ECDYSOZOA

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Contents

1. Introduction to Ecdysozoa
2. History
2.1. Support
2.2. Doubt
2.3. Consequences
3. Internal phylogeny of Ecdysozoa
4. Characteristics and diversity of ecdysozoans: Arthropoda
4.1. Tardigrada
4.2. Onychophora
4.3. Euarthropoda
5. Characteristics and diversity of ecdysozoans: Cycloneuralia
5.1. Nematoda
5.2. Nematomorpha
5.3. Priapulida
5.4. Kinorhyncha
5.5. Loricifera
Acknowledgements
Glossary
Bibliography
Biographical Sketch

Summary

The name Ecdysozoa refers to a taxon (= group of animals) which all have a cuticle that is molted. Many analyses, drawing on diverse kinds of molecular information, support Ecdysozoa as a monophyletic taxon, going back to one common ancestral species.

Ecdysozoa includes the taxa Euarthropoda, Onychophora, Tardigrada, Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera. Ecdysozoa conflicts with thoughts uniting arthropods (Euarthropoda, Onychophora, Tardigrada) to Annelida based upon their segmental body plan. Under the Ecdysozoa hypothesis, segments have to be considered either a plesiomorphic (= phylogenetically very old) character or a character that evolved in parallel in arthropods and annelids.

1. Introduction to Ecdysozoa

Ecdysozoa is a name of a taxon (a group of animals) uniting all those animals that have a cuticle which is molted during growth. It is assumed that all such animals derive from one ancestral species in which the molting of cuticle (ecdysis) originated. Ecdysozoa includes the following recent taxa: Euarthropoda, Onychophora, Tardigrada, Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera. Euarthropoda, Onychophora and Tardigrada are united in the taxon Arthropoda. Nematoda, Nematomorpha, Priapulida, Kinorhyncha and Loricifera comprise the taxon Cycloneuralia. Other names have been used in the literature, e.g. Panarthropoda and Aiolopoda (= Arthropoda) or Introverta (= Cycloneuralia).

2. History

The hypothesis that Ecdysozoa is a monophyletic taxon, i.e. that all descendants are derived from a common ancestor, is a comparably new hypothesis. At least since Cuvier it was believed that arthropods are closely related to annelids in a taxon named Articulata. This was based on the body organization with a series of segments, which is shared between arthropods and annelids. This hypothesis was rarely doubted. The clearest doubt was expressed in 1992 by Eernisse and colleagues as the result of a cladistic analysis of morphological characters, where annelids and mollusks were found to be more closely related to each other than to arthropods. A clustering of arthropod taxa with cycloneuralian taxa (Nematoda, Nematomorpha, Priapulida, Kinorhyncha, Loricifera) could be observed in several molecular analyses based on DNA sequence comparison, but it was explicitly expressed and named as a hypothesis of relationship by Aguinaldo and colleagues in 1997. Since then, Ecdysozoa has been supported by many molecular analyses, but no such analysis is in favor of Articulata.

2.1. Support

The monophyly of Ecdysozoa is supported by the majority of molecular analyses, be it from single genes, multiple genes, nuclear or mitochondrial genes, partial genomes (expressed sequence tags, ESTs), entire genomes or combined molecular/morphological analyses. Single taxa, for example the nematode *Caenorhabditis elegans*, may fall outside Ecdysozoa, probably as a result of long-branch artifacts. Support comes also from an immune response against horseradish peroxidase in the nervous system of several ecdysozoan taxa.

Morphological characters supporting the monophyly of Ecdysozoa refer to the cuticle. Although the cuticle is quite variable in several subtaxa, the presence of three characteristic layers occurs quite often and has been proposed as an autapomorphy.

These layers are an internal layer containing α-chitin (endocuticle), followed externally by an exocuticle and an outer, thin epicuticle which has a trilaminate organization. Other names for the cuticular layers have been applied in certain subtaxa. The cuticle is molted during development, this molt being under control of ecdysteroid hormones, but this is only known for some euarthropod and nematode taxa.

2.2. Doubt

The most serious doubt about the monophyly of Ecdysozoa comes from the characters related to segmentation. A segmented body organization is a common character in Annelida and Arthropoda (united as Articulata) and although metameric patterns occur abundantly among metazoan animals, the extensive segmentation including several organ systems (integument, musculature, nervous system, excretory system, body cavities) is often evaluated as so complex that its convergent evolution appears implausible.

