

External gestation of *Exogone naidina* Örsted, 1845 (Polychaeta, Syllidae): ventral attachment of eggs and embryos

Maria Mastrodonato^{a,*}, Margherita Sciscioli^a, Elena Lepore^a, Miriam Gherardi^a,
Adriana Giangrande^b, David Mercati^c, Romano Dallai^c, Pietro Lupetti^c

^a Dipartimento di Zoologia, Università di Bari, Via Orabona 4, 70125 Bari, Italy

^b Dipartimento di Scienze e Tecnologie Biologiche e Ambientali, Università di Lecce, 73100 Lecce, Italy

^c Dipartimento di Biologia Evolutiva, Università di Siena, Via Aldo Moro 2, 53100 Siena, Italy

Received 4 April 2003; received in revised form 2 May 2003; accepted 19 May 2003

Abstract

The external gestation of sexually ripe females of the species *Exogone naidina* (Polychaeta, Syllidae) is described by means of SEM and TEM analysis. The eggs, embryos and juveniles are attached in close vicinity of each parapodial complex in a position immediately below each ventral cirrus and are connected to the female by a cup like structure. The formation of this adhesive disk is linked to secretory cells scattered between dermal cells of ripe female. This adhesive disk is present only in sexually mature animals and is considered as epitokous structure.

The evolutive significance of ventral and dorsal attachment found within the Exogoninae is also discussed.

© 2003 Elsevier Ltd. All rights reserved.

Keywords: Brood protection; Epitoky; Syllidae; SEM; TEM

1. Introduction

Polychaetes are a group of marine invertebrates which exhibit a remarkable diversity of reproductive strategies (Wilson, 1991; Giangrande, 1997). Among these, brooding is a widespread phenomenon found in 8 different orders, with 12 different modalities and often associated with direct development. Number of eggs produced and parental care are proved to be correlated, being brood protection diffuse especially among small sized species which can produce only a limited number of eggs per offspring (Giangrande, 1997).

A peculiar type of care of eggs and embryos is represented by their individual attachment to the mother body (external gestation). This feature is found in Syllidae, and is particularly frequent in the subfamilies Eusyllinae and Exogoninae (Pierantoni, 1903, 1905; Heacox and Schroeder, 1978; Perkins, 1981). The attachment can be either dorsal or ventral and the eggs develop into juvenile stages of three chaetigers before detaching from maternal body surface, in dorsal brooding and up to six chaetigerous segments, in the

case of ventral brooding. As already pointed out by Kuper and Westheide (1998) dorsal or ventral attachment position seems to be species specific, even if, both types can be found within the same genus. Recently, however, San Martín (2002) discussed about the presence of different brooding methods within the same genus.

Studies about the external gestation in Syllidae are very dated (Quatrefages, 1865; Viguier, 1884; Malaquin, 1890; Pierantoni, 1903, 1905; Potts, 1911; Gravier, 1923). Very few investigations have been performed more recently (Cazaux, 1969, 1972; Cognetti Varriale, 1971; Westheide, 1974; Heacox and Schroeder, 1978; Perkins, 1981; Kuper and Westheide, 1998). Up to now more than 40 syllid species are reported with external gestation (Garwood, 1991), however, most of reported papers are purely descriptive, and little is known about the mechanisms of individual attachment to the mother body.

A good description of external gestation in syllids can be found in Pierantoni (1903) and Potts (1911) who suggested that the ventral attachment of the eggs occurred by means of glandular secretions produced by cells, the exact location and structure of which was not known.

Haswell (1920) reported the existence of dorsal and ventral pedal glands producing adhesive secretions responsible for the attachment of the eggs.

* Corresponding author. Tel.: +39-080-5443344;

fax: +39-080-5443344.

E-mail address: m.sciscioli@biologia.uniba.it (M. Mastrodonato).

A pair of fixing organs producing fibrils, considered equivalent to cilia, and interpreted as means of attachment to the female dorsal surface were described by Goodrich (1930) in *Grubeosyllis neapolitana* (as *Pionosyllis neapolitana*). Some fibrillar structures fixing eggs to the dorsal surface of the mother body were instead described by Cazaux (1969, 1972) for *Grubeosyllis limbata* and some species of the genus *Sphaerosyllis*.

In a more recent ultrastructural investigation, Kuper and Westheide (1998) reported for three Exogoninae species where the presence of eggs and embryos are attached by specialized chaetae dorsally (notochaetae) to the mother body. In *Sphaerosyllis hermafrodita* the chaetae penetrate the egg envelope, while in *Grubeosyllis* sp. and *Grubeosyllis subterranea* chaetae are closely apposed to the eggs. Finally dorsal brooding was found in the recently described genera *Cicese* (Diaz-Castaneda and San Martín, 2001) and in *Nooralia* (San Martín, 2002), involving the presence of capillary notochaetae in the first genus and compound notochaetae in the second one.

In the present paper we report the ultrastructural features of specializations that assure the ventral attachment of eggs and embryos to mother body in *Exogone naidina* Örsted 1845. The description of brooding and reproduction of this species was already performed by Rasmussen (1973).

2. Material and methods

2.1. Origin and collection of samples

Specimens of *E. naidina* were collected on an algal substrate at 0.5–1 m depth along the littoral of Bari (Apulia, Mediterranean Sea).

The specimens were extracted from the algae using the $MgCl_2$ method (Westheide, 1990).

