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Antarctic tardigrades a biological model for geobiology and astrobiology studies: a review

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***Abstract*– Tardigrades (commonly known as "water bears") are microscopic animals whose bodies are usually less than 1 mm long, they are microscopic bilaterian organisms that belong to the phylum Tardigrada. These organisms are best known for initiating and maintaining a state of dormancy known as cryptobiosis. This ability allows them to survive in unfavorable environments and to inhabit places characterized by extreme temperatures, variable water availability, etc. (e.g., Antarctica). Antarctica is of great scientific interest, as the extreme environmental conditions require unique adaptive traits expressed by the organisms inhabiting this region. The presence of tardigrades in Antarctica has been scientifically documented, and their characteristics could be strategic in developing geobiological, astrobiological, and other areas of knowledge.**

***Keywords*-- biodiversity, cryptobiosis, evolutionary adaptations, extreme environment, polar ecology.**

I. Introduction

Limno-terrestrial tardigrades are microscopic bilaterian organisms that belong to the phylum Tardigrada within the larger protostome superclade called Ecdysozoa. [1]. They are also known as water bears or moss piglets [2]. These organisms are close relatives of arthropods and Onychophora [3], with body sizes from 50 μm to 1200 μm, and eight legs [4], [5]. The body of a tardigrade is composed of five segments, which include a head and four trunk segments. Typically, they consist of only about 1,000 cells [6].

Over the years, the number of identified tardigrade species has grown significantly since the initial species description by Schultze [7]. Currently, there are more than 1400 acknowledged species within the phylum [8].

The semi-terrestrial tardigrades are found in soil, sediments, bryophytes, lichens, algae (where they are active when a water film surrounds the substrate), and lotic and lentic environments. They can be found from low to high altitudes and latitude, from tropical, temperate, desert, and polar habitats [9]. Additionally, tardigrades having an estimated life span of three to 30 months, without including their latency or cryptobiosis period [9].

The majority of tardigrades rely on water for growth and reproduction, certain species found in limno-terrestrial habitats possess the remarkable capability to endure drought [10] and tolerate a variety of extreme environmental conditions at any stage of their life because of their ability to enter cryptobiosis, a process in which metabolic activity is temporarily suppressed [11], [12], [13]. This trait enables water bears to survive in extreme environments such as Antarctica [14], [15].

The extreme climatic conditions of Antarctica are of high scientific interest, and has contribute to organisms developing or displaying unique evolutionary adaptations to the environmental extremes that characterise Antarctica: low temperatures, desiccation, high salinity (in coastal regions), high solar irradiance [16]. Research on Antarctic tardigrades started in the early 20th century, but was sporadic and associated with expeditions (e.g. Richters 1904a; Murray 1907; Richters 1908; Murray 1910 [17], [18], [19], [20]). The knowledge of Antarctic tardigrades is still relatively poor. In 2005, Convey and McInnes reported on the presence of tardigrade species on ten of the 11 major islands of the Antarctic Peninsula, and including previous reports, approximately 55 species have been documented in the Antarctic region.

The Antarctic Peninsula has a higher variety of tardigrade species than continental Antarctica [21]. However, knowledge of the biogeographic distribution, abundance, and diversity of tardigrades in Antarctica remains limited [22], making them an attractive research topic. [23], [24]. The relationships between tardigrades, geology, and space research have been even less studied, but with a great perspective of development as a research topic. For this reason, the present article aims to review the research potential of limno-terrestrial tardigrades in Antarctica as a model for geobiological and astrobiological studies.

II. MATERIALS AND METHODS

To analyse the geographic distribution of tardigrade species reported in Antarctica, academic texts were collected and reviewed from different databases from 2022 to 2024. This literature review was conducted using articles found in ResearchGate, SpringerLink, Csiro Publishing, Scopus and Google scholar. The search was conducted using "Tardigrade", Antarctic" and "Antarctica" as keywords. Also, articles found in references section of the articles selected were manually searched and included in the review. Peer reviewed articles presenting information about the occurrence of limno-terrestrial tardigrades in Antarctic were added, including their isolation and identification process.

