

Sexual reproduction of *Nausithoe aurea* (Scyphozoa, Coronatae). Gametogenesis, egg release, embryonic development, and gastrulation*

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SUMMARY: The structure of the ovaries and testes of *Nausithoe aurea*, reared in the laboratory, is described to update the knowledge of coronate scyphomedusae gametogenesis and early development. The testis is similar to those of other scyphozoans. The organization of the ovary agrees with the description for other coronates, with free oocytes in the mesoglea. The oocytes develop in a limited region of the gastrodermis, and a maturation gradient is observed from this point on. Egg release, embryonic development, and gastrulation mode of *Nausithoe aurea* are also described. Egg production was continuous for 55 days, and the output of released eggs oscillated without observed cue. Cleavage was holoblastic and adequal, but after the 8-cell stage, the cleavage became pseudospiral. Gastrulation occurred through multipolar ingression and began 24 hours after fertilization.

Key words: Scyphozoa, Coronatae, *Nausithoe*, sexual reproduction, gametogenesis, embryonic development, gastrulation.

INTRODUCTION

Campbell (1974) reviewed the general aspects of reproduction in the Cnidaria, while the revisions of Beams and Kessel (1983) (oogenesis) and Miller (1983) (spermatogenesis) were especially focused on the Hydrozoa. Lesh-Laurie and Suchy (1991) reviewed the microscopic anatomy of Scyphozoa. Eckelbarger (1994) provided the most complete study of oogenesis on representative species of the four orders of Scyphozoa, and Arai (1997) reviewed the reproduction of the four orders.

Gametogenesis in the Scyphozoa has received little study. Widersten (1965) compared 3 species of

Semaeostomeae and 1 species of Rhizostomeae, of some 200 species of Scyphozoa (Mianzan and Cornelius, 1999). Recent studies have been conducted on the ultrastructure of 12 scyphomedusae (Avian and Rottini Sandrini, 1991; Eckelbarger and Larson, 1988, 1992; Eckelbarger, 1994).

The microscopic anatomy of coronate medusae was studied by Haeckel (1881), Claus (1883), Maas (1897), Vanhöffen (1902) and Komai (1935) including the structure of the gonads, but only the probable significance of the structure to the systematics of Coronatae was discussed. Few coronate develop germ cells in the scyphistoma stage. However, *Nausithoe racemosa* (Komai 1936) and *Nausithoe eumedusoides* (Werner 1974) show precocious gamete production during strobilation (Komai,

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1935; Werner, 1974). The scyphistomae of *Thecoscyphus zibrowii* (Werner 1984) develop eggs which transform into planulae (parthenogenesis) (Werner, 1984; Sötje and Jarms, 1999). Some studies focused on the histology of four species of polyps of the Coronatae (Chapman and Werner, 1972; Kawaguti and Yoshimoto, 1973; Matsuno and Kawaguti, 1991).

There are few studies of embryonic development in Scyphozoa. Most have reported observations on the Semaestomeae and Rhizostomeae (Goette, 1893; Hyde, 1894; Hargitt and Hargitt, 1910; Teissier, 1929; Littleford, 1939; Widersten, 1965). The only investigations on coronate species are Metschnikoff (1886), about *Nausithoe marginata* Kölliker 1853 and Conklin (1908), about *Linuche unguiculata* (Swartz 1788) (= *Linerges mercurius* Haeckel 1880).

Berrill (1949), based on literature data, suggested a relationship between egg diameter and type of gastrulation. In species with large eggs, gastrulation occurs through invagination; in species with small eggs, gastrulation occurs through ingression; and in species with eggs of intermediate size occurs a mix of the two processes.

Mergner (1971) and Arai (1997) presented some review information about the embryonic development of Scyphozoa. Mergner (1971) summarized that the general aspect for Scyphozoa is radial cleavage and gastrulation through invagination, eventually ingression may occur, and that the development was poorly known compared to Hydrozoa. This knowledge has remained little changed up to the present.

This work describes gametogenesis, egg release, early embryonic development, and gastrulation in the coronate *Nausithoe aurea* Silveira and Morandini 1997, and compares the gametogenesis with the findings of Claus (1883) and Maas (1897), the only histological works on coronates not included in recent reviews of sexual reproduction in the Scyphozoa (e.g. Eckelbarger, 1994; Arai, 1997). The aim of the study is to update the knowledge of coronate gametogenesis and to investigate early development of the species.

METHODS

The scyphistomae were sampled by SCUBA diving in August 1997 in the São Sebastião Channel at Ponta do Urubu (23°51.06'S 45°24.77'W) (São Sebastião Island) São Paulo State, Brazil. They were

growing on the calcareous debris of the coral *Mussismilia hispida* (Verrill 1902) at 3-7 m depth. Twenty-four polyps were reared in the laboratory for 92 days to obtain the medusa stage. A total of 232 medusae were reared for 82 days, producing gametes over the last 55 days. For details of the rearing technique see Silveira and Morandini (1997; 1998).

Each batch of medusae, from different strobilating scyphistomae, was kept in separate plastic cups with an airtight cover. A total of 63 female and 169 male medusae were produced by 2 and 4 strobilating scyphistomae, respectively. The total number of batches of female and male medusae were 3 (coded 1, 1', 2) and 8 respectively. One scyphistoma strobilated twice in 40 days, and its ephyrae matured into female medusae at different times - batches 1 and 1'. Each morning (8-9 a.m.), the oocytes were separated from the females, and the medusae were fed for 5 minutes or until their stomachs were completely filled. The medusae were kept in plastic cups at 22°C under a 2h light/22h dark regime. The oocytes were counted, measured, and used for *in vitro* fertilization.

