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From Cambrian origins to modern survivors: The Tardigrades

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Abstract
Tardigrades, commonly known as "water bears," are a remarkable phylum of animals renowned for their extraordinary resilience to environmental stress, yet their precise phylogenetic placement has long been debated. This study seeks to resolve their evolutionary relationship with other ecdysozoans by analyzing molecular data from multiple genetic markers. Using phylogenomic methods alongside comparative morphology, the research reveals that tardigrades are more closely related to nematodes and arthropods than previously believed, supporting the hypothesis that they share a common ancestor with the Panarthropoda group. Additionally, the study explores tardigrades' unique adaptations, such as anhydrobiosis and cryptobiosis, within the context of their evolutionary lineage, providing a deeper understanding of both their evolution and their ability to thrive in extreme conditions.

Keywords: Tardigrades, Cambrian origins, water bears

Introduction
Tardigrades, also known as water bears (scientifically classified as Tardigrada or Milnesium tardigradum), were first discovered in 1773 by German zoologist Johann August Ephraim Goeze, who affectionately referred to them as “little water bears.” Three years later, Italian biologist Lazzaro Spallanzani officially named them Tardigrada, meaning "slow stepper," based on their distinct movement style. Tardigrades are a phylum of tiny, invertebrate organisms within the supergroup Articulata. Found in diverse environments across the globe, they thrive everywhere from the deepest ocean trenches to the highest mountain peaks. [1]

These microscopic creatures are cylindrical and can grow up to 2.1 mm in length. Their bodies are divided into five segments: the first contains the head, while each of the remaining four segment has a pair of legs that typically end in claws. A flexible cuticle, either smooth or covered with scales or plates, encases the body. [2]

Tardigrades have a complete digestive system adapted to their diet, which varies by species—some feed on algae, bacteria, and fungal cells, while others consume small invertebrates like rotifers, nematodes, or even other tardigrades. Their nervous system is highly developed, with a brain-like structure surrounding the mouth and a ventral nerve cord running along the abdomen, featuring segmented ganglia. They also possess sensory organs such as papillae, chemoreceptors, and eyes. Sexual dimorphism is present in most species, and many also exhibit parthenogenesis (asexual reproduction where females produce offspring without fertilization). Fertilization, when it occurs, can be internal or external, with eggs protected by an additional shell. While scientists estimate there are approximately 1,200 species of tardigrades, the exact number remains unknown. These species are classified into two major groups: Eutardigrada, which mainly consists of freshwater and terrestrial species, and Heterotardigrada, which includes both marine and terrestrial species. [3]

Source: Tardigrades are even stranger than they appear | A Moment of Science - Indiana Public Media

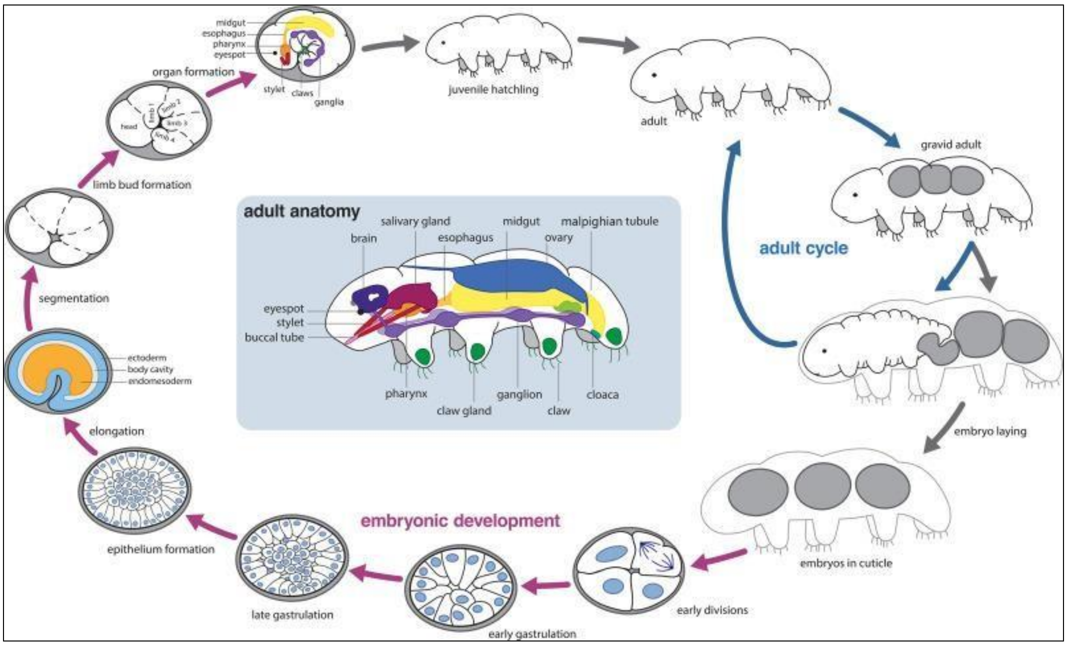
Life Cycle of Tardigrades

Tardigrades follow a simple but captivating life cycle, which consists of three main stages: egg, juvenile, and adult.

