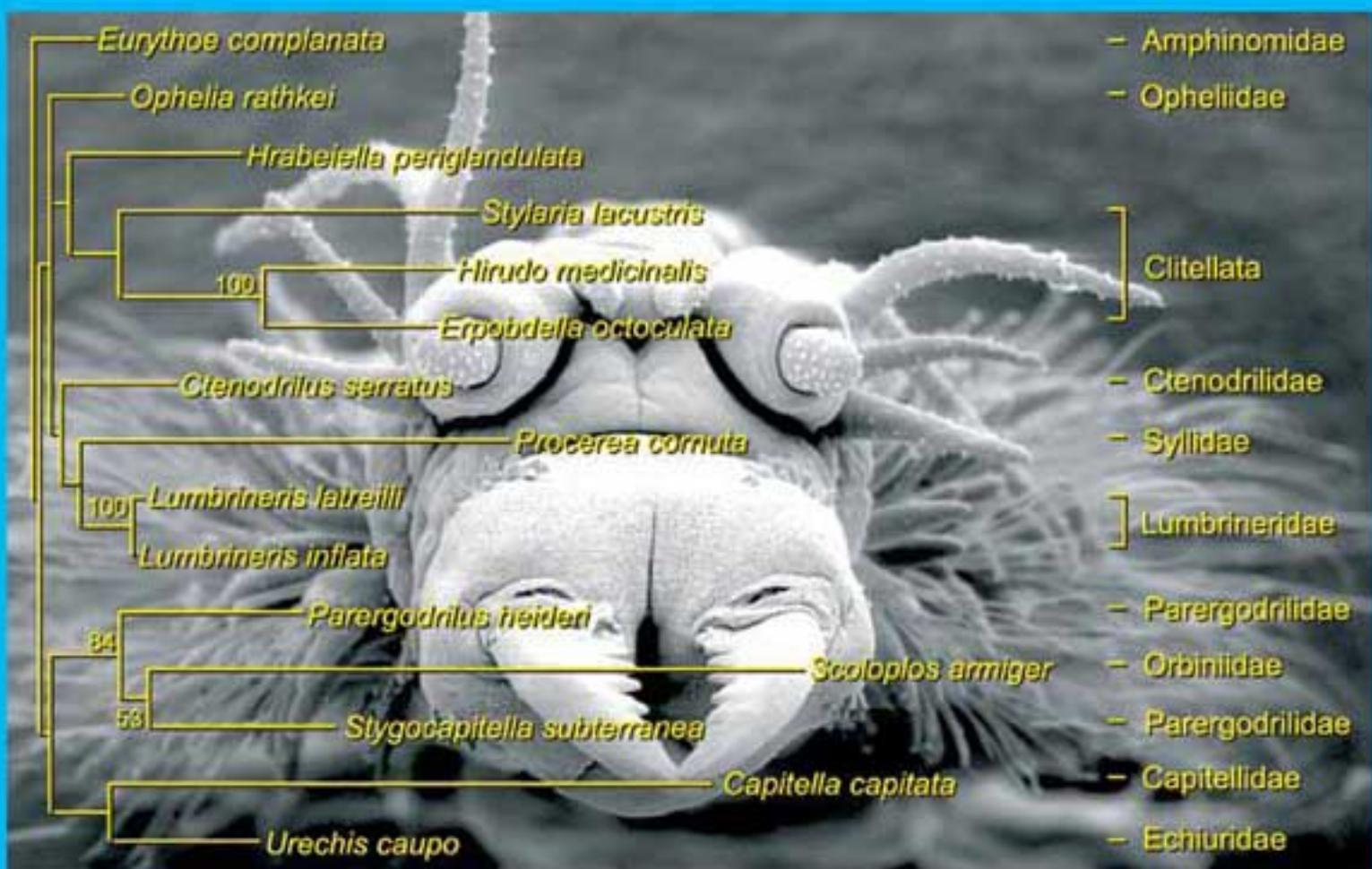


DEVELOPMENTS IN HYDROBIOLOGY

Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa

edited by

Thomas Bartolomaeus and Günter Purschke



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Developments in Hydrobiology 179

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Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa

Edited by

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Cover Illustration: SEM of the anterior end of *Nereis* sp. with everted pharynx and extended jaws. Dorsolateral palps show bundles of sensory cilia at their tip. Cladogram to the fore is based on molecular data and shows Clitellata and Echiura among polychaete taxa. (Original figure by Purschke, cladogram from Jördens et al. (2004): J. Zool Syst. Evol. Res 42: 270–289.)

