Progenetic species in polychaetes (Annelida) and problems assessing their phylogenetic affiliation

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Synopsis

Progenesis is defined as the retention of ancestral juvenile characters by adult stages of descendants due to an acceleration of the sexual maturation and thus is often regarded as a fast evolutionary process. Several small, meiofaunal polychaetes, such as Dinophilidae, some “Dorvilleidae” (for example, Parapodrilus), and Protodrilida, exhibit morphological simplicity in that they lack features typical of larger polychaetes, for example, parapodia and/or head appendages. Due to the general resemblance of adult meiofaunal polychaetes to juveniles of larger forms, progenesis has been invoked to explain evolutionary origins of many smaller taxa with increasing frequency over the past 4 decades. In this review, I summarize the interstitial species of polychaetes for which progenetic origin has been suggested on the basis of morphology. However, critical examination of morphological data that includes larval features reveals that autapomorphic characters uniting supposed progenetic taxa to specific annelid lineages are often missing. Typically larval and juvenile characters, which are argued to support hypotheses of progenetic origin, are often widely dispersed, homoplastic features. Because of this situation, molecular data seem to be the most reliable source for phylogenetic inference. However, other biological data, for example, from life history and morphology, are necessities to substantiate the progenetic evolution of these species.

Progenetic evolution and interstitial species

Retention of ancestral juvenile characters by adult stages of descendants (paedomorphosis) can arise either by a retardation of somatic development (neoteny) or by an acceleration of the sexual maturation (progenesis) (Gould 1977). Westheide (1987) proposed that only a few steps of speciation are necessary in the progenetic adaptation process, because instead of the reduction of several morphological characters like size, parapodia, and chaetae and the retention of others like ciliary bands or protonephridia at the same time to achieve a small body resembling ancestral juvenile stages “only” the sexual maturation has to be sped up. Thus, progenesis combines a maximum of phenotypic alterations with a minimum of genotypic changes (Gould 1977).

The marine interstitium, the space between the sand grains, is an environment characterized by an extreme and rigid requirement for very small body size. Gould (1977) expected progenesis to be the prime evolutionary process in such a case. Furthermore, this requirement for the interstitium can be assumed to very old with limited change during Earth history (Noodt 1974). As long as there have been seas there has been sediment with its pore system (Westheide 1987). Thus, due to this rigid but stable condition a high degree of adaptation for very small body size is required to invade the interstitium. On the other hand, once adapted to small body size alterations of selection pressures are less likely to happen. Therefore, Westheide (1987) concluded that the probability of a successful and permanent invasion of the interstitium by a new species increases with an increasing potential for a fast adaptive process concerning body size. Many marine invertebrates like polychaetes exhibit a biphasic life cycle. During this life cycle larval and/or juvenile stages inhabit the interstitial space temporarily. Due to their small body size this is a “safe haven” against larger predators. Several authors (Gould 1977; Rieger 1980; Westheide 1987) have proposed that a permanent habitation of the interstitium by these species appears to be most rapidly accomplished by progenesis. Although other evolutionary processes have been proposed and demonstrated (for example, Siewing 1963; Werner 1965; Boaden 1975), progenesis is regarded to have a fundamental role in the evolution of interstitial species (Westheide 1987; Warwick 2000).

Common features of several interstitial polychaete species are a small body size, from only a few millimeters down to 300 \(\mu\)m in length, as well as a seemingly
simple organization including only a few segments, missing or few parapodia and chaetae, a ventral ciliary gliding band, a epidermal nervous system, and pro-tonephridia (for example, Westheide 1990). Due to the simple organization many of these taxa including Dinophilidae, Protodrilida, and Nerillidae were initially grouped together as “Archiannelida” and considered to reflect the basal organization of Annelida (see Hermans 1969). However, ultrastructural analyses (for example, Purschke and Jouin 1988), general arguments about annelid origins (for example, Westheide 1997), and 18S rDNA (Struck and others 2002) changed this view. Due to resemblance with larval or juvenile stages independent progenetic origins has been suggested for many of the interstitial polychaete taxa (for example, Westheide 1987). The purpose of this review is to summarize the interstitial species of polychaetes for which a progenetic origin has been suggested, to outline the problems of assessing their phylogenetic position in Annelida, and to examine the support for progenetic hypotheses.