The released oocytes were put together with 5 male medusae for a period no longer than 1 hour, to prevent medusae from eating the oocytes. Embryonic development was observed *in vitro*. The different embryonic phases were preserved according to their developmental stages (2-64 cells) and time periods of development (11, 24, and 48 hours).

The mature medusae were anesthetized with tricaine (3-aminobenzoic acid ethyl ester methane sulfonate salt - C₁₀H₁₅NO₅S) and preserved in 4% formaldehyde solution in seawater. For histological preparations, medusae were refixed in Heidenhain's fixative (SUSA) (Pantin, 1948). The embryos were preserved in a 4% formaldehyde-seawater solution.

For histology the medusae were dehydrated in ethanol series, cleared with Xylene, and embedded in Paraplast®. The specimens were serial sectioned 5µm, stained with Harris haematoxylin + Eosin-Floxin (HE) (Lightner, 1996) or Weigert haematoxylin + Mallory trichromic (Mahoney, 1973), and mounted on slides with Permount®.

Measurements for gametogenesis were made with a Wild M20 microscope and photographs taken with a Carl Zeiss Jenaval mf-AKS microscope with attached camera. The diameters of 20 cells, of each phase, were measured: male germ cells at high power magnification (1000x); female germ cells at intermediate power magnification (400x), and when the nucleoli were visible.

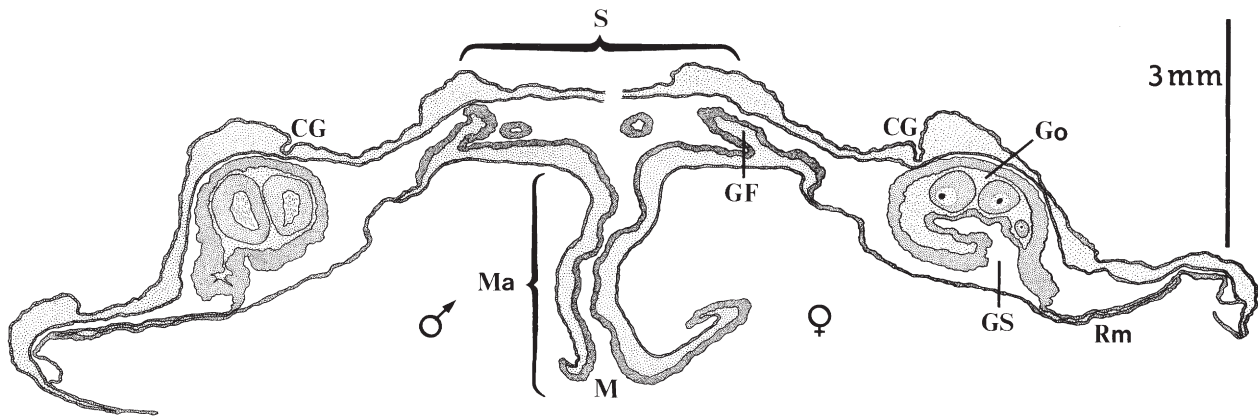


FIG. 1. – Schematic view of a histological section (oral-aboral) of a medusa of *Nausithoe aurea*. A male and a female gonad are represented left and right of the stomach, respectively. Note: the gonads are evaginations of the gastrodermis. CG: coronal groove; GF: gastric filament; Go: gonad; GS: genital sinus; M: mouth; Ma: manubrium; Rm: ringmuscle; S: stomach.

In Figure 6, generated with the graph option of Microsoft, Word 97, we used a best fit regression line adjusted by the polynomial regression ($y = b + c_1x + c_2x^2 + c_3x^3 + \dots + c_6x^6$) (Sokal and Rohlf, 1995: 665). We omitted the first 9 days of data for batch 1 because of variation in the number of medusae in the plastic cup.

Histological sections of the medusae were deposited in the Cnidarian Collection of the Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ 3365-3374).

RESULTS

General structure of the gonads

The medusae are dioecious and produced gametes continuously for 55 days. The gonad forms as an evagination of the floor of the gastric cavity, peripheral to the gastric filaments within the central stomach. The gonads consist of two gastrodermal tissue sheets, filled with mesoglea in which sperm, in follicles, or free oocytes develop (Fig. 1).