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Preface

Polychaetes and Clitellata, which together constitute Annelida, are one of the most significant groups of metazoans, not only because they are so numerous – about 20,000 species have been described – but also because of their remarkable diversity. Recently evidence is accumulating that even some of the groups formerly regarded as independent “phyla” such as Pogonophora (Frenulata and Vestimentifera), Echiura, Myzostomida and perhaps Sipuncula, are most probably nothing else than greatly modified Annelida. The relationship of Clitellata to the other annelids has also recently become controversial. Hence these animals as a whole are highly significant to our understanding of fundamental questions about morphological and adaptive diversity, as well as clarifying evolutionary changes and phylogenetic relationships. In recent years a great deal has been learned about these animals, from morphological studies employing conventional and modern methods plus, increasingly and importantly the use of molecular markers and computer-assisted kinship analyses. This new knowledge has also raised new questions and controversies. By no means everything is known in polychaetes and related taxa and much is still to be disclosed.

So far there has been no modern, comprehensive presentation and discussion of the recent research results, nor has there been a clear statement of the open questions and current problems in the area. Such a summary also seems necessary in particular because the different research groups, as a result of the wide range of methods they employ publish in extremely diverse journals. One aspect of the topic, ultrastructure, has for many years been covered by the comprehensive and much quoted work “The Ultrastructure of Polychaeta”, edited by W. Westheide & C.O. Hermans (Mikrofauna Marina 4, 1988), which resulted from a similar conference held in 1986. Somewhat later than this volume, in the series “Microscopic Anatomy of Invertebrates”, Volume 7 “Annelida” (F.W. Harrision & S.L. Gardiner, eds, Wiley-Liss, Inc., 1992) was published. Although in many

respects these publications are by no means outdated, the first book is out of print now, and furthermore they treat only one aspect, morphology. During the 15 years that have been elapsed since that conference new morphological (e.g., confocal laser scanning microscopy) and molecular (e.g., DNA sequencing) methods came into use. And of course many other new results, obtained with different methods, have become available since then. However, the overall subject area indicated by the title of the symposium including evolution and phylogeny with reference to morphological and molecular characters, is not treated anywhere. The best way to achieve this goal appeared to gather specialists in a workshop and to edit a comprehensive volume with chapters written by these specialists, putting emphasis on open questions, current problems and possible directions of future research as well. We are happy that these specialists were willing to write these contributions. We are also happy that the resulting programme was attractive enough for many others who came and attended this symposium in part with short contributions and posters. We both hope that this book will be a good foundation for future work and will help to keep the topic attractive enough to encourage young scientists to work with polychaetes and related taxa. Last but not least we would like to dedicate this volume to Professor Wilfried Westheide on the occasion of his 65th birthday and retirement in recognition of his outstanding contributions in the fields of annelid systematics, evolution, phylogeny, reproductive biology and morphology.

We thank the Vice President of the University of Osnabrück, Prof. Dr P. Hertel, for his welcoming remarks at the opening of the symposium. We are extremely grateful to the Stiftung Volkswagenwerk, Hannover, Germany, for funds supporting the travel and accommodations of the participants. We are grateful to the President of the University of Osnabrück for additional financial support. Without these supports the workshop and the volume would not have been made pos-

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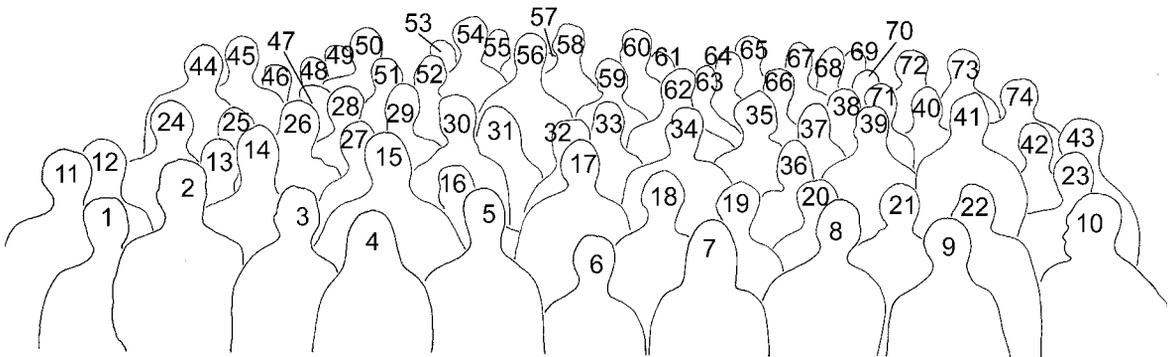
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Group photo taken at the Symposium “Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa”. Numbers in the line drawing indicate position of participants:

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Cell lineage and gene expression in the development of polychaetes

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Keywords: polychaete, cell lineage, determination, gene expression

