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Water Bears in the Land of Diversity: A Comprehensive Review of Tardigrades in India

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ABSTRACT. Tardigrades, also known as water bears, are a group of microscopic invertebrates with four pairs of stout legs. They are known to be found in freshwater, terrestrial and marine environments. An exceptional feature of the tardigrades is their ability to withstand extreme low temperatures, desiccation and other such severe environmental conditions. Globally, 70.8% of the earth is covered with the oceans and seas, while the Indian Ocean accounts for 29% of the global ocean area and is known to be a region of high biodiversity, where India is one of the countries. Tardigrades are known to form a habitat with mosses, lichens, freshwater ecosystems, oceans, and Himalayas in India. One of the main areas of research on tardigrades in India is the diversity and distribution of tardigrade species in different regions of the country, however, very few studies have been conducted on this phylum. Tardigrades have become the subject of increasing interest due to their potential economic importance like their significance in environmental monitoring and space research. Lastly, this phylum needs to be explored in terms of the species distribution and their economic importance, making them a valuable resource for India.

Keywords: Water Bears, Tardigrades, India, Biodiversity, Cryptobiosis, Biogeographic patterns

1. Introduction

Tardigrades are microscopic invertebrates, roughly cylindrical with four pairs of brief stubby legs terminating in claws. Their physical size varies from 50 μm in just hatched individuals to a maximum of 1200 μm in a few exceptionally large species. For fully mature adults, average sizes range typically from 200 to 500 μm. These animals are called “water bears” in many instances due to their bear-like appearance (legs with claws), and sluggish lumbering gait (Nelson et al., 2016). Tardigrades can be found in freshwater, terrestrial, and marine environments. The most well-known tardigrades are those found in terrestrial environments, where they live in the thin film of water on mosses, lichens, algae, other plants, leaf litter, and soil, and are active when there is at least a thin film of water on the substrate. Tardigrades frequently coexist with bdelloid rotifers, nematodes, protozoans, and other animals. Aquatic freshwater tardigrades live on submerged plants or in sediment but they are not water column dwellers. Some tardigrade species can live in both freshwater and aquatic environments.

Over the last couple of decades, the number of studies conducted within the integrative taxonomy has increased, leading to genetically confirmed documentation of tardigrade species from multiple locations for the first time in the history of biogeography. Although the majority of such examples are drawn from a geographically limited sample, i.e. a single continent or a part of it (Michalczyk et al., 2022). Studies show that at least some tardigrades (most with a parthenogenetic mode of reproduction) exhibit wide geographic ranges, but due to the low number of such examples it is not clear whether they reflect the “Everything is everywhere, but environment selects” hypothesis (Baas Becking, 1934) or are a result of anthropogenic dispersal (Gąsiorek et al., 2019; Morek et al., 2021). Thus, tardigrade species distribution patterns are complex, and we need integrative data on more genera and species before drawing sound general conclusions about tardigrade`s biogeography (Michalczyk et al., 2022).

The aim of this study is to examine the variety and occurrence of tardigrade species in various parts of India, and to identify their possible economic significance for environmental assessment and other possible applications in different fields such as space research and

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biotechnology. This study will provide a comprehensive survey of tardigrade diversity and distribution in India, and will highlight the unique features and applications of these resilient microorganisms, which can withstand extreme low temperatures, desiccation and other severe environmental conditions.

2. Classification

According to the recent checklist of tardigrades species as per the studies published by Degma and Guidetti in 2023, there are 1464 species, 159 genera and 33 families present currently (Degma et al., 2019; Degma & Guidetti, 2023). The Tardigrada phylum accepted two classes and four orders. Apochela and Parachela make up Eutardigrada, while Echiniscoidea and Arthrotardigrada make up Heterotardigrada (Jørgensen et al., 2018). Tardigrades are mainly classified into three classes: Heterotardigrada, Eutardigrada and Mesotardigrada. The majority of known species belong to the class Heterotardigrada (Guidetti & Bertolani, 2005). However, the class Mesotardigrada should be considered *nomen dubium* since no such physical evidence is reported for the species namely *Thermozodium esakii* which was known to be placed under class Mesotardigrada evoking the formation of a new class as per the study conducted by Grothman et al., (2017).