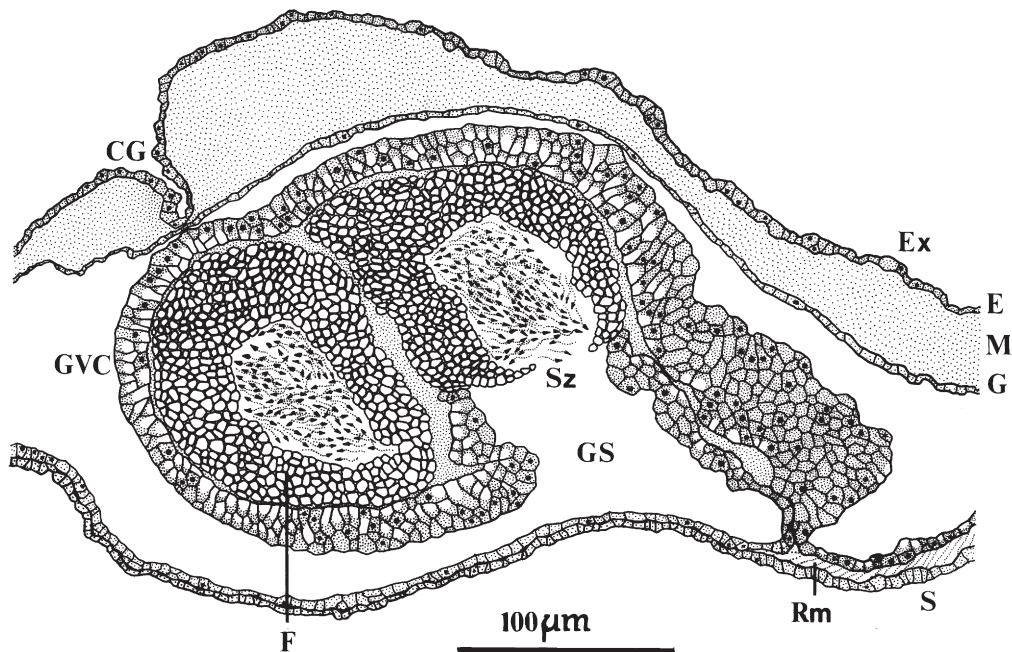


FIG. 2. – Schematic view of a histological section (oral-aboral, to the right of the stomach) of the testis of *Nausithoe aurea*. Note: the gonad is an evagination of the gastrodermis; the follicle opens to the genital sinus. CG: coronal groove; E: epidermis; Ex: exumbrella; F: follicle; G: gastrodermis; GS: genital sinus; GVC: gastrovascular cavity; M: mesoglea; Rm: ringmuscle; S: subumbrella; Sz: Spermatozoa.

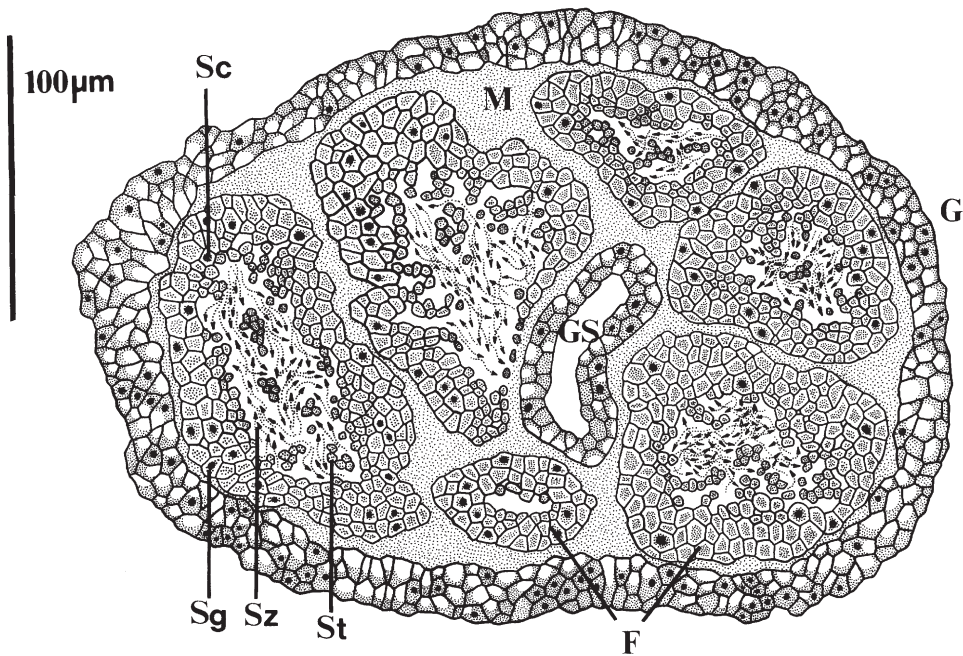


FIG. 3. – Schematic view of a transverse histological section of the testis of *Nausithoe aurea*. Note: the organization of the gonad with follicles; the development of the germ cells in the follicles. F: follicles; G: gastrodermis; GS: genital sinus; M: mesoglea; Sc: spermatocyte; Sg: spermatogonium; St: spermatid; Sz: spermatozoon.

Spermatogenesis

The testis is composed of several follicles (Figs. 2, 3). The maturation of the germ cells in every follicle occurs in a centripetal pattern, and the cell types form distinct layers (Fig. 3). The spermatogonia lie on the margin of the cyst, forming a thin layer. They are spherical with reduced cytoplasm and with nuclei ranging in diameter from 4.8-6.0 μm . The spermatocytes are also spherical cells, with nuclei diameter ranging from 4.8-6.6 μm and with granular chromatin. The spermatids are spherical cells with reduced cytoplasm; in the nucleus (diameter 2.4-3.6 μm) the chromatin is concentrated in clusters. The spermatozoon has a conical head (length 4.2-6.0 μm), followed by a region that does not stain (HE), with the tail pointing to the center of the cyst before becoming mobile.

Oogenesis

The ovary shows distinct areas of gastrodermal epithelium: one, internal, surrounding the genital sinus, with spherical cells and some vacuoles; and the other, external, with columnar cells containing many vacuoles (Fig. 4). The oocytes develop from the gastrodermis (Fig. 5), and lie in the mesoglea. Oocytes were observed in different stages, with no relation to the age of the medusae. Small spherical

cells were observed near a limited region of the gastrodermis (diameter 16.5-36.0 μm), with reduced basophilic cytoplasm, light nuclei (diameter 10.5-22.5 μm), and scattered chromatin. These cells migrate into the mesoglea, and showed two distinct phases: basophilic and acidophilic oocytes. The basophilic oocytes were spherical or elliptical (diameter 31.5-82.5 μm), light nuclei (diameter 18.0-46.5 μm), and conspicuous nucleoli (diameter 6.0-10.5 μm). The acidophilic oocytes were spherical (diameter 73.5-133.5 μm), light nuclei (diameter 24.0-51.0 μm), and nucleoli (diameter 9.0-12.0 μm). In oral-aboral sections, a maturing oocyte gradient was observed towards the free side of the female gonad (Fig. 5). Some of the yolk granules in the oocytes showed a central dark spot, resembling the nucleus of a very small cell (Fig. 4).

