16 October to 6 November 1995, some mature medusae and their embryos/planulae were kept at controlled temperature, 22°C. In summer, from 8 to 28 January 1996, the specimens were kept at controlled temperature, 22°C, and a 12 hr light/dark regime. Table I shows several data of the scyphistomae sampled.

The free-swimming ephyrae, from strobilating scyphistomae, were transferred into single dishes and reared to mature medusae. They were fed with homogenized clam gonads. The ephyrae and the medusae were intensively fed, up to twice a day, for as long as 37 days. They were individually immersed in the homogenized food, observed under the stereomicroscope until their stomachs were full, and removed to a new dish with clean filtered seawater. Thereafter, the mature female medusae released many oocytes. The oocytes and a female medusa were combined with a male medusa. The fertilized eggs were observed until early planula stage.

The free-swimming planuloids, from strobilating scyphistomae, were transferred into single dishes, at 24 hr intervals, and were observed from then on. A batch of 24 planuloids, from a single scyphistoma, was maintained in the same dish with the polyp.

Specimens fixed and preserved in seawater-formalin were prepared for scanning electron microscopy (SEM). The periderm tube was sectioned transversely over and below the middle periderm whorl of internal cusps. The tube and the ring fragment were dehydrated, critical-point dried and mounted. They were coated with 10 nm of gold in a Balzers S-SCD 050 sputter coater. Specimens were examined with a Zeiss DSM 940 SEM.

We studied the cnidome of live specimens and of specimens preserved in seawater-formalin. Only undischarged nematocysts of preserved tissues were measured.

Descriptive part

Nausithoe aurea sp. n.
(Figs. 1–7, Pls. I–II)

Material examined. – Holotype: MNRJ 2899, Museu Nacional Universidade Federal do Rio de Janeiro, Brazil, State of São Paulo, Ilhabela, Praia Grande (23°51'S 45°25'W), 12/X/1995, 1 ♂ medusa reared for 29 days at CEBIMar, FLS/ACM coll.

Paratypes: MNRJ 2900, Museu Nacional Universidade Federal do Rio de Janeiro, Brazil, State of São Paulo, Ilhabela, Praia Grande, 5/X/1995, 6 m depth, on dead stony coral, 1 strobilating chain that originated female medusae, reared for 36 days, FLS coll.; MNRJ 2901, Brazil, State of São Paulo, Ilhabela, Praia Grande, 16/X/1995, 6 m depth, on dead stony coral, 1 scyphistoma that originated male medusae, reared for 47 days, FLS coll.; MNRJ 2902, Brazil, State of São Paulo, Ilhabela, Praia Grande, 16/X/1995, 6 m depth, on dead stony coral, 1 strobilating scyphistoma, reared for 47 days, in whole-mount preparation, FLS coll.; MNRJ 2903, Brazil, State of São Paulo, Ilhabela, Praia Grande, 11/X/1995, 6 ephyrae reared for 2 days at CEBIMar, FLS/ACM coll.; MNRJ 2904, Brazil, State of São Paulo, Ilhabela, Praia Grande, 6/X/1995, 6 planulae reared for 22 days at CEBIMar, FLS/ACM coll.; MNRJ 2905, Brazil, State of São Paulo, Ilhabela, Praia Grande, 15/X/1995, 1 ♀ medusa reared for 35 days at CEBIMar, FLS/ACM coll.; MNRJ 2906, Brazil, State of São Paulo, Ilhabela, Praia Grande, 15/X/1995, 1 ♀ medusa reared for 20 days at CEBIMar, FLS/ACM coll.

Additional paratypes are deposited at: The Royal Ontario Museum, Invertebrate Zoology (ROMIZ) B2898, B2899, and B2900, Canada; The Zoölogisch Museum, University of Amsterdam (ZMA) Coel. 8474, Coel. 8475, and Coel. 8476, The Netherlands; Zoologisches Museum, Universität Hamburg (ZMH) C1132, C1133, C1134, C1135, C1136, C1137, and C1138, Germany; and The Natural History Museum (NHM) 1996.1076, 1996.1077, 1996.1078, 1996.1079–1084 and 1996.1085–1094, United Kingdom.

Etymology. – The specific name is derived from the Latin adjective *aureus* (= golden yellow, fem-