2.2. Transmission electron microscopy and light microscopy

Samples were placed in a solution obtained by adding 3 ml of artificial sea water to 5 ml of 0.1 M sodium-cacodylate buffer solution of pH 7.4. Ripe females with eggs or advanced juveniles onto their ventral surface were then isolated under a stereo-microscope. The first anterior and last posterior segments of females were cut with micro-scissors and discarded. All other segments were then fixed in the above buffer to which 2 ml of 50% glutaraldehyde aqueous solution had been previously added. After 2 h of fixation at 4 °C samples were rinsed in the above buffer and postfixed for 1 h at 4 °C in 1% osmium tetroxide buffered solution. After a few more rinses in buffer, samples were dehydrated in a graded series of ethanol, and embedded in Epon-Araldite. After resin polymerization, ultrathin sections were obtained by a Reichert Ultracut IIE ultra-microtome. Thin sections were routinely contrasted with uranyl acetate and lead cit-

rate and observed with a Philips CM10 transmission electron microscope operated at an accelerating voltage of 80 kV.

For light microscopic observations, 0.5 μ m thick sections, stained for 2 min with an 1% aqueous solution of Toluidine Blue, were observed and photographed with a Leica DMRB light microscope equipped with an Olympus Camedia Z4040 digital camera.

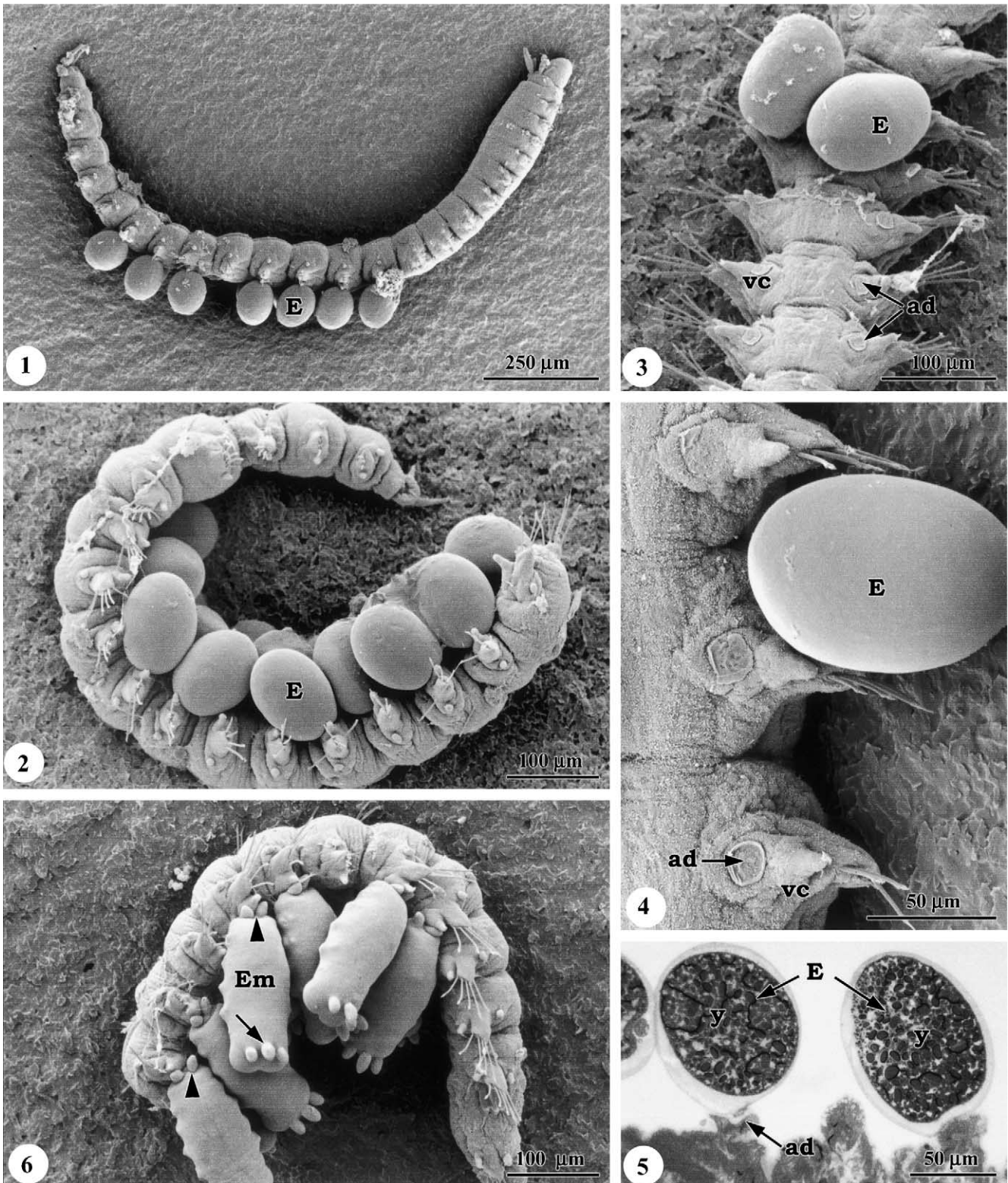
2.3. Scanning electron microscopy

For SEM observations living specimens of *E. naidina* were immersed in the above buffer and ripe females bearing eggs or advanced juveniles were selected under a stereo-microscope. Selected samples were fixed with 2.5% glutaraldehyde in buffer for 4 h at 4 °C. Samples were rinsed in buffer, postfixed for 2 h in 1% osmium tetroxide, rinsed in buffer, and dehydrated in ascending ethanol series. Finally, the specimens were critical-point dried in a Balzers CPD 030 and coated with gold in a Balzers MED 010 sputtering device. Specimens were examined and photographed in a Philips XL20 scanning electron microscope operated at an accelerating voltage of 15 kV.