Egg release, embryonic development and gastrulation

The fertilization is external, with the oocytes released through the mouth. Mature female medusae released oocytes from 11/Sep-5/Nov/1997. The total number of oocytes released varied throughout the period, ranging between 0-485 oocytes per day (Table 1).

Figure 6 shows that the release of oocytes was continuous for the whole study period, but with some variation in the number of oocytes released.

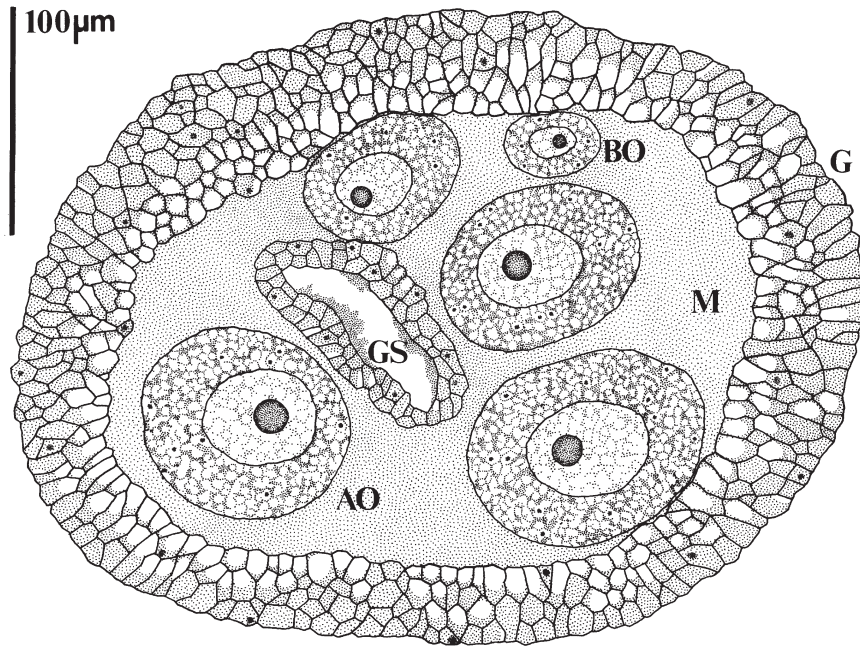


FIG. 4. – Schematic view of a transverse histological section of the ovary of *Nausithoe aurea*. Note: the distinct areas of gastrodermal epithelium, internal with spherical cells and external with columnar cells. AO: acidophilic oocyte; BO: basophilic oocyte; G: gastrodermis; GS: genital sinus; M: mesoglea.

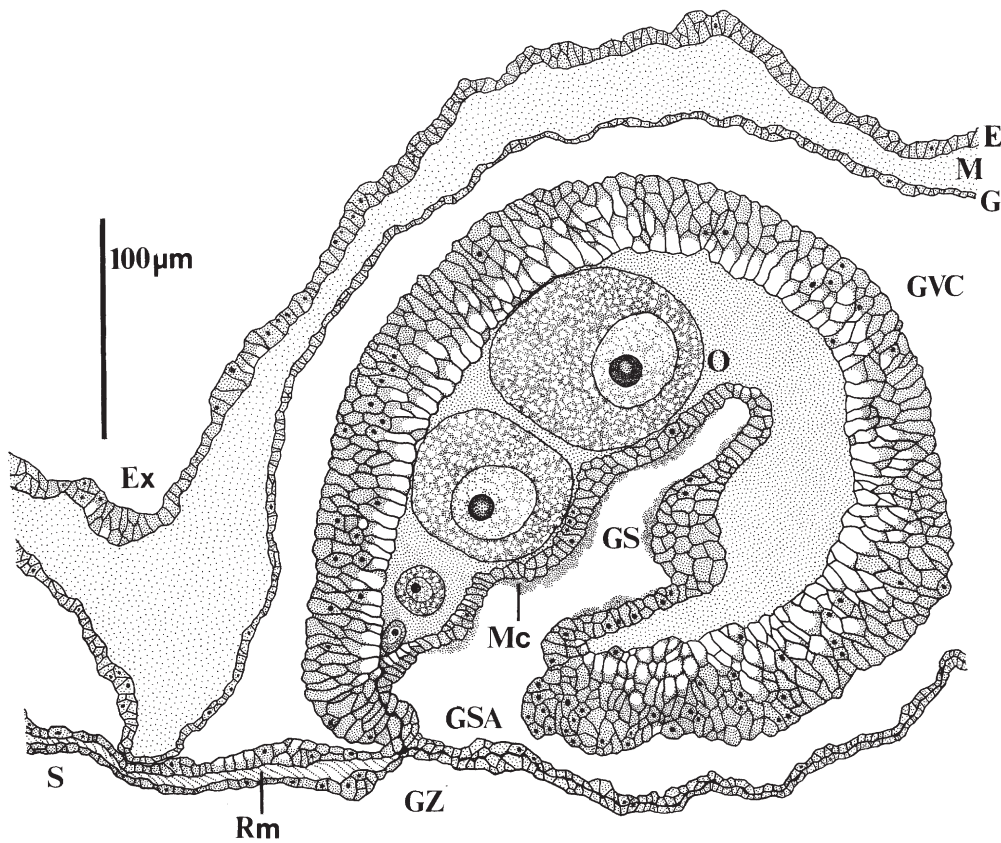


FIG. 5. – Schematic view of a histological section (oral-aboral plane and to the left of the stomach) of the ovary of *Nausithoe aurea*. Note: oocytes in different stages; the differences between the gonad epithelia; the presence of mucous in the genital sinus. E: epidermis; Ex: exumbrella; G: gastrodermis; GS: genital sinus; GSA: genital sinus aperture; GVC: gastrovascular cavity; GZ: germinative zone; M: mesoglea; Mc: mucus; Rm: ringmuscle; O: oocyte; S: subumbrella.

