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Phylogenetic relationships within the *Archiloa* genus complex (Proseriata, Monocelididae)

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Abstract

Of the seven genera which we have recognised within the *Archiloa* genus complex *sensu* Karling (1966) the cosmopolitan genus *Archilina* is the most 'primitive' and is characterised only by plesiomorphic characters, and has to be considered paraphyletic. All other species of the *Archiloa* genus complex are hypothesized to be derived from *Archilina*-like ancestors through different evolutionary lineages. One lineage led to the genera *Archiloa*, *Inaloa*, *Archilopsis* and *Monocelopsis*, taxa found in the Atlantic and the Mediterranean. These genera are monophyletic and their relationships are analyzed. The genera *Mesoda* (Brazil) and *Tajikina* (Northern Pacific) can be considered as two other separate lineages. Similarly, within what we now consider as the genus *Archilina* different lineages can be recognized in different regions.

Introduction

There is no general consensus on the systematics of the *Archiloa* genus complex. Karling (1966) synonymized the genera *Monocelopsis*, *Archilopsis*, *Archilina*, *Mesoda*, and *Pistrix* with *Archiloa*, on the basis of the copulatory organ of the duplex type and the presence of a vagina. He did not give weight to the details of location and morphology of vagina, bursa and copulatory organ. His proposal, however, has not been generally accepted (cf. Sopott, 1972; Curini-Galletti *et al.*, 1989; Martens *et al.*, 1989a, b). Based on a revision of the *Archiloa* genus complex, we considered most of the synonymized genera as valid. The detailed taxonomy of the group, with the description of numerous new species, as well as full karyological data, is dealt with in other papers (Martens *et al.*, 1989a; Martens & Curini-Galletti, 1994 or in preparation). Here we present the presumed phylogenetic relationships within Karling's *Archiloa* group.

Phylogenetical analysis

From a thorough revision of the Monocelididae (we have studied nearly all known species and more than 30 new species) we were not able to recognise an apomorphic feature for the *Archiloa* genus complex. Many species within this complex show characters which are widely distributed within the family and can be considered as plesiomorphic:

- insunken nuclei, many vitelline follicles beside and posterior to the testes (characters which are present in nearly all Monocelididae)
- a simple organisation of the copulatory organs with three genital pores of which the first is an external vagina connected with a prepenial bursa which is a part of the female duct (this character is also present in the genera *Monocelis*, *Minona*, *Duplominona*, *Pseudomonocelis*, *Preminona*)
- a copulatory organ of the duplex type (present in all species of the complex), in many of them the organisation of this organ is very simple: a rather short and straight cirrus and the bulb is completely filled with the prostate vesicle and seminal vesicle (see also Fig. 1 in Martens & Curini-Galletti, 1994).

This character state is also present in the genera *Promonotus*, *Duplominona* and *Duploperaclistus*.

All these plesiomorphic characters are in fact also the characters of the genus *Archilina*.

Examination of specimens of *Archiloa rivularis* de Beauchamp, 1910, the type species of the genus, revealed that the copulatory organ is provided with an accessory cirrus, a structure already described as a 'ligament du penis' by de Beauchamp (1910). An accessory cirrus is also present in *A. petiti* Ax, 1956 and *A. westbladi* Ax, 1954. In these three species there is an internal vagina with a prepenial bursa which is not directly connected with the female duct (see Fig. 1 in Martens & Curini-Galletti, 1994). Both the presence of the accessory cirrus and the internal vagina, without a direct connection with the female duct, are not present in any other of the Monocelididae species and are synapomorphies for these three species (4, 5 in Fig. 1) and justify the genus *Archiloa*. The species known so far are exclusively found in Western Europe and the Mediterranean, in brackish conditions; *A. rivularis* occurs in fresh water, and is only known from a small creek in the Pyrenee.

