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Review article

The polychaete-to-clitellate transition: An EvoDevo perspective

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Annelids, or segmented worms, constitute one of the major animal phyla. The modular organization of the segmental body plan has endowed a high degree of constructional flexibility. This enabled the evolution of a high degree of morphological diversity in the Phylum Annelida, making the annelids a useful system for studying how an animal body plan diversifies and evolves. On the basis of their morphological characteristics, two distinct groups of annelids, Polychaeta and Clitellata, are traditionally recognized (Brusca and Brusca, 1990; Rouse and Fauchald, 1995, 1998). Although this traditional taxonomy is no longer supported by new molecular evidence (see below), it nevertheless suggests that the distinctions between these two groups are indeed evolutionarily significant. Polychaetes constitute a highly diverse group of worms equipped with various body plan features, including parapodia and clusters of chaetae attached to parapodia. Clitellates are defined by the presence of the clitellum (thus Clitellata), a glandular structure producing cocoons that encapsulate eggs, and the absence of the parapodium (Brusca and Brusca, 1990). Other than these taxon-defining characters, there are also additional morphological differences. For example, the sensory nuchal organ can only be found in nearly all polychaete species, but it is absent from all clitellate species; also absent from the clitellate species are characters such as prostomial appendages and epidermal ciliation, (Purschke, 2002). Additionally, the mode of development, which is highly relevant to our discussion, also differs between polychaetes and clitellates. In general, the early embryogenesis of polychaetes is similar to that of other spiralian taxa (Hejnol, 2010; Lambert, 2010; Wilson, 1898) as they develop indirectly, first into a trochophore larva and then morph into the adult form. By contrast, clitellates directly develop into their adult forms, bypassing the trochophore stage (Anderson, 1966a). Here, I compare these two basic modes of annelid development and propose an evolutionary scenario for the developmental changes underlying the evolutionary divergence between these two groups of annelids.

1. Annelida phylogeny and polychaete-to-clitellate transition

Over the past two decades, studies on molecular phylogenetics have firmly placed annelids, together with molluscs, flatworms, nemerteans, lophophorates, and other lesser phyla, into Superphylum Lophotrochozoa (Aguinaldo et al., 1997; Dunn et al., 2008). The phylogenomic approach has been successfully used to elucidate interrelationships between the lophotrochozoan phyla (Dunn et al., 2008; Laumer et al., 2015; Nesnidal et al., 2013; Struck et al., 2014). Annelid is one of the most diverse lophotrochozoan phyla. Therefore, interrelationships between annelid subgroups are a critical issue in lophotrochozoan evolution. Even in the very early days of annelid molecular phylogenies, it had become clear that Polychaeta is a paraphyletic group (Kojima, 1998; McHugh, 1997). Recent phylogenomic studies have also supported this scenario (Andrade et al., 2015; Struck et al., 2015, 2011; Weigert et al., 2014). Several monophyletic groups, such as Clitellata, Echiura, Sipuncula, and Pogonophora, arose from within Polychaeta. Furthermore, phylogenomic data have defined Clitellata as a subgroup of Sedentaria, one of the two major clades within the Phylum Annelida; the other clade is Errentia. However, these studies have not resolved the sister clade of Clitellata. The phylogenetic position of Clitellata within the Phylum Annelida is presented in Fig. 1A.

In any case, the phylogenetic position of Clitellata unequivocally supports directional evolution from polychaetes to clitellates in many morphological traits, and this is also likely the case in the evolution of development. Given that the early embryogenesis of polychaetes is similar to that of some nonannelid lophotrochozoans (*e.g.,* noncephalopod molluscs and polyclad flatworms), the mode of polychaete embryogenesis is likely plesiomorphic in annelids, whereas that of clitellate embryogenesis is apomorphic. Considering this well-defined polarity in character evolution, I use the term “polychaete-to-clitellate transition” (PCT) to refer to evolutionary changes that occurred at the root of clitellates.