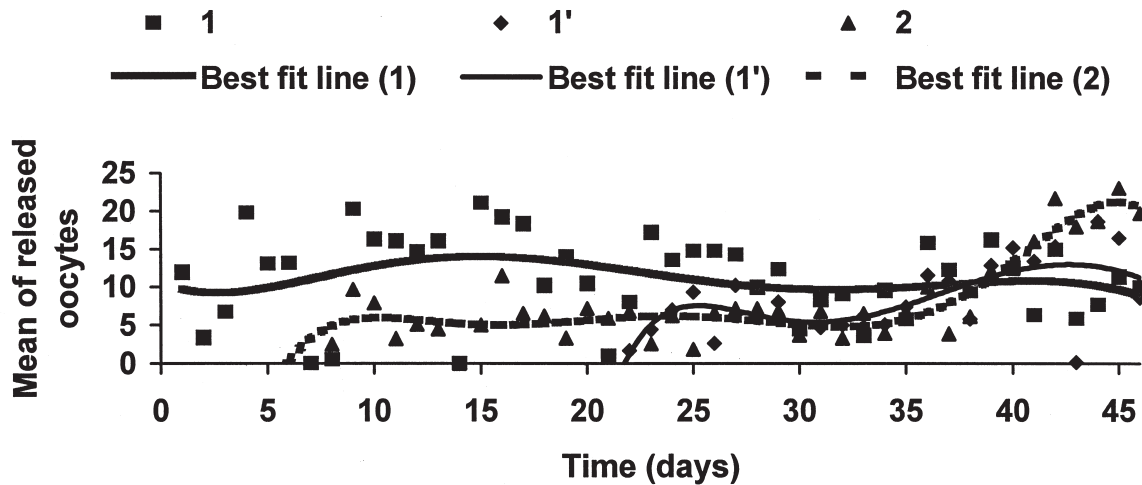


FIG. 6. – Mean number of oocytes per day released by medusae of *Nausithoe aurea* reared from 20/Sep-5/Nov/1997 and best fit regression line. Spawning period for batches are: 1, 20/Sep-5/Nov; 1', 11/Oct-5/Nov; 2, 27/Sep-5/Nov/1997.

TABLE 1. – Data of the 3 batches of medusae of *Nausithoe aurea*, releasing oocytes from 20/Sep-5/Nov/1997. Table shows the range/batch and mean/medusae numbers of released oocytes by batch (total number of oocytes divided by the total number of medusae each day). Variation on medusae number and spawning period is shown.

batch	range/batch	mean/ medusae	number of medusae	spawning period
1	0-168	11	8-7	47 days
1'	3-318	8	17	26 days
2	0-485	8	22-21	40 days

The oocytes remain grouped by a mucus strand. Spawned oocytes were almost spherical, 132-188 x 164-208 μm ($n = 100$; mean \pm SD = 167 \pm 11 x 179 \pm 8.5 μm) in diameter, and are dark brown. Released oocytes are enclosed by the egg envelope, and usually have 2 polar bodies (Fig. 7a); in some cases 3-4 polar bodies were observed. Sometimes the spermatozoa were observed moving in the space between the egg envelope and the oocyte surface.

Cleavage is radial and holoblastic. After 1.5 to 2 hours of mixing the oocytes with male medusae, we observed the first cleavage. The division is meridional (beginning in the polar bodies region, the animal pole), forming a heart-shaped figure (Figs. 7b, 7c). The second cleavage occurs almost 2.5 to 3 hours after fertilization, and is also meridional (Fig. 7d), and the third at 3.5 to 4 hours, and is equatorial. After the 8-cell stage, the cleavage becomes pseudospiral.

After 24 hours following fertilization, the embryo begins to rotate inside the egg envelope until it ruptures and the embryo is freed. At this stage the

embryo is almost spherical (Fig. 7e). After 48 hours, the embryo moves actively in the water column of the rearing vessel (Fig. 7f).

Observations of histological sections of the released oocytes and the first cleavage stages added no more information to that gained from observations on live embryos, except for confirming the absence of any zooxanthellae.

The histological sections of the embryos (24, 48 hours) showed that gastrulation occurs through multipolar ingression (Fig. 8), and may begin approximately 24 hours after fertilization. In the sections of 11-hour-old embryos, no migrating cell was ever observed. No invagination or grouping of cells in one pole was observed in any section.

In the 48-hour embryos we could not see the basal lamina. The presumptive gastrodermis still had few cells, and most of the space inside the stereogastrula was filled with yolk granules. The ectodermal cells were very irregular in shape.

