



## Morphological support for the phylogenetic positioning of Pentastomida and related fossils

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Submetido em 19/11/2007  
Aceito para publicação em 28/04/2008

### Abstract

Pentastomida is a group of parasites that infects the respiratory tracts of vertebrates. They have a mixture of annelid and arthropod characteristics. For that reason, the phylogenetic relationships of the pentastomids have been controversial in proposals of metazoan phylogeny. Forty-seven characters were selected for the analyses of the taxa Annelida, Arthropoda, Kinorhyncha, Loricifera, Nematoda, Nematomorpha, Onychophora, Pentastomida, Priapulida and Tardigrada. The analyses with PAUP resulted in a single shortest cladogram (length 89, ci 0.78, ri 0.86). Our results indicate that Pentastomida is a transitional group between the Arthropoda and some of the Nematelminth groups such as Nematoda and Nematomorpha.

**Key words:** Pentastomida, Ecdysozoa, cladistic analysis

### Resumo

**Suporte morfológico para o posicionamento filogenético dos Pentastomida e fósseis relacionados.** Pentastomida compreende um táxon de animais parasitas que infestam o trato respiratório de vertebrados. Esses endoparasitas possuem uma mistura de características de anelídeos e artrópodes. Por esse motivo, as relações filogenéticas dos pentastomídeos têm sido controversas nas propostas de filogenia dos Metazoa. Foram selecionados 47 caracteres para a análise dos táxons Annelida, Arthropoda, Kinorhyncha, Loricifera, Nematoda, Nematomorpha, Onychophora, Pentastomida, Priapulida e Tardigrada. As análises com o PAUP resultaram num único cladograma mais curto (comprimento 89, ci 0,78, ri 0,86). Segundo nossa análise, Pentastomida deve constituir um grupo de transição entre os Arthropoda e grupos de Nematelminthes como Nematoda e Nematomorpha.

**Unitermos:** Pentastomida, Ecdysozoa, análise cladística

## Introduction

Pentastomida are parasites that infect the respiratory tracts of vertebrates. About 131 species are known, classified into seven recent families and three Middle Cambrian fossil groups ( $\cong$  450 million years) (Almeida and Christoffersen, 1999). These endoparasites have a mixture of annelid and arthropod characteristics. For this reason, the phylogenetic relationships of the pentastomids have been controversial in proposals of metazoan phylogeny.

Following the first descriptions of pentastomids, the group was related to Platyhelminthes (Fröhlich, 1789; Humboldt, 1811) or Nematoda (Diesing, 1850). These hypotheses were soon abandoned, mainly because Dujardin (1845) described striated muscles in Pentastomida. This represented the first step towards relating Pentastomida with Arthropoda. Among the first supporters of this new proposal, controversies surfaced over which group of the arthropods would be closest to the pentastomids. Van Beneden (1849) proposed that the new parasites were crustaceans, while Leuckart (1860) suggested that pentastomids represented modified mites. This latter idea was supported by Sambon (1922), who emphasized the analogous example of how lice became adapted to endoparasitism. Upon studying the embryonic development of *Reighardia* (Pentastomida), Osche (1959, 1963) proposed that the Pentastomida were phylogenetically related to the Myriapoda. Heymons (1935) presented a series of anatomical observations to suggest that pentastomids had greater affinity with the Annelida.

Nevertheless, for Cuénot (1949), Nicoli (1963) and Haffner (1977), pentastomids are neither annelid nor arthropod. These authors argued that pentastomids occupied a unique intermediary position between Annelida and Arthropoda. This latter hypothesis was also supported by Self (1969) and Haugerud (1989), who that argued that Pentastomida should be considered a phylum with indeterminate phylogenetic relationships.

The discovery of similarities in the sperm ultrastructure of *Raillietiella hemidactyli* (Pentastomida) and *Argulus foliaceus* (Crustacea, Maxillopoda, Branchiura) was taken to support the

hypothesis that pentastomids are crustaceans related to the Branchiura (Wingstrand, 1972; Riley et al., 1978; Storch and Jamieson, 1992; see revision of these ideas in Zrzavý, 2001). Molecular analyses conducted with 18S rRNA also seemed to indicate that Pentastomida are related to Branchiura (Abele et al., 1989; Lavrov et al., 2004).