The Heterotardigrada class is defined by their possession of plates on their cuticles, while the Eutardigrada class is defined by the lack of such plates (Guidetti and Bertolani, 2005). This classification helps to distinguish tardigrades based on the presence or absence of certain morphological characteristics. The plates on the cuticles of Heterotardigrada species provide them with protection from predators and help them to conserve moisture. Other physical characteristics which are considered for the identification of these two taxa are: the presence of a separate gonopore and anus in Heterotardigrada and the presence of sclerified structures within pharynx which has a different shape and nature as compared to the Eutardigrada taxa. Moreover, the Eutardigrada taxa differs from Heterotardigrada by showing the presence of a common cloaca and "Malpighian tubules". Classification of tardigrades is important for understanding their diversity and evolution. The three classes of tardigrades are differentiated by their morphological characteristics, such as the presence or absence of plates on their cuticles, their leg structures, and their existence. Further research is necessary to better understand the characteristics and evolution of each class of tardigrades.

3. Characteristics

Tardigrades belong to the phylum Tardigrada and are considered to be among the most resilient micro-animals in the world, as they can withstand extreme environmental conditions such as drought, high pressure, and extreme temperatures (Guidetti & Bertolani, 2005). One of the most notable characteristics of tardigrades is their ability to enter a state of suspended animation, known as cryptobiosis, when faced with harsh environmental conditions. In this state, tardigrades can survive without water or nutrients for extended periods of time (Boothby et al., 2015). Naturalists have long been fascinated by tardigrades ability to 'resurrect' after desiccation, when water becomes available. This phenomenon of cryptobiosis, or anabiosis, has assisted tardigrades in surviving 'normal' as well as 'experimental' adverse conditions such as temperatures ranging from - 272 to > 340°C; gases such as CO_2 and H_2S; strong acids, including osmic acid; and alcohol, as well as radiation under ultraviolet light (McInnes, 1994). This ability to enter cryptobiosis is one of the key characteristics that sets tardigrades apart from other micro-animals. Another key characteristic of tardigrades is their hard exoskeleton, known as a cuticle, which provides them with protection from predators and helps them to conserve moisture (Nelson, 2002). The cuticle of tardigrades is made of a material called chitin, which is also found in the exoskeletons of insects and crustaceans. Tardigrades are also known for their unique leg structure, which consists of four pair of legs that are equipped with claws (Nelson, 2002). These legs provide them with the ability to move quickly and efficiently through their environments. The unique leg structure of tardigrades is a characteristic that sets them apart from other micro-animals. Tardigrades are fascinating micro-animals that are known for their ability to enter cryptobiosis, their hard exoskeleton, and their unique leg structure. These characteristics have helped tardigrades to survive and adapt to a wide range of environmental conditions, making them among the most resilient micro-animals in the world.

4. Aquatic and Terrestrial Habitats

Tardigrades are commonly found in freshwater, saltwater, and brackish water environments. They are able to survive in these aquatic habitats due to their ability to regulate their body fluids and osmotic pressure. Tardigrades that live in freshwater habitats, for example, must be able to deal with hypotonic conditions, which means that there is a lower concentration of solutes outside their bodies than inside. They are able to do this by regulating the amount of water in their bodies and by producing certain solutes to maintain osmotic balance. Marine tardigrades, on the other hand, live in a more isotonic environment, which means that the concentration of solutes is the same inside and outside their bodies. However, they still face challenges in the form of high salinity and pressure, as well as changes in temperature and pH. Tardigrades have adapted to these conditions by developing protective mechanisms, such as the production of antioxidants and the ability to repair DNA damage caused by exposure to ultraviolet radiation (Erdmann and Kaczmarek, 2017). Tardigrades have also been found in brackish water habitats, such as estuaries, where they must be able to tolerate fluctuations in salinity and temperature (Zawierucha et al., 2016). Studies have shown that tardigrades in brackish water habitats have a higher tolerance for exposure to low oxygen levels and can even survive periods of anoxia (Jönsson et al., 2008).