DISCUSSION

General structure of the gonads

The structure of the gonads of *Nausithoe aurea* agrees with other Coronatae species from studies focusing on histology/anatomy (Claus, 1883; Maas, 1897), systematics (Haeckel, 1881; Vanhöffen, 1902), and vitellogenesis (Eckelbarger and Larson, 1992). The general organization of the gonad is similar to other scyphozoan species (Hargitt and Hargitt, 1910; Widersten, 1965; Avian and Rottini San-

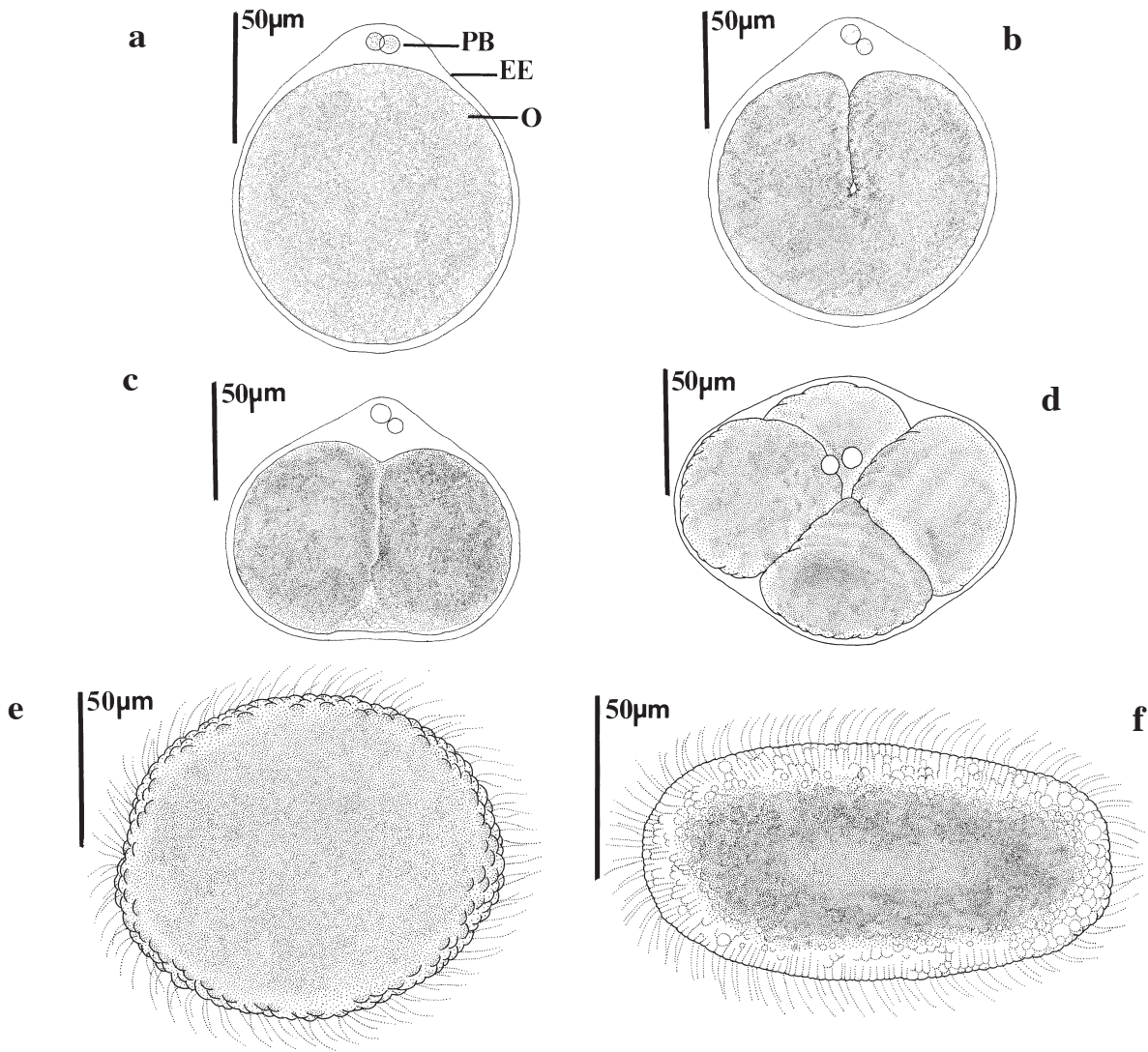


FIG. 7. – Embryonic stages of *Nausithoe aurea*. (a) Newly released oocyte of *Nausithoe aurea*. Note the egg envelope and the polar bodies. O: oocyte; EE: egg envelope; PB: polar bodies. (b) First cleavage. (c) 2-cell stage. (d) 4-cell stage. (e) Embryo 24 hours after fertilization. (f) Embryo 48 hours after fertilization.

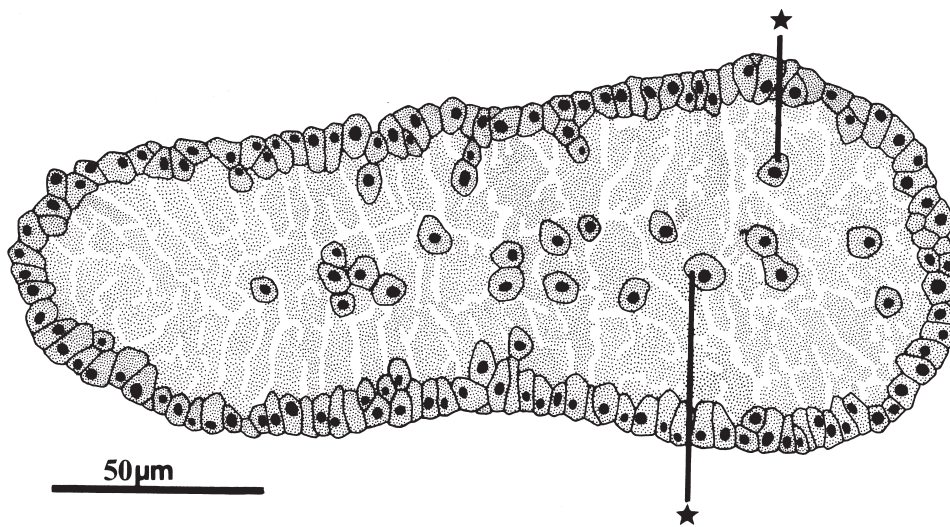


FIG. 8. – Schematic view of a longitudinal histological section of the 48-hour embryo of *Nausithoe aurea*, showing the gastrulation (multi-polar ingression) process. H: migrating cells.

drini, 1991; Kikinger, 1992; Eckelbarger and Larson, 1992; Eckelbarger, 1994) and showed the arrangement of gastrodermis layers as described by Widersten (1965).