Abstract

The developmental strategies of embryos within the various taxa of polychaetes are designed to set up the fate of the cell lines. Some of these traits of pattern formation are considered to be ancestral, but we also find a number of derived developmental characteristics, some of which might be useful indicators for phylogenetic relationships. A combination of ooplasmic segregation and anisotropic cleavage rapidly establishes the fate of several larval cell lines in the polychaete embryo. The setting-up of the primary trochoblasts basically concerns the same cell line ($la^2-l_d^2$) in polychaetes and even in molluscs. Such mechanisms may thus be regarded as ancestral. The determination of the mesoderm precursor occurs very late in both equally cleaving annelids and mollusks, indicating that an equal cleavage pattern may be regarded as an ancestral trait. Since both disproportionate cytoplasmic distribution (either by spindle shift or polar lobe formation) and cell cycle asynchronies appear to speed up the development of the mesoderm-forming cell line, these strategies represent derived traits. An analysis of these derived traits of early development is given and is discussed in the light of the phylogenetic relationships among the polychaetes. These data are extended by an analysis of some of the postlarval structures in polychaetes and the molecular developmental circuitry involved.

Introduction

Numbering approximately 9000 species, annelids belong among the larger groups of invertebrate animals. Although annelids occupy various terrestrial and freshwater habitats, it is beyond a shadow of a doubt that the ancestral life forms in this group initially lived in a marine environment. Even nowadays almost 60% of all annelid species described so far are marine and nearly all of these species are polychaetes. With only few exceptions the majority of the ancestors of the polychaetes related to the marine environment, whereas the ancestors of oligochaete and hirudinean species adopted a terrestrial and/or freshwater life style. Despite the fact that polychaete species have developed a tremendous diversity in body plan, ranging from free living to completely

sedentary life styles, they never show the typical reproductive adaptations found in the clitellates. With only few exceptions, clitellates form cocoons with extremely yolky eggs which develop by a modified spiral cleavage pattern. The precursor cells for the majority of tissues of the adult body are determined at a very early developmental stage. Due to their size they can easily be identified at the posterior dorsal side of the embryo and are therefore called teloblasts (Whitman, 1878; Schleip, 1914). In the hirudinean development the N-, O/P-, O/P-, Q- teloblasts provide for the ectoderm and neural elements of the leech trunk (Stent & Weisblat, 1982). Each of the bilaterally symmetrical positioned M-teloblasts represents the precursor cell

for the formation of a mesodermal germ band. The leech embryo skips a larval stage and develops all 33 segments simultaneously. Even though the number of segments in oligochaete development is not fixed by the end of embryonic development, the same type of germ band leads to the immediate formation of a small adult, thus skipping a larval stage. Shimizu (1982) showed that the isolated precursor of the teloblasts, the D-blastomere, is able to form normal young worms. Not only the adult body plans of the clitellates, but also the developmental strategies of their embryos thus share several derived characters. In contrast, most polychaete embryos develop by a type of spiral cleavage in which the formation of larval structures prevails and leads to the formation of a trochophore larva. Similar developmental strategies leading to similar larvae are encountered in the development of Mollusca, Echiurida, Sipunculida and Nemertea. The larval conditions enable the developing individual to disperse, feed and grow after the termination of embryogenesis. This developmental strategy has several advantages:

- it allows the production of a larger number of small, oligo-lethal eggs, thereby reducing the maternal investments in a single embryo;
- a large number of offspring secures the gene pool of the parental pair in future reproductive cycles;
- the dispersal of numerous small larvae prevents predation and supports the spreading of the species;
- the development and growth of adult tissues (in polychaetes: combined with the formation of segments) can be spread over or postponed until after the larval phase.

These, and a large number of more derived developmental characteristics, can be encountered in the various taxa of the polychaetes. This chapter focuses on the various aspects of pattern formation and the determination of larval and adult cell lines. It also provides some of the recent molecular data we have gathered on the differentiation of such cell lines. Although this chapter predominantly deals with developmental processes of polychaetes it also attempts to answer some questions of phylogenetic descent within the spiralians.