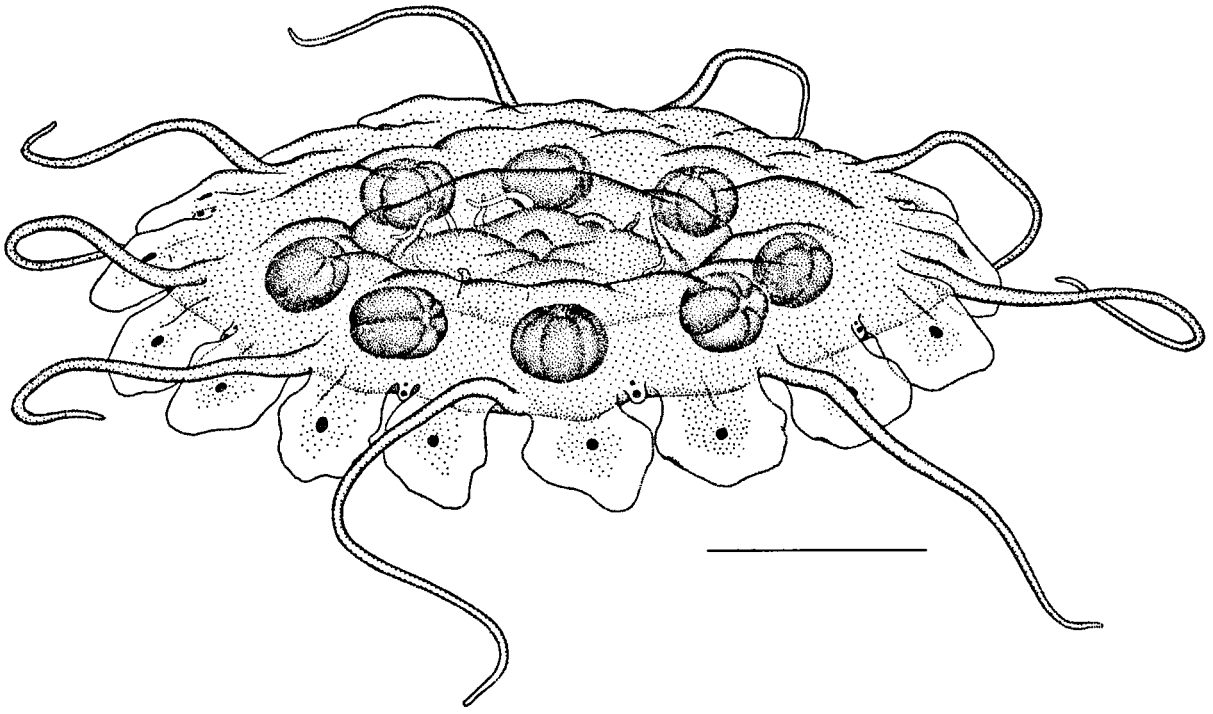

Fig. 1. Mature male medusa of *Nausithoe aurea* n. sp. (MNRJ 2899) showing the 8 testes (side view, after 5 months in seawater-formalin). Scale bar: 1.3 mm.

inine *aurea*), after the color of the pigment spots in the medusa lappets.

Diagnosis. – Metagenic. Polyp solitary with periderm tube dark to light brown, with small basal disk for attachment, ± 0.47 mm. Proportions (diameter/length) at 2 mm height 0.19 ± 0.03, at 5 mm height 0.11 ± 0.02, and total length 0.17 ± 0.06 mm. Tube surface with a pattern of many varied transverse rings, more or less prominent, with longitudinal striations. Inner spines or cusps are arranged in distinct whorls of sixteen cusps; 4 large (perradius), 4 intermediate (interradius) and 8 small (adradius). Scyphistomae with 16–31 filiform tentacles, with one conspicuous irregular white pigment spot in each tentacle base and with few zooxanthellae in the gastrodermis. Medusa with flattened, smooth umbrella, central disk diameter 4.8–10.5 mm, tentacle length up to 5.5 mm in live specimens; few zooxanthellae in gastrodermis; with 16 lappets, most with a yellow pigment spot, 8 filiform tentacles and 8 rhopalia, each with statocyst and red ocellus. Largest mature dioecius medusae with 8 brown round adradial gonads, stomach with 4 pouches and presenting up to 13 gastric filaments (typically 3 in each quadrant); the central filament of each group, the oldest, is always longer than the others. Life cycle: ephyrae retained within periderm cone transform into flagellated planuloids. The same scyphistoma may produce free medusae and planuloids alternately.

Medusa. – The total diameter is 5 mm. The diameter of the central disk (from rhopalium to rhopalium) is 3.69 mm; of the coronal furrow 1.9 mm; of the mouth 0.75 mm; of each gonad about 0.6 mm; of each tentacle base about 0.16 mm. The distances between 2 radial septa are different in the ones that present tentacles (0.75 mm) or rhophalia (0.5 mm) (Fig. 1).

Scyphistomae. – The scyphistomae usually occur in groups of many solitary polyps within the calcareous septa of long-dead stony corals. For the majority, the substrata had to be broken to free

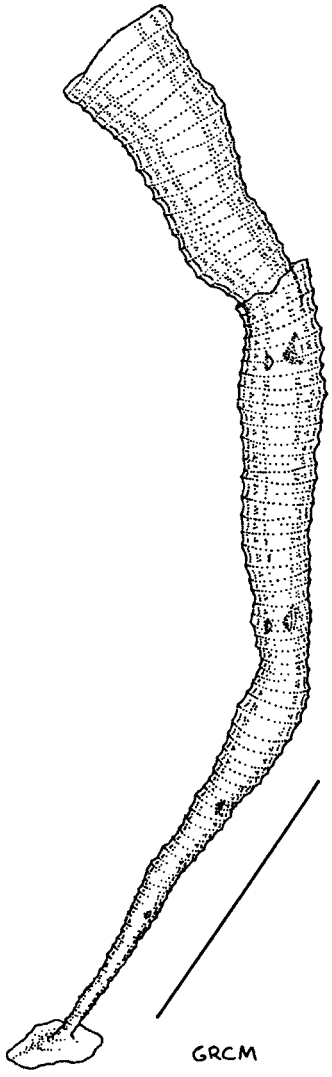

Fig. 2. The scyphistoma of *Nausithoe aurea* n. sp. (MNRJ 2901) showing the periderm pedal disk and tube sculpture (from preserved specimen). Scale bar: 2.5 mm.

the polyps. They attach to the substrate by a small and flattened periderm pedal disk (Fig. 2) and can be well buried by layers of soft mud. Only in a few instances, we found single scyphistomae thriving on other calcareous debris, e.g. much eroded mollusk shells.