The germinative zone (gastrodermis region from which the germ cells migrate to the mesoglea of the gonad) was observed in other coronate species: Haeckel (1881), called the region “germinative epithelia” for *Nausithoe* (*Nauphanta*) *challengeri* (Haeckel 1880); Maas (1897), studying *Periphylla* and some *Atolla* species, called it germinative zone (“*Keimzone*”).

Spermatogenesis

The general structure of the testis of *N. aurea* resembles the descriptions of Claus (1883) for *Nausithoe punctata* (= *N. albida* Gegenbaur 1856, following Mayer, 1910); Widersten (1965) for *Cyanea capillata* (Linné 1746), *Cyanea lamarckii* Péron and Lesueur 1809 (= *C. palmstruchii* Östergren 1909, following Russell, 1970), and *Aurelia aurita* (Linné 1746); and Kikinger (1992) for *Cotylorhiza tuberculata* (Macri 1778).

Claus (1883) reported that the structure of the testis is similar to that of the ovary, but that the mesoglea layer is reduced in the former, because of the development of the follicles. In addition he stated that in oral-aboral sections the follicles were fused. However, we believe that this observation was a misinterpretation of the sections. According to Maas (1897) there was no genital canal inside male gonads of *Atolla* and *Periphylla*. The shedding of spermatozoa occurs through the rupture of the testis wall (Campbell, 1974), and any gastrovascular canal system associated with the gonad region may function as a “genital canal”.

Arai (1997:143) interpreted the misleading figure 7 of Widersten (1965:53), saying that: “*Sperm of scyphozoa ... develop in follicles formed by invagination of the epithelium into the mesoglea of the testis ... (Figure 6.4)*”. Vanhöffen (1902) stated that in male medusae the follicles differentiate in the mesoglea. Widersten (1965:49) and Kikinger (1992:343) corroborated that the follicles are formed by migrating cells of the “genital epithelia” into the mesoglea of the gonad.

The spermatozoa of *N. aurea* do not form sperm packages (“*spermatozeugmata*”) as observed in some Rhizostomeae, such as *C. tuberculata* (Kikinger, 1992) and *Cassiopea andromeda* (Forskål 1775) (Gohar and Eisawy, 1960). The

region of the spermatozoon of *N. aurea*, which does not stain, is the region of the mitochondria according to Afzelius and Franzén (1971) in the ultrastructure study of the spermatozoon of a *Nausithoe* species.

Oogenesis

Claus (1883) observed some differences in the ovary of *N. punctata* between the aboral (thicker layer of columnar cells) and oral epithelia (thinner layer with small vacuoles). The vacuolated aspect of the epithelium covering the genital sinus may be related to secretion. Claus also observed small oocytes migrating to the mesoglea from the germinative zone (“*Keimepitel*”). The comments of Claus (1883) on the vacuolated epithelium, and our observations on sections and live materials, showed that the presence of these vacuoles are related to spawning (oocytes within mucous strand). Avian and Rottini Sandrini (1991) suggested that the large amount of mucus is peculiar to species with external fertilization and may provide a chemoattractant for spermatozoa.

Maas (1897) observed a maturing gradient towards the free sides of the gonads. Vanhöffen (1902, Taf. VII, Fig. 47) showed that in the female gonads of *Atolla wyvillei* Haeckel 1880 (= *A. verrilli* Fewkes 1886) the early oocytes (basophilic oocytes) are attached to the wall by a peduncle, differing from all other known coronate species.

The dark spots in the yolk granules of the oocytes, resembling the nuclei of “shrunk cells” of some Hydrozoa (Tardent, 1985; Thomas and Edwards, 1991) were never mentioned in other works, but they were illustrated in Figure 8 of Avian and Rottini Sandrini (1991: 192), figs. 13-14 of Kikinger (1992: 346), and Figure 3 of Eckelbarger and Larson (1992: 635). The appearance of these dark spots might be a consequence of the histological techniques employed, or might be related to the different stages of the vitellogenesis process occurring in the growing oocytes, as established by Eckelbarger and Larson (1992) and Eckelbarger (1994), using ultrastructure techniques.

According to Eckelbarger (1994), one of the distinguishing features between the different orders of Scyphozoa is the mode of the oocytes nutrition in the female gonad. *Nausithoe aurea* agrees with the pattern defined for Coronatae; free oocytes in the mesoglea without close association to any cell.

Egg release, embryonic development and gastrulation

Jarms (*pers. comm.*) affirmed that medusae of *Nausithoe marginata* in laboratory, after a spawning period, produce eggs again after several weeks. Conklin (1908) had observed for *Linuche unguiculata* that after spawning (= empty gonads) the medusae sank and died, and that the spawning always occurred in the morning (8 a.m.). The continuous egg production of *Nausithoe aurea* seems to differ from *L. unguiculata*, although this is an observation restricted to the laboratory.

Mature medusae are one of the possible results of strobilation-planuloid formation the other (Silveira and Morandini, 1997), and continuous gamete production may maximize the success of sexual reproduction. Thus, continuous egg release in this species is likely an adaptive trait evolved in response to the natural selection of medusae.