The first fossils of larvae of pentastomids from the Middle Cambrian were described by Andrés (1989), Waloszek and Müller (1994) and Waloszek et al. (1994). These new data led Almeida and Christoffersen (1999, 2002), Maas and Waloszek (2001), Tchesunov (2002) and Waloszek et al. (2006) to reinforce the hypothesis that Pentastomida must represent an intermediary evolutionary stage between Annelida and Arthropoda.

The goal of this paper is to deduce the phylogenetic position of the Pentastomida in relation to the Arthropoda and Annelida, thus reconsidering the two main hypotheses that are widely debated today: Pentastomida are closely related to the Arthropoda or even belong as a subgroup (of crustaceans) in this taxon; Pentastomida represent a transitional group between annelids and arthropods, or are included in the Ecdysozoa.

## Material and Methods

The primary source of data was the literature pertaining to all studied groups. We also examined specimens of pentastomids deposited in the collections of the Universidade Regional do Cariri (0021, 0022, 0023, 0043, 0044) and FIOCRUZ (CHIOC 20420, 20421, 20429, 20431, 20432, 20434, 20439, 20402, 30325, 30326, 30327, 20328, 30329a, 30330a-b, 29176a-m, 29185a-o), in addition to non-catalogued specimens of nematodes and onychophorans from the Laboratório de Invertebrados Marinhos and the Laboratório de Entomologia of the Universidade Federal da Paraíba. These examinations allowed the selection and confrontation of comparative data on morphology and anatomy described in the literature contrasting with biological specimens.

The taxa selected for analyses were based on the proposals of Abele et al. (1989), Storch and Jamieson

(1992), Almeida and Christoffersen (1999; 2001 and 2002), Maas and Waloszek (2001), Almeida et al. (2003), Lavrov et al. (2004), and Waloszek et al. (2006). Autapomorphies of the studied groups can be obtained from: Annelida (Rouse and Fauchald, 1997; Rouse and Pleijel, 2001), Arthropoda (Boudreaux, 1979; Hennig, 1981; Weygoldt, 1986), Kinorhyncha (Lorenzen, 1985; Ehlers et al., 1986; Nebelsick, 1992, 1993), Loricifera (Kristensen, 1991a and 1991b; Hou and Bergström, 1995), Nematoda (Lorenzen, 1985; Malakhov, 1994; Hou et al., 1995; Neuhaus et al., 1996; Wallace et al., 1996; Schmidt-Rhaesa, 1996), Nematomorpha (Lorenzen, 1985; Schmidt-Rhaesa, 1996 and 1998), Onychophora (Monge-Nájera, 1995), Pentastomida (Almeida and Christoffersen, 1999), Priapulida (Lemburg, 1995; Ehlers et al., 1986), and Tardigrada (Kristensen, 1994).

Binary and multistate non-ordered characters were admitted in the analyses (see Wilkinson, 1992 and 1995; Slowinski, 1993). Polarization of characters was obtained by the method of comparison of multiple outgroups (Nixon and Carpenter, 1993; Amorim, 2002). All studied groups were considered *a priori* as being monophyletic. The selected outgroups were Platyhelminthes, Sipuncula and Mollusca, following the results obtained by Almeida and Christoffersen (2001) and Almeida et al. (2003).

The phylogenetic analyses followed Hennigian principles (Hennig, 1966; Wiley, 1981; Amorim, 2002) and were carried out using the software PAUP (version 3.1.1; Swofford, 1999). For the construction of the matrix and the graphic visualization of cladograms, the program MacClade (Maddison and Maddison, 1992) was used. The commands used in the analyses with PAUP were according to the *branch-and-bound* option.

The fact that subgroups of arthropods were not used as terminal taxa obviously reduces the ability of the present analysis to test the hypothesis of relationships of the Pentastomida with certain groups of crustaceans. This paper explores the relationships between the topology obtained in the analysis and new paleontological evidence related to the group.

## Results

Forty-seven characters were selected (see list below) for the construction of a data matrix for analyses (Table 1). The analyses with PAUP resulted in a single shortest tree, which is presented in figure 1.