**Supposed progenetic polychaetes**

Supposed progenetic species of polychaetes, which I discuss briefly in this review, are listed in Table 1.

<table>
<thead>
<tr>
<th>Supposed progenetic taxon</th>
<th>Proposed phylogenetic affiliation</th>
<th>Reference</th>
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</thead>
<tbody>
<tr>
<td>Dinophilidae</td>
<td>“Dorvilleidae”</td>
<td>(for example Westheide and Riser 1983; Westheide 1987; Eibye-Jacobsen and Kristensen 1994)</td>
</tr>
<tr>
<td></td>
<td>Non-Eunicidan taxon</td>
<td>(Struck and others 2002; Struck, Halanych, and Purschke 2005)</td>
</tr>
<tr>
<td>Arenotrocha, Microdorvillea, Petrocha, Pusillotrocha, Neotenotrocha</td>
<td>“Dorvilleidae”</td>
<td>(for example Westheide 1982; Westheide 1987; Eibye-Jacobsen and Kristensen 1994; Struck and others 2006)</td>
</tr>
<tr>
<td>Parapodrilus, Apharyngtus, Apodotrocha</td>
<td>“Dorvilleidae”</td>
<td>(for example Westheide and Riser 1983; Westheide 1987; Eibye-Jacobsen and Kristensen 1994; Struck and others 2002; Struck and others 2006)</td>
</tr>
<tr>
<td>Nerillidae</td>
<td>Eunicida/Amphinomida</td>
<td>(Westheide 1990; Rouse and Pleijel 2001; Worsaae and others 2005)</td>
</tr>
<tr>
<td>Protodrilida</td>
<td>Spionida</td>
<td>(H. Hansen, Personal communication, Free University Berlin)</td>
</tr>
<tr>
<td>Psammodrillus aedificator, Psammodrilidae fauali</td>
<td>Psammodrilidae</td>
<td>(Swedmark 1958; Swedmark 1964; Kristensen and Narrevang 1982)</td>
</tr>
<tr>
<td>Microphthalmus</td>
<td>Hesionida</td>
<td>(for example Westheide 1967; Wolff 1969; Westheide 1987; but see Pleijel and Dahlgren 1998; Dahlgren and others 2000)</td>
</tr>
<tr>
<td>Metaxypsomma uebelackerae</td>
<td>Aphroditiformia/Pholoidae</td>
<td>(Wolf 1986)</td>
</tr>
<tr>
<td>Pisionida</td>
<td>Aphroditiformia</td>
<td>(Struck, Purschke, and Halanych 2005; Wiklund and others 2005)</td>
</tr>
<tr>
<td>Protoarcinia oerstedi</td>
<td>Orbinidae</td>
<td>(for example, Eisig 1914; Purschke and Tzetlin 1996; Bleidorn 2005)</td>
</tr>
<tr>
<td>Branchiornaldane</td>
<td>Arenicolida</td>
<td>(Bartolomaeus and Meyer, 1999; Bleidorn and others 2005)</td>
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<tr>
<td>Malicenidae</td>
<td>Arenicolida</td>
<td>(Tzetlin 1991; op. cit. Purschke and Tzetlin 1996)</td>
</tr>
<tr>
<td>Protis, Protula, Apomatus</td>
<td>Serpulidae</td>
<td>(Knight-Jones and others 1997)</td>
</tr>
<tr>
<td>Poeobius meseres</td>
<td>Flabelligerida</td>
<td>(Burnette and others 2005)</td>
</tr>
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</table>

