

Bathybic ostracods: Old, diverse, and plenty of memories on past oceans

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Abstract: Research on deep-sea ostracods – hereafter referred to as bathybic – and its contribution to the understanding of past oceans is the theme of this paper. Its development is an outcome of the strategic expansion of oceanography by European nations during the 19th century and subsequent improvements in deep-sea sampling technology, during the 20th century. The bathybic ostracodology has revealed unusual ecological and taxonomic patterns over the last 140 years. Since its full-establishment by the end of the 1960s, the field has followed three main paths: (i) the faunal approach; (ii) the geochemical approach, and (iii) the morphometric approach. Advancements in the knowledge on recent and fossil assemblages expanded the use of bathybic ostracods as hydrological markers, enhancing their application in the study of changes in the oceans through time. In spite of limitations imposed by the inadequate taxonomy of some genera, the astounding diversity, and the long evolutionary history of ostracods make them critical organisms for the understanding of deep oceans. This paper reviews some crucial studies on bathybic assemblages, since the pioneering work by George Stewardson Brady, with an emphasis on their contribution to the development of ostracodology and oceanography.

Key-words: Deep-sea research; Paleooceanography; Ostracoda; paleontology

Ostracodes batílicos: antigos, diversos e repletos de memórias sobre os oceanos pretéritos

Resumo: A pesquisa sobre ostracodes de águas profundas – doravante referidos como batílicos – e sua contribuição ao estudo dos oceanos pretéritos é

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o tema deste trabalho. Seu desenvolvimento resulta do fomento estratégico da oceanografia conduzido por nações europeias durante o século 19, e ao subsequente aperfeiçoamento de tecnologias de coleta em águas profundas ao longo do século 20. A ostracodologia batfílica revelou, em seus quase 140 anos de existência, padrões ecológicos e taxonômicos peculiares. Desde seu pleno estabelecimento ao final da década de 1960, seguiu três rumos principais: (i) a abordagem faunística; (ii) a abordagem geoquímica, e (iii) a abordagem morfométrica. Avanços no conhecimento sobre ostracodes batfílicos fósseis e viventes propiciaram a expansão de seu uso como marcadores hidrológicos, reforçando sua aplicação paleoceanográfica. Apesar das limitações impostas pelo ainda frágil conhecimento taxonômico sobre alguns gêneros, a notável diversidade e longa história evolutiva tornam os ostracodes elementos-chave à compreensão dos oceanos profundos e suas mudanças ao longo do tempo. Alguns trabalhos relevantes sobre assembleias batfílicas desde o pioneiro estudo de George Stewardson Brady são aqui discutidos, com ênfase em sua contribuição ao desenvolvimento da ostracodologia e da oceanografia.

Palavras-chave: águas profundas; paleoceanografia; Ostracoda; paleontologia

1 INTRODUCTION

The appeal of ostracods is inversely proportional to their size. It is simply amazing how much information these tiny crustaceans hold in their sometimes smooth, sometimes intricately carved carapaces. No matter the habitat or age, they help us to understand changes in our planet in the last ~ 485 Ma¹. Ostracods have long caught the attention of naturalists for the study of past climates or rock dating (Bergue, 2010). This paper, however, focuses on a branch of this broad research field known as ostracodology: the study of ostracods from the deeper oceanic regions.

Some valuable papers have already been written describing advancements on the knowledge of bathybiic ostracods between the late 19th and 20th centuries (e.g., Benson, 1988; Whatley, 1996; Cronin *et al.*, 2002). So, the purpose of this new contribution is twofold: firstly, to discuss how these bivalved Lilliputian organisms improved our comprehension on past oceans, providing complementary data to the papers above mentioned; secondly, to contextualize the origin and development of this research area. Naturally, this article does not

¹ Ma = millions of years. The Ordovician Period (which began ~ 485 Ma) holds the oldest records of Ostracoda known so far.

intend to discuss details of each work on bathybiic ostracods published up to now; instead, this paper comments in more detail on innovative or outstanding studies, which in many cases have become lodestars for subsequent research.