The periderm tubes are usually light brown and transparent, but they can be dark brown and opaque. Some specimens showed a second periderm tube growing out the aperture of another tube. A pattern of many variable transverse rings

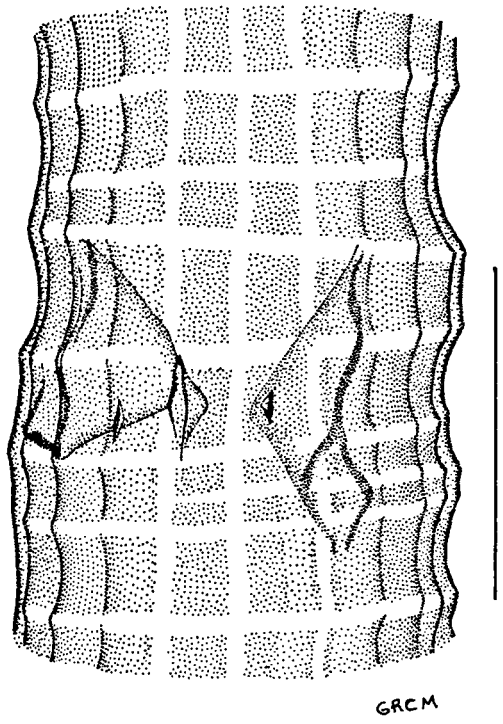

Fig. 3. Segment of the periderm cone of *Nausithoe aurea* n. sp. showing the spines of 3 sizes. Notice that in the perradial cusps the proximal end is bulging (from preserved specimen). Scale bar: 0.5 mm.

Table II. Measurements from *Nausithoe aurea* n. sp. scyphistoma MNRJ 2900; total length of the tube = 5.94 mm.

Whorl	Height (mm)	Diameter (mm)
1	0.42	0.21
2	0.9	0.3
3	1.65	0.405
4	2.475	0.525
5	3.6	0.6

Table III. Measurements from *Nausithoe aurea* n. sp. scyphistoma MNRJ 2901; total length of the tube = 9.12 mm.

Whorl	Height (mm)	Diameter (mm)
1	0.52	0.18
2	1.05	0.22
3	1.8	0.34
4	3.15	0.43
5	5.17	0.66

with longitudinal striations is observed on their surface (Fig. 2 and Plate Ia). The cusps are arranged in distinct whorls, almost in the same plane. Under the stereomicroscope they are variable in number. The SEM preparations showed a regular number of 4 larger cusps (perradius), placed cross-wise, with 4 smaller cusps (interradius) between them, and 8 small cusps (adradius) (Plate Ib). The axis of cusp base outline is long, narrow and parallel with the longitudinal axis of the tube; in the perradial cusps the proximal end is crescent (Fig. 3). In the SEM pictures, the apexes are arrow-shaped with jagged edges in large cusps and pointed edges in small cusps (Plate Ib). Tables II and III show measurements from the two scyphistomae deposited in MNRJ 2900 and 2901. Tables IV and V show measurements, sensu Jarms (1990; 1991), of all cultivated scyphistomae during spring and summer.

The coloration of the soft body is provided by the zooxanthellae, mainly in the gastrodermis of the oral disk. There are few zooxanthellae in the tentacles. However, distinct white pigment spots are irregularly placed at or near the base of the tentacles (Plate Ic).

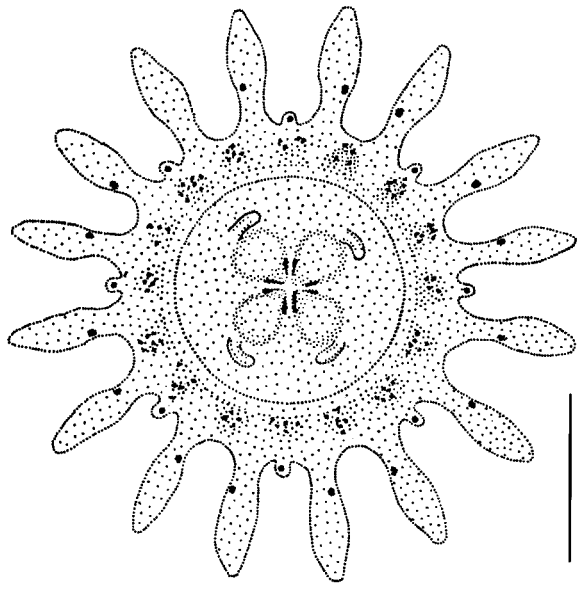

Fig. 4. Ephyra of *Nausithoe aurea* n. sp. showing 4 gastric filaments and early pigment spots in the lappets. Notice that the zooxanthellae are concentrated beyond the coronal groove (from photomicrograph). Scale bar: 350 µm.

Life cycle

At the start of strobilation, the polyp has a strobilating region just below the oral disk. By the time this center shows a cross-fission process, the tentacles are resorbed and the oral surface produces an operculum that closes the periderm cone aperture (Plate IIa). For about twelve hours, the former distal end of the polyp soft body –'head'– remains below the operculum and above the strobilating chain (Plate IIa). Later this region is resorbed as well.

After strobilation, we noted two possible devel-

Table IV. Measurements and proportions, sensu Jarms (1990; 1991), of *Nausithoe aurea* n. sp. scyphistomae kept in culture during August–October 1995 (for legends see Table V).