Pattern formation in early embryos

Polarity of the oocyte

In a previous review of the ultrastructural aspects of development in polychaetes, Dorresteijn & Fischer (1988) stated that pattern formation in part is prepared by the setting up of egg polarity during oogenesis. Most polychaete eggs develop within an ovary and are frequently accompanied by somatic cells (follicle or nurse cells) or they are attached to the epithelium of the ovary wall, of the peritoneum, or of a blood vessel. The diversity of polychaete oogenesis and of ovarian types has been treated by Eckelbarger (1988; this volume) and will not be repeated here. The oocytes of some polychaete groups, like the Nereididae, Phyllodocidae, Sphaerodoridae and Alciopidae, sprout from still unknown tissues and undergo previtellogenic and vitellogenic development in a free-floating condition within the coelomic fluid. But even in such cases of diffuse oogenesis the eggs show signs of polarity which must have been set up at earlier stages. In the Nereidid *Platynereis dumerilii* the mature oocyte represents a rotational ellipsoid with an equatorial radius of 75–80 μm and a rotational axis of approximately 135 μm (Fig. 1a and b). Kluge (1991) showed that the rotational axis corresponds to the future animal-vegetal axis of the embryo and the antero-posterior axis of the larva. The oocytes of *Pomatoceros triqueter* show an even more pronounced degree of animal-vegetal flattening, giving the unfertilized egg the appearance of a discus (Fig. 1c and d). Similar egg forms were also described in other polychaetes, e.g. *Arenicola marina* (Meijer, 1979) and *Podarke obscura* (Treadwell, 1901). Within the non-spherical ellipsoidal eggs, the short axis of which relate to the animal-vegetal axis, developmental factors may have been allocated in the cortex at the future polar regions. Dorresteijn & Fischer (1988) described the presence of such cortical fields with accumulations of ribosomes, ER and numerous vesicles during polar body formation of the fertilized egg of *Pomatoceros*. Other egg forms have been described by Villa (1976) for the sternaspid *Sternaspis* which produces spindle-shaped eggs with polar accumulations of mitochondria. But even in the spherical eggs of *Sabellaria alveolata* (Hatt,

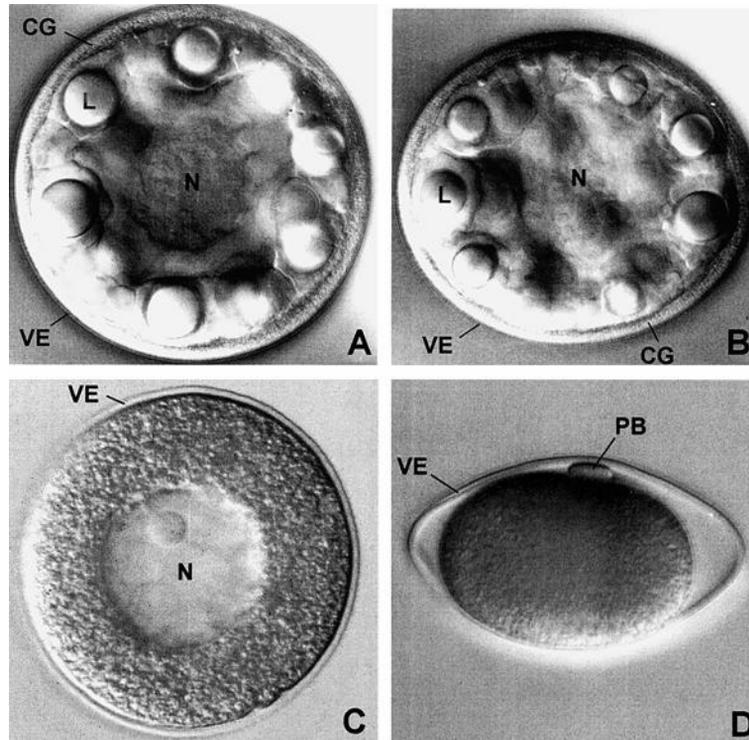


Figure 1. Oocytes of most polychaete species show signs of a preexisting polarity. The oocytes of *Platynereis dumerilii* (A, B) are shaped as rotational ellipsoids, the rotational axis of which corresponds to the animal-vegetal axis. The oocytes of the serpulid *Pomatoceros triqueter* are lense-shaped (C: top view). Although the egg slightly rounds up after fertilization the initial lense-shape of the vitellin envelope remains (D). The position of the polar body in this image labels the animal pole. The rotational axis of the oocyte thus foreshadows the future egg axis. CG: cortical granules; L: lipid droplets (surrounded by protein yolk granules); N: nucleus; VE: vitellin envelope; PB: polar body. Egg diameters: *Platynereis* (160 μm), *Pomatoceros* (65 μm).