Since the late 18th century, ostracods have been studied either by paleontologists or zoologists whose works are ruled by distinct conceptual principles. Paleontologists study assemblages, which in some cases assemble fossils of different ages and provenances; zoologists, on the other hand, work on living populations (faunas) that are usually autochthonous. As a result of evolution in response to ecological and biogeographic constraints, ostracods from shallow regions became somewhat different taxonomically from those of deeper ones to such a degree that separation also emerged between the scientists studying them.

2 THE HISTORY OF A CONCEPT

Bathybiic ostracods occur at least since the Devonian Period (419-358 Ma) when a distinctive deep-water Thuringian Mega-assemblage appeared that could be distinguished morphologically from the shallower Eifelian Mega-assemblage (Crasquin & Horne, 2018). This characterization of shallow thermospheric (warm water) and deeper psychrospheric (cold water) faunas became subdued during the Jurassic and Cretaceous (201-66 Ma). However, since the inception of modern thermal stratification in the Eocene (56-33 Ma), some taxa became more abundant and diverse in deepwaters, continuing through evolution toward a Neogene mega-assemblage. Benson (1972) argues that Cenozoic bathybiic ostracods originated probably from older stocks of species living in shallow waters which adapted through evolution to deeper environments.

In the literature, “deep-sea” is the most common designation for ostracod species living either in bathyal or abyssal domains (or both, in some cases). They are also referred to as psychrospheric; however, the use of this term as a synonym of deep-sea may not always be appropriate, because psychrospheric environments, i.e., dominated by cold waters (<10°C), are also present in shallow regions of high latitudes. Bathybiic ostracods do not possess a specific set of particular morphological traits, notwithstanding the presence of some

adaptations in limbs and physiology likely facilitate living in a dark, cold and low-productivity realm (Danielopol *et al.*, 1996).

Research on bathybic ostracods is strongly associated with the name of Richard Hall Benson (1929-2003) (Fig. 1) whose work traces the construction of several concepts not only in this area but in ostracodology as a whole, including the adoption of the term “deep-sea” to designate marine bathybic ostracods. Benson (1969) used the word “abyssal” in his first publication on the subject, to refer to both abyssal and bathyal species. A few years later he used the hyphenated term “deep-sea” for this group (Benson, 1971; Benson & Sylvester-Bradley, 1971), and in the following year adopted the term “psychrospheric” in a monumental taxonomic work where the genus *Poseidonamicus* was proposed (Benson, 1972). It is noteworthy that in the latter work, the adjective “deep-sea” is used to refer to environments and sample provenance, but not to the species that occur there. This hyphenated adjective was not used much in the following decade or so. Guernet (1982) used the term “abyssal” to refer to deep-water fossil ostracodes from the Bahamas, and Cronin (1983) choose the term “bathyal” in his study in the southeast coast of the United States. From the 1990s onwards, however, the adjective “deep-sea” became widespread among ostracodologists, occasionally substituted by the non-hyphenated form “deep water” (Whatley & Coles, 1991).



Fig. 1. Richard Hall Benson (1929-2003) at his laboratory in Smithsonian Institute (1980). Photo by Chip Clark. Courtesy of Carlita Sanford.

Although some of the terms previously discussed convey the same meaning, i.e., designate ostracods that live in deep oceanic waters, they also bring some confusion. The designation as “abyssal” is inadequate because not the entire deep-sea environment is abyssal. The word “psychrospheric” has more relation to water temperature than to bathymetry and therefore does not seem to be correct. The adjective “deep-water” seems not to be the most suitable for the case in point because deep waters also occur in non-marine environments (e.g., the lakes Tanganyika and Baikal, both deeper than 1000 m).