3. Results

3.1. Scanning electron microscopy and light microscopy

Ripe females of *E. naidina* carry two eggs of 80–90 μ m of diameter on each chaetigerous segment (Figs. 1 and 2). The adhesion of eggs to the body surface is maintained through a discoidal structure adhering on female cuticle and becoming better visible when eggs are mechanically removed with the help of a thin needle after critical-point drying (Figs. 3, 4 and 7). Egg removal also helps to visualize their exact location on each chaetigerous segment allowing the description of the ultrastructural details of the attachment site. Eggs are attached in close vicinity of each parapodial complex, immediately below each ventral cirrus (Figs. 3 and 4), and their cross sections reveal the presence of abundant yolk granules surrounded by a thin egg envelope (Fig. 5). Eggs and later advanced juveniles are held in the ventral position until these latter have reached 170 μ m in length (Fig. 6). At this stage, juveniles have lost the egg envelope and are attached to the parent only by their posterior end, and show lateral buddings of their first four chetigerous segments (Fig. 6). In front position it is possible to observe the incomplete prostomium and three antennae; in the posterior segment the anal cirri are visible (Fig. 6). Later on, when they have reached 200 μ m in length, they are released in the environment. When the early embryos are removed it is still possible to observe in their exposed cytoplasm residual spherical yolk granules embedded in an amorphous matrix (Fig. 9). Occasionally the egg removal exposes a domain closer to the body surface of female (Fig. 7). This domain where eggs adhere to the body surface of female is a circular area with a



Figs. 1 and 2. Scanning electron micrographs showing a lateral view of a ripe female of *E. naidina*. The eggs (E) are brooded ventrally on chaetigerous segments. Figs. 3 and 4. SEM micrographs showing a ventral view of a ripe female. The adhesive disks (ad) located below ventral cirrus (vc) are visible after the mechanic removal of the eggs (E). Fig. 5. Semithin section in which the connection of the eggs (E) to the body of the mother by an adhesive disk (ad) is visible. Note the presence of abundant yolk granules (y). Fig. 6. SEM micrograph showing a ripe female with embryos (Em) ventrally attached by the posterior end. The incomplete prostomium with three antennae (arrow) is visible. The anal cirri (arrowheads) are also observable.