### List of analyzed characters with their respective states (0-4).

- 1 **Cuticle:** 0. Absent/ 1. Present, but not sclerotized/ 2. Present and sclerotized (Budd, 1993, 1998).
- 2 **Ecdysis:** 0. Absent/ 1. Present (Zrzavý et al., 1998).
- 3 **Ultrastructure of epicuticle:** 0. Not laminated/ 1. Trilaminar (Neuhaus et al., 1997).
- 4 **Acellular layers in cuticle:** 0. Absent/ 1. Present.
- 5 **Cuticular specializations** (spines and chaetae): 0. Absent/ 1. Present.
- 6 **Cuticularized stomodaeum:** 0. Absent/ 1. Present (Brusca and Brusca, 2003).
- 7 **Cuticularized proctodaeum:** 0. Absent/ 1. Present (Brusca and Brusca, 2003).
- 8 **Eggs with cuticularized covering:** 0. Absent/ 1. Present (Neuhaus et al., 1997).
- 9 **Epidermic thickenings:** 0. Absent/ 1. Present, but not arranged into longitudinal nerve chords/ 2. Present and arranged into longitudinal nerve chords (Schmidt-Rhaesa, 1998).
- 10 **Chitin:** 0. Absent/ 1.  $\beta$ -chitin present/ 2.  $\alpha$ -chitin present (Karuppaswamy, 1977; Nielsen, 2001).
- 11 **Locomotory cilia:** 0. Present/ 1. Reduced/ 2. Absent (Zrzavý et al., 1998).
- 12 **Scalids on introvert:** 0. Not forming more than one circle on introvert/ 1. Introvert with several rows of scalids, but without clavoscalids/ 2. Clavoscalids present (Lemburg, 1995).
- 13 **Coelom:** 0. Absent/ 1. Well developed/ 2. Modified into a hemocoel/ 3. Modified into a heterocoel (Budd, 1993; Nielsen et al., 1996; Nielsen, 2001).
- 14 **Lorica:** 0. Absent/ 1. Present (Hou and Bergström, 1994).

- 15 Metameria:** 0. Absent/ 1. Present/ 2. Reduced or absent (Almeida and Christoffersen, 2001; Almeida et al., 2003).
- 16 Number of primary metameres:** 0. More than 13/ 1. Less than 13 (Brusca and Brusca, 2003; Giribet, 2003).
- 17 Locomotory appendages:** 0. Absent/ 1. Parapodia present/ 2. Parapodia modified into lobopods and arthropods/ 3. Reduced or absent (Almeida and Christoffersen, 2001; Almeida et al., 2003).
- 18 Number of locomotory appendages:** 0. More than seven pairs/ 1. Seven or four pairs/ 2. Secondarily absent (Almeida and Christoffersen, 1999; Almeida et al., 2003).
- 19 Articulation on locomotory appendages:** 0. Absent/ 1. Present, but not articulated/ 2. Articulated/ 3. Secondarily absent (Weygoldt, 1986).
- 20 Musculature:** 0. Non-striated/ 1. With striations arranged in the form of a cross (Weygoldt, 1986).
- 21 Circular musculature:** 0. Well developed/ 1. Reduced (Wallace et al., 1996).
- 22 Longitudinal musculature:** 0. Absent/ 1. Present and continuous/ 2. Present and divided into four or five bands/ 3. Secondarily reduced or absent (Rouse and Fauchald, 1995, 1997; Rouse and Pleijel, 2001).