The above discussion shows that standardized terminology would bring benefits to scientific communication. Therefore, the adoption of the classic, though rarely used term “bathybic” is herein recommended to designate marine ostracod species living in deep waters. The word “bathybic” was widely employed by naturalists in the late 19th and early 20th centuries to designate organisms that lived at or near the bottom in deep oceanic waters. Its use includes the following benefits to ostracodology: (i) it is specifically restricted to deep water marine species; (ii) the ecological terms bathyal and abyssal can be reserved to their respective bathymetric intervals; (iii) the Greek root of the word facilitates its use and improves communication; and (iv) it provides a shorter form for both Germanic and Romance languages speakers.

3 CHALLENGING PARADIGMS: FROM THE AZOIC TO A “POLYTHEISTIC” REALM

Historically, oceanography developed mostly in nations steeped in nautical tradition due to either commercial or military reasons. Before the advent of jet fighters and intercontinental ballistic missiles, the navy ensured the power of a nation. The sea was the pathway to reach new lands and their resources: the further one might sail, the higher one’s capacity of exploring economically oceanic and transoceanic regions.

Hence, triumph over mysterious and unpredictable oceans demanded the acquisition of reliable knowledge, which along the years would shape a discipline called oceanography. But, exactly where and when did oceanography start? It can be hard to pinpoint the beginning of human intellectual achievements (principles, ideas, or theories) since they are usually products of cooperative and cumulative efforts. A favorable choice to hammer a golden spike to mark the ground zero of

oceanography would be on October 21st, 1805. The victory of the British Navy over the French-Spanish coalition fleet in the Battle of Trafalgar promoted Great Britain as the dominant power of the world's seas, sustaining and reinforcing its economic and geopolitical influences. The outcome of this event would influence several sectors of activities, including science, establishing a close relationship between marine studies and naval affairs. As knowledge of the oceans became a *sine qua non* condition to maintain an efficient navy (both in military and commercial aspects), investments in exploratory expeditions became strategic during the 19th century. Consequently, it is possible to assume that oceanography benefited from military development, analogous to space exploration in the 20th century.

Although deep-oceans nowadays increasingly attract the attention of scientists, the perception in the early 19th century was somewhat different. The zoologist Edward Forbes (1815-1854), for instance, considered it a sterile environment (“azoic zone”), where animal life would be limited to 300 fathoms (540 m water depth). Strange as it might sound nowadays, this reasoning prevailed among naturalists for some time. However, by the late 1860s the short-range oceanographic expeditions of Charles Wyville Thomson (1830-1882), professor of Natural History at the Edinburgh University, demonstrated the existence of animal life in the deep sea and refuted Forbes' concept. These findings positively impressed the Royal Society and the British Navy to the degree that they allowed Thompson to use the adapted gunboat H.M.S. Challenger for the first around-the-world oceanographic expedition, from 1872 to 1876 (Bailey Jr., 1975).

4 THE VOYAGE TO THE BOTTOM OF THE SEA

Modern seas are usually represented in our minds by bluish and wavy waters full of swimming animals. However, one of their most fascinating parts lies unseen beneath the seas: oceanic sediments. Oceanic sediments constitute historic archives that allow scientists to understand the oceans of the past. Access to that history literally demands a journey to the bottom of the sea, sometimes very deeply. Whereas the field of biological oceanography deals with organisms living both in the water column (planktonic and nektonic) and on the seafloor (benthonic) to understand the modern oceans, the field of

paleoceanography uses the accumulations of organisms in sediments on the seafloor to understand the oceans of the past. Difficulties in studying the deep sea stimulated improvements in sampling technology, which ultimately modified our perception of oceanic processes completely. Bathybiic ostracod research commenced in the late 19th century with the H.M.S. Challenger expedition in the 1860s, when the British naturalist George Stewardson Brady (1832-1921) (Fig. 2) described 52 ostracod species in samples from several regions at depths beyond 500 fathoms (900 m water depth) (Brady, 1880). Years of subsequent research has revealed that the deep sea, instead of being an azoic realm, houses a virtual palace of Ryugu, where Poseidon, Neptune, and Yemanja inhabit². And why not Mars?