Dinophilidae is the classical example of progenesis in polychaetes. Due to convincing similarities to developmental stages of larger eunicidans and their relatively small size (Fig. 1), progenetic origin of Dinophilidae within Eunicida has been repeatedly assumed, already as early as the 19th century (Meznikow 1866; Svesnikov 1958; Westheide 1987). Westheide (1982) and Westheide and Riser (1983) also discussed a phylogenetic hypothesis that the 2 dinophilid genera *Dorvilleus* and *Trilobodrilus* are extremely derived. The most substantial evidence for a close relationship between dinophilids and eunicidans was derived from Åkesson’s (1977) experiments demonstrating reciprocal infection with coelomic coccidian of the genus *Grellia*, parasites that are regarded as host-specific. Finally, Eibye-Jacobsen and Kristensen (1994), on the basis of a morphological cladistic analysis, merged Dinophilidae with “Dorvilleidae.” In their analysis Dinophilidae and other supposedly progenetic dorvilleid species follow each other step by step and develop out of each other with gradually increasing juvenile organization (see also Fig. 2A). However, molecular analyses based on 18S and 28S rDNA significantly rejected a closer relationship of Dinophilidae to any eunicidan taxon and thus Dinophilidae are
not of progenetic origin within Eunicida (Struck and others 2002, Struck and others 2005a). However, their progenetic origin from another polychaete taxon cannot be excluded (Müller and Westheide 2002).

To date “Dorvilleidae” (Eunicida) is proposed to contain the greatest number of progenetic species. Eunicida (sensu Rouse and Pleijel 2001) is a species-rich taxon for which monophyly has been well established by at least one morphological autapomorphy: a ventral pharyngeal organ with conspicuous jaw apparatus, consisting of cuticular mandibular and maxillary elements which can, at least partially, be regarded as homolog throughout the various extant and fossil taxa (Kielan-Jaworowska 1966; Wolf 1986; Purschke 1987; Orensanz 1990).

Several dorvilleid genera are hypothesized to be of progenetic origin: Arenotrecha, Microdorvillea, Petrocha, Puillotrecha, Ikosipodus, and Neotenotrecha (for example, Westheide 1982; Eibye-Jacobsen and Kristensen 1994). Additionally, the jawless Parapodrilus (Fig. 1), Apharyngtus, and Apodotrocha have also been included (Westheide 1965; Westheide and Riser 1983; Eibye-Jacobsen and Kristensen 1994). Adults of these species and Dinophilidae can be arranged in morphological series, which resemble the developmental series of larger eunicidans. Although Eibye-Jacobsen and Kristensen (1994) recovered in their cladistic analysis phylogenetic relationships similar to the order of the morphological series (see also Fig. 2A), the arrangement in morphological series may not necessarily reflect phylogenetic relationships (Westheide 1987). Molecular data provided additional support for the progenetic origin of the jaw bearing Microdorvillea (Struck and others 2006) and the jawless Parapodrilus (Struck and others 2002). Both taxa evolved independently from each other in a dorvilleid clade comprising the large genera Protodorvillea, Dorvillea, Schistomeringos, and Parougia. Furthermore, Ophryotrocha derived within this clade and thus, they might also be of progenetic origin (Struck and others 2006). In contrast to Eibye-Jacobsen and Kristensen’s (1994) analysis molecular data support the hypothesis of several independent progenetic events (Westheide 1987).

Similar to Dinophilidae, progenesis has also been proposed for the other former archiannelids Protodrilida and Nerillidae. Nerillidae resemble Aciculata in the morphology of sensory palps, prostomial antennae, compound chaetae, muscular pharynx, parapodial cirri, and one pair of pygidial cirri (Rouse and Fauchald 1997; Rouse and Pleijel 2001; Worsaae and others 2005). Westheide (1990) mentioned the superficial resemblance of adult Nerillidae and juvenile Onuphidae (Eunicida) (Hsieh and Simon 1987). However, except for the consistence of body configuration Nerillidae do not share any other feature with these or other juvenile stages (Westheide and Purschke 1996). Nonetheless, Rouse and Pleijel (2001) suggested that such a relationship should be considered. The presence of a ventral buccal organ has been pointed out as a possible synapomorphy for Nerillidae, Eunicida, and Amphinomida (Rouse and Fauchald 1997; Worsaae and others 2005). However, the different ventral organs are very likely not homolog (see Purschke and Tzetlin 1996). A study using 18S rDNA and morphological data reconstructed a closer, but poorly supported relationship of Nerillidae to Amphinomida and Eunicida (Worsaae and others 2005).