Some authors point at several differences between Cycloneuralia and Arthropoda, neglecting that for the reconstruction of phylogeny only shared characters are important, not differences. Molting may even occur in some annelids, but hormone-driven molting of the entire cuticle has to be clearly distinguished from shedding of partial cuticle or layers. Molting is likely to occur in the deeply nested annelid taxon Hirudinea (or at least in certain species such as the medical leech *Hirudo medicinalis*), but there is no indication that molting could represent an ancestral character within Annelida.

Some genomic analyses do not reveal monophyletic Ecdysozoa, although none of these analyses supports Articulata. Most of these investigations have in turn been criticized themselves and may be the result of differing analytical methods or the inclusion of genomic data from the nematode *Caenorhabditis elegans*, which is known to notoriously cause unreliable results in analyses.

2.3. Consequences

The proposal of Ecdysozoa as a monophyletic taxon required a major shift of an important taxon, the Arthropoda, within the tree of life. A strong character complex, the segmentation, had to be interpreted as convergent. This caused some debate, not least because one had to decide which is stronger: the morphological signal coming from segmentation or the molecular signal and other morphological characters such as cuticle structure and molting. The morphological support for Ecdysozoa is supplemented by an additional body of morphological evidence: the Articulata hypothesis forces the shared characters of annelids, mollusks and other spiral-cleavers with trochophora larvae to be lost in arthropods.

These ad hoc losses and evolutionary reversals are not forced under the Ecdysozoa hypothesis. If Ecdysozoa is a real taxon, the consequence is that a complex set of characters can evolve convergently (or, alternatively, is a plesiomorphic character that is strongly reduced in most taxa but was retained in two derived taxa).

If Articulata were a real taxon, the consequence would be that molecular analyses consistently give a wrong signal (including the strong molecular support for annelids grouping with mollusks rather than arthropods). However, although Ecdysozoa is generally accepted, this debate should not stop to interest us and motivate further investigations, refine analyses of molecular data and take a closer look at segmentation and molting.

3. Internal Phylogeny of Ecdysozoa

The internal phylogeny of Ecdysozoa is not unequivocally resolved. From the morphological perspective, Ecdysozoa is composed of two sister groups, Arthropoda and Cycloneuralia (Fig. 1). Cycloneuralia is characterized by a unique organization of the brain, which is circular around the pharynx and has neuronal somata anterior and posterior to the central ring neuropil. Arthropoda are characterized by the segmental body organization, with paired, segmental ventrolateral appendages. The reconstruction of the arthropod ancestor depends for many characters on the position of the three taxa Tardigrada, Onychophora and Euarthropoda (Fig. 1). It is not yet known whether the microscopically small tardigrades are derived from larger ancestors or whether they conserve the body size from small ancestors.

Molecular analyses rarely show the monophyly of both Arthropoda and Cycloneuralia. Usually, Euarthropoda and Onychophora cluster together, as do Nematoda and Nematomorpha. However, internal phylogeny is generally not supported by very high support values.