Unfortunately, after this start, little research was done on bathybiic ostracods for several decades. British paleontologist (settled in Australia) Frederick Chapman (1864-1943) (Fig. 3) examined 60 samples collected between 912 and 4887 m water depth near Funafuti Island (Pacific Ocean) by an expedition of the H.M.S. Penguin in 1896. The study revealed several species, most of the genera *Bairdia*, *Bythocypris*, *Xestoleberis*, *Krithe*, and *Argilloecia* (Chapman, 1910). About two decades later, the research vessel H.M.S. Willebrord Snellius surveyed waters around Dutch colonies in the Indian and Pacific oceans between 61 and 4483 m water depth (van Riel, 1930). The ostracod results appeared with some delay, but demonstrated the occurrence of 14 species, among them the new taxa *Bairdia ceramensis*, *Krithe droogeri*, and *Bythocythere kueneni* (Keij, 1953).

In spite of the lack of bathybiic ostracod studies during the first decades of the 20th century, the peculiarity of their assemblages attracted the attention of scientists. Considering that deep-sea samples were scarce at that time, the old saying, “One man’s meat is another man’s poison” fits perfectly for this phase of the ostracod research. Due to methodological similarity, the residue of samples initially prepared for the study of a fossil group can be used in the study of others, i.e., samples prepared for foraminifers can, in some cases, be used by ostracodologists.

² These marine deities inspired the etymology of some typical bathybiic ostracod genera, i.e., *Ryugucivis* Yasuhara *et al.*, 2015; *Poseidonamicus* Benson, 1972; *Philoneptunus* Whatley *et al.*, 2002; and *Yemanja* Brandão, 2010.



Fig. 2. George Stewardson Brady (1832-1921). Courtesy of the Natural History Society of Northumberland, Great North Museum: Hancock.



Fig. 3. Frederick Chapman (1864-1943). Courtesy of Bruce W. Hayward.

A case in point of beneficial sample reuse is the work by Willis Lattaner Tressler (1903-1973) (Fig. 4), a biologist at the University of Buffalo, who studied material collected in 1936 by the *Western Union Co* cable ship *Lord Kelvin* between Europe and North America. The voyage was undertaken for repairs to the North Atlantic telegraph cable and additionally provided an opportunity for testing a new deep-sea coring apparatus designed by the geologist Charles Snowden Piggot (1892-1973). Eleven cores obtained between 1280 and 4820 m water depth supplied 184 samples for foraminiferal study; subsequent examination for ostracods resulted in recognition of 27 species (Tressler, 1941). Tressler's work, therefore, represents a turning point in bathybic ostracodology. The sampling methodology and distribution of samples resulted in pioneering ideas about abundance, diversity, and the geographic and bathymetric distribution of species in the Atlantic Ocean. In another work, Tressler (1954) added critical preliminary data on ostracod bathymetric distribution in the Gulf of Mexico from the shelf down to 3630 m water depth.



Fig. 4. Willis Lattaner Tressler (1903-1973). Courtesy: Limnology Library, Center for Limnology, University of Wisconsin-Madison.

5 TURNING TO THE PAST

Perhaps the most important developments in 20th-century oceanography were advancements in coring technology. Circulation, sedimentary processes, and oceanic crust dynamics are examples of processes whose comprehension was strongly influenced by high-quality cores. The birth of paleoceanography is as subjective as the origin of oceanography itself, but it surely lies somewhere near to the first recognition of the relationship between the occurrence/abundance of a taxon and prevailing hydrological conditions.