Tardigrades are also found in a variety of terrestrial habitats, including soil, moss, lichens, and leaf litter. These habitats pose different challenges than aquatic environments, such as fluctuations in temperature and humidity, as well as exposure to desiccation (drying out). Tardigrades have evolved a number of strategies to deal with these challenges, including the ability to enter a state of suspended animation known as cryptobiosis. During cryptobiosis, tardigrades are able to shut down most of their metabolic processes and become almost completely dehydrated, reducing their water content to as little as 1% of their normal level. This allows them to survive for extended periods of time in harsh conditions (Rebecchi et al., 2007). When conditions improve, tardigrades are able to rehydrate and resume normal activity. Tardigrades in terrestrial habitats also face exposure to radiation from the sun, which can cause DNA damage. To protect against this, tardigrades have developed the ability to produce special proteins that protect against radiation damage and repair DNA damage caused by exposure to high levels of ultraviolet radiation (Jönsson et al., 2008).

5. Global Distribution of Tardigrades

According to a study conducted on Global distribution of tardigrades in freshwater by (Garey et al., 2008), out of 910 species, only 62 species representing 13 genera were found to be the only ones in aquatic habitats. Five genera namely *Carphania*, *Dactylobiotus*, *Macroversum*, *Pseudobiotus*, and *Thermozodium* were found to be exclusively aquatic while other genera like *Hypsibius*, *Isohypsibius*, *Amphibolus*, *Mixibius* had some species that were aquatic as per the study. According to the literature studies, there are over 50 Antarctic and Neotropic species present in freshwater habitats, which primarily are Eutardigrades belonging to 2 orders and 8 families as per (Degma et al., 2009; Nelson et al., 2016). Due to difficulty in access and fewer researchers, the total number of species reported in the regions of Antarctica and Neotropic are much less than other zoographic regions, except for the regions namely Argentina, Chile, Costa Rica and the Antarctic Penisula.

As for previous literature by (Nelson et al., 2020), there are two endemic genera: *Ramajendas* (currently belonging to family Isohypsibiidae), which are found in freshwater sediment, mosses and lichens of the Antarctica and Sub-Antarctica islands. However, in the recent study proposed by (Tumanov, 2022), through the molecular phylogenetic analysis and morphological description of the Antarctic Tardigrade of genus Ramajendas, evoked the formation of a new family named Ramajendidae to place these Ramajendas species. The second monospecific genera are Acutuncus, which previously belonged to family Hypsibiidae but currently the study conducted by Vecchi et al. in 2023 revealed the extension of Acutunus species into a new family named Acutuncidae based on the phylogenetic analyses and morphological studies (Vecchi et al., 2023).

Acutuncus antarcticus is a pan-Antarctic species, most abundant and common tardigrade in Antarctica with a habitat in freshwater ecosystems and terrestrial soils, mosses, algae and lichens in non-glacial areas. Whilst, the Neotropical region contributes to a very diverse freshwater habitats like the tardigrades are found in rivers, streams and lakes in tropical lowlands (in Central America and Northern South America) up to high mountain lakes, ponds and glaciers in the Andean Mountains. The freshwater tardigrades are known to be found in very cold ponds, rivers, lakes and in cryoconite holes on glaciers in the southern end of South America. Meanwhile, the central region provides freshwater habitats in temporary dry or very hot climate zones of South America. Also, the Neotropic regions are known to provide some unusual freshwater habitats for tardigrades, which include tree holes and bromeliads (Nelson et al., 2020).

6. Indian Scenario

Globally, 70.8% of the earth is covered by the oceans and seas, with a global coastline of 1.6 million km. The Marine and Coastal Ecosystem occur in 123 countries worldwide. These ecosystems generally include sand dune areas (where freshwater and sea water mix), nearshore coastal areas and open ocean marine areas. The Indian Ocean constitutes 29% of the global ocean area and is known to be a region of high biodiversity, where India is one of the countries in the region. The land of biodiversity, India is known to be a part of the list of 12 mega-biodiversity countries and 25 hotspots of the richest and highly endangered eco-regions of the world. It is known to have a coastline of about 8000 km. It is also the only country amongst the Asian countries, which has a long record and complete list of coastal and marine biodiversity dating back at least two centuries old (Venkataraman and Wafar, 2005)

In India, Tardigrades happen to be found as meiofauna on the sandy beaches up to 2-3 meters from the sea's edge. Out of the three classes of the phylum Tardigrada, the Heterotardigrada is known to prevail in the marine, freshwater and high-altitude mountain regions of the country. As for the reports, only 10 species under 2 families and 3 genera occur as the meiofauna of the marine regions in India (Venkataraman et al., 2020). Tardigrades are also known to form a habitat with mosses, lichens, freshwater ecosystems, oceans, and Himalayas (Chandra et al., 2018)

Scientific studies on tardigrades have known to be increased throughout the world in the 20th century, yet this phylum remains unexplored and little-known to the scientific community. With regards to India, very few studies have been conducted on this phylum. To know more about this phylum and understand its diversity, detailed studies should be conducted (Dey and Mandal, 2018).