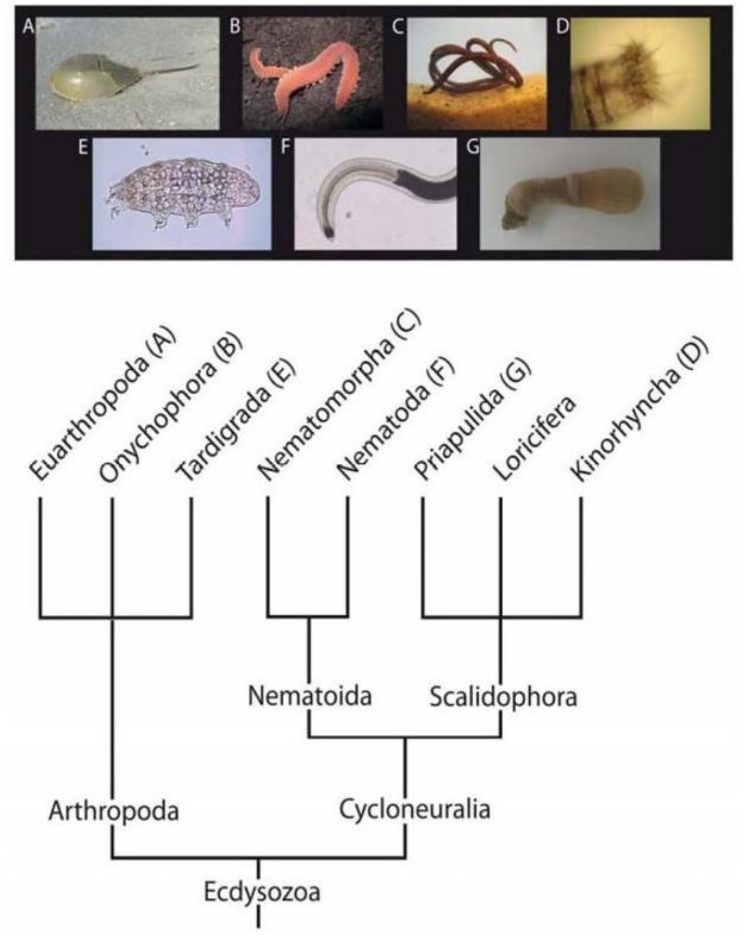

Figure 1. Cladogram showing one hypothesis of internal relationships of Ecdysozoa. The exact relationships within Arthropoda and Scalidophora are not well settled and are represented here as trichotomy.

4. Characteristics and Diversity of Ecdysozoans: Arthropoda

Arthropoda is a large and diverse taxon that can be divided into three monophyletic subtaxa: Tardigrada, Onychophora and Euarthropoda. Different terminologies are sometimes applied (see above). The uniting character for all arthropods is the presence of segmental, ventrolateral appendages. These are present as cone-like structures with apical claws in onychophorans and tardigrades or as segmented (articulated) legs in euarthropods.

Sister-group relationships within Arthropoda are not fully resolved, because there are sets of characters supporting Tardigrada as sister taxon of Euarthropoda and others supporting Onychophora as sister taxon of Euarthropoda. Tardigrades are exclusively small animals, this may either be the product of a secondary reduction or it may reflect a primary small body size. Such considerations have great impact on phylogenetic considerations, because with an evolutionary miniaturization, some characters may have become lost (such as for example a dorsal heart). On the other hand, tardigrades show some characters, such as the triradiate pharynx, which can be interpreted as plesiomorphies in the Ecdysozoa concept, because such a pharynx is present also in several cycloneuralians. The terminal mouth opening is another such character.

4.1. Tardigrada

Tardigrades are microscopically small animals living in aquatic or moist habitats. Several species of the taxon Heterotardigrada are marine and inhabit the interstitial system of benthic sediments. Some species of Heterotardigrada and all Eutardigrada live in mosses or comparable terrestrial habitats and have developed effective mechanisms for periodic desiccation. They usually live in the moist film of water around moss, but when this dries up, tardigrades go into a physiologically almost inactive stage. They can desiccate almost completely and thereby change their morphology into a tun-like appearance. After rehydration, they resume their normal life. This capability to survive hostile environmental conditions is reflected by a general tolerance to all kinds of extreme factors. Tardigrades can survive extreme hot or cold temperatures and even cosmic radiation.

All tardigrades have four pairs of legs, which gives them a somewhat bear-like appearance and led to the name water bears. The first three pairs are usually oriented laterally, while the last, the fourth pair of legs, is oriented posteriorly and pushes the body forward. Species of Heterotardigrada have terminal claws or sucking discs on their legs. Their cuticle is structured into plates of stronger cuticle. Several cuticular bristles are present in various positions, especially in the head region. In eutardigrades, the body is less strongly structured, lacking cuticular plates and bristles. They have terminal claws on their appendages.

Tardigrades have a sucking pharynx. This function is performed by a triradiate lumen and a radial orientation of muscles, which open the lumen quickly when contracting. In the anterior part of the pharynx, paired stylets are present. With these stylets, tardigrades puncture plants or animals (rotifers, nematodes) and then suck fluids out. The pharynx leads into the intestine and to a subterminal anus.

The four pairs of legs reflect a segmentation that is reflected internally by the nervous system, which has segmental ganglia. The structure of the brain is not completely clear. Some authors describe it as tripartite, comparable to proto-, deuto- and tritocerebrum of euarthropods, but according to other investigations, this is not clear and the brain may be composed of one dorsal mass of neurons with probably paired extensions. The musculature is composed of isolated muscles. Sets of muscles run into each leg, these sets differ slightly between the first three legs and strongly in the fourth leg. Longitudinal muscles without recognizable segmental structure run through the entire body. Some further muscles are present.