Foraminifers rose as the most reliable proxy for past oceanic conditions and became, somewhat, a staple of paleoceanographic studies. Their potential as indicators of temperature and salinity is rivaled only by a few fossil groups, and the high abundance, preservation potential, and fast evolution allowed robust biostratigraphic/climatic zoning. But why, among the myriad of fossils preserved in marine rocks, are only foraminifers and, to a lesser degree, calcareous nannofossils (coccolithophorids) of such importance to paleoceanography? Part of the answer lies in an extrinsic attribute of

foraminifers: the taxonomy. Ostracods lag behind foraminifers due to weaker taxonomy. So, considering that it is virtually impossible to infer ages or propose paleoecological models without solid taxonomic knowledge, foraminifers have a clear advantage over ostracods in paleoceanographic studies. This disparity has its reasons. Foraminifers are much more diverse compared to ostracods; the number of specialists in foraminifers is higher, and some biological traits of ostracods, such as ontogenetic instars, sexual dimorphism, and ecophenotypic variability make the species identification more complex. The increase in the number of specialists and resulting taxonomic improvement, however, began gradually to change this situation. Though ostracods were an underutilized group early in the history of paleoceanographic research, they have significantly increased in importance to paleoceanography in the second half of the 20th century.

Although Piggot's coring system represented a significant improvement compared to the first deep-sea cores obtained by the Challenger expedition, a real revolutionary technique resulted from the piston corer, created by the oceanographer Börje Kullenberg (1906-1991) (Fig. 5). In the oceanographic expedition of the Albatross (1947-1948)³, the piston coring allowed unprecedented retrieval of cores up to 60 feet long (Cowen, 1960). However, paleoceanography would substantially change during the 1960s with the establishment of multi-institutional oceanographic programs aiming precisely at the coring of deep regions. From 1966-83 the Deep Sea Drilling Project (DSDP) supplied samples and field data which promoted immense development in oceanography. This program would continue from 1983-03 under the name Ocean Drilling Program (ODP), and from 2003-13 as IODP, the Integrated Ocean Drilling Program. Since 2013 it has been named the International Ocean Discovery Program (Passow *et al.*, 2013).

³ This is also the name of an U.S. oceanographic ship, which worked from 1883 to 1919.



Fig. 5. Börje Kullenberg (1906-1991). Courtesy of Gunnar Kulleberg.

Although the advent of the DSDP spurred the growth of the study of fossil bathybiic ostracods, the actual beginning of this research dates some years earlier. The Eocene–Oligocene “open sea facies” described by Willem Aaldert van den Bold (1921-2000) (Fig. 6) in Trinidad included *Kritbe* (e.g., *K. trinidadensis*, *K. morkehoveni*, *K. dolichodeira*), *Bairdia*, *Bythocypris*, *Bythoceratina*, among other typical Cenozoic bathybiic taxa (van den Bold, 1960). He presented some insights on this in his Ph.D. thesis on ostracods from the Caribbean (van den Bold, 1946) where he comments that the assemblages studied corresponded to different facies (= environments). Comparing the occurrence of ostracods with other fossils, he concluded that those assemblages were deposited under different paleoenvironmental conditions, although he did not use the term deep-sea (van den Bold, 1946). Hence, W. A. van den Bold should be considered the forerunner of the fossil bathybiic ostracod research because he was the first paleontologist to publish taxonomic studies on them.

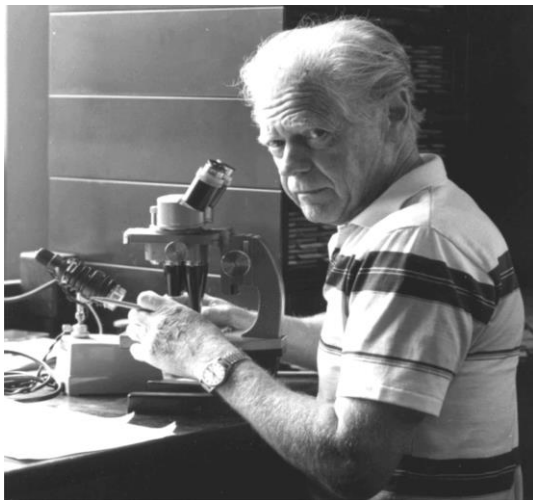


Fig. 6. Willem Aaldert van den Bold (1921-2000). Courtesy of Peter McLaughlin and Thomas W. Dignes.

