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## POGONOPHORA (SIBOGLINIDAE) ARE NOT POLYCHAETES: A SYSTEMIC VIEW OF METAMERIAN ANIMALS

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### RESUMO

***Pogonophora (Siboglinidae) não são poliquetas: uma visão sistêmica dos animais metaméricos.*** Trabalhos recentes têm revisado a história dos pogonóforos com o paradigma cladístico, e concluem que este grupo não mais representa um táxon deuterostomado, mas constitui uma simples família de poliquetas, os Siboglinidae. Entretanto, alguns autores estranhamente omitiram capítulos recentes em sua revisão histórica. Primeiro, eles ignoraram opiniões contrárias que indicam que Annelida e Polychaeta são parafiléticos. Numa abordagem sistêmica, tanto anelídeos como poliquetas devem ser referidos a um clado mais abrangente, os Metameria. Nesta perspectiva, faz pouco sentido considerar Siboglinidae como pertencente ao táxon não existente "Polychaeta". Segundo, nós reforçamos que há fortes evidências, não citadas por autores recentes, de que pogonóforos representam um clado transicional entre vermes metaméricos esquizocélicos (Oweniidae em particular), e radiários oligoméricos enterocélicos. Os principais caracteres discutidos aqui, que estabelecem relacionamentos entre poliquetas, pogonóforos e deuterostômios são: 1) sistema nervoso; 2) padrão de clivagem e celoma; 3) tagmose e redução de segmentos; 4) desenvolvimento assimétrico; 5) larva modificada. A história não pode ser feita ignorando evidências contrárias. Por isso, adicionamos uma discussão sobre a história dos pogonóforos (ou Siboglinidae), baseado em uma sistemática filogenética sustentada pelos princípios de Hennig.

**Palavras-chave:** Metameria, poliquetas, pogonóforos, deuterostômios, clado de transição.

### ABSTRACT

***Pogonophora (Siboglinidae) are not polychaetes: a systems view of the metamerian animals.*** Recent papers have reviewed the history of pogonophores with the cladistic paradigm, and conclude that this group no longer represents a deuterostome taxon, but consists of a single clade of polychaetes, the Siboglinidae. However, some authors strangely skip some chapters in their historical review. First, they ignore recent alternative opinions, which indicate that Annelida and Polychaeta are paraphyletic. Under a systemic approach, both annelids and polychaetes must be

referred to a much larger clade, the Metameria. Under this perspective, it makes little sense to consider Siboglinidae as belonging to the nonexistent taxon "Polychaeta". Second, we reinforce that there is strong evidence, not cited by the recent references, that pogonophores represent a transitional clade between schizocoelous metamerian worms (Oweniidae in particular), and enterocoelous oligomerian radialians. The main characters discussed herein that establish relationships among polychaetes, pogonophores, and deuterostomes are: 1) nervous system; 2) cleavage pattern, and coelom; 3) tagmosis, and reduction of segments; 4) asymmetrical development; 5) modified larva. History cannot be made by ignoring contrary evidence, so we conclude discussing the history of Pogonophora (or Siboglinidae), based on phylogenetic systematics under Hennigian principles.

**Key words:** Metameria, Polychaetes, Pogonophores, Deuterostomes, transitional clade.

## INTRODUCTION

The taxonomy and phylogenetic position of Pogonophora, including Frenulata, Monilifera (which including *Sclerolinum* and Vestimentifera), and recent *Osedax*, has been debated since their discovery by French biologist Maurice Caullery, in 1914, which described a long slender tube living worm.

Several important papers on histology (CAULLERY, 1914; USCHAKOV, 1933; JOHANSSON, 1937, 1939; BEKLEMISHEV, 1944; IVANOV, 1955, 1963; WEBB, 1964; JONES, 1985a, b, MAÑÉ-GRAZÓN and MONTERO, 1985; SOUTHWARD, 1993; SCHULZE, 2001, 2002; MATSUNO and SASAYAMA, 2002; SASAYAMA *et al.*, 2003), blood biochemistry (SOUTHWARD and SOUTHWARD, 1963; MILL, 1972; TERWILLIGER *et al.*, 1987; SUZUKI *et al.*, 1989), and ontogeny (JÄGERSTEN, 1957; NØRREVANG, 1970a; SOUTHWARD, 1975; IVANOV and GUREEVA, 1976; GUREEVA, 1979; GUREEVA and IVANOV, 1986; IVANOV, 1988; YOUNG *et al.*, 1996), were motivated by the desire to clarify obscure aspects of these worms and to place these animals among the Metazoa.