Excretory structures are Malpighian glands leading into the intestine. Tardigrades are dioecious, the gonads are unpaired sacs. Some terrestrial tardigrades reproduce by parthenogenesis, the other species deposit eggs. In some species, eggs are deposited inside the female exuvia, which is used as a shelter. Tardigrades have a direct development without larval stages.

Figure 2. Tardigrada. Undetermined representative of the Eutardigrada extracted from terrestrial moss. The four pairs of legs and the round pharynx in the anterior end (to the right) are visible. Photo: Andreas Schmidt-Rhaesa.

4.2. Onychophora

Onychophorans or velvet worms are large animals in the centimeter-range. They mostly occur in the southern hemisphere. Two subtaxa (families) are known, Peripatidae and Peripatopsidae. Both occur in South America, Africa and Southeast Asia, with Peripatidae being distributed further north on all continents than Peripatopsidae. In Australia and New Zealand, only Peripatopsidae occur.

All onychophorans have an elongated trunk with numerous pairs of legs. The legs are cone-like extensions of the body with terminal claws. In the anterior end, conspicuous head appendages called antennae or palps are present. The antennae and legs show external constrictions to form numerous rings. This is also present on the body cuticle and reflects a superficial structure of the cuticle, but not the segmental structure.

Below the antennae, a pair of oral papillae is present, through which voluminous salivary glands open. The sticky saliva can be squeezed out of the animal and thereby spit netlike over prey organisms. These are usually insects. With paired cuticular jaws (not homologous to mandibles within euarthropods), prey is then opened and digestive fluids are secreted into the prey. After extraintestinal digestion, the prey is sucked out. The long intestine ends with a terminal anus.

The nervous system is composed of a dorsal brain, which does not show any tripartition as in euarthropods. A pair of ventral nerve cords emerges, the two cords are connected by numerous fine commissures. However, segmental ganglia are absent and the commissures do not reflect segmental patterns. The musculature forms sheets of external circular and internal longitudinal musculature, with additional muscles running into the legs.

A large central body cavity is present. In early embryos, this body cavity is a coelom. With growth a primary body cavity extends next to the coelom. At a certain time the coelom opens into the primary body cavity, forming a so-called mixocoel. Then the tissue of the coelom becomes restricted to the excretory structures, the sacculus and its duct which opens at the base of the legs. Numerous fine trachea are present and serve as respiratory structures. A circulatory system is present, composed of a long dorsal tube-like heart with segmental openings.

Onychophorans are dioecious. Many species transfer sperm in a spermatophore, which is attached somewhere on the female body. In some species, a transfer of a spermatophore to the female genital opening or even direct transfer of sperm is possible. Species can be oviparous, ovoviviparous or viviparous. In viviparous species, a uterine tissue is present that nourishes the developing embryos.

Figure 3. Onychophora. Undetermined representative of the Peripatidae, adult specimens with juvenile. Photo: Andreas Schmidt-Rhaesa.

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Biographical Sketch

Andreas Schmidt-Rhaesa received his PhD at the University of Göttingen in Germany in 1996, and did a postdoc at Duquesne University in Pittsburgh and at the University of South Florida in Tampa. He then moved to Bielefeld, Germany (1998-2007), where he worked as an assistant in the working group of Thomas Bartolomaeus. Since 2007 he has been working at the Zoological Museum in Hamburg as curator for lower invertebrates. He has published many scientific papers, in addition to a book on the evolution of organ systems. He is a member of several scientific societies. He currently serves as Chief Editor of *Zoomorphology*, of the *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* and of the *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg*. From 2004-2011 he was Associate Editor of *Meiofauna Marina*. He currently works on several book projects including the *Handbook of*

Zoology. He has studied the morphology, systematics and evolution of Nematomorpha, Gastrotricha and Priapulida, further projects of his team dealt with various groups including Hydrozoa, Cestoda, Tardigrada, Oligochaeta, Kinorhyncha and Rotifera. He mainly works with microscopy methods such as scanning and transmission electron microscopy and confocal laser scanning microscopy.