The new perspectives revealed by the DSDP and the previous results by G.S. Brady and W.L. Tressler, inspired, as previously mentioned, R.H. Benson to publish a state of the art treatment of bathybiotic ostracodology, which laid out the upcoming challenges of this research (Benson, 1969). However, 15 years later Benson *et al.* (1984) published a comprehensive synthesis of the relation between climatic events and Cenozoic assemblages, discussing for the first time the relationship between assemblages composition and oceanographic events. Although some of the ostracod global events proposed in that work were not recorded in subsequent studies (e.g., Majoran & Dingle, 2001), it revealed bathybiotic ostracods to be reliable oceanographic markers, sealing an alliance with foraminifers and calcareous nannofossils in paleoceanography.

6 BRUSHES, NEEDLES, AND SPECTROMETERS IN ACTION

From 1969 onwards, bathybiotic ostracodology, now established as a substantial research field, followed three main paths: (i) the faunal approach (focused on taxonomy and zoogeography); (ii) the

geochemical approach (focused mainly on trace-element analysis), and (iii) the morphometric approach (focused on the environmental influence on morphology). During 1970s bathybiic ostracodology aimed at the origin, dispersal and evolutionary response of some taxa to climatic events, mostly in the Mediterranean Sea (e.g., Benson & Silvester-Bradley, 1971) and the Atlantic Ocean (e.g., Benson, 1983). R.H. Benson's contribution to the faunal approach also included the description of the genera *Atlanticythere*, *Abyssocythere* and, perhaps the most famous one, *Poseidonamicus* ("Poseidon's friend"), all widespread in bathyal and abyssal depths (Benson, 1971; Benson, 1972; Benson, 1977). During the same period, Jean-Pierre Peypouquet was also an influential contributor to this research for investigations on the species response to sea-level and OMZ (oxygen minimum zone) changes (e.g., Peypouquet, 1977, 1979). Two outstanding zoologists also made a valuable taxonomic contribution: Evgeny Ivanovich Schornikov (1940-2016) (Fig. 7) and Rosalie Maddocks, revealed more about bathybiic ostracod biodiversity, making some of their papers essential references on the subject.



Fig. 7. Evgeny Ivanovich Schornikov (1940-2016) in Berlin during the European Ostracodologists Meeting (2007). Photo by Ekaterina Tesakova.

During the 1980s, other essential studies appeared, among them a classic work of Thomas Mark Cronin, which supplied crucial insights on the post-mortem transport and bathymetric distribution of North Atlantic taxa, influencing many subsequent studies (Cronin, 1983). A few years later Robin Charles Whatley (1936-2016) (Fig. 8) and Graham Coles publish a milestone paper on North Atlantic bathybiic ostracods, proposing 22 new species and a genus (*Rimacytheropteron*) in Late Miocene–Quaternary sections of several DSDP sites (Whatley & Coles, 1987). At the end of the decade, those authors would publish a complementary study covering the older Cenozoic strata (i.e., the Paleocene–Miocene) completing their coverage on fossil North Atlantic bathybiic ostracods of the Cenozoic (Coles & Whatley, 1989).

Any historical review on bathybiic ostracod studies of the 1980s that does not mention Maddocks & Steineck (1987) would be incomplete, because of the critical faunal insight yielded by a novel experimental design. Their study analyzed the colonization of wood parcels placed in deep regions of the North Atlantic and the Caribbean by a submersible. The experiment revealed a very distinctive fauna composed mostly by Bythocytheridae, Cytheruridae, Paradoxostomatidae, Pontocyprididae, and Paracyprididae. Among its essential results are the description of four species of *Xylocythere*, a new genus therein proposed, whose etymology makes clear allusion to wood. No other study developed so far can be compared to that, and it is arguably the most important ecological study published on bathybiic ostracods. The large volume of work presented at the 9th Ostracoda International Symposium held in Shizuoka, Japan, in 1985, provides the measure of the development of this area of research during the previous years of that decade, resulting in the largest compilation of ostracod papers ever published (91 articles) (Hanai *et al.*, 1988). It was also the first meeting with a section exclusively for bathybiic work, including the review by Whatley & Ayress (1988) of their general characteristics and dispersal from two main centers of origin: the Indo-Pacific and the Caribbean.