III. TARDIGRADES AND CRYPTOBIOSIS

Tardigrades can be categorized into two primary evolutionary lineages: eutardigrades and heterotardigrades. Among these, the heterotardigrades exhibit greater diversity in terms of species and characteristics [25].

Tardigrades do not possess specialized respiratory organs; instead, gas exchange occurs through diffusion across the epidermis and cuticle [5]. Similarly, they lack circulatory organs like a heart, and instead rely on a fluid-filled body cavity for circulatory functions. This cavity accommodates storage cells of varying sizes and quantities, which move passively along with the animal's movements [26]. The storage cells play important roles in nutritional maintenance, vitellogenesis, and potentially contribute to immune defense mechanisms [27]. Tardigrades possess longitudinal muscles and excretory systems. Males, females, and hermaphrodites capable of self-fertilization exhibit a singular dorsal sack-like gonad. In certain species, reproduction solely occurs through parthenogenesis, with only female individuals present [28].

Tardigrades have the capacity to undergo cryptobiosis, a state of reversible standstill often referred to as latent or hidden life, is prevalent across various kingdoms of life [29]. Among metazoans, nematodes, rotifers, and tardigrades possess the remarkable ability to enter cryptobiosis at any stage of their life cycle, including as eggs, juveniles, and adults [30].

The entry into the cryptobiotic state involves a sequence of anatomical and physiological transformations. The presence of a water film is crucial for tardigrades to maintain their physiologically active state [31]. When faced with desiccation, during which tardigrades can lose over 95% of their water content, they undergo longitudinal contraction. In this process, they retract their head and legs, assuming a dormant and barrel-shaped structure known as a "tun" [32]. In this state, oxygen consumption almost stops, and the metabolic rate decreases considerably [33], [34], [35]. Nonetheless, there is compelling evidence suggesting that certain species of tardigrades can endure substantial levels of environmental stress even while in an active state [36]. Cryptobiosis can be triggered by various extreme conditions, leading to different stages of cryptobiotic dormancy. Notably, stressors such as; water loss (desiccation), increased external osmotic pressure (osmobiosis), freezing (cryobiosis), lack of oxygen (anoxibiosis), and exposure to environmental toxins (chemobiosis), can induce a state of quiescence [37], [38], [39], [40], [41], [42], [43]. Anhydrobiosis, osmobiosis, and potentially chemobiosis are cryptobiotic states characterized by the formation of tuns. The ability to form tuns is observed in some existing tardigrade lineages, indicating that it is an ancient and shared characteristic [44].

The interest in the investigation of tardigrade physiology is growing because of their ability to withstand a diverse range of abiotic challenges. These challenges encompass desiccation [31], [38], elevated levels of ionizing and UV radiation [45], [46], the vacuum of space [47], [48], contact with harmful heavy metals and metalloids [49], [50], extreme temperatures spanning from very low to high [40], [51], [52], and varying atmospheric conditions, including both low and high pressures [41], [53], and even oxygen deprivation [54], [55].

Despite the limited understanding of the cryptobiosis process, the mounting evidence indicates that tardigrades produce a diverse array of molecules with bioprotective properties [56], [57]. These molecules include proteins, such as DNA repair systems, as well as carbohydrates, among other substances [58]. For instance, there is a unique protein called Damage suppressor (Dsup) found in tardigrades that plays a crucial role in safeguarding DNA. This tardigrade-specific protein can bind to DNA and nucleosomes [59], [60], [61].

When introduced into human cultured cells, Dsup effectively mitigates the occurrence of DNA breaks induced by radiation and reactive oxygen species (ROS). As a result, the expression of Dsup enhances the survival of cells exposed to a semi-lethal dose of X-ray irradiation [62]. Tardigrades possess additional unique proteins called Cytosolic Abundant Heat-Soluble (CAHS) and Secretory Abundant Heat-Soluble (SAHS) proteins. These proteins have been associated with the tardigrades' capacity to endure desiccation, enabling their survival in extremely dry conditions [63]. These biological capabilities and the ability to enter a cryptobiosis state facilitate and increase the survival and presence of tardigrades in Antarctica.