- 23 Musculature in digestive tract:** 0. Present/ 1. Absent (Brusca and Brusca, 2003).
- 24 “Muscle scars” in cuticle:** 0. Absent/ 1. Present (Kristensen, 1991a).
- 25 Anterior tagma (proboscis/introvert):** 0. Proboscis without mouth at apex/ 1. Proboscis with mouth at apex (Schmidt-Rhaesa, 1996).
- 26 Pharynx:** 0. Muscular pharynx prehensile/ 1. Muscular pharynx suctorial (Nielsen, 2001; Brusca and Brusca, 2003).
- 27 Mioepithelial pharynx:** 0. Absent/ 1. Present (Rieger and Tyler, 1995).
- 28 Symmetry of pharyngeal structures:** 0. Radial/ 1. Hexaradial/ 2. Pentaradial (Hou and Bergström, 1994).
- 29 Salivary glands:** 0. Absent/ 1. Present (Brusca and Brusca, 2003).
- 30 Circulatory system:** 0. Absent/ 1. Present/ 2. Open/ 3. Secondarily absent (Rouse and Fauchald, 1995, 1997; Rouse and Pleijel, 2001).
- 31 Heart with ostia:** 0. Absent/ 1. Present (Weygoldt, 1986).
- 32 Adhesive tubules:** 0. Absent/ 1. Present (Brusca and Brusca, 2003).
- 33 Caudal appendages (“toes”):** 0. Absent/ 1. Present (Brusca and Brusca, 2003).
- 34 Cloaca:** 0. Absent/ 1. Present (Brusca and Brusca, 2003).
- 35 Metanephridia:** 0. Absent/ 1. Present/ 2. Modified into coxal, antennal or maxillary glands (Almeida and Christoffersen, 2001).
- 36 Protonephridia in adult stages:** 0. Absent/ 1. Present (Rouse and Fauchald, 1997; Rouse and Pleijel, 2001, Almeida et al., 2003).
- 37 Cerebral ganglia:** 0. Only one protocerebral ganglion present/ 1. Protocerebral and deutocerebral ganglia present/ 2. Protocerebral, deutocerebral, and tritocerebral ganglia present/ 3. Cerebral ganglia reduced in adults, nerve cells positioned around subterminal nerve ring (“cycloneurialian” condition)/ 4. “Cycloneurialian brain” positioned terminally (Schmidt-Rhaesa, 1998; Nielsen, 2001).
- 38 “Mushroom-bodies” in brain:** 0. Absent/ 1. Present (Pleijel and Dahlgren, 1998; Wägele et al., 1999).
- 39 Ventral nervous chords ganglionated:** 0. Absent/ 1. Present/ 2. Secondarily absent (Brusca and Brusca, 2003).
- 40 Fusion of ventral nerve chords:** 0. Not fused/ 1. Fused (Schmidt-Rhaesa, 1996, 1998).
- 41 Sensory structures:** 0. Not specialized into cells with cilia containing apical openings; 1/ Specialized into cells with cilia containing apical openings (Brusca and Brusca, 2003).
- 42 Sperm:** 0. With posterior flagellum/ 1. Flagellum absent (Neuhaus et al., 1996; Schmidt-Rhaesa, 1996).
- 43 Cleavage:** 0. Spiral/ 1. “Cross-like”/ 2. Centrolecithal (Scheltema, 1993; Budd, 1993).
- 44 Progenesis:** 0. Absent/ 1. Present (Lorenzen, 1985).