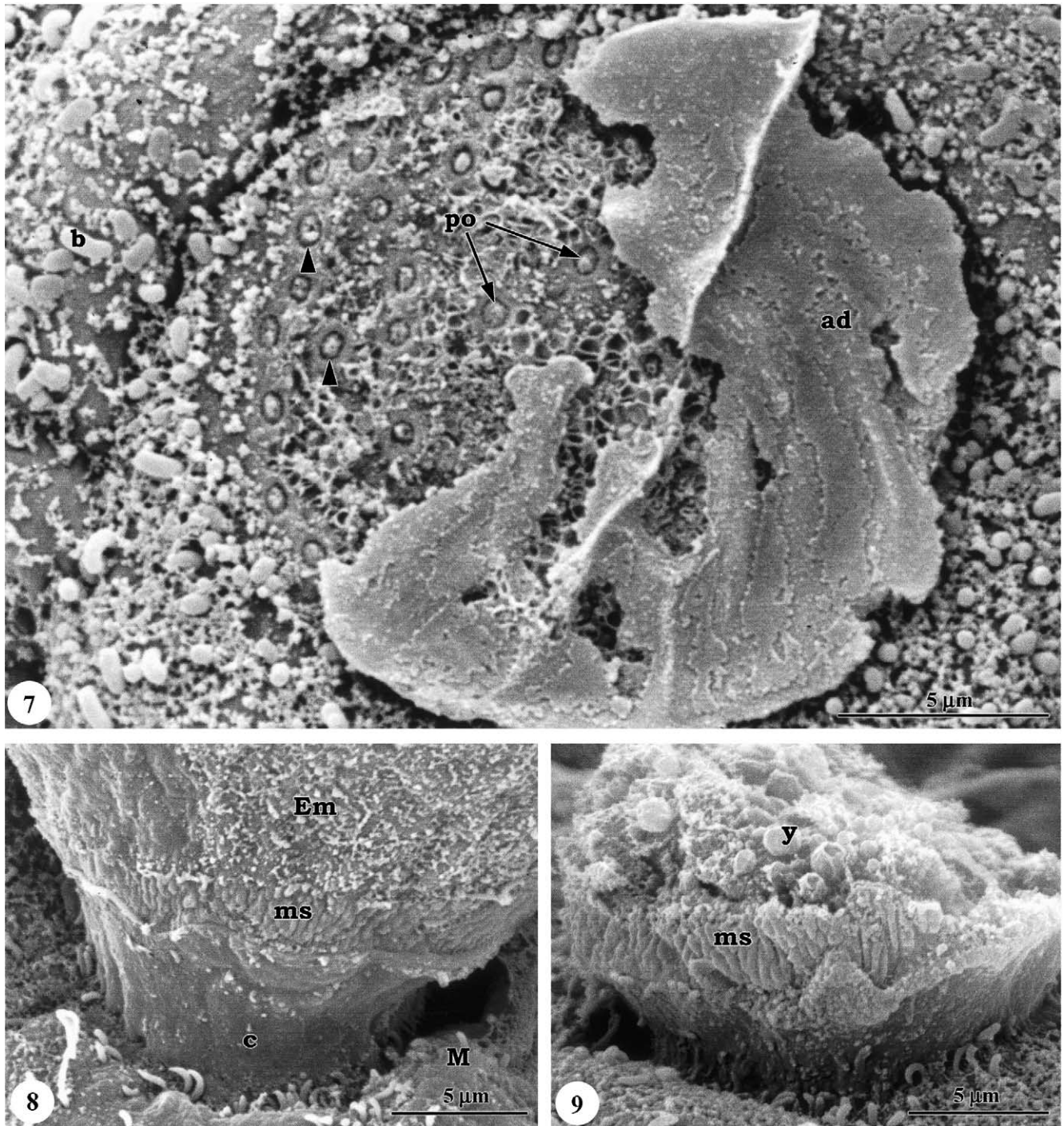
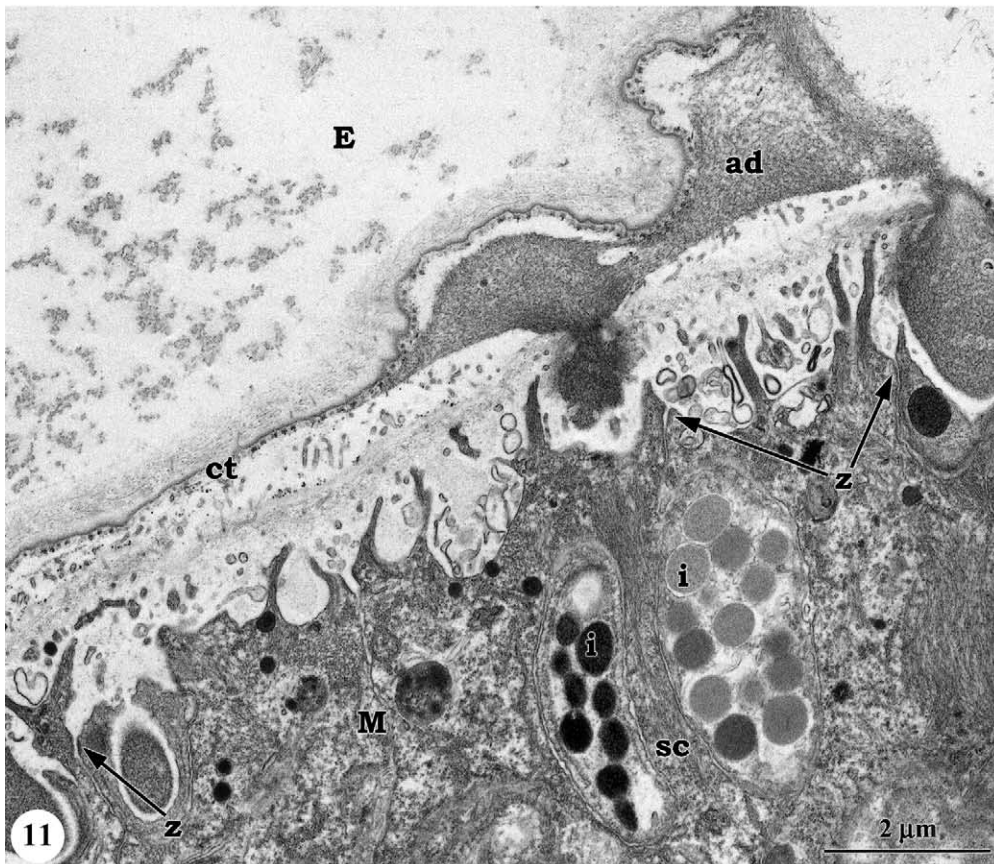
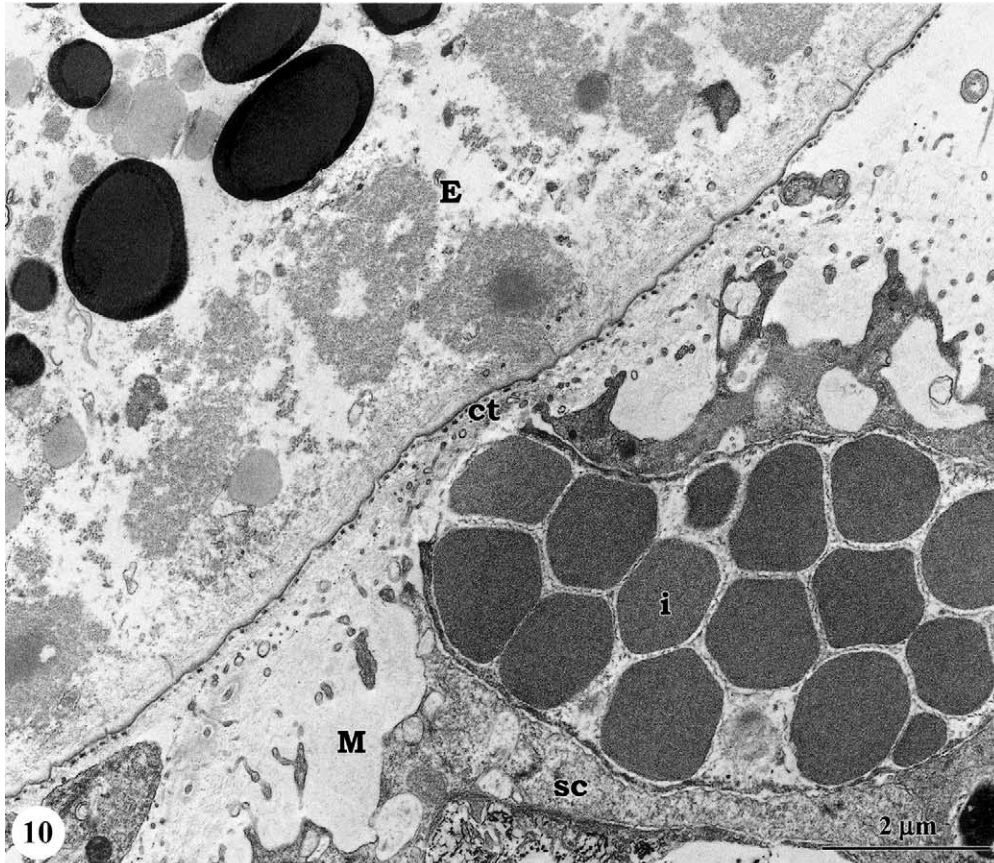