1932; Rander, 1983; Speksnijder & Dohmen, 1983; Dorresteijn & Fischer, 1988) there are experimental and ultrastructural correlates for the localization of developmental potential in the vegetal hemisphere. Jeffery (1984) demonstrated an asymmetric distribution of mRNA in the cortex of the oocytes of *Chaetopterus*. As in many other animals, the oocytes of polychaetes are liable to produce maternal factors which are allocated during oogenesis or by ooplasmic segregation during early development. The localisation of preformed factors rather than the *de novo* synthesis of such factors speeds up the processes of early development by setting up and determining the fates of some of the early blastomeres. The properties of the egg cortex, recently reviewed by Sardet et al. (2002), not only offer a chance for this precocious localization of developmental factors, it also allows a rapid reorganization of

such factors upon fertilization, and, due to the interactions with mitotic spindles, set up the site of polar body formation and the various cleavage furrows. Since most polychaete eggs are not perfectly spherical and the shape relates to the animal-vegetal polarity, developmental factors may well be or get distributed in a polar fashion (Fig. 2). Unfortunately, our knowledge about the existence and the distribution of developmental factors in the polychaete egg and early embryo is still very limited. After the successful isolation of larval and postlarval developmental factors (Arendt et al., 2001; Seaver et al., 2001; Arendt et al., 2002) we should now focus on those factors involved in the earliest stages. So far, experimental studies disturbing the cortex by means of destabilizing the microfilament or microtubule network indicate that this influences both the position of the spindles as well as the determina-

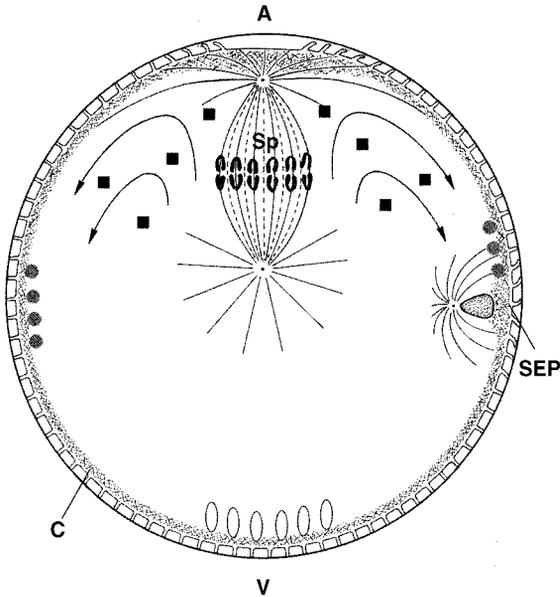


Figure 2. The animal-vegetal polarity of polychaete oocytes and eggs could well be instrumentalized for the prelocalization of developmental potential. The egg cortex (C) plays a crucial role in the allocation of determinants (indicated by the grey rounded symbols). Part of the determinants (depicted by black squares) may reside in the cytoplasm and get segregated during the cleavage process. A break of the initial rotational symmetry the axis of which gets manifest by the position of the spindle of the first meiotic division is caused by the sperm entry point (SEP). A: animal pole; V: vegetal pole.

tion of cell fates (Dorresteijn et al., 1987; Dorresteijn & Kluge, 1990)

The cleavage pattern

As in the Mollusca, Nemertea, Sipunculida and Echiurida, the embryos of the Annelida follow a quartet spiral cleavage. According to Siewing (1980), Ivanova-Kazas (1981) and several authors ever since, spiral cleavage is a autapomorphy of animal taxa grouped together as the spiralian and most likely evolved from the radial cleavage pattern of the diploblasts. The cleavage pattern of spiralian embryos is the result of the inclination of the mitotic spindles with respect to the animal-vegetal axis. In most spiralian embryos the first sign of this inclination can be encountered at second cleavage (Fig. 3F), when the spindle in either blastomere is not oriented in the horizontal plane, but stands at an angle to it. As a result, each of the

two cells divides into an animal and a vegetal daughter cell. In such cases the animal cells contact each other at the animal pole, whereas the vegetal cells broadly contact each other at the so-called vegetal cross furrow. So, even at the four-cell stage the blastomeres of the spiralian egg are not in a perfect radial arrangement. The eggs of only few polychaete species, like *Pomatoceros triquetter*, lack such animal and vegetal cross furrows and then show a perfect radial arrangement of the blastomeres at the four-cell stage. This may well represent the ancestral condition.

