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Phylogeny of the digonoporid Proseriata

PAUL M. MARTENS and ERNEST R. SCHOCKAERT

Department SBM, Limburgs Universitair Centrum, B-3610 Diepenbeek, Belgium

Introduction: the history

MEIXNER (1938) subdivided the Monocelididae Hofsten, 1907 into the Monocelidinae, Coelogynoporinae and Archimonocelidinae. The latter subfamily contained two genera: *Archimonocelis* and *Monotoplana* for which a new family was erected by Ax, 1958. KARLING (1966) elevated the Coelogynoporinae to the family level and united all other Monocelididae into one taxon. In 1978, he introduced the subfamily Minoninae, provisionally keeping all remaining monocelidids in the subfamily Monocelidinae. The taxon Archimonocelidinae in MEIXNER's sense had disappeared.

One of the main diagnostic features of the Monocelididae *sensu* KARLING (1966) is the separation of the male and female genital pores, the digonoporid condition. The Nematoplanidae Meixner, 1938 and Polystyliphoridae Ax, 1958 also have two genital pores but have never been incorporated in the Monocelididae because they lack a statocyst. On the contrary, Nematoplanidae and Polystyliphoridae were united as Unguiphora and considered the adelpho-taxon of all other Proseriata, the Lithophora, with a statocyst (SOPOTT-EHLERS, 1985).

From a comparative study of the ultrastructure of the hard parts in the copulatory organ of the Proseriata, E. MARTENS (1984) concluded for the monocelidid genera she studied that in all exept the genus *Archimonocelis*, the spines and stylets are basal lamina differentiations : the autapomorphy for the monophylum Monocelididae (block 2 in fig.). *Archimonocelis* has intracellular hard parts as in all other Proseriata, clearly the plesiomorphic condition (see E. MARTENS, 1984 and BRÜGGEMANN, 1985). At the same time it was also found from a karyological viewpoint that there are arguments that *Archimonocelis* does not belong to the Monocelididae at all (CURINI-GALLETTI et al., 1984).

What we now want to consider is: What is the adelphotaxon of the Monocelididae? Are there other genera which should be excluded from the Monocelididae and if so, where do they belong? Is there a relationship between the Proseriata with separate genital pores?

The adelphotaxon of the Monocelididae

From extensive comparative karyological studies on 36 Monocelididae, the karyotype of the monocelidid ancestor can be reconstructed. It consists of a haploid set of one large metacentric, a medium-sized metacentric and a small heterobrachial chromosome. Different karyological events can be recognised which occurred during evolution and which lead

to the karyotypes found within the Monocelididae (fission, fusion, translocations, pericentric inversion and genome growth). The data and extensive discussions can be found in CURINI-GALLETTI et al., 1985; 1988, MARTENS and CURINI-GALLETTI, 1987 and MARTENS, et al., submitted).

From the study of the karyotypes of 35 non-monocelidids (including Unguiphora) it appeared that the great majority had six or more chromosomes in the haploid set (only four exceptions were to be found in the Otoplanidae). In each family at least one species was found with a haploid set of six chromosomes: two large and two medium sized metacentric ones and two more or less heterobrachial ones, clearly the basic set for the non-monocelidids. The morphology of this karyotype strongly suggests that it may have originated by polyploidy from a karyotype very similar to that of the Monocelididae. The hypothesis of polyploidy is also strenghtened by measurements of the DNA content in the nuclei of five Monocelididae and of five non-monocelidids (including a *Nematoplana* and an *Archimonocelis* species). The DNA content in the C nuclei of the Monocelididae ranges from 1 to 2.3 pg and in the non-monocelidids from 2.4 to 4.8 pg. All raw data, methodology and an extensive discussion of the matter can be found in MARTENS et al. (submitted).

From the karyological data summarized above it can be concluded that a «basic» karyotpye can be recognised not only for the Monocelididae but also for all non-monocelidid Proseriata. Moreover the non-monocelidid basic karyotype has most probably arisen by polyploidy from a karyotype very similar to the basic karyotype of the Monocelididae. The polyploidy may be considered as an autapomorphy for all non-monocelidid Proseriata (incl. the Unguiphora) (block 3) which thus form a monophyletic taxon, the Paramonocelida, adelphotaxon of the Monocelididae. This apomorphy is congruent with the fact that in all polyploid Proseriata the brain is surrounded by a capsule, this is lacking in Monocelididae, Tricladida and other Platyhelminthes. The basic karyotype of the Monocelididae (or at least one very similar to it) may be regarded as the basic karyotype for the Proseriata (Seriata?) (see MARTENS et al. submitted).

Since in both adelphotaxa: the Monocelididae and the Paramonocelida, a statocyst is found (see SOPOTT-EHLERS, 1985), this statocyst must be considered as another autapomorphy for the Proseriata in addition to the characters recognised by EHLERS (1985) (block 1). Hence the absence of the statocyst in the Unguiphora, a taxon of the Paramonocelida, must be regarded as the result of a secondary loss (see however SOPOTT-EHLERS, 1985 and EHLERS, 1985 for an opposing point of view).

The digonoporid taxa within the Paramonocelida

The digonoporid condition is clearly a plesiomorphy within the Proseriata, and hence the common gonopore of the Coelogynoporidae and the Otoplanidae may be considered a possible synapomorphy for these two families (block 5).

The Unguiphora may be considered as a monophyletic taxon characterised by the multiplication of the ovaries (SOPOTT-EHLERS, 1985) and the loss of the statocyst (see above) (block 7).