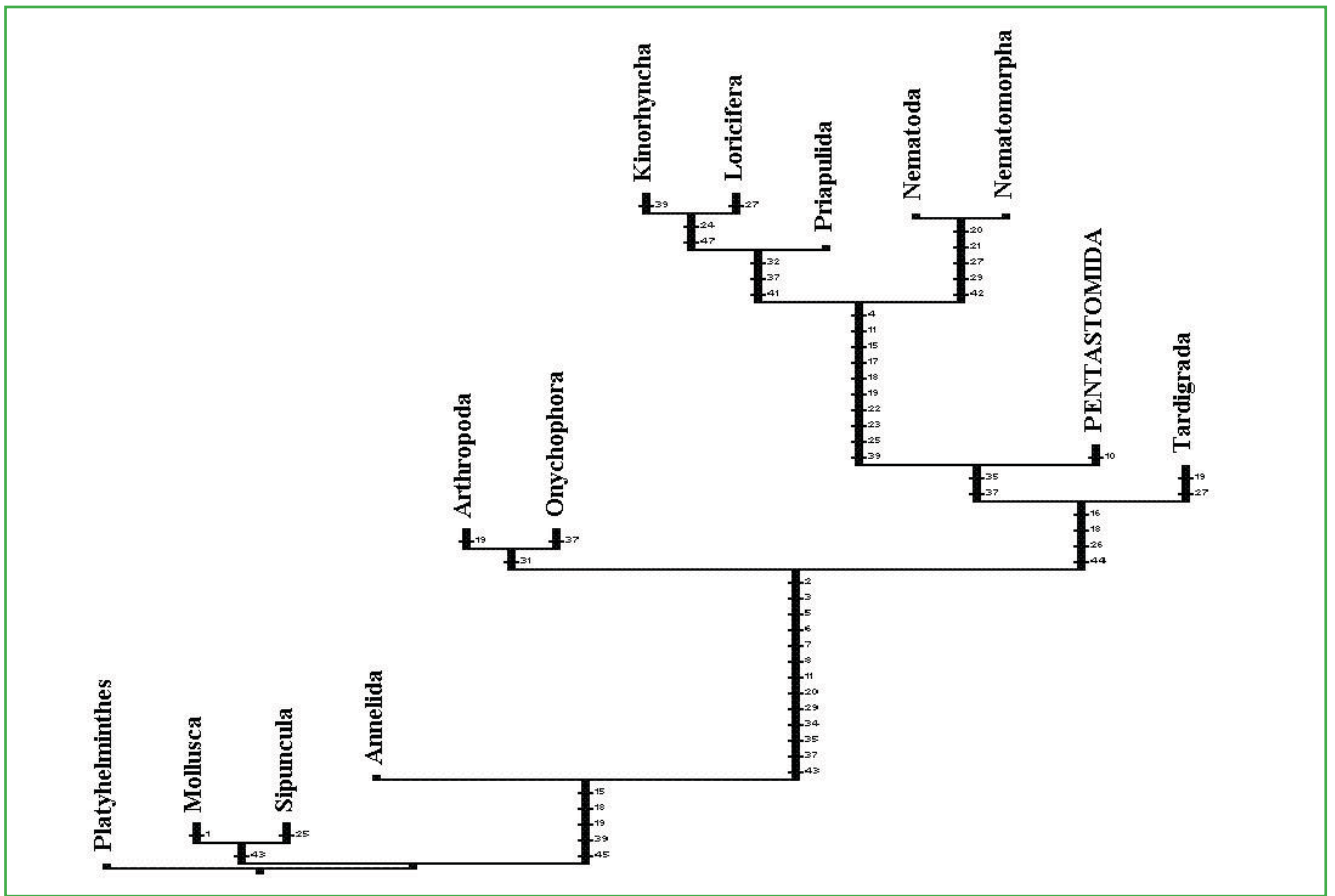


FIGURE 1: Most parsimonious cladogram (length 89, ci 0.78, ri 0.86) representing the hypothesis of phylogenetic positioning of Pentastomida.

TABLE 1: Character matrix of data for the investigation of interrelationships of Pentastomida. 0-4, character states arranged into transformation series; “?”, uncertainty or absence of information on the state of a character.

Taxa	Characters				
	1	111111112	222222223	333333334	4444444
	1234567890	1234567890	1234567890	1234567890	1234567
<b>Platyhelminthes</b>	000000000	000000000	000000000	000010000	00000?0
<b>Mollusca</b>	100000000	?01000000	011000002	000010000	00100?0
<b>Sipuncula</b>	100000000	101000000	011010001	000010000	00100?0
<b>Annelida</b>	100000001	101010110	021000001	0000100110	00001?0
<b>Arthropoda</b>	2110111102	2020102121	021000012	1001202110	00201?0
<b>Kinorhyncha</b>	211?111112	0230210031	0301110213	0101014010	1021121
<b>Loricifera</b>	211111???2	0231210031	0301111213	0111014020	1021121
<b>Nematoda</b>	211?111122	00302100301	1300111103	0001013021	0121110
<b>Nematomorpha</b>	21111?1122	0030210030	1300111103	0001013021	0121110
<b>Onychophora</b>	2110111102	2020102111	021000012	1001?01110	00201?0
<b>Pentastomida</b>	2110111101	2030112211	0210010013	00010?3?10	002?1?0
<b>Priapulida</b>	211?111?12	0131210031	0300110213	0111014021	1021120
<b>Tardigrada</b>	2110111102	2030112221	0210011013	0001202?10	00211?0



- 45 Development:** 0. Indirect/ 1. Direct (Almeida and Christoffersen, 2001; Almeida et al., 2003).
- 46 Stages in juvenile development:** 0. Absent/ 1. Four stages/ 2. More than four stages (Neuhaus, 1995).
- 47 Neck region in juveniles:** 0. Not forming a closed apparatus/ 1. Forming a closed apparatus (Neuhaus, 1995).