Each of the blastomeres of the four-cell stage is the founder cell of an embryonic quadrant. We discern the A-, B-, C-, and D-quadrant. Later in their development, the cells of these quadrants participate in the formation of specific structures pertaining to dorsal, ventral or lateral fates and can then be denominated according to their fates. Conventionally, the D-quadrant is the dorsal quadrant of Mollusca and Annelida and produces the stem cell of the mesoderm, i.e. the mesentoblast 4d. The cell material within a quadrant is generated by a series of alternating dextrotropic and laetotropic spiral cleavages. For example, at third cleavage the spindles are oriented slightly tilted with respect to the animal-vegetal axis (Fig. 3H). As a result the otherwise equatorial cleavage plain becomes slanted and produces an animal daughter cell to the left and a vegetal daughter cell to the right, viewed on from lateral aspect of the embryo. Viewed from the animal pole, the animal daughter cells, the micromeres 1a–1d, are shifted clockwise (dextrotropic) with respect to the vegetal daughter cells, the micromeres 1A–1D. The fourth cleavage is characterized by the formation of a second generation of micromeres, the blastomeres 2a–2d. Almost simultaneously the first generation of micromeres divides and produces two cell tiers: 1a¹–1d¹ round the animal pole and 1a²–1d² in a vegetal direction. During these cleavages the mitotic spindles stand at a 90° angle to the positions of spindles at the third cleavage. Consequently, this cleavage is a counter-clockwise (laetotropic) cleavage. This pattern of alternating spindle positions in embryos of polychaetes (and other organisms with spiral cleavage) is repeated at subsequent cleavages. The alternation of dextrotropic and laetotropic cleavages results in an animal-vegetal zig-zag orientation of

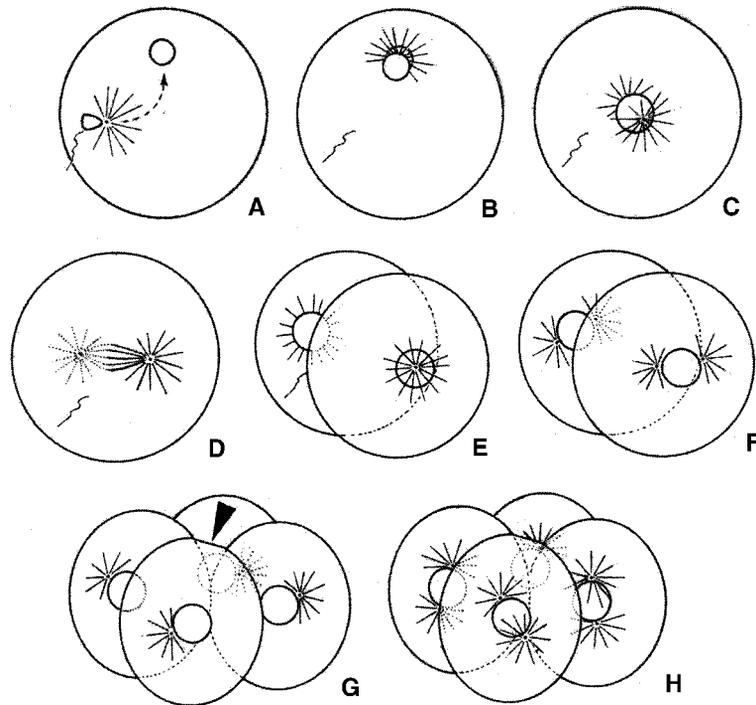


Figure 3. This simplified diagram shows the destiny of the paternal centrosome from fertilization up to the third cleavage. Initially, it forms the sperm aster which pulls the paternal pronucleus towards the maternal pronucleus (A, B). The centrosome (possibly enriched by centrosomal material of maternal origin) divides and forms the asters of the first cleavage spindle (C). The spindle stands at right angles to the path followed by the sperm aster after fertilization (D). As a result the first cleavage cuts through the sperm entry point (E). The centrosomes in either blastomere divide, and the daughter centrosomes take opposite positions on the nuclear perimeter (F). Note that one of the asters lies slightly shifted towards the animal pole and causes the spindles to take positions deviating from the equatorial plane. Due to this tilt two opposing blastomeres form a cross furrow at the animal pole (arrowhead), the other two form a cross furrow at the vegetal pole.

the blastomeres in each of the quadrants. On the basis of its cleavage history, each of these blastomeres has a unique position and set of neighbors. The constancy of spiral cleavage seems to obey certain mathematical laws. In his important study on the orientation of centrioles in embryos of the turbellarian *Polychoerus*, Costello (1961) proposed that the remnant of the previous cleavage, the so-called mid-body, might orientate the spindle at the subsequent cleavage. The same kind of cortical bias is proposed by Morris et al. (1989) in their comparison of cleavage patterns in *Nereis*, *Styela* and *Xenopus*. But can a single directional cue be sufficient to explain the alternation of dextrotropic and laeotropic spindle positions? Although we cannot rule out the role of the cortex and will discuss it later on in the setting up of dorsoventral polarity and of cell fates, we dare not forget the

behavior of the centrosome. Polychaete eggs inherit a single centrosome after the mitotic divisions of the oogonium. This centrosome supports meiosis by the formation of the polar bodies. However, after polar body formation the quality of the maternal centrosome seems weakened. Studies on artificially activated eggs of *Platynereis dumerilii* (Spek, 1930; Kluge, 1991) and *Chaetopterus* (Brachet, 1937) demonstrated that the postmeiotic centrosome cannot form a bipolar mitotic spindle. The bipolar cleavage spindle must thus originate from or predominantly relate to the paternal contribution, the sperm centrosome. Let us follow the history of this centrosome, which is schematically shown in the center of the asters in Figure 3. This sperm centrosome accompanies the paternal pronucleus towards the maternal pronucleus (Fig. 3A and B). It then replicates and the sister