Scyphistoma	Dbd (mm)	Db (mm)	Ltot (mm)	D/L_{2mm}	D/L_{5mm}	Do (mm)	nwc	nwc_{5mm}	D/Ltot
1 (MNRJ 2901)	0.51	0.15	9.12	0.180	0.114	0.90	4	3	0.098
2	0.63	0.12	9.18	0.159	0.09	0.72	5	4	0.078
3	0.468	0.21	6.06	0.159	0.0924	0.75	4	4	0.123
4	0.45	0.126	6.00	0.180	0.144	1.02	7	7	0.170
5 (MNRJ 2900)	–	0.24	5.94	0.228	0.132	0.738	5	5	0.124
6	–	0.24	5.28	0.159	0.09	0.522	3	3	0.098
7	–	0.18	5.76	0.240	0.144	0.78	4	4	0.135
8	–	0.15	5.17	0.127	0.078	0.45	5	5	0.086
9	0.525	0.195	4.65	0.195	–	0.57	4	4	0.122
10	0.855	0.195	4.66	0.240	–	0.84	5	5	0.180
11	0.48	0.195	3.85	0.217	–	0.81	5	5	0.210
12	0.405	0.12	3.13	0.225	–	0.525	3	3	0.167

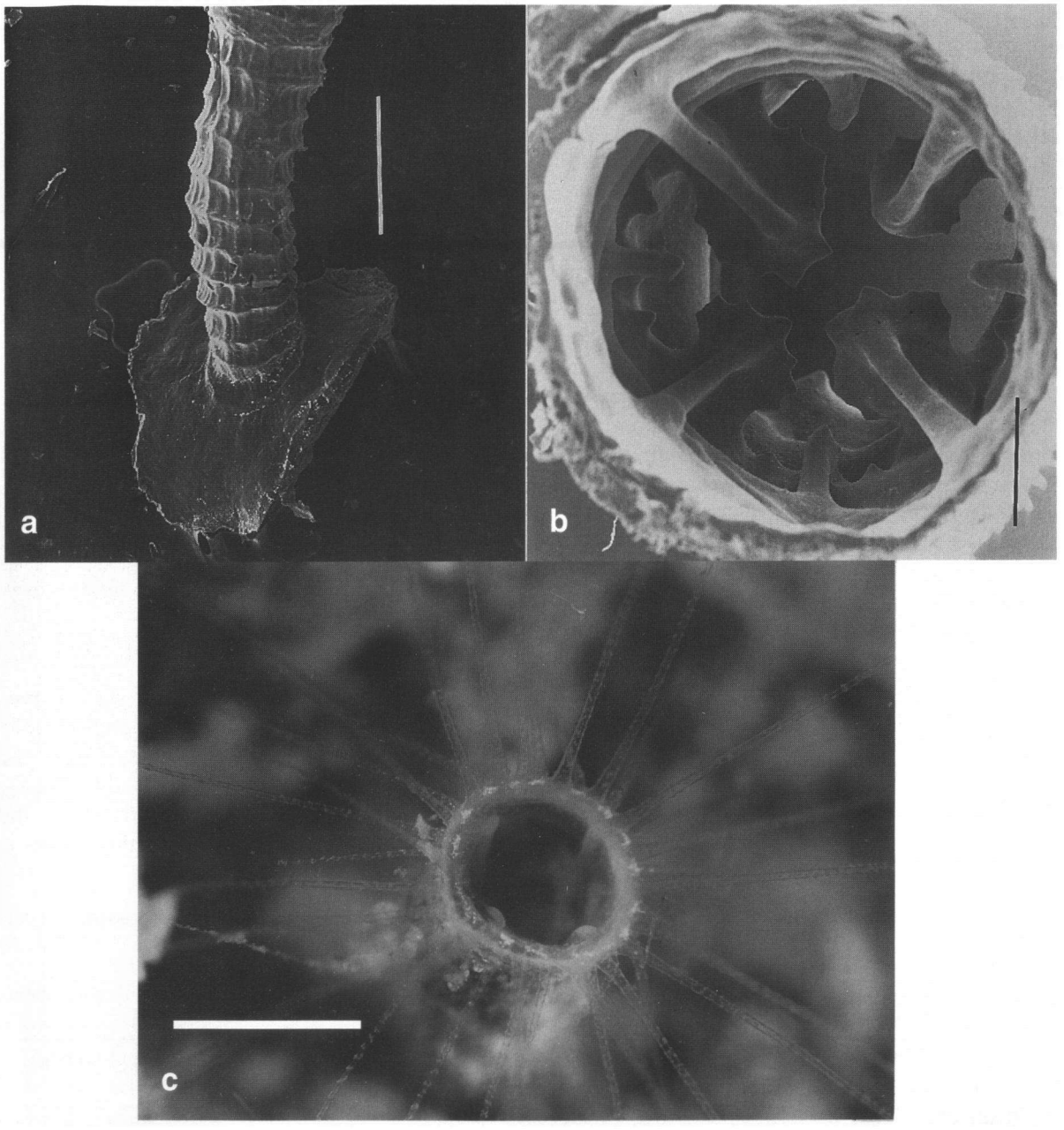

Plate I. (a) SEM of the scyphistoma pedal disk of *Nausithoe aurea* n. sp. Scale bar: 200 μm. (b) SEM of some of the 16 internal cusps in the distal whorl of *Nausithoe aurea* n. sp. Scale bar: 200 μm. (c) Photomicrograph of the scyphistoma oral disk, with mouth wide open, of *Nausithoe aurea* n. sp. showing the white pigment spots near or at the base of the tentacles and the 4 gastric septa. Scale bar: 0.6 mm.

opmental patterns of the ephyra: (1) polydisk strobilation, liberating as many as 89 ephyrae; (2) polydisk strobilation, producing a chain of many young detached ephyrae that are not liberated. The ephyrae transform into planuloids, always within the periderm cone, giving rise to as many as 29 flagellated planuloids. It takes 3 to 14 days to liberate the planuloids.