7. Species Diversity in India

Initial studies on tardigrades found in India was conducted as early as in the beginning of 20th century (Murray, 1907) followed by (Iharos, 1969) in the second part of the century. Though, very little was known about the terrestrial tardigrades of India. As a part of the Zoological Survey of India, a review study was conducted, which depicted that 41 species of Tardigrades were known to India, out of which 23 species were found in the Indian Himalayas (Chandra et al., 2018). The above study also referred to the presence of *M. hufelandi* in India, showing the progress in our understanding of the taxonomy of this genus, which is known to be a different species than the last recorded by Murray in 1907 (Murray, 1907). Apart from the larger studies conducted in India, there were also some smaller islands around the subcontinent, like different species of tardigrades found in Andaman and Nicobar Islands by McInnes in 1994 (McInnes, 1994). Geographic representation on a map (Figure 1) followed by a list (Table 1) of Tardigrades species found in various regions of India is given below.

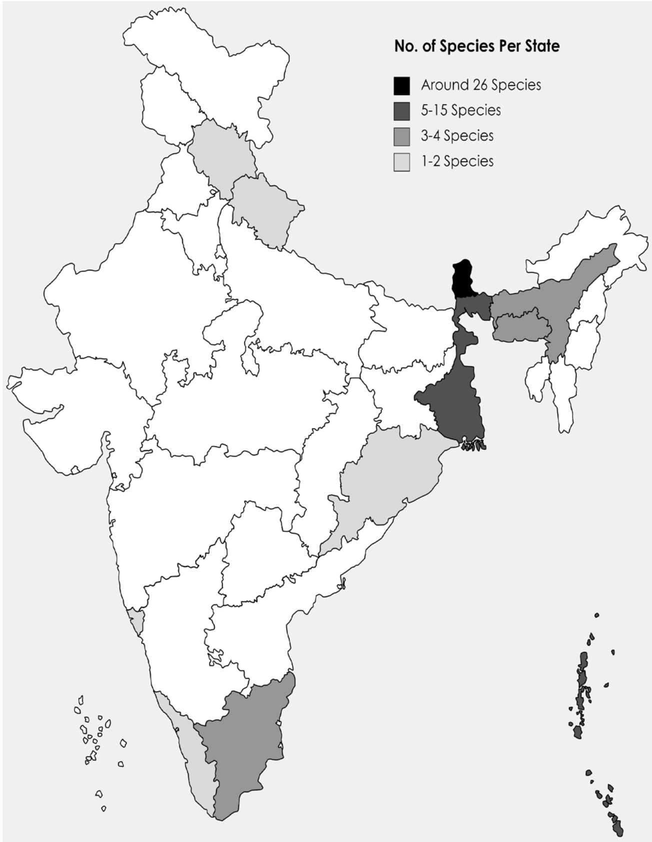

Fig.1. Geographic distribution of Tardigrade species found in different regions of India (1. Sikkim 2. Andaman Islands, West Bengal 3. Assam, Meghalaya, Tamil Nadu 4. Goa, Himachal Pradesh, Kerala, Odisha, Uttarakhand)

8. Research Scenario of Tardigrades in India & it's Ecological Importance

Aquatic meiofauna and terrestrial invertebrate species can be used as a biomonitoring tool to indicate environmental quality. Tardigrade being a meiofauna has also been studied and used as an indicator of pollution in different freshwater habitats (Nelson et al., 2010). A recent study was conducted to inspect the meiofaunal biodiversity of the Dahisar River, Mumbai, the urban development and its impacts in the environmental management by (Salian et al., 2022). This study concluded the presence of tardigrades species in Sanjay Gandhi National Park and Borivali, which were found to be more polluted as compared to other areas, which indicated that tardigrades could survive in polluted areas, thus, acting as an important pollution indicator. This has important implications for industries that are reliant on the health of ecosystems, such as agriculture and forestry, as well as for the development of new technologies for environmental monitoring (Jönsson et al., 2008)