A major habitat change likely triggered the PCT. Most polychaetes are found in marine habitats, whereas clitellates are predominantly found in freshwater and terrestrial habitats (Fig. 1B). The last common ancestor of living clitellates was likely a freshwater species, and extant marine clitellates are generally considered to be secondarily evolved from their freshwater ancestors (Rousset et al., 2008). It was proposed that the first clitellate arose in a coastal lagoon or brackish water before further invading inland freshwater habitats (Omodeo, 1998). In contrast to the stability of marine environment, physical and chemical factors are constantly changing in the environs where the first clitellates evolved. Adaptations to such challenges had provided ancient clitellates the ability to further invade and colonize hostile inland habitats. Therefore, in the present study, clitellate developmental traits are examined in the context of adaptive strategies adopted by ancient clitellates to conquer freshwater and terrestrial habitats.

Fossil records and molecular time trees have suggested that all major animal phyla arose in the Precambrian ocean. By contrast, fossil

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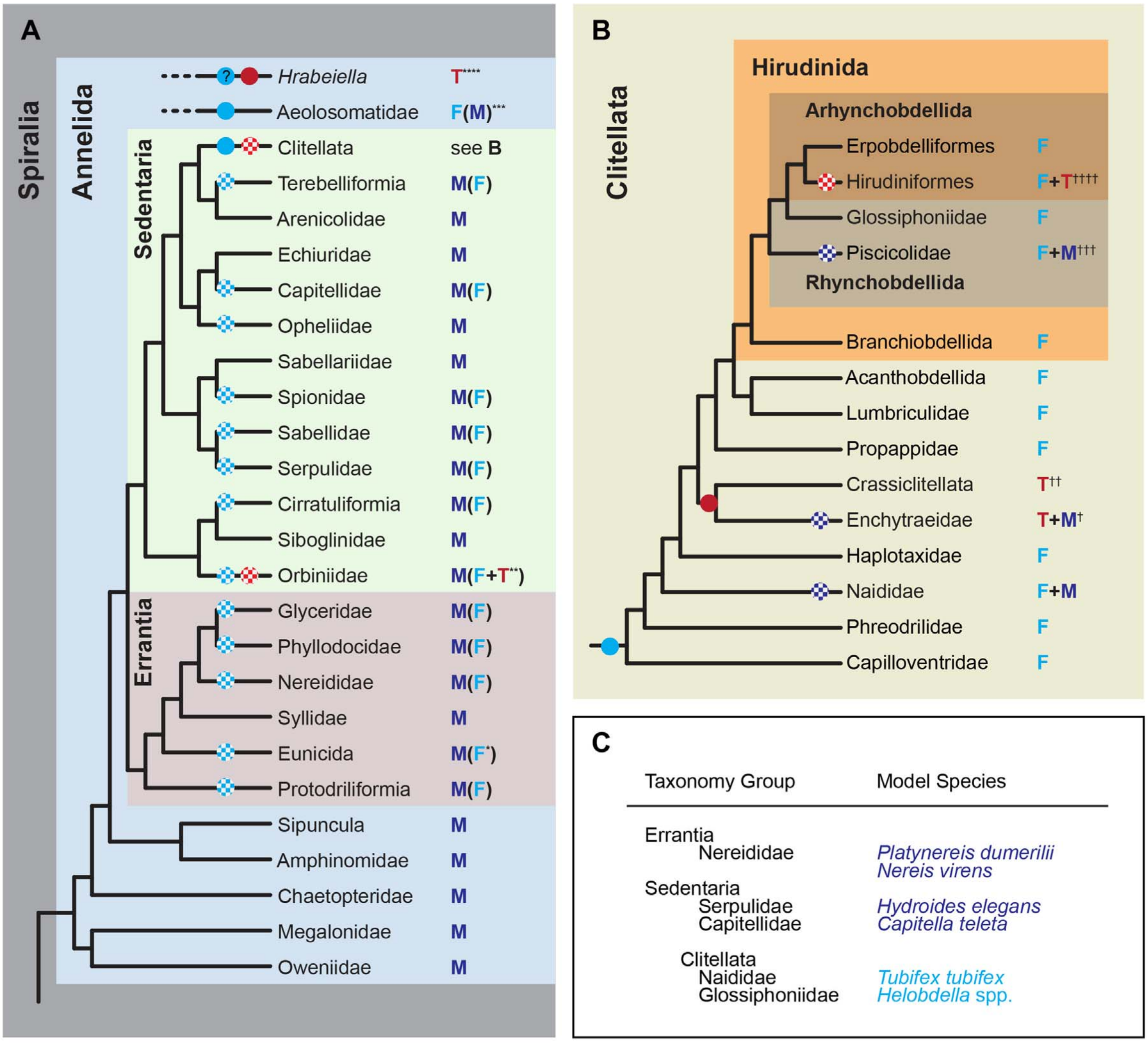