The central disk diameter of newly liberated ephyrae measured around 0.78 mm. They had 8

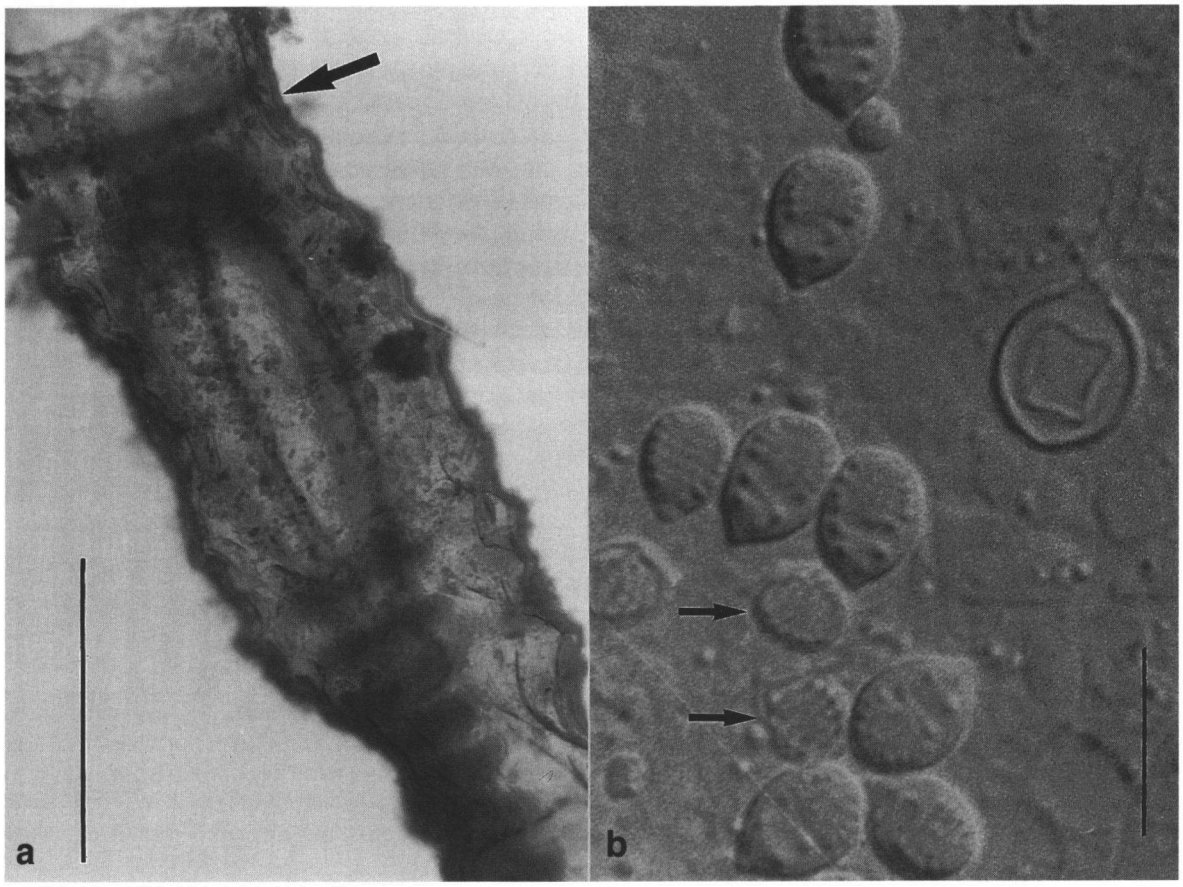

Plate II. (a) Photomicrograph of the strobilation chain of *Nausithoe aurea* n. sp. showing the operculum (arrow) and the 'head'. Scale bar: 0.65 mm. (b) Photomicrograph of the nematocyst types of *Nausithoe aurea* n. sp. medusa showing holotrichous isorhiza (arrows) and heterotrichous microbasic eurytele. Scale bar: 10 μm.

rhopalia with statocyst and without ocellus, 16 pointed marginal lappets and 4 gastric filament buds. The zooxanthellae were concentrated in 16 small groups (8 perradial and 8 interradial) peripheral to the coronal groove (Fig. 4). During the free-swimming ephyra stage we noted the following main changes in a more or less regular and progressive series: (1) development of the first 4 gastric filaments; (2) appearance of tentacle buds within the rhopalial lappets; (3) development of an adaxial ocellus (eye) on the rhopalium; (4) development of a conspicuous yellow pigment spot on the lappet. Some late ephyrae had a few lappets without pigment spot. This condition remained in the maturing medusae.

The end of the ephyra stage, i.e., the young medusa, is marked by the development of 8 round, adradial, gonad primordia. By this time, the 4 gastric filament primordia have developed into long and mobile structures.

From this last phase on we observed some female medusae producing oocytes, that were liberated through the mouth via stomach and manubrium (Fig. 5), and male medusae in which the development of testes was seen (Fig. 6).

Some medusae developed up to 13 gastric filaments; usually a pair of new filaments budded alongside each of the 4 older filaments, and these older filaments grew distinctly longer than the others. Therefore, the even number of 12 filaments was usually observed, although there was some variation with either smaller or larger uneven numbers. Table VI presents a summary of the main features observed in 12 scyphistomae.