IV. ANTARCTIC TARDIGRADES

According to the literature, the presence of tardigrades in Antarctica was first validated in 20th century [64]. Richters [65], was the first to report the presence of tardigrades in Antarctica. Until 1962, only four genera had been identified, namely, *Echiniscus, Pseudechiniscus, Hypsibius,* and *Milnesium*. These genera were mostly collected from the South Orkney Islands, Victoria Land, South Shetland, and other locations in Antarctica [66]. In Larsemann Hills, East Antarctica, surveyed in 1987, five genera and six species of Tardigrada were identified, and dynamics linked to dispersal capabilities of tardigrades in Antarctica were proposed [67].

In 1988, A total of 28 species of tardigrades were known from the Vestfold Hills in Antarctica (Miller et al., 1988). These species have been reported in Gaussberg [69], Syowa, Queen Maud Land (Japanese base) [70], Vestfold Hills (Davis Base), and the Clark Peninsula (Wilkes Base) [67], [71]. Understandably, the first reports of tardigrades were of locations near bases; therefore, most knowledge of tardigrades in Antarctica was focused on East Antarctica and the Antarctic Peninsula [67], [72], [73]. There have also been reports of tardigrades in Enderby Land, Coast of Alasheev Bight, Antarctic Peninsula, and South Shetland Islands - King George Island.

At the end of the 20th century, Dastych redescribed the species *Hypsibius antarcticus* to prevent it being confused with *Hypsibius arcticus* and reassigned all Antarctic tardigrades cited as *Hypsibius arcticus* in the literature to *Hypsibius antarcticus* [74], [75]. Pilato & Binda [76] revised the genus to *Acutuncus antarcticus*. Other species of tardigrades reported during the 20th century have been redescribed due to the improving taxonomic methods in the last decades and the increasing interest in studying these organisms to help classify them according to their similarities. For example, the species *Echiniscus pseudowendti* was reassigned to *Claxtonia pseudowendti*. In summary, around 35 tardigrade species were documented in the 20th century such as *Pseudechiniscus suillus, Acutuncus antarcticus, Ramajendas frigidus, Diphascon chilenensis, Dip. pingue, Dip. polare, Dip. dastychi*, and *Dip. victoriae* [77].

In 2000, a new species of eutardigrade, *Diphascon (Adropion) tricuspidatum* (now *Adropion tricuspidatum*) was found with *Acutuncus antarcticus* in a small lake in the Crater Cirque (Victoria Land) [78]. The following year, more information on tardigrades obtained from the 1977 to 78 Australian Museum Expedition was published, expanding on information highlighting the evolutionary relationships of tardigrades in Antarctica and confirming the biogeographic distinctiveness of *Adropion tricuspidatum*.

TABLE I
TARDIGRADES DOCUMENTED IN ANTARCTICA DURING THE 20TH CENTURY

	Genera	Species	Reference
1	*Acutuncus*	*antarcticus*	[18], [69], [72], [74], [80], [81], [82]
2	*Adropion*	*greveni*	[72]
3	*Barbaria*	*jenningsi*	[72], [80], [83]
4	*Claxtonia*	*pseudowendti*	[74]
5	*Dastychius*	*improvisus*	[74]
6	*Dianea*	*papillifer*	[84], [85]
7	*Diphascon*	*alpinum*	[72], [74], [86]
8	*Diphascon*	*chilenensis*	[83], [87]
9	*Diphascon*	*mirabile*	[74]
10	*Diphascon*	*pingue*	[72], [81]
11	*Diphascon*	*puniceum*	[86]
12	*Diphascon*	*sanae*	[80], [88], [81]
13	*Diphascon*	*polare*	[77]
14	*Diphascon*	*dastychi*	[77]
15	*Diphascon*	*victoriae*	[77]
16	*Echiniscus*	*kergeuelensis*	[84]
17	*Echiniscus*	*darienae*	[80]
18	*Echiniscus*	*punctus*	[85]
19	*Grevenius*	*asper*	[85]
20	*Grevenius*	*laevis*	[85]
21	*Hebesuncus*	*schusteri*	[74]
22	*Hebesuncus*	*conjungens*	[82]
23	*Hypsibius*	*convergens*	[89]
24	*Hypsibius*	*dujardini*	[72]
25	*Hypsibius*	*simoizumii*	[90]
26	*Mesobiotus*	*blocki*	[80]
27	*Mesobiotus*	*fuciger*	[72], [91]
28	*Mesobiotus*	*harmsworthi*	[84], [87]
29	*Milnesium*	*tardigradum*	[72], [85], [82]
30	*Minibiotus*	*weinerorum*	[67], [88]
31	*Minibiotus*	*stuckenbergi*	[92], [88]
32	*Mixibius*	*saracenus*	[82]
33	*Oreella*	*mollis*	[85]
34	*Pseudechiniscus(Meridioniscus)*	*novaezeelandiae*	[68], [93]
35	*Pseudechiniscus(Pseudechiniscus)*	*suillus*	[85], [93]
36	*Ramajendas*	*heatwolei* sp.	[80]
37	*Ramajendas*	*frigidus*	[94]
38	*Ramajendas*	*renaudi*	[72], [95]
39	*Ramazzottius*	*oberhaeuseri*	[96], [97]