Fig. 7. SEM micrograph: circular area at the surface of the female below the adhesive disk (ad). Its fracture surface reveals the presence of pores (po). A small pillar (arrowheads) emerges from each of them, b: bacteria. Figs. 8 and 9. SEM micrographs: embryo (Em) attached to body of the mother (M). The adhesive disk is transformed in a cup like structure (c). In Fig. 9 residual cytoplasm with spherical yolk granules (y) after the removal of embryo are visible, ms: microsculptures.

diameter of 15–20 μm. Its fracture surface reveals the presence of 120–150 pores, each 1.5 μm in diameter and with a regular distribution. Pores cross a smooth discontinuous surface and a small pillar emerges from each of them. A trabecular matrix, likely the fibrous cuticle, is evident beneath the smooth surface in which pores are embedded (Fig. 7).

When the egg begins to develop in embryo the adhesive disk assumes a cup like shape of about 10 μm. Close up views of the eggs attachment region revealed that eggs are connected to the female by a smooth cup like structure about 10 μm wide. This connection becomes wider up to 20 μm at its distal end giving origin to a thin rim where it contacts the



Figs. 10 and 11. Cross sections through the contact point between the egg (E) and the mother (M). The epidermis of the mother presents secretory cells (sc) with large electron-dense inclusions (i). In Fig. 11 the secretory material gives origin to the adhesive disk (ad) located between the egg and the mother; ct: cuticle; z: zonulae adherentes.

early embryo (Fig. 8). A small area (3 μm wide) of the early embryo surface in close vicinity of the rim is wrinkled and characterized by the presence of longitudinal microsculptures (Figs. 8 and 9). Bacteria are present on the surface of both the ripe female and the eggs in the surroundings of the contact region (Fig. 7).

3.2. Transmission electron microscopy (TEM)

During formation of adhesive disk and the successive transformation in cup, secretory cells scattered among dermal cells of ripe female are evident. Epidermal cells are elongated with their nucleus in basal position. Apically they are joined by zonulae adherentes (Figs. 11 and 14) and show thick microvilli which branch in thinner extensions crossing the fibrous cuticle. A few dense droplets are visible in the cytoplasm of dermal cells; this material is released in the basal layer of the cuticle overlaying the cells (Fig. 11). Secretory cells appear rich in rough endoplasmic reticulum with many spherical secretory granules of variable electron density stored in large compartments surrounded by plasma membrane (Figs. 10 and 11). Products of secretory activity are released from the apex of cells beneath the fibrous cuticle through a narrowed neck region (Figs. 11 and 14). The accumulation of this secretory material gives origin to a consistent dense structure that crosses the cuticle and expands in the inter space between the external body surface of female and the egg envelope (Fig. 11). At the end of secretion and shaping of adhesive disk, this fibrous electron dense structure appears very peculiar. It consists of a disk connected to the female cuticle by 1.5 μm wide pillars that deepen into cuticular layers and reach the apical plasma membrane. The inner tip of these pillars is frequently swollen giving origin to wider knobs sometimes with lateral expansions (Figs. 12–15). On the opposite side, facing towards the egg, the adhesive disk begins to originate a cup like structure. When the egg develops in early embryo, the apical edge of this cup is thicker, rimmed, and appears finely wrinkled, as previously observed by SEM (Fig. 8). This cup like structure adapts to the early embryo surface. Peripheral extensions of fibrous adhesive structure are frequently visible at a more basal level (Fig. 13). These structures induce the formation of 3 μm long superficial invaginations of the embryo surface (Fig. 13).

4. Discussion

The external gestation of *E. naidina* is performed through eggs, embryos, and juveniles attached in latero-ventral position of the mother body. The fixing system here described is in accordance with the previous observations relative to other Exogoninae species brooding eggs in ventral position, where the presence of ventral glandular secretion was enhanced (Pierantoni, 1903; Potts, 1911; Haswell, 1920).