## Discussion

Analyses using the molecular marker 18S rRNA led to the proposal of the taxon Ecdysozoa, which includes all animals presenting ecdysis (periodical moulting during development): Pentastomida, Onychophora, Tardigrada, Arthropoda, Nematoda, Nematomorpha, Priapulida and Loricifera (see Aguinaldo et al., 1997; Giribet and Ribera, 1998; Giribet, 2003). The congruence between molecular and morphological data was also demonstrated by Schmidt-Rhaesa et al. (1998). Our analysis corroborates the monophyly of the Ecdysozoa. However, data derived from the DNA analysis diverge in different degrees from morphological studies.

The problem of the incongruence between morphological and molecular data has already been discussed by Wägele (1996) and Nielsen (2001). These authors demonstrated that the results of molecular analyses vary according to the selected species, sample size, and particular methods of analysis used. Although still controversial, there is additional evidence that at least the sequences of 18S rRNA may not contain consistent phylogenetic information for cladogenetic events as old as the Median Cambrian (Philippe et al., 1994). Regarding the phylogenetic positioning of the Pentastomida, our results do not corroborate conclusions obtained based on spermatological (Wingstrand, 1972; Riley et al., 1978; Storch and Jamieson, 1992) or molecular data (Abele et al., 1989; Lavrov et al., 2004). Our results agree with the proposals of Waloszek and Müller (1994), Maas and Waloszek (2001) and Waloszek et al. (2006), in which neither the Cambrian fossils nor the recent forms of pentastomids present any morphological evidence for their inclusion within any specific group of euarthropods.

Among the characters studied we stress the implications of metamery (#15) and the number of metameres (#16) for the phylogenetic position of the Pentastomida and for the history of the fossils related to them. In the first case (#15) we agree with Aguinaldo et al. (1997) and Lavrov et al. (2004), whose results indicate that the absence of metamery in ecdysozoan groups (e.g., Nematoda and Nematomorpha) must be secondary.

In the second case (#16), the reduction in the number of metameres is a character related to the reduction in body size of the animals and to adaptations to other modes of life (for example, parasitism). In this evolutionary scenario the position of the Pentastomida in our results would indicate that, before the loss of metamery, some groups reduced their number of somites. According to Moura and Christoffersen (1996), depending on some premises of homology of the cephalic structures, there are 22 metameres present in the groundplan of the Arthropoda, and this number becomes reduced to 13 in higher arthropods. Tardigrada has only eight nervous ganglia and Pentastomida has seven. This reduction is also related to the reduction in the size and number of the locomotory appendages. In Tardigrada there are three pairs of legs for locomotion. The fourth pair, located in the posterior region of the body, similar to those of †*Aysheaia* and Onychophora, has the function of embracing the substrate, only occasionally being used for walking. However, in the basic plan of the Tardigrada there are seven pairs of appendages, the first three being reduced on the cephalic tagma. In Pentastomida, there are two distinct pairs of appendages, as well as two pairs of vestigial anterior appendages in the fossil †*Bockelericambria* (Waloszek and Müller, 1994) and in the groundplan of the Pentastomida. Almeida and Christoffersen (1999) considered the basic number of segments in Pentastomida to be seven.

The evolutionary scenario presented herein has profound implications for the positioning of several enigmatic Cambrian fossils. Integrating our results with those obtained by Eloy (2001), fossils of some lobopodian animals must be positioned at the *stem-group* of Ecdysozoa. Others, such as †*Anomalocaris* and related forms, must belong to the *stem-group* of

Arthropoda (Figure 2). Hou and Chen (1989) described five pairs of appendages for †*Facivermis*, but Hou and Bergström (1995) considered the differences between †*Facivermis* and the lobopodians to be profound. Hou and Bergström (1995) argued that the appendages of †*Facivermis* were restricted to the anterior region of the body and were arranged along the midventral line of the body, not ventrolaterally as in lobopodians (Figure 2). The appendages become vestigial in the heads of some of the nemathelminths (Chang et al., 1998a and 1998b). However, we understand that these differences are not significant, because the appendages of †*Facivermes* are similar in shape to those of the remaining lobopodians. Furthermore, other characters (e.g., the presence of cutaneous papillae) indicate that †*Facivermes* must be interpreted as a lobopodian. Its proximity to Pentastomida and other nemathelminths is also indicated by the fact that its long and delicate spines at the tips of the lobopodes were probably not used for walking, but rather for anchorage to the substrate or to a host animal.