Previous reports and descriptions of tardigrades were usually studies focusing on which tardigrades are to be found in Antarctica; however, more studies on abundance, frequency, species richness, and their correlation with others species have been published. A study conducted in the nunataks of the Schirmacher Oasis found that the highest densities of tardigrades were observed at sites with mosses, lichens, liverworts, or algae [99]. The most abundant and frequently occurring tardigrade genera were found to be *Mesobiotus and Hebesuncus* [99]. In addition, studies on tardigrade colonization and dynamics have also been published (e.g. Smykla et al. 2012). Results showing post-glacial and Holocene dynamics were obtained through the assessment of tardigrade eggs and exuviae from Antarctic lake sediments and paleosediments [101].

A new species of Heterotardigrada, *Echiniscus corrugicaudatus* (now *Claxtonia corrugicaudatus*) was discovered by McInnes (2010) in the nunataks of Ellsworth Land, West Antarctica. In 2012, *Milnesium antarcticum* was documented in inland Antarctica for the first time, more specifically in Victoria Land [100], [103]. The *Mil. antarcticum* specie were also found with *Acutuncus antarcticus* and were present in 23 of 41 samples. The occurrence of these two tardigrades species in Victoria Land is linked to the high water availability in the soil [100];

overall, abiotic conditions influence the abundance of these animals [104].

The location near Syowa station is one of places in continental Antarctica [105], [106]; therefore, an update of tardigrade diversity was reported in this area, and three new species were documented: *Claxtonia pseudowendti, Hebesuncus ryani,* and *Pseudechiniscus* sp.§ [106]. Another location is Victoria Land, where numerous species of tardigrades have been reported. Pilato et al. (2017) included new information on the Tardigrada biodiversity, updating the presence of *Diphascon sanae* and reporting two new species, namely, *Mixibius felix* and *Milnesium validum*.

In recent years, molecular characterisation in conjunction with morphological descriptions, i.e. integrative taxonomy, has been used to facilitate the identification of new taxa. The species *Mopsechiniscus franciscae* [108], *Cryoconicus antiarktos,* and *Ramazzottius sabatiniae* [109] were identified using this technique.

With the advent of technological advances, modern molecular studies have been applied to understanding the evolutionary relationships of Antarctic tardigrades. For example, an 18S rRNA sequencing was performed to confirm a culture of tardigrades from near Syowa station, and the presence of *Acutuncus antarcticus* was confirmed. Older records had confused this species with *Hypsibius articus* [105]. The use of molecular techniques to identify mitochondrial operational taxonomic units (OTUs), resulted in potentially more putative species in the genera *Acutuncus, Milnesium*, and *Echiniscus* than have been reported using older morphological methods [110].

These new tools used for identification methods allow a faster classification [111], [112]. For example, various species have been redescribed, such as *Hypsibius dujardini* [113], *Hypsibius murray* [114], and the genus *Ramajendas* [115]. However, taxonomic studies of Antarctic tardigrades have developed slowly and the diversity and distribution of these animals in this extreme continent remains largely unknown. This is mainly due to difficulties associated with working in the extreme climatic conditions of Antarctica, distance, transport and mobility, which make most of the continent inaccessible and prevent comprehensive studies (Fig 1). A list of tardigrade species documented since 2000 is provided in.