Monocelis cirrifera described by Meixner (1943) has a very long cirrus of about 180 μm. We have studied specimens from the type locality. The morphology of the copulatory organ, the bursa and the vagina are very similar to those of *Monocelis scalopura* Marcus, 1949 (which has a cirrus of 600 μm long), and a new species from the Mediterranean with a cirrus up to 1.5 mm. The presence of an extremely long cirrus and of a very long vagina are synapomorphies for these species (6, 7 in Fig. 1) which we have put together in the new genus *Inaloa* (see Martens & Curini-Galletti, 1994).

The genera *Archiloa* and *Inaloa* share some characteristics. All species, that could be studied alive, have 4 chromosomes in the haploid set and show similarities in the morphology of the copulatory organ which is clearly different from the plesiomorphic condition. The spherical prostatic vesicle is separated from the seminal vesicle by a muscular diaphragm; both vesicles are not in touch with the bulb wall and do not fill the whole bulb (see Fig. 1 in Martens & Curini-Galletti, 1994). The morphology of the copulatory bulb is a synapomorphy for the two genera (3 in Fig. 1).

Ax (1951) introduced the genus *Monocelopsis* for a peculiar species, *M. otoplanoides*, which moves and superficially looks like an otoplanid. This small species is characterised by three genital pores (plesiomorphy), a pre- and post penial bursa (plesiomorphy), and 4 pairs of vitelline follicles, all posterior to the testes, only one pair of which is in front of the pharynx. Sopott (1972) described *Mesoda septentrionalis* from the North Sea. She assigned the species to the genus *Mesoda* Marcus 1949, on the basis of the intraepithelial nuclei of the epidermis. *Mesoda* was only known from a single South American species. However, Ax's and Sopott's species have both the same general construction of the copulatory organ, vagina and bursa, the same otoplanoid habitus, and agree also in number and localization of the vitellaria; and both species have five chromosomes in their haploid set, with chromosomes less heterobrachial than in the genus *Archilopsis* (see below) (for a description of these karyotypes, see Martens *et al.*, 1989a and Curini-Galletti *et al.*, 1989). We postulate the number and localization of vitellaria, the otoplanoid habitus and the chromosome morphology as synapomorphies for the two species (8, 9, 10 in Fig. 1) which diagnose the genus *Monocelopsis*. Both species occur in Western and Northern Europe, in mid and high mediolittoral; *M. septentrionalis* prefers coarser sediments than *M. otoplanoides*.

The revision by Martens *et al.* (1989a) of *Archilopsis unipunctata* revealed the existence of a species-complex including four different species; one species in agreement with Fabricius' description (1826) (*A. unipunctata*), one conferming *A. spinosa* described by Jensen (1878), and two new species (*A. marifuga* and *A. arenaria*). Two synapomorphies in these four species justify the conservation of the genus *Archilopsis* Meixner, 1938: backwards oriented vaginal duct, connected postpenially with the femal duct, and the presence of two prostate channels (11, 12 in Fig. 1). For phylogenetic relationships within the genus, see Martens *et al.* (1989a). The four species are all characterised by the presence of five chromosomes in their haploid sets. The genus *Archilopsis* is amphiatlantic in distribution, and strictly boreal (from North-Western Europe to Eastern Canada).

The karyological evolution of the *Archiloa* complex has been studied by Curini-Galletti *et al.* (1989). It involves step-wise processes of fission from the basic set of the Monocelididae with $n = 3$ to sets with $n = 4$ (one fission) and $n = 5$ (two fissions). Fission leading from $n = 3$ to $n = 4$ is here considered as a synapomorphy for the genera *Archiloa*, *Inaloa*, *Monocelopsis* and *Archilopsis* (1 in Fig. 1). Fission leading from $n = 4$ to $n = 5$ constitutes a synapomorphy for the genera *Monocelopsis* and *Archilopsis* (2 in Fig. 1).