Fig. 1. Phylogenetic context of the Polychaete-to-Clitellate Transition. **A**. Phylogenetic distribution of the invasion events (circles on the branches indicate the occurrence of invasion events; freshwater: cyan; terrestrial: red) across Phylum Annelida. This distribution pattern suggests multiple independent invasion events in Annelida. Solid label indicates the invasion event occurred at the base of the clade, and hatch label indicates that the invasion events occurred in subgroups of the clade. Type(s) of the habitat for each group is labeled on the right side of the taxon name. M (dark blue): marine; F (cyan): freshwater; T (red): terrestrial. *: Family Histriobdellidae in the Eunicida is predominantly freshwater. **: *Parergodrilus heideri* is one of the only two identified terrestrial polychaete species. ***: phylogenetic position of Family Aeolosomatidae (predominantly freshwater) is undetermined. ****: the enigmatic terrestrial polychaete species *Hrabeiella periglandulata* is not assigned to any family yet. Habitat information is taken from Glasby and Timm (2008) and Purschke (1999). **B**. The Clitellata represents the most successful annelid clade in the freshwater and terrestrial habitats. The ancestral clitellates were probably freshwater, and the Enchytraeidae ('white worms' or 'pot worms') + Crassiclitellata (common earthworms) clade and the Hirudiniformes (jawed leeches, including the medicinal leeches) further invades the terrestrial habitats. Note that the leeches forms a monophyletic group within the paraphylectic Oligochaeta. †: in the wild, members of the Enchytraeidae are found in soil but can also survive in fresh water and they are thus amphibious; some enchytraeid species are found in marine sediment, and they probably represent a secondary invasion of marine habitat. ††: most members of Crassiclitellata are exclusive terrestrial. †††: The piscicolid leeches are ectoparasites of fishes, and the marine piscicolid are considered to be secondarily evolved. ††††: The terrestrial leeches are surface species and are usually amphibious. Phylogenetic tree and habitat information are taken from Rousset et al. (2008). **C**. The annelid model species in which a substantial amount of experimental data related to embryonic development has been produced in the past three decades and their taxonomic affiliations.
The phylogenetic tree is adapted from Struck et al., (2011, 2015) and Weigert et al. (2014).

records of terrestrial animals were only found later in the Ordovician and the Devonian (Shear, 1991), suggesting that terrestrial animals arrived later and were descendants of their marine ancestors. The invasion of land had occurred multiple times in various metazoan lineages (Little, 1983), and the PCT was the most significant invasion-of-land event in the Phylum Annelida. The exact timing of the PCT remains unknown. Molecular dating has placed the origin of annelids in the Ediacaran and the diversification of crown groups between the Cambrian and the Lower Ordovician, and the expansion of Clitellata groups in the Lower Permian (Edgecombe et al., 2011; Erwin et al., 2011). Given that the last common ancestor of clitellates was likely a freshwater species, the PCT event must have occurred before the expansion of the clitellate clade. Therefore, the PCT could have taken place at any point between the Upper Cambrian and the Lower Permian. The Paleozoic fossil records of possible clitellate species are scant and poorly preserved, and most candidate specimens were from the Ordovician shallow water marine sites (Conway Morris et al., 1982). If these fossils are indeed those of clitellates, they may represent the earliest stage of the PCT event.

2. Evolutionary conservation of cell lineage and fate maps

In terms of developmental evolution, a key PCT event was the reorganization of development to remove the trochophore larval stage from the life history of clitellates (Fig. 2A). To identify and reconstruct developmental changes during the PCT, one approach is to compare homologous developmental pathways between the members of these two taxa. Homology is the central element in comparative biology (Hall, 2003), but identifying homology is not often straightforward, particularly when comparing distantly related taxa. However, the