Notwithstanding these efforts, a consensus has not been reached on whether: (1) pogonophores represent an independent Phylum within Protostomia (JONES, 1985a, b, SOUTHWARD, 1975); (2) pogonophores represent an independent phylum within Deuterostomia (JOHANSSON, 1937, 1939; JÄGERSTEN, 1957; HYMAN, 1959; AX, 1960; IVANOV, 1960, 1975a, b, 1988; ULRICH, 1972; SIEWING, 1975; MALAKHOV *et al.*, 1997; IVANOVA-KAZAS, 2007); (3) these worms must be reduced to a family among the polychaete worms - Siboglinidae (ROUSE and FAUCHALD, 1995, 1997; ROUSE, 2001; SCHULZE, 2003; BARTOLOMAEUS *et al.*, 2005, PLEIJEL *et al.*, 2009); or (4) pogonophores emerge from a common connecting link between advanced coelomate gastroneuralian and oligomeran organization (LIVANOV and PORFIREVA, 1965, 1967; SALVINI-PLAWEN, 1982, 1998, 2000; SMITH *et al.*, 1987; CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994, ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003).



The aims of this paper are to present five points of view regarding the phylogenetic position of the pogonophores, and to support the view which we consider most coherent in an evolutionary context: that pogonophores represent a transitional clade between oligomeric Radialia (Phoronida + Deuterostomia), with three anterior enterocoelic tagma (tricoelomate pattern), and multimetameric polychaetes, with a schizocoelic pattern (multicoelomate pattern), such as is still found in the opisthosome of pogonophores.

### COMPLEMENTING THE HISTORICAL ACCOUNT

Recent papers pointed a new concept of the pogonophores, arguing for their placement as a monophyletic family within the Polychaeta. However, because their essay was presented as a historical account of the group, we were surprised not to find mention of recent authors who defend an alternative point of view. Several papers explicitly reject considering pogonophores a family of polychaetes (RIEDL, 1963; GARDINER, 1978; CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; SOUTHWARD, 1999, 2000; SMIRNOV, 2000a, b; ALMEIDA and CHRISTOFFERSEN, 2001; SOUTHWARD *et al.*, 2002; MATSUNO and SASAYAMA, 2002; SASAYAMA, *et al.*, 2003; ALMEIDA *et al.*, 2003; KOJIMA *et al.*, 2002, 2003; IVANOVA-KAZAS, 2007).

Others further sustain that, because of their oligomeric organization into anterior body tagmas, pogonophores represent an clade of Deuterostomia (JOHANSSON, 1937, 1939; JÄGERSTEN, 1957; IVANOV, 1960, 1963, 1975a, b; IVANOVA-KAZAS, 2007), or a clade intermediary between paraphyletic polychaetes (more closely related to the oweniids or, even more specifically, to *Owenia fusiformis*) and the Radialia (Phoronida + Deuterostomia) (RIEDL, 1963; LIVANOV and PORFIREVA, 1965, 1967; ULRICH, 1972; SIEWING, 1975; GARDINER, 1978; MALAKHOV *et al.*, 1997; SALVINI-PLAWEN, 1982, 1998, 2000; SMITH *et al.*, 1987; CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003).

Some authors aimed to resolve dissent by furnishing a new authoritative chapter on the evolutionary history of these animals. However, they do not refute some arguments that have been discussed more recently in the primary literature. In their historical review, they consider mainly the formation of the nervous system and of the coelom, but it is possible to interpret their conclusions differently. Before considering these and other characters, we posit the following reflection: How can pogonophores belong to Polychaeta if both Polychaeta and Annelida represent paraphyletic taxa?

The monophyly of Annelida and Polychaeta remain inconclusive or has been definitively rejected based on several studies involving morphology (CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; NIELSEN, 1995; EIBYE-JACOBSEN, 1996; WESTHEIDE, 1997; ALMEIDA and

CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003; PURSCHKE *et al.*, 2000), and molecules such as 18S rRNA (BLEIDORN *et al.*, 2003a, 2003b), EF1 $\alpha$  (MCHUGH, 1997, 2000; KOJIMA, 1998), 18S rRNA in combination with histone H3, U2, snRNA, and gene fragments (JENNINGS and HALANYCH, 2005, BLEIDORN *et al.*, 2006), or 18S rRNA in combination with other genes fragments such as 28S rRNA, 16S rRNA, histone H3 or *cox1* (ROUSSET *et al.*, 2004, 2007; COLGAN *et al.*, 2006).

CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA (1994) reconstructed the phylogeny of Enterocoela and questioned the monophyly of Annelida and Polychaeta, proposing that the smallest clade that contains all animals previously referred to as polychaetes should be named Metameria. They further positioned pogonophores as the sister group of Radialia (Phoronida + Deuterostomia) (Figure 1A). These results were further corroborated by ALMEIDA and CHRISTOFFERSEN (2001), and ALMEIDA *et al.* (2003). In this last paper, four main lineages of Metameria were established: 1 – Echiura, with an uncertain position within polychaetes (NIELSEN, 1995; EIBYE-JACOBSEN, 1996; MCHUGH, 1997), although Sternaspidae has been suggested as the most likely sister group (ALMEIDA and CHRISTOFFERSEN, 2001, ALMEIDA *et al.*, 2003). Presently, phylogenetic analyses with morphological and molecular data indicate that echiurans are related to Capitellida (STRUCK and PURSCHKE, 2005; COLGAN *et al.*, 2006; and ROUSSET *et al.*, 2007), that echiurans are the sister-taxon of *Capitella*, and that sipunculans are placed among other annelids (DUNN *et al.*, 2008). In previous analyses, sipunculans appeared as the sister-taxon of mollusks, at the base of annelids (HALANICH, 2004); 2 – Ecdysozoa, including Arthropoda, a lineage in which arthropodia were hypothesized to be derived from the parapodia of polychaetes (WALTON, 1927; MANTON, 1977), and homologies have been suggested between the elytrae of the Aphroditiformia and the dorsal plates of marine lobopodians (DZIK and KRUMBIEGEL, 1989), suggestions that have been further developed in ALMEIDA and CHRISTOFFERSEN (2001) and ALMEIDA *et al.* (2003, 2008); 3 – Clitellata, which is strictly related to Questidae (ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003; GARRAFFONI and AMORIM, 2003; CHRISTOFFERSEN, 2009), 4 – pogonophores, a lineage derived from sedentary tubicolous polychaetes such as *Owenia* and related to the oligomeric animals, the radialians (Figure 1B) (GARDINER, 1978; SALVINI-PLAWEN, 1982, 1998, 2000; SMITH *et al.*, 1987; CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003).

An important series of papers on the ontogeny of the neuropodial chaetae were published by BARTOLOMAEUS (1995, 1996). These authors compared the uncini of several polychaetes with those of pogonophores, concluding that the clades Oweniida, Terebellida, Pogonophora and Sabellida are strictly related.

ROUSE and FAUCHALD (1995, 1997) were the first to establish

pogonophores as a family of polychaetes, on the basis of a cladistic analysis of morphological characters. They renamed the pogonophores as Siboglinidae and placed them together with Sabellariidae, Sabellidae, Serpulidae, and the more basal Oweniidae, within the Sabellida. The latter taxon was based on the following synapomorphies: a limited fusion of the prostomium and the peristomium, and a peristomium that is not limited exclusively to the lips. However, the first of these characters is homoplastic in other polychaetes and the second represents a reduction of an earlier evolved character, making both characters inconsistent to support a valid clade (BARTOLOMAEUS *et al.*, 2005).

ROUSE (2001) provided further cladistic data to support the inclusion of pogonophores and vetimentiferans as a family of polychaetes. SCHULZE (2003) conducted a phylogenetic analysis of Vestimentifera, also accepting the Siboglinidae. BARTOLOMAEUS *et al.* (2005) established Sabellida (including Sabellidae and Serpulidae) as the sister group of pogonophores, on the basis of the following synapomorphies: nephridia in segment 2 and presence of dorsal nephridiopores. ROUSSET *et al.* (2007) argued, on the basis of a molecular phylogeny of 28S rRNA, 16S rRNA, histone H3, and cox1 molecules, that Annelida and all its component taxa, including Polychaeta and Sabellida, are not monophyletic.