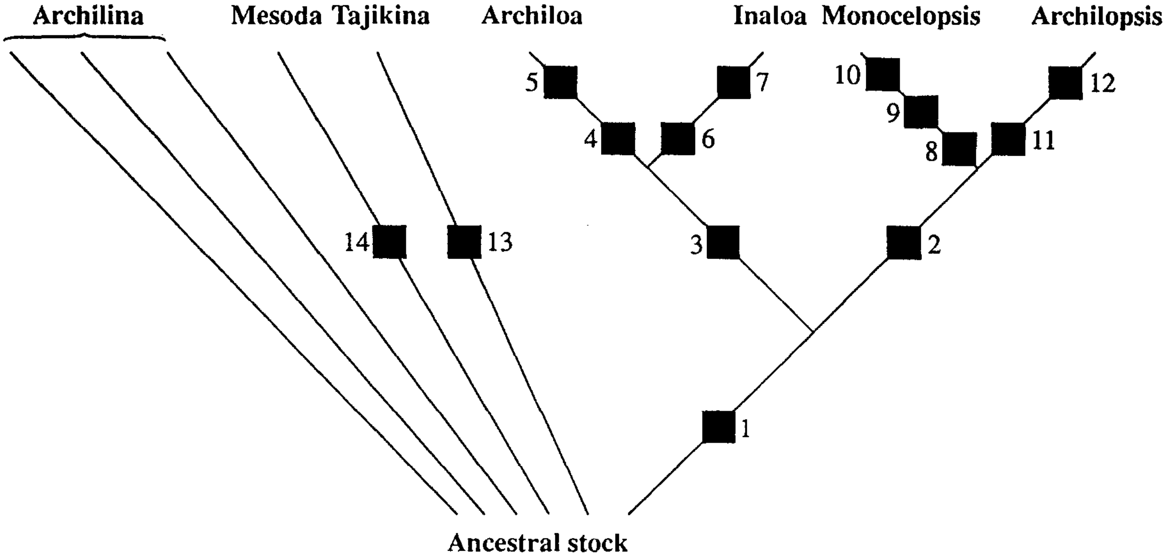

Fig. 1. Cladogram for the *Archiloa* genus complex. Numbers refer to the hypothesized apomorphies. 1. $n=4$: fission of the first metacentric chromosome of the basic set. 2. $n=5$: fission of the second metacentric chromosome of the basic set. 3. Spherical seminal vesicle and prostatic vesicle separated by a muscular diaphragm, both vesicles are more or less not in touch with the bulb wall. 4. Accessory cirrus. 5. Internal vagina ending in the prepenial bursa without direct connection with the female duct. 6. Extremely long cirrus. 7. Extremely long vagina. 8. Four pairs of vitelline follicles, only one pair of which is in front of the pharynx. 9. Otoplanoid habitus. 10. Karyotype nearly symmetrical. 11. Copulatory organ with prostatic channels. 12. Vaginal duct connected postpenially with the female duct. 13. Vagina interna. 14. Intraepithelial nuclei.

Two other species, described as *Archiloa juliae* by Tajika (1982) and *Archiloa tajikai* by Ax & Armonies (1990), both from the Northern Pacific have an internal vagina. An internal vagina, but not connected with the female duct, is also present in *Archiloa* as defined above. However, in these two species the seminal and the prostate vesicle fill the whole bulb, and the female duct is connected with the vagina. In addition, the geographic distribution of these species is different and *Archiloa juliae* has only two chromosomes in the haploid set. We consider the presence of an internal vagina as a parallelism. These species cannot conveniently be assigned to any of the other genera. We therefore proposed the new genus *Tajikina* Martens & Curini-Galletti, 1994, with the internal vagina as the provisional autapomorphy for this genus (13 in Fig. 1).