A close relationship of Protodrilida to Spionida has been proposed, but is not sustained by clear morphological synapomorphies. This proposal was based on evident structural correspondences of the
anterior end, the nervous system, specific structure of the palps, and nuchal organs (Orrhage 1974; Schlötzer-Schrehardt 1987; Purschke and Jouin 1988; Purschke 1990a; Purschke 1993). In particular, these workers highlight the similarities between the central nervous system and the innervations of the palps. Protodrilida’s progenetic origin within Spionida is inferred from the presence of a prostomial, probably light sensitive statocyst in adult protodrilids and juvenile spionids (H. Hansen, Personal communication, Free University Berlin and Purschke 1990b,c, 1992).

Another example of neoteny appears within the enigmatic interstitial Psammodrilidae. Psammodrilus aedificator and Psammodriloides fauveli are thought to be of progenetic origin from Psammodrilus balanoglossoides with P. fauveli possessing more neotenic features (Swedmark 1958; Swedmark 1964; Kristensen and Nørrevang 1982).

The position of another interstitial genus, Microphthalmus, is also controversial. These Nereidiformia species were regarded as Hesionidae (for example, Westheide 1967; Wolff 1969; Westheide 1987). Westheide (1987) pointed out the apparent paedomorphic character of these small species in comparison with juvenile stages of larger Hesionidae (for example, Schram and Haaland 1984). However, a cladistic analysis of Nereidiformia placed Microphthalmus in a basal position or closely related to Pilargidae and Hesionides, and not closer to Hesionidae (Pleijel and Dahlgren 1998). Furthermore, a molecular analyses based on a 660 bp fragment of the mitochondrial cytochrome c oxidase subunit I (COI) also resulted in a close relationship of Pilargidae and Microphthalmus with Hesionidae as sister to this group (Dahlgren and others 2000). However, nodal support for these results was low in all analyses. Additionally, neither a combined
analysis nor a molecular analysis omitting the highly variable third position of COI caused a significant increase of nodal support (Dahlgren and others 2000). Within Microphthalamus the species group of M. listenis, M. nahantensis, and M. carolensis is thought to be one of the few convincing examples of step-by-step progenetic evolution similar to a morphological series as exemplified above for dorvilleids and dinophilids (Westheide 1987; Westheide and Rieger 1987). For example, with a decreasing number of setigers larval features like the ciliary gliding band become increasingly persistent.

Metaxypsamma uebelackerae, an interstitial species in fine to coarse sands and typically attributed to Aphroditiformia, has paired mounds of papillae very similar to structures in nectochaete I and II larval stages of Pholoe synophthalmaica, leading to speculation of a progenetic origin within Pholoidae (Aphroditiformia) (Wolf 1986). Additionally, M. uebelackerae shows considerable similarities to the interstitial Pholoe swedmarki (Laubier 1975), which still possesses elytra. Both show similar adaptations to the interstitial habitat including reduced number of segments (up to 24 or 27, respectively, in contrast to up to 90 in other Pholoidae), reduced or absent notopodia, and reduced tentacular cirri (Wolf 1986). The loss of elytra could have enabled M. uebelackerae to invade even smaller interstitial spaces than P. swedmarki (Wolf 1986). Recent molecular analyses supported the highly derived position of the interstitial Pisionidae within Aphroditiformia, the scale worms, and corroborated a closer relationship to Pholoidae and Sigalionidae (Struck and others 2005b; Wiklund and others 2005). Pisionidae lack elytra like M. uebelackerae and show at least heterochrony in the earlier developmental appearance of the venom glands and their associated styli than in other Aphroditiformia (Ákesson 1961). The evolution within Pisionidae is regarded as a transition from middle-sized infraunal species to small true interstitial species (Westheide 1987). However, the alternative direction from interstitial species to infuunal ones due to a secondary increase in size is also possible, especially taking into account that other infraunal Aphroditiformia still possess their elytra. To address this question the phylogenetic relationships within Pisionidae have to be studied in more detail.