Larson (1986) suggested that the coronates *Atolla chuni* Vanhöffen 1902 and *Atolla wyvillei* Haeckel 1880 release a few eggs at a time, continuously. Jarms *et al.* (1999) believe that the life cycle of *Periphylla periphylla* (Péron and Lesueur 1809) lasts for some decades, and may be related to continuous and scanty egg release. Eckelbarger and Larson (1992) stated that deep sea coronates produce few eggs per day. In contrast, *L. unguiculata*, an epipelagic species, releases more than 100 eggs per day (Kremer *et al.*, 1990). Thus, the mean number of eggs released by *N. aurea* medusae fits the values for the deep sea coronates. Arai (1997:145) summarized that oceanic scyphomedusae produce a low number of eggs throughout the year, while neritic temperate species have a strong seasonality in the production of ephyrae and gametes. Silveira and Morandini (1998) suggested that the observed seasonality of medusae swarming of *L. unguiculata* (following their gametogenesis) is related to the marked strobilation period. *N. aurea* is so far a neritic species (considering the zooxanthellate scyphistomae), subtropical-tropical, and its medusae release eggs in laboratory for 55 days. In the laboratory and throughout the year, the scyphistomae always strobilated a few days after they were collected (*pers. obs.*). There were oocytes in different stages in the gonads (*in vivo*) and in histological sections.

Considering the discussion of sexual reproduction of Scyphozoa by Arai (1997), we suggest that *N. aurea* is indeed a neritic species and produces gametes throughout the year. This condition repre-

sents a new pattern for the biology of *N. aurea*. In the São Sebastião Channel, it remains to be answered which factors may account for the absence of ephyrae/medusae in plankton samples and intensify the mechanisms of asexual reproduction of coronates (Silveira and Morandini, 1997, 1998).

The early development of *N. aurea* resembles that of *L. unguiculata* observed by Conklin (1908), and agrees with the brief description of Silveira and Morandini (1997). Conklin (1908) observed that the eggs were released with a mucus strand and that the egg envelope persisted until the gastrula stage. Montgomery and Kremer (1995) showed that the transmission of zooxanthellae from the female to the embryo of *L. unguiculata* occurs through the mucus strand.

Hargitt and Hargitt (1910) stated that the polar bodies were formed prior to or at fertilization. Widersten (1965) observed that the expulsion of the polar bodies occurs while the oocytes are in the mesoglea of the gonads. We always observed polar bodies with released oocytes, which suggests that meiosis is completed prior to fertilization, following Campbell (1974:171) and Tardent (1985:175).

The water in which female medusae were maintained ("egg water", *sensu* Giese and Pearse, 1974:33) induces male medusae of *N. aurea* to spawn, but the release of her eggs is independent of males.

Mergner (1971:24) stated that, in general, cleavage in Scyphozoa [e.g., *Aurelia aurita* (Linnaeus 1746)] is radial, aequal, and holoblastic, although in some species a pseudospiral cleavage might be observed as a complementary phenomenon. The cleavage of *N. aurea* conforms to this last type, with pseudospiral cleavage after the 8-cell stage.

Following the hypothesis of Berrill (1949), Larson (1986) suggested that large eggs would indicate direct development (see Table 2), based on medusae of *P. periphylla* and *Atolla* species. Recently, Jarms *et al.* (1999) described the holopelagic life cycle of *P. periphylla*, which agrees with the hypothesis of Berrill and Larson (large eggs - direct development).

According to Conklin (1908), the gastrulation of *L. unguiculata* occurs through invagination. He observed that sometimes gastrulation occurs through a mass of endodermal cells migrating from the vegetal pole (unipolar ingression). Hargitt and Hargitt (1910) stated that for *Aurelia* the gastrulation occurs mainly through invagination, but that it is not the only process. Table 2 shows some literature data

TABLE 2. – Comparison of egg sizes and gastrulation in different species of Scyphozoa. Ø: diameter; (rel): size of released eggs; ing: ingression; inv: invagination; del: delamination; *: species with direct development.

Order	Species	Ø egg (µm)	Gastrulation	Author
Coronatae	<i>Linuche unguiculata</i>	240 (rel)	inv-ing	Conklin, 1908
	<i>Nausithoe aurea</i>	132-208 (rel)	multipolar ing	present work
	<i>Nausithoe marginata</i>	230	inv	Metschnikoff, 1886
	<i>Periphylla periphylla</i> *	1280-1680	del	Jarms <i>et al.</i> , 1999
Rhizostomeae	<i>Cotylorhiza tuberculata</i>	120	ing	Berrill, 1949
Semaestomeae	<i>Aurelia aurita</i>	150-230	ing-inv	Hyde, 1894
	<i>Chrysaora hysoscella</i>	47	ing	Teissier, 1929
	<i>Chrysaora quinquecirrha</i>	70-190 (rel)	inv	Littleford, 1939
	<i>Cyanea capillata</i>	120-150	ing	Hyde, 1894
	<i>Pelagia noctiluca</i> *	300	inv	Goette, 1893

concerning gastrulation in several scyphozoan species. The data reinforce the hypothesis of Berrill (1949) about the relation between egg size and mode of gastrulation.

The elongate appearance of the 48-hour embryos is similar to that of the planuloids produced asexually by the polyps (see Silveira and Morandini, 1997).

The absence of the basal lamina from the histological sections of 48-hour embryos of *N. aurea*, suggests 2 possibilities: that the ingression of cells at gastrulation continues for a period over the initial 2 days; or, the basal lamina is so thin that it was not distinguishable with the microscopy employed.

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