#### BRIEF REFLECTIONS ON SOME CHARACTERS DISCUSSED IN THE LITERATURE

##### Nervous system

The pogonophores typically have an intraepithelial nervous system as is characteristic for Epineuralia (Oligomera + Chordata). With the acceptance of the mid-longitudinal nerve cord as being ventral, this differentiation corresponds to the midventral nerve cord in Pterobranchia and Enteropneusta (SALVINI-PLAWEN, 1998, 2000; SMITH *et al.*, 1987). This mid-ventral concentration of the intraepithelial nervous system is likewise present in oweniids (MCINTOSH, 1917; BUBKO and MINICHEV, 1972; SALVINI-PLAWEN, 1982; SMITH *et al.*, 1987; LAGUTENKO, 1985). PLEIJEL *et al.* (2009) infer from NØRREVANG (1970a, b) that Ivanov was mistaken in attributing a dorsal position for the nervous cord in pogonophores. However, SALVINI-PLAWEN (1998, 2000), ULRICH (1972), and IVANOV (1988) rejected the arguments of NØRREVANG (1970a, b), and reaffirmed their previous conclusions. SALVINI-PLAWEN (2000) explained that the internal cell mass of the diploblastic stage separates a frontal enterocoelic sac which enlarges posterior along both sides between the ectoderm and entoblastema, losing its connection to the latter. Yet the paired coelomic sacs subsequently subdivide from back to front into four compartments: the first tentacle is formed left-dorsally and is provided with a coelom from the not-yet-subdivided compartment. This corresponds to

the oligomeric mesocoelom and protocoelom, a condition found in many Echinodermata. In our conception, a sedentary and tubicolous animal with a crown of sulcate tentacles surrounding the head for feeding and respiration, such as occurs in Spionida, Terebellida, Sabellida, Oweniida, Pogonophora, Phoronida, among others, are functionally radiate in organization, at least in the head region. For example, many species of sabellids and serpulids have groups of ocelli on the radioles, which are distributed over the entire branchial crown, and thus perceive light incidence coming from all directions. However, KUPRIYANOVA *et al.* (2006) indicate that this character still needs more study. The crown is innervated by what in other polychaetes would be the palpal nerves; the dorsal lips are more complexly innervated, but do not correspond to either antennae or palps (ORRHAGE, 1980; ROUSE and FAUCHALD, 1997). In sabellariids, sabellids and serpulids, the border between thorax and abdomen is marked by chaetal inversion, with the dorsal notochaetae and the ventral comb-shaped neurochaetae (uncini) of the thorax changing positions, so that abdominal uncini become dorsal (notopodial) and abdominal chaetae become ventral (neuropodial) in the abdomen (TEN HOVE and KUPRIYANOVA, 2009). Thus, also in the abdomen the ventral side is considered dorsal, and the dorsal side becomes ventral. Because the nervous cord remains in the same position, it becomes effectively dorsal, in our opinion.

Other closely related polychaetes, such as maldanids (tubicolous), and capitellids arenicolids (not tubicolous, but remaining sedentary), excavate galleries and have thus lost their cephalic structures, a precursor condition for the derivation of the clitellate lineage. We believe these polychaetes are related to pogonophores based on the presence of well-developed body tagma and on the presence of hooks and uncini, two structures that form a transformation series, as hypothesized by BARTOLOMAEUS *et al.* (2005). It may thus make little sense to distinguish dorsal from ventral in tubicolous worms. On the other hand, the evolution of the tubicolous condition may explain the transition of a ventral nervous cord to a dorsal nervous cord that occurred along the transition from a schizocoelous to an enterocoelous metameric animal.

In the last decades a series of important papers have been published on the anatomy and physiology of the brain (DENES *et al.*, 2007; TESSMAR-RAIBLE *et al.*, 2007; TOMER *et al.*, 2010), demonstrating that the neurosecretory control centers form part of the forebrain in many animal phyla, and indicating that vertebrates, insects, and annelids have a common origin, although the evolutionary origin of these centers is largely unknown.

Another paper (ARENDRT *et al.*, 2004) showed that insect and vertebrate eyes use rhabdomeric and ciliary photoreceptor cells, respectively. In the marine ragworm *Platynereis*, both cellular types are found: rhabdomeric photoreceptor cells in the eyes, and ciliary photoreceptor cells in the brain, indicating that this worm shares a common ancestry with insects and vertebrates.