Another example of progenesis can be found in Orbiniiidae. The ventral pharyngeal organ, pygidial cirri, and the shape of the thoracic neuropodia of Protoaricia oerstedi and juveniles of Naineris and Phryo exhibit a high degree of similarity and thus the progenetic origin of Protoaricia has been invoked (for example, Eisig 1914; Purschke and Tzetlin 1996). On the other hand, validity of Protoariciinae has been questioned due to considerations that these species are actually juveniles of other Orbiniiidae taxa (Blake 1996). A molecular phylogenetic analysis using 16S and 18S rDNA data recovered a significantly supported clade of P. oerstedi and Naineris species and thus corroborated their progenetic origin (Bleidorn 2005). Furthermore, several individuals of P. oerstedi in this analysis had visible eggs.

Species of Branchiomaldane, typically considered as Arenicolidae, are characterized by a small body and the resemblance to juvenile stages of Arenicolides including the possession of tiny, largely unbranched gills and the lack of an achaetous, gill-less tail, which is typical for juvenile stages in other genera of Arenicolidae (Fauvel 1899; Ashworth 1912; Fournier and Barrie 1987; Bartolomaeus and Meyer 1999). Furthermore, juvenile stages of arenicolid species and adult Branchiomaldane possesses pigmented photoreceptors, which are absent in the adults, and at least in Arenicola marina and Branchiomaldane these photoreceptors possess lenses (Nogueira and Rizzo 2001; Bleidorn and others 2005). Molecular data of 18S, 28S, and 16S rDNA also confirmed a derived position of Branchiomaldane within Arenicolidae as sister to Arenicolides caudata (Bleidorn and others 2005). Thus, both morphological and molecular data support the hypothesis of their progenetic origin (Bartolomaeus and Meyer 1999).

The foregut structures of different maldanid species, the “bamboo” worms, can be arranged in sequences resembling the ontogeny of the foregut structures of Arenicolidae and a progenetic origin of Maldanidae in general has not been discarded (Tzetlin 1991; op. cit. Purschke and Tzetlin 1996). Furthermore, the Clymenites larvae of Arenicolidae exhibit similarities to adult Maldanidae (Rouse 1992). However, preliminary analyses based on 18S rDNA only revealed a sistergroup relationship of Maldanidae and Arenicolidae and thus it still remains unresolved whether maldanid species show a plesiomorphic condition of the foregut structure or an apomorphic, progenetic (Bleidorn and others 2005). Therefore, it is necessary to include more maldanid and arenicolid, as well as outgroup species to deduce the basal foregut structures of both taxa and thus to conclude on the most parsimonious process explaining their evolution.

Finally, paedomorphic processes have often been invoked in the evolution of species in abyssal depth due to low temperatures and poor feeding (Zezenia 1994). Within the well known Serpululidae, the Christmas tree worms, the genera Protis, Protula, and Apomatus are thought to be of paedomorphic origin (Knight-Jones and others 1997). Whereas Protula and some species of Protis lack an operculum, other
Protis species and Apomatus possess a terminal vesicle at a pinnulated radiole. In that, these 3 genera resemble the development of 2 other serpulid genera, Serpula and Hydrodias. After metamorphosis, a terminal vesicle is developed on one of the second dorsal pinnulated radioles. This vesicle differentiates into the first operculum. Thus, the first operculum is on a pinnulated radiole. Later it is replaced by other opercula on stalks without pinnules (Szent-Braconnot 1964). Alternatively, the lack or reduction of opercula in Serpulidae has been regarded as an adaptation for respiratory necessities. For example, the lack of an operculum in Hyalopomatus cancerum may be due to a low oxygen environment (Knight-Jones and others 1997). Nonetheless, even a low oxygen habitat must not necessarily exclude paedomorphic processes. The former might be the driving selective force and the latter the adaptive process, which would also increase the body surface to volume ratio.