Table V. Measurements and proportions, sensu Jarms (1990; 1991), of *Nausithoe aurea* n. sp. scyphistomae kept in culture during January 1996.

Scyphistoma	Dbd (mm)	Db (mm)	Ltot (mm)	D/L_{2mm}	D/L_{5mm}	Do (mm)	nwc	nwc_{5mm}	D/Ltot
1 (ROMIZ B2899)	0.444	0.156	5.22	0.192	0.093	0.54	3	3	0.103
2	0.30	0.12	5.64	0.186	0.127	0.792	5	5	0.140
3	0.45	0.15	5.17	0.157	0.078	0.495	7	7	0.095
4	0.465	0.195	8.10	0.225	0.138	0.825	6	6	0.101
5	0.45	0.255	2.55	0.217	–	0.615	3	3	0.241
6 (ZMH C1136)	0.36	0.12	3.78	0.240	–	0.672	3	3	0.177
7	0.465	0.18	2.32	0.187	–	0.45	3	3	0.193
8	0.465	0.15	2.10	0.202	–	0.39	2	2	0.185
9 (ZMA 8475)	0.36	0.144	2.58	0.204	–	0.60	3	3	0.232
10	0.315	0.165	3.01	0.217	–	0.48	3	3	0.159
11	–	0.18	3.82	0.165	–	0.60	3	3	0.156
12	–	0.18	2.88	0.225	–	0.54	3	3	0.187
13	–	0.24	3.90	0.15	–	0.525	5	5	0.134
14	0.435	0.27	1.65	–	–	0.345	2	2	0.209
15	0.45	0.18	1.96	–	–	0.42	3	3	0.213
16	0.51	0.15	1.89	–	–	0.45	3	3	0.238
17	0.456	0.18	1.68	–	–	0.54	3	3	0.321
18	0.60	0.225	1.69	–	–	0.375	2	2	0.221
19	0.495	0.18	1.42	–	–	0.405	2	2	0.284
20	–	0.21	1.80	–	–	0.375	3	3	0.208

Dbd = diameter of basal disk; Db = diameter of tube just above the basal disk; Do = diameter of opercular aperture; Ltot = total length of tube; nwc = total number of whorls of internal cusps; nwc_{5mm} = number of whorls of internal cusps in basal 5 mm; D/L_{2mm} = proportion at 2 mm ($D_{2mm}/2$); D/L_{5mm} = proportion at 5 mm ($D_{5mm}/5$); D/Ltot = proportion (Do/Ltot).

Table VI. Observations on 12 solitary scyphistomae of *Nausithoe aurea* n. sp. during 37 days (August–October 1995). Abbreviations: 'S' = length of period of strobilation, p = planuloids that did not leave the periderm cone; m = medusae that did not shed gametes.

Scyphistoma specimen	1 (MNRJ 2901)	2	3	4	5 (MNRJ 2900)	6	7	8	9 (ZMH C1135)	10	11	12
'S' originating ephyrae (days)	4 and 7	–	–	7	3 and 3	–	4	–	4	–	–	2
Number of ephyrae	41 and 57	–	–	89	28 and *	–	23	–	16	–	–	10
'S' originating planulae (days)	–	4	4	–	–	5	–	4	1	7	1	–
Number of planuloids	–	29	11	–	–	19	–	7	13	9	3+p	–
Minimum period for completion of ephyra development (days)	20	–	–	13	23	–	20	–	18	–	–	23
Minimum period for maturation of medusa (days)	m	–	–	m	m	–	10	–	11	–	–	3

*The chain of ephyrae not liberated from the tube was preserved.

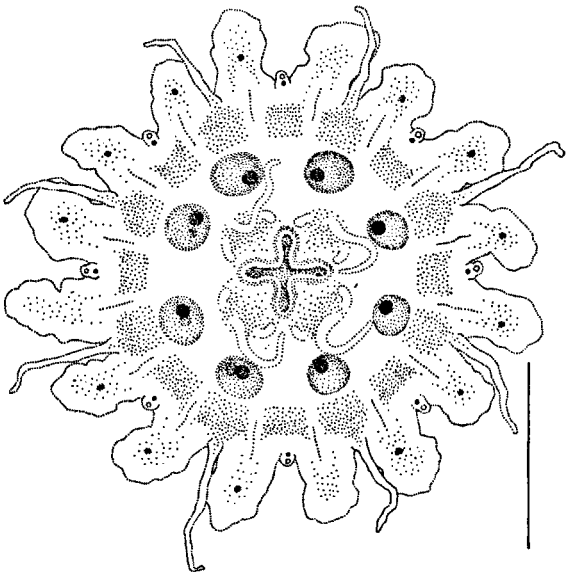

Fig. 5. Oral view of mature female medusa of *Nausithoe aurea* n. sp. showing the 8 ovaries with some oocytes ready to spawn (from photomicrograph). Scale bar: 1.5 mm.