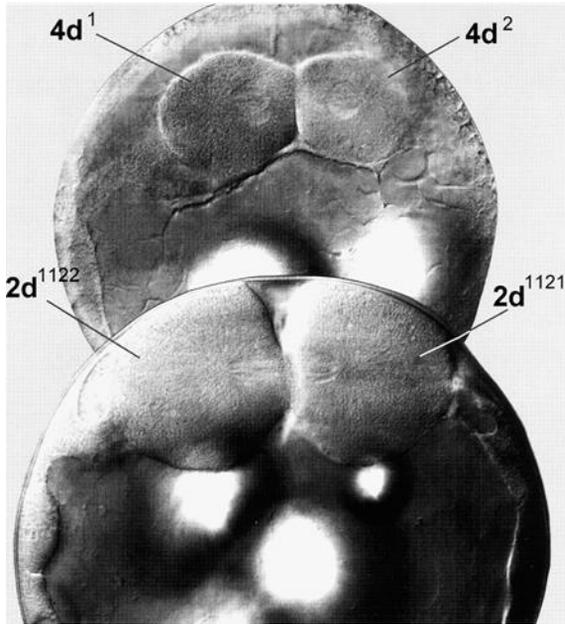


Figure 4. Photographic montage of two different focal planes within *Platynereis* embryos showing the dorsal positions of the descendants of the 2d and 4d blastomeres. As an expression of their determined state these cells no longer cleave in a spiral mode, but divide in a bilaterally symmetrical pattern. The sister blastomeres $2d^{1121}$ and $2d^{1122}$ in the equatorial level and $4d^1$ and $4d^2$ at the vegetal pole take perfect mirror positions with respect to the dorsal median.

centrosomes move and take opposite sides at the conjunction of the pronuclei (Fig. 3B and C). Although the astral microtubules interact with the cortex of the egg, the primary orientation of the spindle is nevertheless within a plane perpendicular to the direction of the movement of the sperm centrosome (Fig. 3D). This also explains why the first cleavage in polychaete eggs with high incidence cuts through the sperm entry point (Fig. 3E). If the position of a centrosome after cleavage is at the far side of the reconstituting nucleus within a blastomere and if the sister centrosomes developing from it take opposite sides of that nucleus, then the subsequent cleavage should always be at right angles with respect to the previous cleavage (Fig. 3E and F). Although the proposed mechanism does not explain the oblique position of spindles at the third cleavage, it accounts for the perpendicular spindle positions of each of the subsequent cleavages (compare Figs. 3 C, F, H). As in molluscs, the obliqueness of the spindles at second and third cleavage may be

caused by the inheritance of maternal cytoplasmic and/or cortical factors (Sturtevant, 1923; Boycott et al., 1930; Freeman & Lundelius, 1982).

The number of cleavages with a spiral character is not indefinite in polychaete eggs. After the formation of the fourth generation of micromeres morphogenetic cell movements set in, and gastrulation positions the germ layers. Although cell divisions continue during gastrulation, there is no sign of spiral cleavage. In *Platynereis dumerilii* the pattern of cell divisions after sixth cleavage is bilaterally symmetrical, which is most clearly shown in the pattern of $2d^{112}$ and 4d, the descendants of the D-quadrant lying on the dorsal median (Fig. 4). The reasons for the change of a spiral mode to a bilateral mode of divisions have not been investigated so far, but are certainly indicative of the determined state of these cells.

Cellular diversity and determination of cell fate

In the previous sections we focused on the development of egg polarity and a multicellular pattern in the polychaete embryo, stressing some of the similarities studied. Basically, polychaete eggs show an architecture with animal-vegetal polarity and form quartets of cells by spiral cleavage. Although the development of egg polarity is a general feature in the development of metazoans, the spiral cleavage with its alternating dextrotropic and laeotropic spindle positions is so uniquely different from radial and bilateral holoblastic cleavage that we may regard it as a sound autapomorphy for the Spiralia. This is also supported by molecular data (Peterson & Eernisse, 2001). In the following we seek explanations for the diversity of embryos and larvae found in the various groups of polychaetes. In their historic paper on the cleavage patterns and phylogenetic relations within the monophyletic gastropods, van den Biggelaar & Haszprunar (1996) describe the variations of a single ontogenetic character, i.e. the timing and mode of determination of the mesentoblast, and place this in relation to the evolution of body plans. They provide strong evidence that an equal cleavage pattern within the molluscs is to be regarded as the ancestral condition. All deviating modes of spiral development, such as polar lobe development and unequal cleavage by spindle shift (Dorresteijn &