#### Cleavage pattern and coelom

The cleavage pattern varies strongly between *Siboglinum* and *Oligobranchia*, depending on egg shape and the proportion of yolk in the eggs (IVANOVA-KAZAS, 2007). Slight differences occur between cleavage in polychaetes and pogonophores that are related to the prospective value of the blastomeres. In polychaetes, such important primordia as the ectoblast 2d and mesoblast 4d are derivatives of the postero-dorsal quadrant D, whereas in pogonophores a great role in development is played by the anterior quadrant B, comprising materials for the archenteron and coelomic mesoderm (IVANOV, 1988; IVANOVA-KAZAS, 2007). Notwithstanding, the larval development of two vestimentiferans, *Lamellibrachia* and *Escarpia*, apparently reflect the typical pattern of polychaetes (SALVINI-PLAWEN, 2000; YOUNG *et al.*, 1996). Developmental patterns clearly need to be elucidated in more detail. Observations on coelom development were made on whole mounts and paraffin sections of post-gastrulation stage embryos of *Siboglinum caulleryi* and *Nereilinum murmanicum* (IVANOV, 1957, 1963, 1975a, b; GUREEVA and IVANOV, 1986). These authors concluded that coelomic sacs appear from an anterior ectodermal pouch that grows posteriorly as in Enteropneusta. On the other hand, NØRREVANG (1970b) used semi-thin (2-4 µm) Epon sections of *Siboglinum fiordicum* embryos and suggested that the mesoderm is not of entodermal origin, but is formed at two different phases, as in Annelida. IVANOV (1975a, b) disagreed with the conclusions of NØRREVANG (1970b), and investigated *Nereilinum murmanicum*. Together with Gureeva (GUREEVA and IVANOV, 1986), he described the enterocoelic formation of the coelom of *Siboglinum caulleryi*, and further observed that the blastopore opens inside the lumen of the primitive gut. Finally, these authors concluded that NØRREVANG (1970a, b) was wrong about his interpretations of the mesoderm. The enterocoelic pouch mode of coelom formation is derived in relation to the schizocoelic mode resulting from the internal spaces appearing among teloblastic cells (CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003; IVANOVA-KAZAS, 2007). In polychaetes, the coelom is multisegmented and appears by schizocoely, being divided by transversal septae that may be more or less complex. The septae are perforated by the intestine and by the longitudinal blood vessels, while the remaining organs become arranged metamerically. It is still not clear whether the coelom formation in pogonophores is schizocoelic and/or enterocoelic. We hypothesize that the coelom of the three anterior tagma may be formed by enterocoely, while the posterior opisthosomal metameres may retain the primitive schizocoelic mode of coelom formation. This corroborates CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA (1994): "Pogonophora thus still retain a primarily schizocoelic pattern of metamere formation in the posterior part of the body, while a novel enterocoelic and tricoelomate pattern has become superimposed from fore to aft in the anterior region of the body". In this case, both Ivanov and Nørravang were partially

correct. The head coelom – protoel – extends into the tentacles and forms the pericardium of the dorsal heart (IVANOV, 1957, 1994; SOUTHWARD, 1993; GARDINER and JONES, 1993). The second tagma has a coelomic cavity – mesocoel – separated from the first by a mesentery (SOUTHWARD, 1993; GARDINER and JONES, 1993; IVANOV, 1994). The third body tagma has a pair of coelomic sacs – metacoels – running longitudinally along the trunk, and separated by longitudinal mesenteries. This pattern is similar to the tri-coelomate (oligomeric) pattern described by SALVINI-PLAWEN (2000) for the Deuterostomia. The fourth body region – the opisthosoma – has a series of simple coelomic spaces divided by transversal septae as in arenicolids, maldanids and oweniids. This pattern represents strong evidence for an evolutionary transition from the multi-metameric condition of polychaetes to the oligomeric condition of Radialia (Phoronida + Deuterostomia) (CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003).

#### Tagmosis, and segment reduction

The transformation series is the most important evidence for the positioning of pogonophores within the Metameria (CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994), because it represents a transitional stage linking annelids with radiates (Figure 1A-B). Tagmosis consists in the grouping of a number of segments to form new specialized body regions, such as a head, a collar region, a trunk, or a tail. Different tagmata have been formed in the errant polychaete + arthropod lineage on the one hand, and in the sedentary-tubicolous polychaetes + deuterostome lineage on the other (CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003). Among the sedentary polychaetes, tagmosis is well established in the following groups: (1) Spionida – Spionidae, Apistobranchidae, Chaetopteridae, Longosomatidae, Magelonidae, Poecilochaetidae, and Trochochaetidae; (2) Terebellida – Terebellidae, Tricobranchidae, Acrocirridae, Alvinellidae, Ampharetidae, Cirratulidae, Flabelligeridae, and Pectinariidae; (3) Sabellida – Sabellidae, Serpulidae, Sabellariidae, and Oweniidae; and (4) a portion of the “scolecids” – Ophelidae, Capitellidae, Arenicolidae, and Maldanidae. In these groups, the body becomes divided into three distinct regions: (a) a well-defined head without appendages, as in ophellids, capitellids, arenicolids, maldanids, and some representatives of the oweniids, a head tagma with palps or a crown of tentacles in Spionida, Terebellida, Sabellida, and in *Owenia* (in this oweniid the postomium is fused to the peristomium and there is a basal collar); (b) a trunk region that is composed by a more prominent and shorter anterior thorax and a posterior less prominent and more elongate abdomen; and (c) a pygidium, that contains the anus. In arenicolids, maldanids, oweniids, and pogonophores, the median body segments are elongate. In pogonophores the coelom is further divided into three compartments (SALVINI-PLAWEN, 2000).