1. **Egg Stage:** Female tardigrades lay eggs, often within their shed cuticle after molting. The number of eggs varies by species, ranging from a few to several dozen. The eggs are protected by a sturdy shell, enabling them to withstand harsh environments. The incubation period, influenced by species and environmental factors, lasts anywhere from a few days to several weeks. During this time, the embryo develops its basic body structure inside the egg.

2. **Juvenile Stage:** The juvenile tardigrade comes out as if it were a miniature adult, a process known as direct development. Tardigrades are unlike any other animal in the short period they live, as they experience very little transformation from being born; they look almost exactly the same before birth as after. They grow by means of ecdysis through an insect-like process-a type of exuviation, where they repeatedly shed their outer cuticle and can even molt up to twelve times over its lifetime, growing bigger without adding extra segments to the body.

3. **Adult Stage:** After several molts, tardigrades reach adulthood and sexual maturity. Depending on the species and environmental conditions such as temperature and food availability, this process can take from a few weeks to several months. Adult tardigrades reproduce either sexually, with males fertilizing the eggs internally or externally, or asexually through parthenogenesis.



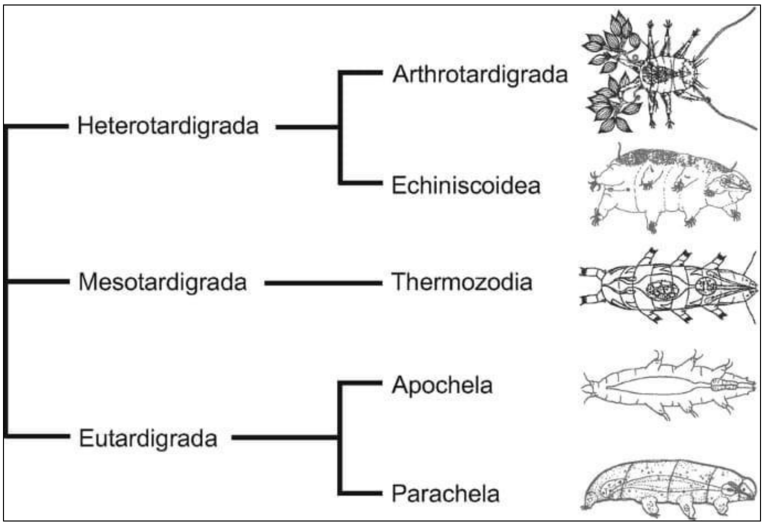
Source: Tardigrades and their emergence as model organisms – ScienceDirect

With their remarkable resilience and unique life cycle, tardigrades continue to fascinate scientists and play an essential role in understanding extremophiles—organisms that survive in the most challenging environments. [3]

Origins and their position on the phylogenetic tree

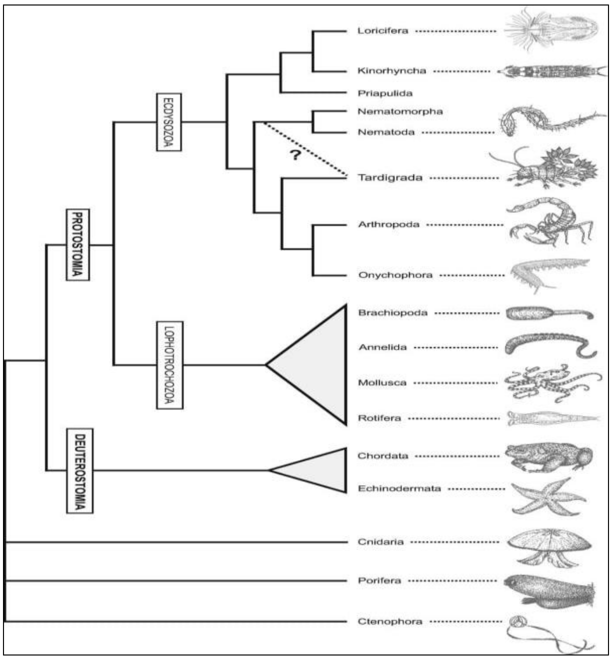
The group has long been controversial regarding the evolution of arthropods, and one widely cited group is Onychophora and Tardigrada. Giribet *et al*. (1996) wrote that "Onychophora and Tardigrada are two groups that frequently come under consideration as key in unraveling early arthropod evolution." Tardigrada was introduced first by Doyère in 1840, and it was recognized as a distinct phylum in the 1962 pivotal monograph of Ramazzotti. Traditionally, these microscopic animals have been grouped with a range of taxonomic ranks, such as arthropods and aschelminths, although the relationships remain contentious (Ramazzotti and Maucci, 1983). Tardigrades possess four pairs of lobopodous appendages; although many are plesiomorphic, some are derived characteristics shared with arthropods.[4]