Fischer, 1988) thus originated during the phyletic development of the gastropod taxa. If an equal cleavage pattern is the ancestral condition for the gastropods and even characterizes the embryonic development of the polyplacophorans, we must expect an equal cleavage pattern at the base in each of the spiralian phyla, including the polychaetes. If the development of ancestral polychaetes was characterized by an equal cleavage pattern, the various mechanisms to accomplish cellular diversity must have developed later in phylogeny. Should there be an evolutionary pressure to accelerate the creation of cellular diversity in a dorsoventral pattern, as we find it in the gastropods, then the eggs of more derived polychaetes should also convergently develop polar lobes, spindle shifts and asymmetrical segregation of cytoplasm to create immediate differences among the early blastomeres. Table 1 summarizes the data on the symmetry or asymmetry of the first cleavage of polychaete eggs collected from the available literature of the past 130 years. The most striking conclusion after a careful survey of the data presented must be that only very few polychaete embryos actually show an equal cleavage pattern. One can even question whether the equal first cleavage shown for *Myrianida fasciata* by Malaquin (1893) might not have been based on the fact that he missed the formation of a very small polar lobe, because other members of the Syllidae form polar lobes. Nevertheless, a limited number of small polychaete eggs, like those of the ophelids *Armandia*, *Ophelia*, and *Euzone*, the polynoids *Harmothoe* and *Lepidonotus*, the hesionid *Podarke*, the sigalionid *Sthenelais*, as well as the serpulids *Pomatoceros*, *Hydroides*, and *Serpula* really cleave symmetrically or almost so at the first and second cleavage. This results in a homo-quadrantal development in which all the blastomeres have equal developmental capacities and divide in perfect synchrony. In the ophelid *Armandia brevis* even the third cleavage turns out equal, making the “micromeres” of the animal pole (1a–1d) just as large as the “macromeres” at the vegetal pole (1A–1D) (Hermans, 1964). In this case the micromeres can only be identified by the position of the polar bodies. The thorough developmental study by Hermans also shows that fourth cleavage is equal too and thus produces four quartets of equal-sized cells. Fifth cleavage is

only slightly asynchronous between the four tiers of cells, but the homologous cells in each of the quadrants cleave synchronously. This cleavage leads to the first visible size difference between the blastomeres. The animal quartet 1a¹¹–1d¹¹ and the vegetal macromeres 3A–3D are clearly larger than all the other cells. Nevertheless, the radial symmetry remains unperturbed. The sixth cleavage is strongly asynchronous. The largest blastomeres 3A–3D and 1a¹¹–1d¹¹ divide first. As in other polychaetes, the diversity in the nuclear-cytoplasmic ratio (for explanation see Dorresteijn & Lutjens, 1994) may be the cause of this asynchrony between the various tiers of blastomeres. As shown for molluscs by van den Biggelaar (van den Biggelaar & Haszprunar, 1996), the determination of the mesentoblast would lead to asynchronous cell proliferation among the cells within the tier of macromeres or of the micromere quartets. In *Armandia brevis* this is postponed until after the 64-cell stage. Hermans (1964) describes how the macromeres and the fourth quartet of micromeres 4a–4d protrude deeply into the blastocoel. It is predictable that these cells come into contact with animal micromeres and that a single micromere of the fourth quartet is induced to become the mesentoblast 4d. So it seems that the cleavage pattern of this species represents the ancestral pattern at the base of the polychaete tree. It would be interesting to examine the cleavage patterns of other ophelids which on the whole appear to have an equal cleavage pattern. *Armandia brevis*, the other ophelids, but also the maldanids belong to the Scolecida and also the latter polychaete taxon shows an equal spiral cleavage pattern. This thus supports the phylogenetic tree proposed by Rouse & Pleijel (2001) in which the branch of the Scolecida starts at the very base of annelid phylogeny. However, we must bear in mind that even within the Scolecida we encounter groups like the orbinids and the Arenicolidae with an unequal spiral cleavage. The groups Scolecida thus contain groups that have conserved ancestral conditions of development and others that have developed a rapid diversification among the early blastomeres. We cannot rule out that these developed from two different ancestors, one already having developed an unequal spiral cleavage.

The embryos of the species within the Eunicida seem to follow an unequal cleavage. No data