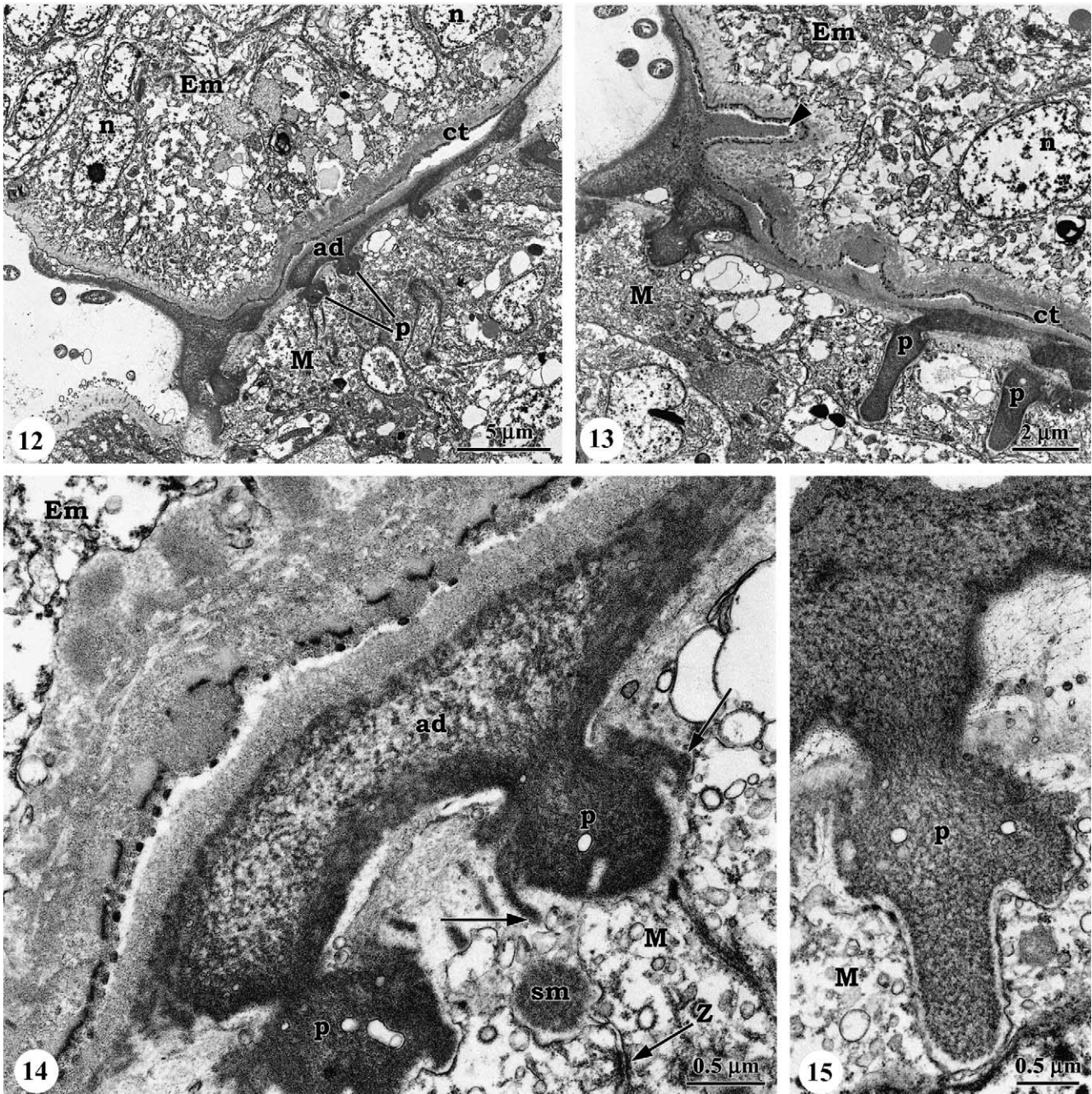
The adhesive disk present on the ventral surface of the female of *E. naidina*, easily recognizable after mechanical ablation of eggs, is present only in ripe specimens and can be considered an epitokous structure. This interpretation is further confirmed by the identification of active secretory cells intercalated among the epidermal cells in close vicinity of the adhesion structure. The disk ultrastructure strongly suggests its function to ensure an efficient and firm connection between the cuticle of ripe female and the egg envelope and successively the cuticle of juveniles. Its efficiency in holding developing embryos in place is consistently implemented by the shape of fibrous pillars whose detachment from cuticle is prevented by their terminal swallowings and lateral extensions. Our observations seem also to indicate that the adhesive structure is totally secreted and shaped by the female with a passive role of eggs. Pierantoni (1903) described in some dorsal broaders *Parapionosyllis* species the gut of juveniles remaining closed until their detachment from maternal cuticle, suggesting that no active role was played by embryos in energy supply other than processing of egg yolk.

The position of eggs in *E. naidina* is quite different from that described by Kuper and Westheide (1998) in other Exogoninae species. These authors observed eggs and embryos attached to the dorsolateral body surface above the parapodia by means of chaetae penetrating the egg envelope in *Sphaerosyllis hermaphrodita*, or closely apposed to the eggs in *G. subterranea* and *Grubeosyllis* sp., suggesting that different position and arrangement of chaetae could indicate an independent evolution of the dorsal system attachment in the two genera. These dorsal chaetae are not recognizable by light microscope; therefore, as the authors suggest, the paired spherical sacs described by Goodrich (1930) in *G. neapolitana* could be referable to the epidermal sac found in *G. subterranea*. It is hypothesized that the same system is also present in all the species fixing eggs dorsally as for instance *G. limbata* (Cazaux, 1969, 1972).