The understanding of ecophysiology of tardigrades and their responses to different environmental conditions becomes a pre-requisite to use them as a tool for biomonitoring of environmental pollution or as an indicator of environmental change (Massa et al., 2023). For instance, a study on the prevalence and distribution of different tardigrades species in some tropical areas of Tamil Nadu and their different temperature tolerance capacity was conducted by (Abirami et al., 2021). This study showed that most of the isolated species belonged to the genus *Milnesium sp.*, others were found to be *Murrayon sp.*, and *Macrobiotus sp.* It was also observed that *Milnesium tardigradum* exhibited higher tolerance to all different temperature conditions as compared to *Macrobiotus sapiens*. This research has important implications for the conservation and management of ecosystems in India. There has been a growing interest in the study of tardigrades in India in recent years. Research on tardigrade diversity and distribution, ecophysiology, and potential as bioindicators has contributed to our understanding of these unique micro-animals and their significance in the Indian environment (delBarco-Trillo, 2019).

Tardigrades have become the subject of increasing interest due to their potential economic importance. Despite their small size, tardigrades play a significant role in several key industries and have the potential to be valuable resources in the future. One area where tardigrades have economic importance is biotechnology. Tardigrades are known for their ability to withstand extreme environmental conditions, including high temperatures, radiation, and desiccation. This resilience has led to their use in the development of new technologies, such as cryopreservation methods for the storage of cells and tissues (Bertolani et al., 2004). In addition, tardigrade genes have been used in the development of new methods for the production of proteins, such as the production of vaccines (Boothby et al., 2017). Apart from this, the mechanism behind the physiological adaptations made by tardigrades to survive extreme environmental conditions drives the scientific community to develop products having application in various fields. For instance, a recent study published in 2023, conducted by (Mredha et al.,

Table 1. List of Tardigrade species found in India

No.	Species	Location	References
1	*Adropion scoticum*	Sikkim	(Chandra et al., 2018)
2	*Batillipes carnonensis*	Odisha	(Rao, 1971)
3	*Bryodelphax ortholineatus*	Andaman Island	(McInnes, 1994)
4	**Calcarobiotus gildae*	Andaman Island	(McInnes, 1994)
5	**Claxtonia wendti*	Sikkim	(Chandra et al., 2018)
6	*Cornechiniscus madagascariensis*	Himachal Pradesh	(Abe and Takeda, 2000)
7	*Dactylobiotus macronyx*	Sikkim	(Chandra et al., 2018)
8	**Dianea acuminata*	Sikkim Tamil Nadu	(Chandra et al., 2018) (Degma and Guidetti, 2023)
9	**Dianea sattleri*	Sikkim	(Chandra et al., 2018)
10	*Diphascon chilenense*	Sikkim	(Murray, 1907) (Chandra et al., 2018)
11	*Diphascon pingue*	Sikkim	(Chandra et al., 2018)
12	*Echiniscus arctomys*	Sikkim	(Murray, 1907) (Chandra et al., 2018)
13	**Pseudechiniscus suillus*	Sikkim	(Murray, 1907) (Degma and Guidetti, 2023)
14	*Echiniscus quadrispinosus*	Sikkim West Bengal	(Chandra et al., 2018) (Murray, 1907)
15	*Echiniscus testudo*	Assam Meghalaya West Bengal	(Degma and Guidetti, 2023) (Murray, 1907)
16	*Hypsibius convergens*	Andaman Islands Sikkim	(Degma and Guidetti, 2023) (Chandra et al., 2018)
17	**Kristenseniscus kofordi*	Andaman Island	(McInnes, 1994)
18	*Macrobiotus echinogenitus*	Sikkim West Bengal	(Chandra et al., 2018) (Murray, 1907)
19	*Macrobiotus gemmatus*	Sikkim	(Chandra et al., 2018)
20	*Macrobiotus hufelandi*	Assam Meghalaya Sikkim West Bengal	(Degma and Guidetti, 2023) (Shil, 2001) (Chandra et al., 2018) (Murray, 1907)
21	*Macrobiotus kamilae*	Uttarakhand	(Coughlan and Stec, 2019)
22	*Macrobiotus polyopus*	Andaman Island	(McInnes, 1994)
23	*Macrobiotus rubens*	Sikkim	(Chandra et al., 2018)
24	*Macrobiotus sapiens*	Tamil Nadu	(Abirami et al., 2021)
25	*Macrobiotus topali*	Sikkim	(Chandra et al., 2018)
26	**Mesobiotus coronatus*	Andaman Island	(McInnes, 1994)
27	**Mesobiotus furciger*	Andaman Island	(McInnes, 1994)
28	**Mesobiotus harmsworthi*	Andaman Island	(McInnes, 1994)
29	**Mesobiotus mauccii*	Andaman Island	(McInnes, 1994)
30	*Milnesium tardigradum tardigradum*	Andaman Island Sikkim Tamil Nadu West Bengal	(McInnes, 1994) (Chandra et al., 2018) (Abirami et al., 2021) (Murray, 1907)
31	**Minibiotus aculeatus*	Andaman Island Sikkim West Bengal	(McInnes, 1994) (Chandra et al., 2018) (Murray, 1907)
32	**Minibiotus furcatus*	Assam Meghalaya West Bengal	(Degma and Guidetti, 2023) (Shil, 2001) (Murray, 1907)