Phylogenetic assessment of progenetic species

This steadily growing assemblage of independent polychaete lineages indicates that progenesis, or more general paedomorphism, is not an infrequent evolutionary process in polychaetes. Although not thoroughly investigated yet it seems especially frequent in the colonization of the interstitial habitat. As suggested by Westheide (1987) the biphasic life cycle of many polychaetes with larval and/or juvenile stages temporarily inhabiting the interstitial space may predispose them for a successful and permanent colonization of this space by means of progenesis. However, as discussed above and shown in Table 1 the phylogenetic assessment of many of the progenetic species is still uncertain based on morphology. For example, even though the supposed progenetic origin of Dinophilidae is well substantiated especially by investigations of the nervous system showing apparent larval and juvenile characters (Müller and Westheide 2002), their phylogenetic affiliation within Annelida, except for the exclusion from Eunicida, is unresolved (Struck and others 2002, Struck and others 2005a). The phylogenetic position of other taxa including Microphthalmus, Protodrilida, Nerillidae, and Psammodrilidae is also unresolved (see Dahlgren and others 2000; Rouse and Pleijel 2001). In contrast, placement of several other species in specific polychaete taxa is well established by morphological autapomorphies. For example, the inclusion of Microdorvillea and Ikosipodus within at least Eunicida is well established because of the possession of a ventral pharyngeal organ with a complex jaw apparatus consisting of mandibles and rows of maxillary pieces (for example, Eibye-Jacobsen and Kristensen 1994). However, even the position of these better-established taxa within that particular polychaete taxon is often uncertain. For example, based on the cladistic analysis of Eibye-Jacobsen and Kristensen (1994) Microdorvillea and Ikosipodus are members of a highly derived, unique crown group of progenetic dorvilleids and dinophilids comprising also Arenotrocha, Petrocha, Pusillotrocha, Neotenotrocha, Parapodrilus, Apodotrocha, Aphyangtus, Trilobodrilus, and Dinophilus (see Fig. 2A). Alternatively, Westheide (1982) and Westheide and Riser (1983) also suggested a close relationship of a group containing Pusillotrocha, Ikosipodus, Petrocha, Arenotrocha, and Microdorvillea, but far away from another group including Parapodrilus, Apodotrocha, Aphyangtus, Trilobodrilus, and Dinophilus. Furthermore, Westheide (1987) acknowledged the possibility that independent progenetic origins of species might occur even more often within dorvilleids. Molecular data substantiate the hypothesis of several independent progenetic origins of dorvilleid and dinophilid species (Struck and others 2002, Struck, Halanych and Purschke 2005a, 2006). Thus, the phylogenetic assessment of progenetic taxa in polychaetes is problematic and may be misled by morphology. This has also recently been shown for progenetic salamanders using a comparative approach between molecular and morphological data (Wiens and others 2005).

Problematic factors

Several factors may be responsible for the problems occurring in the phylogenetic assessment of progenetic taxa. In cladistic analyses of morphological data usually only adult stages are compared with each other to establish a common basis for judgment and homology. However, in the case of progenetic species, this means that adult taxa with larval features are compared with other adults, which already possessed a similar stage or features in an earlier phase of their development. Thus, one could argue that comparable life history stages are not being used to score the taxa.

Especially within the salamander literature the possession of similar larval characters in the adult stages of distantly related paedomorphic taxa has been suggested and shown to obscure phylogenetic analyses based on “adult” morphology (for example, Hecht and Edwards 1976; Good and Wake 1992; Larson and Dimmick 1993; Wiens and others 2005). Similar to salamanders, larval characters in polychaetes exhibit an overall
structural similarity. For example, and as mentioned above, investigations on the nervous system of the Dinophilidae clearly show larval and juvenile characters indicating progenetic evolution (Müller and Westheide 2002), but these structures are widespread among larval and juvenile polychaetes belonging to various taxa. This is also true for other typical larval features of progenetic species like protonephridia or ciliary gliding bands.