Fig. 8. Robin Charles Whatley (1936-2016). Courtesy of Caroline Maybury.

While the studies in the 1970s and 1980s were aimed mostly at unraveling diversity and evolution trends, reinforcing the role of climate as a modulator, the focus of research along the 1990s turned to the influence of the hydrologic structure on the occurrence and dispersal of taxa. No other author is more promptly linked to this theme than Richard Vernon Dingle. Dingle & Lord (1990) and Dingle *et al.* (1990) proposed the existence of ostracod assemblages associated with different deep-water masses of the Atlantic Ocean. The sensitivity of species to hydrological parameters and their influence on ostracod bathymetric and latitudinal distribution is also extensively discussed in those papers. The 1990s also represents the period of expansion of bathybiotic ostracod research towards the Southwest Pacific and Australia (e.g. Whatley *et al.*, 1992; Ayress *et al.*, 1995; Ayress *et al.*, 1997 and Ayress *et al.*, 1999). Among those studies, however, Ayress *et al.* (1996) deserve additional remarks since it registers the occurrence of unusual morphologic features whose significance has never been thoroughly understood. The latter is a typical example of how limited is our knowledge on some paleobiologic aspects of bathybiotic biotas. An innovation arising in the 1990s was the spread of geochemical analyses as temperature tracers. Using paleotemperature concepts previously applied to freshwater species, Gary Dwyer and collaborators adjusted the analytical techniques for species of the marine genus *Krithe* (Dwyer *et al.*, 1995). The results would ultimately reveal the close relationship

between oceanic productivity, temperature, and deep-sea benthonic diversity (Cronin *et al.*, 1999).

Turning towards the 21st century, the study of both fossil and recent bathybiotic assemblages expanded not only along the Atlantic but also to other oceanic basins, bringing new data and reinforcing previous discoveries. However, the most innovative approach during the first and second decades of the 21st century is the study of climatically induced morphological variations. Insights on the influence of water temperatures and dissolved oxygen levels in carapace morphology and size had been discussed previously by authors such as R. Maddocks, R.H. Benson, and J.-P. Peypouquet. However, two critical works that more deeply explore this complex subject were published in 2007 (Hunt, 2007; Aiello *et al.*, 2007) dealing with distinct ostracod genera. While the first of them (Hunt, 2007) investigated evolutionary trends based on selected morphological structures in *Poseidonamicus*, the second (Aiello *et al.*, 2007) applied different morphometric analyses on *Krithe* from the Mediterranean region, aiming at more precise species identification.

The pandemism of bathybiotic taxa is, perhaps, one of the most discussed subjects in ostracodology. Since earlier studies, pandemism has been presented as a rule for bathybiotic species, possibly inspired by patterns observed in other meiofaunal groups (Giere, 2009). Some studies, however, maintain that pandemic patterns resulted from misidentifications of ring species (“ring species” are a series of similar species that can interbreed with nearby related populations in the series, but not necessarily with the more distant ones). Swanson & Ayress (1999) provided a seminal work on this theme, developed in more detail in the first decade of the 21st century. The pandemism is essentially a taxonomic matter, intimately linked to the troublesome concept of species, which holds some divergences among paleontologists and neontologists. Ostracodology, however, has some good examples demonstrating that a taxonomy common to both fossil and living species is far to reach a consensus.

7 CONCLUSION

The research on bathybiotic ostracods successfully merges traditional and innovative approaches in taxonomy, geochemistry, and

morphometry. It provides complementary data for a comprehensive understanding of both past and modern deep-sea ecosystems, and crustacean evolution as well (e.g., Cronin *et al.*, 2010; Cronin *et al.*, 2014; Yasuhara *et al.*, 2017; Yasuhara *et al.*, 2018). These approaches demonstrate the dynamism of this research and its continuing importance to the understanding of oceanic environments.

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