In arenicolids and maldanids a fourth tagma is present differently of the anterior setigers, which becomes elongate tail in *Arenicola* and *Abarenicola*, and in the maldanids this structure becomes reduced. We consider this fourth tagma homologous to the fourth tagma of oweniids and to the opisthosoma of pogonophores (CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003).

#### Asymmetrical development of anterior pair of coeloms

Dexiothetica JEFFERIES (1979) was attributed to a group of organisms in which a new plane of bilateral symmetry was formed (in Enteropneusta and Chordata), following the suppression of the right side of the body in Echinodermata. The new symmetrical body thus became completely reorganized from the original left side (JEFFERIES, 1979). Evidence for assymetry in the protocoelom occur in pogonophores and in all enterocoels. In the groups in which this pattern was described, the right protocoelom is modified into a pericardium, or a proosomal cardiac vesicle appears and becomes suppressed during development (SALVINI-PLAWEN, 2000). With the subsequent individuation of the proto and mesocoeloms, the tentacular crown becomes associated exclusively with the left protocoelom, while the right protocoelom forms the pericardium. For this reason, we consider the two types of tentacular apparatuses found in pogonophores and deuterostomes to be homologous. Pterobranchia and Enteropneusta also display a tendency for the protocoeloms to become asymmetrical, including an assymetry in the prosomal coelomopore (SALVINI-PLAWEN, 1998).

Pogonophores present an asymmetric pattern of development of the anterior pairs of coeloms, like all deuterostomes. The pericardium, in pogonophores and hemichordates, and the madreporic vesicle in echinoderms, develop at the expense of the right anterior coelom (IVANOVA-KAZAS, 2007). The derivatives of the left anterior coelom and tentacular coelom of pogonophores, the coelom of the proboscis in hemichordates, and some parts of the stone canal of the ambulacral system in echinoderms, all develop in a similar way (IVANOVA-KAZAS, 2007; SALVINI-PLAWEN, 2000).

#### Larval development

Amongst the adaptive diversity of larval forms found in the Metazoa, the mitraria larva of *Owenia* (in our opinion, a modified trochophore), surprisingly presents deuterostome characters, such as monocilliary cells, prototroch with parallel bands of cilia, presence of food groove, metatroch forming sinuous curves, and a deuterostome-like nephridium (SMITH *et al.*, 1987; EMLET and STRATHMANN, 1994; ALMEIDA *et al.*, 2003). These characters indicate that the larva of *Owenia* presents true homologies linking this larval type to the larva of deuterostomes (WILSON, 1932; GARDINER, 1978; ALMEIDA *et al.*, 2003). The larva of *Owenia*, with its so-called catastrophic metamorphosis (WILSON, 1932; ANDERSON, 1974), seems similar to the

groups of Enterocoela, such Phoronida (NIELSEN, 1995). In the mitraria larva the new segments accumulate within the larval hyposphere, until the larva bursts and all the segments are freed catastrophically, differently from other typical polychaete larva, in which somites are added at the posterior region of the animal one by one, and the larvae transform into the adult gradually (ALMEIDA *et al.*, 2003).

### DISCUSSION AND CONCLUSIONS

GEOFFROY SAINT-HILLAIRE (1822), and DOHRN (1875) were the first to propose the origin of Vertebrata from a common ancestor similar to Annelida. The idea that we are but worms has also been reinforced from paleontological evidence (CONWAY MORRIS, 2003a, b). Later studies on hox genes have shown that these are responsible for the dorso-ventral and anterior-posterior orientation of the body axis, and for the segmentation of polychaetes, arthropods and vertebrates (MCGINNIS *et al.*, 1984; LAWRENCE, 1990; FRANÇOIS and BIER, 1995; HOLLEY *et al.*, 1995; JONES and SMITH, 1995; HOLLAND *et al.*, 1997; TAUTZ, 2004; BROWN *et al.*, 2008). Embryological evidence points to a dorso-ventral inversion in the possible derivation of a deuterostome from a protostome ancestor (ARENDRT and NÜBLE-JUNG, 1995a, b, 1997, 1999; NÜBLE-JUNG and ARENDRT, 1999). Ivanov placed the pogonophores as a phylum more closely related to the hemichordates (IVANOV, 1963, 1994; IVANOVA-KAZAS, 2007). JÄGERSTEN (1957) agreed with the homology established between dentate plates and uncini, comparing them with the chaetae of brachiopods. Thus, the pogonophores could be placed as oligomeric deuterostomes, with a double nervous cord placed ventrally, a conclusion also accepted by IVANOV (1975b, 1994).