No.	Species	Location	References
33	*Minibiotus intermedius*	Andaman Island Sikkim	(McInnes, 1994) (Chandra et al., 2018)
34	*Nebularmis indicus*	Goa	(Gąsiorek, Vončina, Ciosek et al., 2021)
35	**Nebularmis reticulatus*	Sikkim	(Murray, 1907) (Chandra et al., 2018)
36	**Paramacrobiotus areolatus*	Sikkim	(Murray, 1907)
37	**Paramacrobiotus chieregoi*	Andaman Island	(McInnes, 1994)
38	**Paramacrobiotus richtersi*	Andaman Island Sikkim Tamil Nadu	(McInnes, 1994) (Chandra et al., 2018) (Abirami et al., 2021)
39	**Pseudechiniscus (Meridioniscus) juanitae*	Sikkim	(Chandra et al., 2018) (Gąsiorek, Vončina, Zając et al., 2021)
40	*Ramazzottius oberhaeuseri*	Sikkim	(Chandra et al., 2018)
41	*Stygarctus keralensis*	Kerala	(Vishnudattan et al., 2021)
42	**Stygarctus bradypus*	Odisha	(Rao, 1971) (Schulz, 1951)
43	**Testechiniscus macronyx*	Sikkim	(Murray, 1907)
44	**Ursulinius mihelcici*	Sikkim	(Chandra et al., 2018)

Note: * – indicates changed taxa as for updated checklist by (Degma and Guidetti, 2023)

2023) depicted the development of an extremotolerant glycerogels by studying the tun formation process in tardigrades and taking inspiration from this process. These gels have varied applications in the field of biomedicine, energy storage devices, sensors, and soft robotics.

Another remarkable study showing the natural occurrence of a fluorescence against ultraviolet radiation in the Eutardigrade *Paramacrobiotus* species conducted by (Suma et al., 2020). The study provided experimental evidence that the *Paramacrobiotus* species produces a protective fluorescent shield that absorbs ultraviolet radiation and thus, this can be used to protect UV-sensitive tardigrades and nematode like *Caenorhabditis elegans* from UV radiation used as a germicide.

Another interesting area where tardigrades have economic importance is space research. Tardigrades have been found to survive in the harsh conditions of space, including extreme temperatures and high levels of radiation (Jönsson et al., 2008). This has led to their use in space research and the development of new technologies for space exploration. Tardigrades have significant economic importance in several key industries, including biotechnology, environmental monitoring, and space research. As research of these micro-animals continues, it is likely that their importance will only increase, making them valuable resources for the future.

9. Conclusion

Little or very few studies have been conducted and there are still areas, which remain unexplored in terms of the species diversity and distribution pattern in India. Increasing research on tardigrade diversity and distribution, ecophysiology, and potential as bioindicators has contributed to our understanding of these unique micro-animals and their significance in the Indian environment. Tardigrades have also become a subject of interest due to their potential economic importance in fields like Biotechnology, environmental monitoring, and space research. The rise in research of these microscopic invertebrates will increase their significance and make them a valuable resource for future applications.

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Conflict of Interest

The authors declare no conflicts of interest.

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