Four digonoporid genera remain to be considered: *Archimonocelis* MEIXNER, 1938, *Meidiama* MARCUS, 1946, *Asilomaria* KARLING, 1966 and an undescribed genus with two species from the Bay of Calvi, Corsica (MARTENS in prep.). For the last three genera it can be concluded from light microscopical observations that the spines are intracellular and so these genera can no longer be placed within the Monocelididae.

A number of *Archimonocelis* species, *Asilomaria* and the two species of the new genus, possess an accessory glandular organ (prostatoid). This is surrounded by long needles

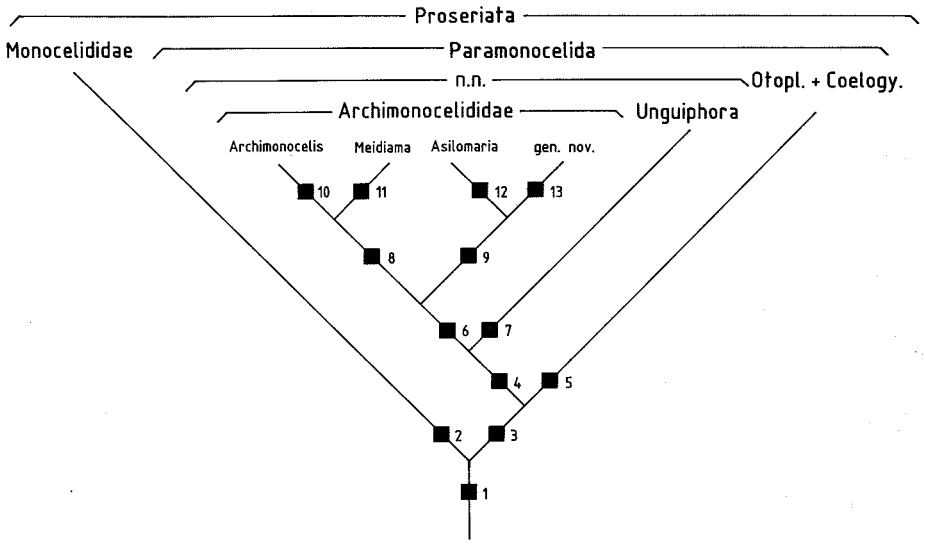

Fig. 1: Phylogenetic relationships within the Proseriata. The numbers refers to the hypothesized autapomorphies: 1. Statocyst, see EHLERS, 1985. 2. Hard structures basal lamina differentiations. 3. Polyploidy, brain capsule. 4. Monociliary receptors, with dense intracellular ring and located between epidermal cells. 5. Common gonopore. 6. Accessory glandular organ. 7. Multiplication of ovaries. 8. Ovaries in front of the vitellaries. 9. Short common female duct. 10. Cnidoblasts. 11. Loss of the accessory glandular organ. 12. No spines in male atrium, postpenial invagination. 13. Accessory glandular organ with its own pore.

similar to those found in the male atrium, a structure which is not found in other Proseriata. It is connected to the male atrium in the *Archimonocelis* species and in *Asilomaria*. In the new genus it has its own pore in front of the male pore. This accessory glandular organ may be considered a common evolutionary novelty for these genera (block 6) which constitute the monphylum Archimonocelididae Meixner, 1938 n. grad. The genus *Meidiama* (adelphotaxon of *Archimonocelis*, see later) also belongs to the Archimonocelididae but here the accessory organ has been secondarily lost like in some *Archimonocelis* pecies.

In Coelogynoporidae, Otoplanidae, *Archimonocelis* and in *Meidiama* a copulatory organ is found that consists of separate seminal and prostatic vesicles (not enclosed in a common bulb as in the Monocelididae), a stylet and a number of spines in the male atrium. This is the plesiomorphic situation within the Paramonocelididae. The stylet has been lost in *Asilomaria* and in the new genus, a synapomorphy. This sister-group relationship is substantiated by a second characteristic. In both genera the right and left ovovitelloducts open almost directly into the female pore. The «common female duct» is confined to a short section with cement glands (block 9) while in all other digonoporid Proseriata this common female duct is much longer (the plesiomorphic condition). *Asilomaria* has also lost spines from the male atrium, an autapomorphy of the genus along with the ventral postpenial invagination (block 12). In the new genus the atrium is extremely wide with very numerous spines and the accessory glandular organ has its own pore, not opening into the male atrium as in the other genera (block 13).

Archimonocelis and *Meidiama* have the ovaria in front of the vitellaria (block 8); both genera may be united in one taxon. The most obvious autapomorphy for *Archimonocelis* is the capacity to store cnidoblasts in its epidermal cells (block 10). Within this genus species are found which lack the accessory glandular organ as is the case in *Meidiama* (block 11). Is this a convergence or should *Meidiama* be considered an *Archimonocelis* that lost the capacity to store cnidoblasts?

The Unguiphora may be united in one taxon together with the Archimonocelididae. It has been pointed out by Sopott-Ehlers (1984) that in *Nematoplana*, in *Polystyliphora* and in *Archimonocelis* the monociliary receptors are located between the epidermal cells, while in all other Proseriata those receptors pierce the epidermal cells. Moreover, in both taxa these receptors are provided with a dense intracellular ring under the surface. From outgroup comparison at least within the Proseriata we considered both characters as synapomorphies for the Archimonocelididae + Unguiphora (block 4). For the latter taxon, in addition to the autapomorphies given by Sopott-Ehlers (1985) we can add the loss of the statocyst and the absence of spines in the male atrium (block 7).

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