Kuper and Westheide (1998) referred that the different type of egg attachment observed within syllids, ventrally by glandular secretion and dorsally by chaetae can be present in a same genus, indicating an independent evolution of the brooding at a specific level. This is not in accordance to the high conservativeness of reproductive features within subfamilies of syllids (Franke, 1999; Nygren, 1999; Giangrande et al., 2002).

It seems that in Syllidae there is a tendency to brood protection, probably linked to the small size. This protection ranges from the external storage of egg masses as in some Autolytinae and Eusyllinae to the attachment to the mother body as in some Eusyllinae and Exogoninae, with a maximum development among Exogoninae, where ventral and dorsal attachment can be found as well.

As far as the presence of the two attachment types within the same genus, however, misidentifications of species must also be taken into consideration. For instance, *P. neapolitana*, which brood dorsally is now inserted in the genus *Grubeosyllis* (San Martín, 1991; Jimenez et al., 1994), while



Figs. 12–15. Cross sections showing the fibrous material that forms the adhesive disk (ad) between the embryo (Em) and the mother (M). This structure consists of some pillars (p) that deepen into cuticular layers (ct) and exhibit lateral expansions (arrows). The adhesive disk produces cuticular embryo invaginations (arrowhead), n: nucleus; z: zonulae adherentes; sm: secretory material.

the brooding system of *Pionosyllis* genus could be different, as occurs in *Pionosyllis pulligera* which carries its offspring dorsally on the cirrus and not attached to the mother's body (Pierantoni, 1905).

Within the genus *Exogone*, only the ventral type of brooding by maternal secretions was found so far, while in the genus *Grubeosyllis*, only the dorsal type seems to be present. This type is also prevalent in the closely related genus *Brania*, with the few exceptions described by Perkins (1981).

The features described for dorsal egg anchoring by Kuper and Westheide (1998) are probably common among all Exogoninae brooding dorsally. Fibrillar structures were described by several authors in the dorsal anchoring of the eggs, in other species closely related to *Grubeosyllis* (Goodrich, 1930; Cazaux, 1969, 1972).

Therefore, at present, the genera which seem to have both dorsal and ventral brooding types are *Brania* and *Sphaerosyllis*. However, recently San Martín (2002), describing the

new genus *Nooralia*, and considering all the species that he examined personally, pointed out that, dorsal brooding is present only in *Grubeosyllis*, in the closely related *Nooralia*, and in the recently described genus *Cicese* (Diaz-Castaneda and San Martín, 2001); whereas in *Brania*, *Parapionosyllis* and *Exogone* only ventral brooding is found. According to this author, dorsal brooding is associated with the development of capillary or compound notochaetae, whilst ventral brooding is associated with the development of glands producing adhesive secretions. The same author is also doubtful about the occurrence of these different methods, involving strong morphological variations, within the same genus.

Kuper and Westheide (1998) discuss about an environmental influence on the evolution of the brooding type, suggesting that interstitial forms brood dorsally because this system would give a major support for movement in the sediment, whilst species living within algae can also adopt the different ventral system. However, a first analysis of the environment colonized by species for which data on brooding type are available, does not seem to reveal any strong correlation (see Perkins, 1981; where numerous interstitial *Sphaerosyllis* species are reported brooding indifferently in ventral or dorsal position).

In our opinion, the two different brooding types could be constrained by the body size. When species are very small and have few segments, they have to brood dorsally to carry a greater number of eggs per female, in dorsal brood in fact eggs are often carried in masses, while in ventral brooders only two eggs are carried on each segment, so that more elongated species, with more segments, can adopt the ventral system. In the dorsal brooding species, where eggs are carried close to each other, only embryos are protected, and juveniles hatch when they are three chaetigers long (Cazaux, 1969). In this case, in fact, the mother is not able to carry dorsally bigger juveniles. If the mother broods ventrally instead there is only one egg at each side of every segment and juveniles can be protected until they reach six to seven chaetigers.

Size, however, could also be seen as a preadaptation to life in the interstitial environment, and the type of brooding in Syllidae could be linked to genealogy more than adaptation. The genus *Sphaerosyllis*, where both types of brooding seem to be present, comprises about 70 species with high variability; it is thus possible that the genus is in reality composed by a complex of genera. According to San Martín (2002), the genus *Sphaerosyllis* Claparède, 1863, is not a monophyletic group, and he proposed to revise it with species remaining within *Sphaerosyllis* brooding ventrally, whilst *Prospiraosyllis* San Martín (1984, 1994), and the “erinaceous” group brooding dorsally.

Only a detailed phylogenetic analysis could clarify this aspect, and probably the mode of reproduction could represent a diagnostic character. At present, however, the paucity of the observations impairs any phylogenetic inference.

Further structural studies are needed to ascertain the role played by juveniles during their maturation on the female

body surface. The mechanism leading to release of juveniles also needs further structural analyses.

Acknowledgements

This study was supported by 60% funds MURST (Italian Ministry of University and Research).