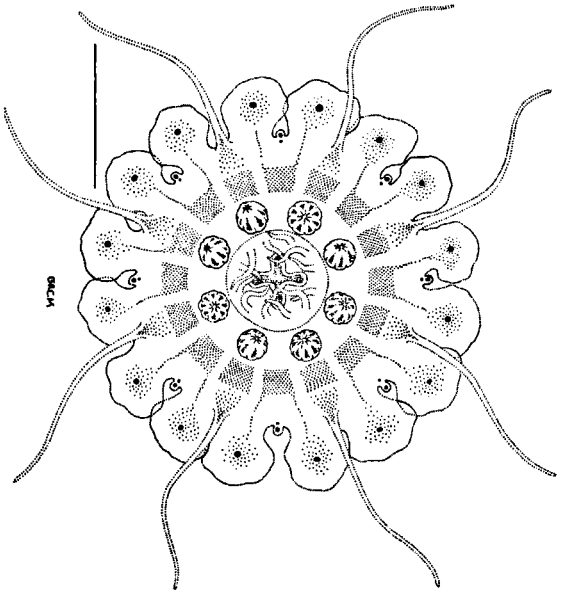

Fig. 6. Aboral view of mature male medusa of *Nausithoe aurea* n. sp. showing the 8 testes (from photomicrograph). Scale bar: 2.5 mm.

Note that scyphistoma specimen 9 strobilated twice, producing planuloids and later ephyrae.

Early embryonic development

Two female medusae released 66 dark brown eggs within 4 days. A third female medusa released 50 eggs within 3 days. The eggs were fertilized externally in less than 24 hours when in the presence of sperm from a male medusa. During fertilization the 2nd polar body is formed while the 1st divides. The zygote undergoes holoblastic adequal cleavage, with close to radial symmetry, but after the 8 cell stage the cleavage is pseudospiral. After fertilization, the early embryo reached the 2, 4, 8, and 16 cell stages, respectively, at 15, 50, 97, and 240 minutes intervals. After the 16 cell stage the cleaving embryo rotates within the egg capsule. The blastula is not hollow. The mode of germ layer formation was not investigated. The early egg capsule, the oolemma, contains the embryo until the early gastrula stage. In about 10 hours the embryos had reached the early gastrula stage, following which they are liberated. Motile planulae were observed for a few days without any perceptible changes occurring (Fig. 7A–F).

Cnidome

Holotrichous isorhizas and heterotrichous microbasic euryteles were noted (Plate IIb). They were recorded in all life-cycle stages. Nevertheless, capsule size tended to increase successively from one stage to the next (Table VII).

Table VII. Measurement of cnidae of cnidome of *Nausithoe aurea* n. sp. The range was taken from 20 nematocysts of each type at each stage.

	Holotrichous isorhiza (μm)	Heterotrichous microbasic eurytele (μm)
Scyphistoma	7.8–6.0×5.4–3.6 5.4–3.6×4.2–2.4	15.0–9.0×4.8–3.0
Ephyra	7.2–5.4×6.0–3.6	12.6–10.2×11.4–9.0
Medusa	6.0–4.2×4.2–3.0	9.0–6.6×7.2–5.4
Planula	6.0–4.8×4.8–3.0	10.8–7.2×9.0–6.0

Discussion

Werner (1973) recognized two "species groups" of solitary scyphistomae, sensu Kramp (1959), typified by *Stephanoscyphus simplex* Kirkpatrick, 1890 and *Stephanoscyphus corniformis* Komai, 1936. However, Werner affirmed that these species groups cannot be considered as valid, because there is a great number of species resembling them, and emphasized that the only way to know a species is to study its life cycle.

Following the summarizing key to the known species of coronate polyps of Jarms (1991), from periderm characters (arrangement and number of the internal cusps) we recognized one species broadly similar to our material: *Nausithoe maculata* Jarms, 1990. There are no exclusive characters in the soft body of the scyphistomae to separate these two species. The white pigment spots at the base of the tentacles and tentacle number in our material are very similar to *N. maculata* and *N. planulophora* (Werner, 1971). The size and proportion of our material were within the ranges of *N. planulophora* and *N. maculata* (cf. Jarms, 1990; 1991; and Werner, 1971b; 1983). However, the present species differs in having some zooxanthellae within the gastrodermis, mainly in the tentacles and oral disk. So far, the colonial *Nausithoe racemosa* (Komai, 1936) and *Linuche unguiculata* (Swartz, 1788) are the only scyphistomae known to have this symbiont (Werner, 1973; Ortiz-Corp's et al., 1987). Moreover, the base outline of the perradial cusps in our material is entirely different from all other species described so far.

The general characters of the ephyra and the medusa in our material resemble those of different Nausithoidae. The most distinctive character, always present, was the conspicuous yellow pigment spot in most or all the lappets of both very young and mature medusae. We suspect variation in the number of pigment spots to be a response to varying culture conditions. In a few specimens, some of the rhopalia had no ocellus or the statocyst was placed at the tip of a lappet. Ortiz-Corp's et al. (1987) noted that the medusae of *L. unguiculata* may present some altered structures under laboratory conditions. Even when zooxanthellae were quite abundant, the yellow spot could be easily seen.

The spawning and fertilization of this species resembles the pattern of many broadcasting invertebrates, i.e., the oolemma plays the role of the early embryonic cover; the stage in which the female gametes are released is that of oocyte (secondary oocyte + 1st polar body), and with fertilization the 2nd polar body is formed while the 1st divides (Giese & Pearse, 1974; Mergner, 1971).

The cnidome of Coronatae has seldom been used in systematics, though it has been investigated to describe some species (Werner, 1971b; 1974) and to study the development of one species (Ortiz-Corp's et al., 1987). All known nematocyst types of Coronatae species include holotrichous isorhizas and heterotrichous microbasic euryteles. Calder (1974: 172) proposed to call the holotrichous isorhizas of Scyphozoa as heterotrichous anisorhizas, though he recognized the spines to be "somewhat indistinct under light microscopy".