Due to the deletion of potential paedomorphic characters from their data set Wiens and others (2005) were able to show the negative influence of synapomorphic characters of adult stages of nonpaedomorphic taxa on the phylogenetic placement of paedomorphic taxa. Because of the retention of a larval status these synapomorphic characters, completely developed only after metamorphosis, are absent in paedomorphic taxa and thus their placement in phylogenetic reconstructions may be misled. In the analysis of Eibye-Jacobsen and Kristensen (1994) the group of supposedly progenetic dorvilleids and dinophilids is only supported by absent characters, which are present in the adult stages of nonpaedomorphic ingroup and outgroup taxa. But not only with regard to paedomorphic taxa are reductions or even losses of characters problematic. The interpretation of absent morphological characters in a phylogenetic context as either plesiomorphic absent or secondary lost and thus apomorphic absent is difficult (for example, Purschke and others 2000; Collin and Cipriani 2003; Jenner 2004).

At last, Wiens and others (2005) demonstrated the negative impact on the phylogenetic assessment of paedomorphic salamanders by convergent adaptation to the aquatic habitat. Similar adaptations of the same morphological characters could be shown in aquatic, nonpaedomorphic salamanders and even other aquatic tetrapods. In contrast to terrestrial, nonpaedomorphic salamanders with aquatic larval stages, paedomorphic salamander lineages lack the constraints imposed by terrestrial adult morphology and can more freely adapt to the aquatic niche (Wiens and others 2005). As most of the presented supposedly progenetic polychaetes inhabit the same environment, the marine interstitium, convergent adaptation might also be a factor to consider.

Therefore, due to these reasons morphological analyses would most likely lead to one clade of taxa with presumed progenetic evolution, irrespectively whether these characters evolved independently or not. However, molecular phylogenies should be able to facilitate the distinction between homolog and convergent morphological characters, because neither the specific selection pressures of the new habitat nor the change in life history do affect this kind of data.

The sequence of a gene will be the same independent from the developmental stage it is determined from. Thus, future taxonomic and phylogenetic studies of supposedly progenetic species should integrate the results from both molecules and morphology to obtain a more holistic knowledge of their evolution.

Example of phylogenetic reconstruction using a hypothetical progenetic descendant

The principal of progenesis assumes that a larval stage becomes sexual mature and arrests the further somatic development (Gould 1977). Accordingly, the coding of a larval stage of a recent species as a sexual mature stage would simulate this process with the advantage of knowing a priori the ancestor/sister taxon (that is, the sexual mature stage of the recent species). To show the validity of the arguments made above, I reanalyzed the absence/presence data matrix of Eibye-Jacobsen and Kristensen (1994) with the Eunicidae/Tetraprionidae outgroup including such a hypothetical progenetic descendant. Therefore, the early developmental stage of Schistomeringos rudolphi without appendages, jaws and parapodia, shown left in Fig. 1 (Richards 1967), was coded according to the character state description provided by Eibye-Jacobsen and Kristensen (1994) resulting in the following 38 character states:

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1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 ? 0 0 0 0 0.
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To be conservative the nonpaedomorphic characters 37 and 38 addressing sperm morphology were coded the same as in the adult stage of *S. rudolphi*. Exhaustive searches for the most parsimonious (MP) trees were performed using the branch and bound option in PAUP*4.0b (Swofford 2002). All character state transitions were unordered and characters were weighted as assigned in the final stage of the successive weighting (Table IV, Eibye-Jacobsen and Kristensen 1994). Strict consensus trees were drawn from the obtained MP trees. Additionally, bootstrap analyses of 1000 replicates were performed using a heuristic search with 10 random additions of taxa in each replicate with no more than 10000 trees saved per replicate (Nchuck = 10000 ChuckScore = 1). The strict consensus tree of 135 MP trees of the analysis without the larval *Schistomeringos* (Fig. 2A) is congruent with the one tree chosen by Eibye-Jacobsen and Kristensen (1994), except this analysis did not recover a sister-group relationship of *Parougia* and *Ougia*. The analysis of the data set with the larval *Schistomeringos* generally revealed the same topology (Fig. 2B). The larval stage is not closely related to the adult *Schistomeringos* but to the jawless *Parapodrilus*, *Apodotrocha*, *Apharyngtus*, *Dinophilus*, and *Trilobodrilus*. Additionally, this clade is supported by the highest bootstrap value (91) in
this analysis. Interestingly, the parapodia-bearing Parapodrilus is more closely placed to the other 4 taxa without parapodia than the parapodia-less larval stage. If the actual origin of the larval stage would have been unknown, as is the case for all included progenetic species, this bias of the morphological series may have been inferred to be credible. Thus, this analysis figuratively demonstrated the problems in assessing the phylogenetic position of progenetic species.