References

- Cazaux, C., 1969. Etude morphologique du développement larvaire d'Annélides Polychètes (Bassin d'Arcachon). II. Phyllocodidae, Syllidae, Nereidae. Arch. Zool. Exp. Gén. 110, 145–202.
- Cazaux, C., 1972. Développement larvaire d'Annélides Polychètes (Bassin d'Arcachon). Arch. Zool. Exp. Gén. 113, 71–108.
- Cognetti Varriale, A.M., 1971. Sur un syllidien des eaux polluées du Port de Livorne: *Syllides edentula* Claparède. Cah. Biol. Mar. 12, 111–115.
- Diaz-Castaneda, V., San Martín, G., 2001. Syllidae (Polychaeta) from San Quintin lagoon, Baja California, Mexico, with the description of a new genus. Proc. Biol. Soc. Wash. 114 (3), 708–719.
- Franke, H.D., 1999. Reproduction of the Syllidae (Annelida: Polychaeta). Hydrobiologia 402, 39–55.
- Garwood, P.R., 1991. Reproduction and the classification of the family Syllidae (Polychaeta). Ophelia Suppl. 5, 81–87.
- Giangrande, A., 1997. Polychaete reproductive patterns, life cycles and life historie: an overview. Oceanogr. Mar. Biol. Annu. Rev. 35, 323–386.
- Giangrande, A., Sciscioli, M., Lepore, E., Mastrodonato, M., Lupetti, P., Dallai, R., 2002. Sperm ultrastructure and spermiogenesis in two *Exogone* species (Polychaeta, Syllidae, Exogoninae). Invert. Biol. 121 (4), 339–349.
- Goodrich, E.S., 1930. On a new hermaphrodite syllid. Q. J. Microsc. Sci. Oxford. 73, 651–666.
- Gravier, C., 1923. La ponte et l'incubation chez les Annélides Polychètes. Ann. Sc. Nat. Zool. Ser. 10 (6), 153–247.
- Haswell, W.A., 1920. Observations on some Australian Polychaeta. Part III. The Exogoneae. J. Linn. Soc. 34, 217–242.
- Heacox, A.E., Schroeder, P.C., 1978. First report of brooding in *Syllides japonica* Imajima (Syllidae: Polychaeta). Bull. South. Calif. Acad. Sci. 77, 142–144.
- Jiménez, M., San Martín, G., Lopez, E., 1994. Redescription of *Pionosyllis neapolitana* Goodrich, 1930 and *Pionosyllis nutrix* Monro, 1936, referred to the genus *Grubeosyllis* Verrill, 1900 (Polychaeta, Syllidae, Exogoninae). Polychaete Res. 16, 52–55.
- Kuper, M., Westheide, W., 1998. External gestation in exogonine syllids (Annelida: Polychaeta): dorsal egg attachment by means of epitokous chaetae. Invert. Biol. 117 (4), 299–306.
- Malaquin, A., 1890. Sur la reproduction des Autolyteae. Rev. Biol. Nord. France 3, 172–183.
- Nygren, A., 1999. Phylogeny and reproduction in Syllidae (Polychaeta). Zool. J. Linn. Soc. 126 (3), 365–386.
- Perkins, T.H., 1981. Syllidae (Polychaeta), principally from Florida, with descriptions of a new genus and twenty-one new species. Proc. Biol. Soc. Wash. 93 (4), 1080–1172.
- Pierantoni, U., 1903. La gestazione esterna (Contributo alla biologia ed alla embriologia dei Sillidi). Arch. Zool. 1, 231–252.
- Pierantoni, U., 1905. Una nuova maniera di gestazione esterna della *Pionosyllis pulligera* Krohn. Ann. Mus. Zool. Univ. Napoli. N.S. 2, 1–10.
- Potts, F.A., 1911. Methods of reproduction in the syllids. Ergeb. Fortsch. Zool. 3, 1–72.
- Quatrefages, A., 1865. Coup d'oeil sur la famille des Syllidiens. Histoire naturelle des Annelés 2, 145–153.

- Rassmussen, E., 1973. Systematics and ecology of the Isfjord marine fauna (Denmark). *Ophelia* 11, 1–495.
- San Martín, G., 1984. Estudio biogeográfico, faunístico y sistemático de los poliquetos de la familia Siliidos (Syllidae: Polychaeta) en Baleares. Publ. Univ. Complutense de Madrid. No 187, pp. 529.
- San Martín, G., 1991. *Grubeosyllis* and *Exogone* (Exogoninae, Syllidae, Polychaeta) from Cuba, the gulf of Mexico, Florida, and Puerto Rico, with a revision of *Exogone*. *Bull. Mar. Sci.* 49 (3), 715–740.
- San Martín, G., 1994. Descripción de una nueva especie y revisión de género *Sphaerosyllis* (Polychaeta: Syllidae). *Cah. Biol. Mar.* 25, 375–391.
- San Martín, G., 2002. A new genus and species of Syllidae (Polychaeta) from Australia dorsally brooding eggs by means of compound notochaetae, with comments on external brooding in the family. *Proc. Biol. Soc. Wash.* 115 (5), 333–340.
- Viguié, C., 1884. Sur l'*Exogone gemmifera* (Pagenstecher) et quelques autres Syllidiens à gestation. Etudes sur les animaux inférieurs de la baie d'Alger. *Arch. Zool. Expér. Gén.* 2, 69–110.
- Westheide, W., 1974. Interstitielle Fauna von Galapagos. XI. Pisionidae, Hesionidae, Pilargidae, Syllidae (Polychaeta). *Mikrofauna Meeresboden* 44, 1–146.
- Westheide, W., 1990. Polychaetes: Interstitial families. In: Kermack, D.M., Barnes, R.S.K., (Eds.), *Synopses of the British Fauna (New Series)*, vol. 44. Universal Book Services, Oegstgeest, 152 pp.
- Wilson, W.H., 1991. Sexual reproductive modes in polychaetes: classification and diversity. *Bull. Mar. Sci.* 488 (2), 500–516.