Histological evidence from the mioepithelial mesoderm demonstrated a transition from the bilaminar layers of most polychaetes to the multilaminar layers of *Owenia fusiformis* and deuterostomes (RIEGER and LOMBARDI, 1987; SALVINI-PLAWEN, 2000; RIEGER and LADURNE, 2003). Concomitantly, GARDINER (1978) also observed the mioepithelial pattern of the visceral mesoderm of *Owenia fusiformis*, including septae, mesenteries, digestive tube, blood vessels, parapodial glands and chaetal sacs, inferring that these differ from the remaining polychaetes and belong to the deuterostome pattern. Other papers added evidence for a transition from protostomes and deuterostomes; SMITH *et al.* (1987) indicated that the monociliate podocytes of the terminal protonephridial cells of *Owenia* were more similar to the larvae of deuterostomes than to the larvae of polychaetes; EMLET and STRATHMANN (1994) observed a prototroch and metatroch of simple cilia and an ascending pattern of particle collection in the mitraria larvae of *Owenia*, similar to the pattern of Deuterostomia. This hypothesis

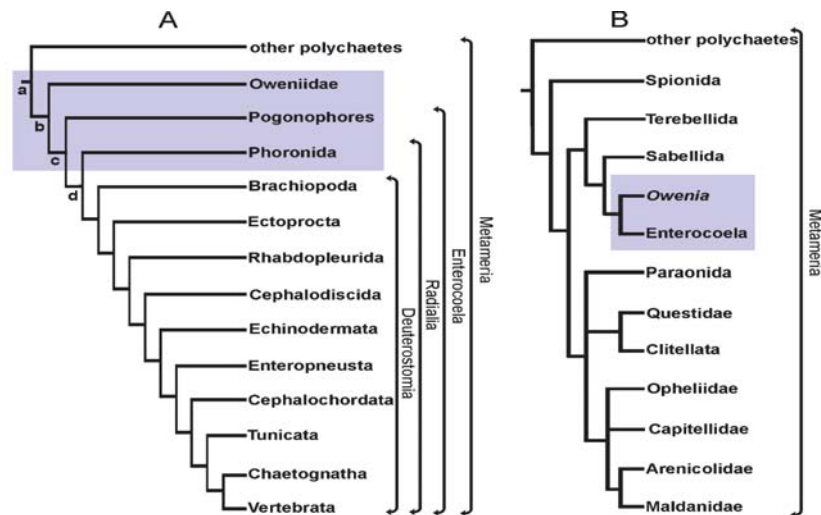


has been corroborated by molecular data (ROUSSET *et al.*, 2004). In our opinion, tagmosis represents an important character appearing in sedentary and tubicolous polychaetes, which derives from a metameric ancestral with non-specialized segments (FAUVEL, 1923; DAY, 1967; FAUCHALD, 1977). Tagmosis and successive reduction of metameres are considered apomorphic conditions that link more basal protostome annelids with deuterostomes (Figure 1A-B) (CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; ALMEIDA and CHRISTOFFERSEN, 2001; ALMEIDA *et al.*, 2003). This hypothesis has been corroborated by a series of homologous genes for segmentation and tagmosis (MCGINNIS *et al.*, 1984; LAWRENCE, 1990; FRANÇOIS and BIER, 1995; HOLLEY, *et al.*, 1995; JONES and SMITH, 1995; HOLLAND *et al.*, 1997).

SALVINI-PLAWEN (2000) critically compared the main characters of pogonophores and its relationships with Annelida-Polychaeta (particularly with oweniids) and to Oligomera. He concluded that the tendency to include pogonophores in annelids is based on convergent/homoplastic characters. We may add that the similarities between annelids and pogonophores are based preponderantly on plesiomorphic similarities shared between the two groups.