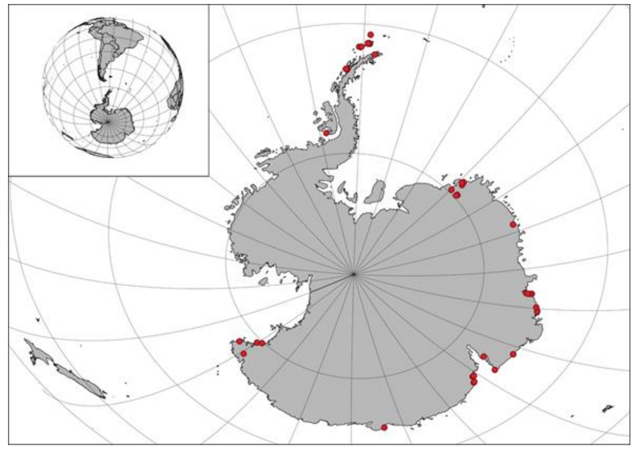

Fig. 1 Location of tardigrades collected from different locations of the Antarctic continent.

V. Geobiological relationships

Geological processes can be understood from the established biological relationships; in turn, geological dynamics can model diverse biological processes. This relationship between life and a planet's geological history is known as geobiology [116]. Depending on the biological scale at which one works, the geological processes that may impact will vary [117]. Biogeochemical cycles are one of the most important relationships between microorganisms and geology [117], [118].

In addition, changes such as sea level, volcanic activity, or mineralogical composition of rocks directly affect the distribution and diversity of microorganisms [119], [120]. Some of the most determinant geological parameters for the presence and abundance of certain species of microorganisms are soil type, water availability, and the presence of certain minerals [121], [122], [123]. On the other hand, some microorganisms can serve as bioindicators of geological changes [124].

For most microorganisms, it has been evidenced that they tend to be more abundant and diverse in soils rich in organic matter [117], [125]. However, in the case of tardigrades studied in Antarctic sectors, it has been found that the determining factor was the water content in the soil, this taking into account that in Antarctic sectors with ornithogenic soils, major presence and diversity of tardigrades was observed [100], [126].

On the other hand, it has been identified that limnoterrestrial tardigrades could be an indicator of geological history. Tardigrades though not part of the fossil record and, until recently, thought to be ubiquitous due to their aerial dispersal and cryptobiosis [127], have shown that they are associated with specific geological and environmental characteristics and with the scale of geological time (Pilato and Binda 2001; McInnes and Philip 2007; Guidetti et al. 2017). Finally, tardigrades could be diverse in mineralogical environments, being organisms that can tolerate toxicity, contribute to nutrient cycling, and use nutrient diversity [130], [131].

VI. Astrobiological perspectives

Considering the characteristics mentioned above, which allow tardigrades to survive in extreme conditions, they have been considered a possible model organism for the search for life outside Earth [47]. Tests on several tardigrade species suggest they could survive in conditions similar to those found on other planets and moons [132].

TABLE II
ANTARCTIC TARDIGRADES DISCOVERED IN THE 21ST CENTURY

	Genera	Species	Reference
1	*Adropion*	*tricuspidatum*	[78]
2	*Bryodelphax*	*olszanowskii*	[133]
3	*Claxtonia*	*corrugicaudatus*	[102]
4	*Cryoconicus*	*antiarktos*	[109]
5	*Dactylobiotus*	*ovimutans*	[134]
6	*Diphascon*	*puchalskii*	[133]
7	*Diphascon*	*rudnickii*	[133]
8	*Hebesuncus*	*ryani*	[99], [106]
9	*Hebesuncus*	*mollispinus*	[64]
10	*Hypsibius*	*conwentzii*	[133]
11	*Mesobiotus*	*aradasi*	[135]
12	*Mesobiotus*	*hilariae*	[22]
13	*Mesobiotus*	*krynauwi*	[99]
14	*Milnesium*	*validum*	[107]
15	*Milnesium*	*rastrum*	[136]
16	*Milnesium*	*antarcticum*	[100], [103], [137]
17	*Milnesium*	*quadrifidum* cv	[64]
18	*Mixibius*	*felix*	[107]
19	*Mopsechiniscus*	*franciscae*	[108]
20	*Paramacrobiotus*	*fairbanksi*	[64]
21	*Pseudechiniscus*	*titianae*	[22], [106]
22	*Ramajendas*	*dastychi*	[138]
23	*Ramazzottius*	*sabatiniae*	[109]