How to assess the phylogenetic position of progenetic taxa

Different strategies have been proposed how to assess the phylogenetic position of progenetic taxa using morphological data sets. A possibility would be to use only larval features (Wiens and others 2005). However, the developmental stages of different species have to be homologized to each other to provide a reasonable basis for the judgment of primary character homology. Furthermore, in continuously developing taxa like dorvilleids, the different developmental stages have to be defined first, which might provide an additional source of systematic error due to other unknown processes of heterochrony. Furthermore, due to the fact that progenetic evolution can take place in many different developmental stages (for example, see morphological series of dorvilleids (Westheide 1984)) no developmental stage can be neglected. Thus, the entire life histories of the investigated taxa have to be known and included based on an appropriate coding matrix. At last, as already mentioned larval features are often widespread among polychaetes belonging to various taxa. This is also known from salamanders (Wiens and others 2005).

The exclusion of paedomorphic characters, defined as the presence of character states in both larval or juvenile stages of nonpaedomorphic taxa and adults of paedomorphic taxa (Wiens and others 2005), has been suggested for phylogenetic analyses of salamanders (for example, Duellman and Trueb 1986). However, this requires that such characters can be identified. Furthermore, Wiens and others (2005) showed that other factors like synapomorphies of adult characters in nonpaedomorphic taxa and convergent evolution have an impact on the phylogenetic assessment of paedomorphic taxa and thus they proposed to code the adult morphology of paedomorphic taxa as unknown, given the assumption that comparable life history stages are not being used to score the taxa. Whereas both approaches are possible with salamander data sets (30 paedomorphic excluded or 317 coded unknown out of 326 characters in Wiens and others 2005), in the analysis of Eibye-Jacobsen and Kristensen (1994) either only the characters 37 and 38 addressing sperm morphology would be regarded as nonpaedomorphic or all 38 characters in the supposed progenetic taxa had to be coded unknown. The latter effectively means that the progenetic taxa are excluded from the analysis.

Nevertheless, to discriminate between the different types of characters is the most promising approach in the case of progenetic/paedomorphic taxa. Ideally the characters should be either exclusive to a certain stage (for example, reproductive or exclusively larval characters) or not alter during development (for example, the number of chromosomes). Sequence data of genes typically used in molecular phylogenetic analyses (for example, 18S rDNA or cytochrome c oxidase subunit I) are not altered neither by developmental processes nor by evolutionary processes like progenesis or adaptation to a specific habitat (for example, Hillis and others 1996; Wiens and others 2005). Therefore, given data availability, number of characters and effort to generate new data molecular data are the data type of choice to elucidate the phylogenetic affiliations of supposed progenetic taxa. However, molecular phylogenetic analyses only produce trees and additional data are necessary to put the results into a biological context. With regard to progenesis this means to positively deduce the progenetic origin of a taxon the biology and life history of the particular taxon, as well as of the closest relatives has to be compared with further related taxa.

Recent molecular phylogenetic analyses of Poeobius meseres and Flabelligeridae were able to show the highly derived position of this holopelagic taxon within the benthic flabelligerids (Burnette and others 2005). P. meseres possesses only 11 poorly defined segments with no setae (Rouse and Pleijel 2001). Based on midwater spawning, relatively late development of setae (that is, at or after the 11 setiger stage) and feeding larvae in Flabelligera commensalis (Spies 1977), a progenetic origin of the holopelagic Poeobius seems reasonable (Burnette and others 2005). Thus, progenetic origin within polychaetes not only occurs in the colonization of the interstitial space.

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References