The Pentastomida must, hence, have evolved from an ancestor similar to †*Facivermes* and seem to be related to Tardigrada and other groups of nemathelminths. Today, even though very modified towards the parasitism of terrestrial vertebrates, pentastomids still retain vestiges of the early stages of the evolution of a group that originated more than 450 million years ago and that resulted in a great diversity of ecdysozoans, containing groups as different as nematodes and priapulids. The presence of the onychophorans as the sister clade of the Arthropoda differs from other recent phylogenetic studies of the group that point to the Panarthropoda (including Tardigrada and Arthropoda) as monophyletic, implying that the presence of the tritocerebral ganglia would be a synapomorphy. We agree with this later hypothesis, and the connection of Onychophora and Arthropoda in a clade may result from the undersampling of features involving onychophorans and secondary losses in the evolution of the group.

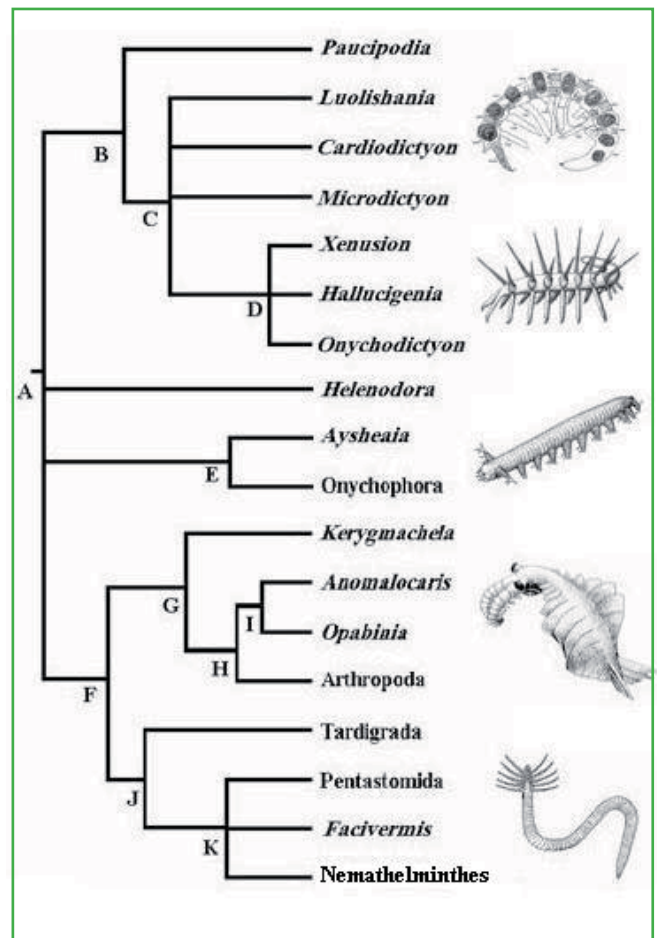


FIGURE 2: Cladogram of phylogenetic relationships of the Ecdysozoa according to Eloy (2001). (A) Ecdysozoa; (B) armoured lobopodians; (C) unnamed clade; (D) spiny lobopodians; (E) Onychophora (including †*Aysheaia*); (F) unnamed clade; (G) unnamed clade; (H) Arthropoda (including †*Anomalocaris* and †*Opabinia*); (I) Anomalocaridea; (J) Myzopharyngea; (K) unnamed clade. Fossil illustrations from top to bottom: †*Microdictyon* (modified from Chen et al., 1995), †*Hallucigenia* (modified from Ramsköld and Hou, 1991), †*Aysheaia* (modified from Whittington, 1978), †*Anomalocaris* (modified from Collins, 1996), and †*Facivermis* (modified from Delle Cave and Simonetta, 1991).

## Acknowledgements

We are very grateful to F. R. Schram, R. Jenner (University of Amsterdam) and Antônio C. Marques (USP) for criticisms and suggestions on a first version of this paper. We acknowledge the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico – FUNCAP for financial support to Waltécio de Oliveira Almeida (9913/ 06 – Convênio 0006-00/ 2006). We

thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq for support to Martin L. Christoffersen and Dalton S. Amorim. Special acknowledgements are due to Dely Noronha, curator of the Coleção Helmintológica do Instituto Oswaldo Cruz, for the loan of specimens of pentastomids.

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