Some experiments related to short-duration flights demonstrated the ability of tardigrades to survive in an anhydrobiotic state in open space environments in low-Earth orbit [47], [139]. Furthermore, tardigrades offer valuable insights into the origin and evolution of life, enriching our understanding of the intricate tree of life on Earth and shedding light on the potential for life to arise in diverse environments [47]. The study of tardigrades provides valuable insights into organisms' adaptability and survival strategies. Their unique characteristics make them fascinating objects of study that contribute to expanding our understanding of the potential for life in the universe [140].

VII. Tardigrades and their potential applications

The study of tardigrades is of great importance for several reasons. First, tardigrades exhibit remarkable survivability, which allows them to withstand extreme conditions such as desiccation, high radiation, and temperature extremes. By delving deeper into the mechanisms driving their exceptional resilience, valuable insights can be gained into adaptations and survival strategies in hostile environments [1]. Tardigrades, such as *Macrobiotus hufelandi*, are well known for their remarkable temperature tolerance, showing resistance to temperatures above 100°C for up to 30 min [30]. *Ramazzottius varieornatus* is also classified as a highly tolerant species [141], and *Richtersius coronifer* presents a resistance to high temperature, making both particularly intriguing in their adaptation to global warming [142]. Exploring cryptobiosis and anhydrobiosis mechanisms holds excellent promise for diverse fields, such as medicine, biotechnology, and stress-resistant plant breeding [42].

On the other hand, Antarctica is a relatively unexplored habitat, with limited knowledge about their biodiversity, despite harboring a great variety of unicellular and multicellular organisms. Tardigrades, in particular, play an essential role in these ecosystems, and their study contributes to a better understanding of their ecological dynamics and functions within these niches [143]. For example, limnoterrestrial tardigrades play crucial roles within Antarctic ecosystems, where terrestrial microinvertebrates provide carbon and nutrient cycling roles in soil environments, as a consecuence of the absent of larger macroinvertebrates [144]. This role becomes particularly relevant in the absence of other regulatory agents, highlighting the importance of these tardigrades in maintaining ecological balance [145], [146]. The study of these ecological functions not only guides the development of appropriate conservation strategies but also improves our understanding of the factors influencing the dispersal and distribution of organisms in glacial ecosystems [147].

Finally, tardigrades could play a vital role in the field of health in the future. Such is the case of *Ramazzottius varieornatus*, one of the tardigrades mentioned above and one of the most tolerant to stressful environmental conditions. From this organism, it was possible to extract a protein exclusively associated with tardigrades, which, when added to a human cell culture and subjected to X-rays and dehydration, generated a cell culture that was 40% more radioresistant and tolerant to water deficit [62]. The above highlights an existing potential in tardigrade proteins as gene protectors.

VIII. CONCLUSION

Antarctica is a continent with very extreme conditions [148], [149], [150], [151]; 152], [153]; it is an ideal place for the study of tardigrades. These are extraordinarily resilient organisms. Their ability to survive in extreme conditions such as desiccation, radiation, and extreme temperatures makes these organisms tolerant and resistant to extreme ecosystems such as Antarctica. They are interesting candidates for understanding the possibility of life on other planets making these organisms a coveted model for astrobiology research. Also tardigrades can enter cryptobiosis and anhydrobiosis holds promising prospects in fields such as medicine and biotechnology. Studying tardigrades in Antarctica can provide insights into how microorganisms adapt to and influence geological processes and could be a key factor in understanding climate change and their role in glacial ecosystems. The Antarctic Peninsula has a higher variety of tardigrade species than continental Antarctica [148]. However, knowledge of the biogeographic distribution, abundance, and diversity of tardigrades in Antarctica remains limited making them an attractive research topic. The relationships between tardigrades, geology, and space research have been even less studied, but with a great perspective of development as a research topic. For this reason, the present article aims to review the research potential of limno-terrestrial tardigrades in Antarctica as a model for geobiological and astrobiological studies.

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