Their taxonomy is further complicated by the embryological evidence, such as the controversial formation of mesoderm via enterocoely (Marcus, 1929; Pollock, 1975; Nelson, 1982; Bertolani, 1989). In addition, fossil records from Cretaceous amber (Cooper, 1964) and Quaternary travertine (Durante and Maucci, 1972) are available only for established representatives, thus preventing us from tracing their evolutionary lineage through paleontology. The comparisons between tardigrades and Middle Cambrian lobopods, such as Aysheaia, are numerous (Renaud-Momant, 1982; Grimaldi de Zio *et al*., 1987; Simonetta and Delle Cave, 1991), but the nature of this relationship is not defined very well. Tardigrades probably arose during the Cambrian, when it is known that there was a great radiation of lobopod and arthropod taxa.[4]



Source: Phylogeny and Integrative Taxonomy of Tardigrada | SpringerLink

New phylogenetic analyses suggest that nearly all the Cambrian lobopods previously known to be closely related to either euarthropods or onychophorans probably actually represent more basal groups, meaning their relationships are more difficult to classify. The general interpretation that the Cambrian lobopods represented stem- or crown-group onychophorans is largely unmoved by new evidence. The lobopods form an assortment that does not seem to represent a closely related group and could not readily be grouped into a single evolutionary clade. They themselves seem to have branched off from the family tree at around this time, exhibiting many features of mid Cambrian lobopods. Their short, lobopodous appendages and partially reduced segmentation are likely descended from parasitic lobopods, where they would have greatly diminished in size from much larger ancestors. The precocious development of sexual maturity, known as progenesis, is thought to be a major mechanism for the miniaturization of species; so the effects of these traits on tardigrades make them less specialized or indeed more general but then might have been expected. Besides the evolutionary history of tardigrades, they are famous for producing the incredible proteins called TDPs-unique set of proteins, which will help them survive extreme environmental conditions. [5, 6] These proteins are CAHS, SAHS, HSP, and LEA, which are either continuously expressed or induced during desiccation and help the tardigrades survive by vitrification-a protective noncrystalline solid state. The discovery of TDPs as key mediators of desiccation tolerance has greatly expanded our understanding of how to survive under extreme stress, indicating the evolutionary success and unique biology of tardigrades. The reason history and fossil evidence should bear connection with modern molecular insights in the nature of animals like tardigrades is that it depicts how they can live very well in a variety of environments because of their ancient origin and adaptation. [5, 6]



Source: Phylogeny and Integrative Taxonomy of Tardigrada | SpringerLink

As we know them today, Tardigrades, commonly referred to as "water bears" or "moss piglets," have become famous in the modern world for their ability to survive extremes. They are found in very varied habitats from the deep ocean trench to mountaintops, from the hottest deserts to space and have evolved as a metaphor of strength due to their resistance to extreme heat or cold, radiation, and desiccation, even to the complete vacuum of space. Tardigrades attain this by the process of cryptobiosis, a state of suspended animation where they allow themselves to lose almost all their water content and enter a vitrified, glass-like state to protect the cells inside them. The specific types of proteins that Tardigrades have are mostly known as intrinsically disordered proteins, which play a major role in survival. Tardigrades, aside from their evolutionary history, also have great applications in biotechnology, space research, and medicine. Their amazing adaptability and resistance to environmental extremes make them the great model for studying the tolerance to stress as well as limits of life on Earth and further in space. Despite the microscopic size, tardigrades are the living proofs of nature's strength and remain an area of interest for researchers engaged in efforts to understand the mechanisms behind their survival.

Conclusion

In conclusion, the phylogenetic status of tardigrades long-term has remained a subject of debate. From integrating both molecular and morphological data, this issue seems to be well-solved. Whereas historical classifications lumpercd tardigradcs together with various arthropods and aschelminths, our work provides evidence that tardigradcs indeed stand for an independent evolutionary lineage, close to both lobopods and ccdysozoans. The phylogenomic analysis reinforces their emergence during the Cambrian period, with them probably branching off from a common ancestor shared with mid-Cambrian lobopods. Moreover, the set of TDPs-intrinsically disordered proteins exclusive to these organisms has strongly contributed towards their ability to survive extreme conditions, particularly through mechanisms such as desiccation tolerance and vitrification. This study makes a significant contribution to the tardigrades' evolutionary history, especially its relationship with early other arthropod lineages, even though advancing the knowledge of their mechanisms of tolerance to stress. It underlines the biological uniqueness of the tardigrades and draws on biotechnology potential application providing a basis for further studies on how these proteins can be exploited for use in extreme conditions. Ultimately, it improves our understanding of tardigrades as evolutionary enigmas that turned out to be the best surviving assets in modern times and closes gaps in scientific understanding of early metazoan evolution and resilience mechanisms.

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