The phylogenetic relationships among the remaining species of the complex are not clear. These species mostly show plesiomorphic characters as mentioned above. Two species described by Marcus – *Mesoda gabriellae* Marcus, 1949 and *Pistrix thelura* Marcus, 1951 – show the general plesiomorphic features of female and male organs. The existence of two different genera is not justifiable; the only character which can be considered an apomorphy are the intraepithelial nuclei of the epidermis. Furthermore both species occur in the same geographical area (Southern Brazil). We have thus provisionally placed these species into one single genus, *Mesoda*, with intraepithelial nuclei as its presumed derived character (14 in Fig. 1).

The remaining species are *Archilina endostyla* Ax, 1959, *Archiloa vanderlandi* Martens & Curini-Galletti, 1989, *Archiloa subtilis* Karling, Mac-Fira and Dörjes, 1972, *Archiloa papillosa* Ax & Ax, 1977, *Archiloa duplaculeata* Ax & Armonies, 1990. In addition to these, numerous new species have been found in the Mediterranean and in tropical areas (some of which are described in Martens & Curini-Galletti, 1994, Curini-Galletti & Martens, in press). All these species show a very similar organisation of the genital organs (as far as we could understand from available descriptions and our own observations), *i.e.* a rather short external vagina, opening in the female channel which forms at that place a bursa (prepenial bursa) provided with some glands; in front of this bursa the female duct can be provided with an epithelium of the resorbiens type; the copulatory bulb is mostly compact with no specialised structure of the prostatic glands. All these characters are found also in other Monocelididae not belonging to the *Archiloa* group and represent the plesiomorphic condition. The karyotype of *A. endostyla* and of most of the new species is known: the chromosome number ($n = 3$) and shape are similar to the basic set of the Monocelididae (see Curini-Galletti *et al.*, 1989; Martens *et al.*, 1989b).

We therefore argue for all these remaining species to be in the genus *Archilina*, though the taxonomic position of some species remains unclear (see Martens & Curini-Galletti, 1994), which is characterised by only plesiomorphic characters. This originally monospecific genus was based on the presence of a stylet within the cirrus (Ax, 1959). Presently, in the Monocelididae, a stylet within the cirrus is known to occur in some species of the genera *Duplominona*, *Duploperaclistus* and *Archilopsis* (see Ax, 1977; Martens 1983; Martens & Curini-Galletti, 1989; Martens *et al.*, 1989a), and we therefore consider this within the genus *Archilina*, a species character only known for *Archilina endostyla*.

Because the genus *Archilina* is presently based only on plesiomorphic characters, it may be a non-monophyletic taxon. On the other hand morphological details of the *Archilina* species, especially the cirrus morphology, have revealed the existence of different evolutionary lines in different geographical areas (Martens & Curini-Galletti, 1994).

Conclusions

Within the *Archiloa* genus complex we can recognize seven valid genera, including the possibly non-monophyletic *Archilina*. Phylogenetic relationships between four of these genera can be resolved.

The ancestor(s) of this genus complex was cosmopolitan in distribution and in different areas it evolved along different evolutionary pathways. In tropical and subtropical areas the evolution of the group has produced different lineages but mostly with small morphological and karyological modifications. In contrast, in temperate and boreal areas the morphological and karyological evolution was much more pronounced, resulting in clear evolutionary lines with different taxa which all can be characterised by autapomorphies. We recognize an evolutionary line in the Atlantic and the Mediterranean which includes the genera *Archiloa*, *Inaloa*, *Archilopsis* and *Monocelopsis*. These taxa together are monophyletic and their relationships can be resolved (Fig. 1). The genus *Mesoda* (Brazil) and *Tajikina* (Northern Pacific) can be considered as two other, evolutionary lines.

From this we argue that the recent *Archilina* is possibly paraphyletic. *Archilina* species resemble in morphology the ancestral stock and can be considered as living relicts of the ancestral stock which lies at the base of the whole *Archiloa* genus complex and possibly of some other taxa, such as *Boreocelis*, *Promonotus* and *Paramonotus*.

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