The peculiarity of *Nausithoe aurea* n. sp. is its life cycle. The solitary scyphistoma strobilates and liberates ephyrae and/or planuloids. The transformation of the ephyrae into planuloids resembles fairly well the description by Werner (1971b; 1983) and Werner & Hentschel (1983) of *N. planulophora* (= *Stephanoscyphus planulophorus*). In this manner, the material of the present study presents an intermediate life cycle between the metagenetic *Nausithoe* species and the *Nausithoe* species which have reduction of the medusa stage.

It is inferred that we found a species of *Nausithoe* that has a less evolved life cycle compared with *N. planulophora*, a species endemic in submarine caves of the western Mediterranean. The species we studied might represent an earlier evolutionary step in the lineage that originated this cave-dwelling species. Werner (1973; 1974) stated that the reduction of the medusoid stage is a response to environmental conditions prevalent where the scyphistomae live (submarine caves). We suggest that liberation of planuloids by the present species accounts for the observation of the scyphistoma aggregates. Furthermore, we hy-

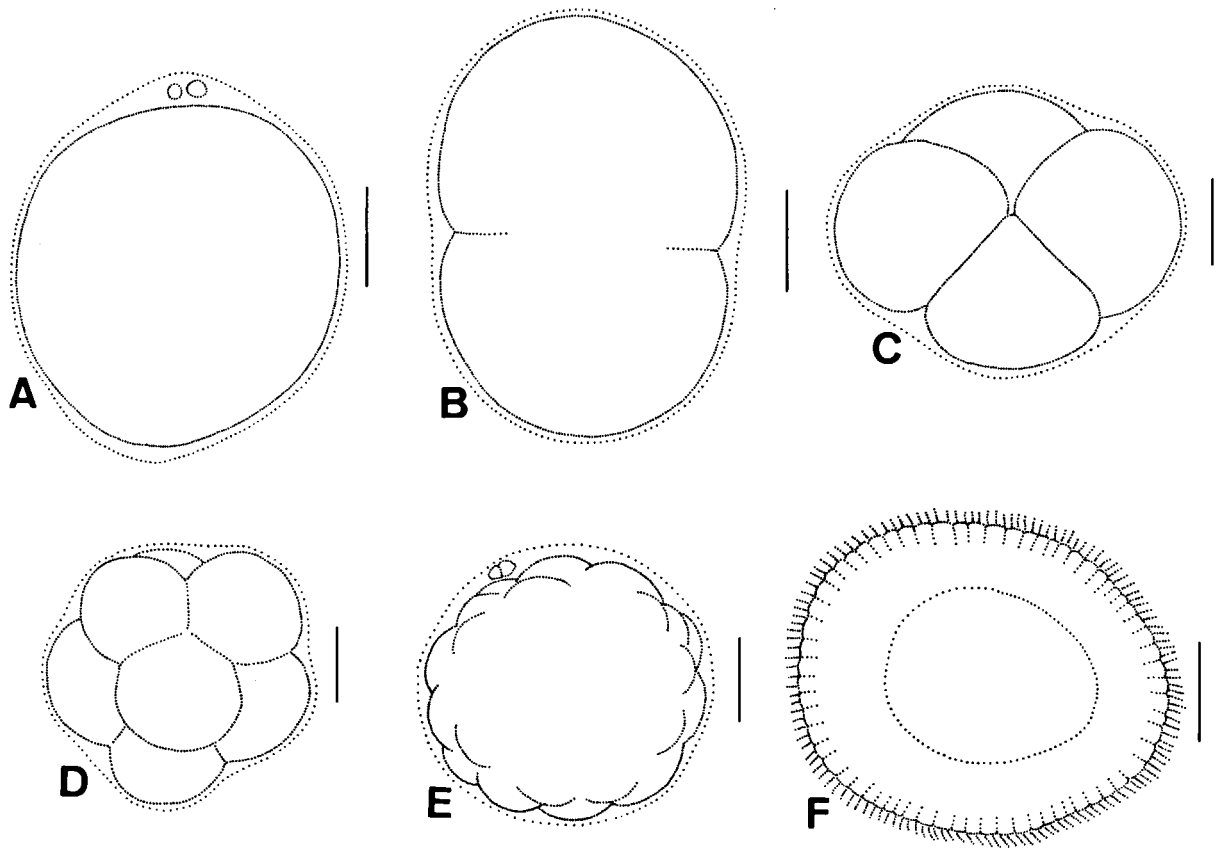

Fig. 7. Early embryonic development of *Nausithoe aurea* n. sp.: A to D, 1, 2, 4, 8 cell stages, respectively (in A two polar bodies are observed); E, late blastula or early gastrula stage – notice that two polar bodies are still observed; F, planula (all from photomicrographs). Scale bar: 50 μm.

pothesize that the aggregates show a tendency of the polyp stage towards philopatry, an adaptive behaviour to secure clonal perpetuation of the species in particular habitats. Cornelius (1992a; 1992b) reviewed some data for leptolid hydrozoans on the significance of medusa reduction, perennation, and philopatry. He believes this is not the trend so far observed in most leptolids, but he reminds us that "a tendency towards philopatry has been reported in several invertebrate groups ancestrally having a long-dispersing stage" (Cornelius, 1992a: 89) when they enter habitats – such as remote islands – having a limited extent. Possibly the cave inhabited by *N. planulophora* provided a parallel stimulus to evolve an abbreviated life cycle.

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