The important point for us is not whether pogonophores are categorized as a family (Siboglinidae) or a phylum (Pogonophora), but that this monophyletic taxon is characterized by having a frenulum, a trunk, ridges with pyriform glands on the anterior trunk, an opisthosoma, uncini with opposed teeth, an occluded gut, and a collapsible tube, all considered unambiguous apomorphies in a multistate analysis (ROUSE, 2001). This clade represents a key group for our understanding the evolution of deuterostomes from "protostomes". Beyond elucidating the worm origins of our own lineage, important phylogenetic consequences of these views are that Polychaeta, Annelida and Protostomia are all paraphyletic assemblages based on plesiomorphic similarities. The smallest monophyletic group which includes the polychaetes and annelids should be referred to as Metameria. More inclusive groups are represented by the Coelomata and Bilateria, with the consequence that protostomes, radialians, lophotrochozoans, and related plesiomorphic groupings represent paraphyletic taxa and must be excluded from the system of the Metazoa. Although some recent papers have attempted to sustain these groups with molecular data, these remain, in our opinion, phylogenetically inconsistent (HOLLAND, 2000; HALANICH, 2004; GIRIBET *et al.*, 2007).

We believe that conflicting conclusions regarding the phylogenetic position of pogonophores reflect different methods of phylogenetic inference, rather than being due to insufficient or inadequate empirical data. Evolutionary systematics does not adequately distinguish plesiomorphic from apomorphic character states, while total evidence and a *posteriori* methods of character polarization in quantitative cladistics may interpret plesiomorphic groups as



**Figure 1 - A.** One of the phylogenetic trees proposed for the Enterocoela based on morphological data; (a) other polychaetes include also Ecdysozoa, Echiura, Sipuncula, and Clitellata, schizocoelic metamerians, with body divided into multiple, similar segments; (b) schizocoelic metamerians, with segments grouped into four body tagma: 1) anterior region (head) formed by the fusion of the prostomium and peristomium; 2) a collar region; 3) a trunk containing several reduced and greatly elongated segments; 4) a pygidium, containing few and greatly reduced or vestigial body segments; (c) metamerians with three anterior enterocoelic tagma (tri-coelomate pattern), similar to the deuterostomes, have 1) a head or cephalic lobe, the protosome; 2) a middle segment or collar region, the mesosome; 3) an elongate trunk segment, with dorsal papillae and a posterior girdle of uncini, the metasome), and retaining a posterior, vestigial, fourth tagma with a schizocoelic organization 4) the opisthosome, with multiple similar segments retaining peg-like chaetae or uncini; (d) Radialia (Phoronida + Deuterostomia), with a tri-coelomate, oligomeric organization. The relationships among the taxa of Deuterostomia are not study focus of this paper. (Modified from CHRISTOFFERSEN and ARAÚJO-DE-ALMEIDA, 1994; see this reference for more details).

**B.** One of the phylogenetic trees proposed for the Metameria, showing the position of the Enterocoela, which include pogonophores among sedentary polychaetes, following ALMEIDA *et al.*, (2003). The *Owenia* appear as sister group of Enterocoela by having 1) larval deuterostome-like nephridia, and 2) larval development catastrophic metamorphosis, with the mitraria larva presenting deuterostome characters. The phylogenetic tree is based on a parsimony analysis of morphological data. (Modified from ALMEIDA *et al.*, 2003, see this reference for more details).



apomorphic, because plesiomorphies tend to be more numerous than apomorphies, so that the quality of characters, their distribution, and the evidence for character conflicts must be investigated (CHRISTOFFERSEN, 1995, 2009; MOOI and GILL, 2010). For this reason, plesiomorphic and convergent data represent noise that must be pruned as far as possible from data matrices before cladistic analysis, as proposed initially in the systemic approach of HENNIG (1966). Only hypotheses of transformation series of apomorphic character states, not rigorous assessments of overall character similarities, are capable of unambiguously revealing the hierarchical pattern of past evolutionary history (HENNIG, 1966; WILEY, 1981). When a systems view is applied to phylogeny reconstruction under a broad evolutionary context (CHRISTOFFERSEN, 1995; AMORIM, 2002), pogonophores are simply understood as sharing plesiomorphic similarities (schizocoel, homonymous metamerites) with groups of polychaetes and apomorphic similarities (enterocoel, oligomerism) with radialians.

We certainly have not seen the end of this story. We are convinced that a more detailed reinterpretation, and more adequate analyses of characters is still imperative. Phenetic clustering of character similarities resulting from present cladistic analyses need to be replaced by a phylogenetic approach, which more adequately considers characters as resulting from an evolutionary process. Only then will the new paradigm of replacing overall similarities by evolutionary relationships, as envisioned originally by HENNIG (1966), be implemented. And only then we will be able, at long last, to say farewell to phenetics and essentialism in systematics.

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