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Unifying Retaria Research: A Common Framework for Studying Foraminifera and Radiolaria

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ABSTRACT

Spanning over 500 million years, the fossil record of Retaria is a cornerstone of paleobiology, paleoclimate reconstruction, and stratigraphy. Yet, the constitutive branches of Retaria, Foraminifera, and Radiolaria, not only have been studied independently, but just a fraction of this research has focused on living representatives of these lineages. Here we tentatively identify the "Big Five" areas of biological research into Retaria, articulated around novel and transformative understanding of their evolution and diversity, role in ocean biogeochemistry, life cycles, and ecology. Through this perspective, we argue that a unified Retaria framework that seamlessly integrates biological and paleontological data will benefit the scientific community at large, train the next generation of researchers broadly and open novel perspectives to understand the global ocean's evolution.

1 | Introduction

Retaria are an ecologically important group of predominantly marine, free-living, amoeboid single-celled eukaryotes. Their body sizes span several orders of magnitude, typically from 5-20 μm to several 100s μm, but some benthic foraminifera can reach up to 25 cm [1], and some Radiolaria form colonies extending over a few meters [2]. They are best known for their ability to produce biomineralized skeletons of varied structures and compositions (Figure 1). The intricate nature of these mineralized structures captivated 19th century naturalists, whose elegant drawings popularized these organisms and facilitated the first classification of both Foraminifera [3] and Radiolaria [4], the two major clades of Retaria. In 1826, Alcide d'Orbigny established the Foraminifera as 'hole-bearers' due to the perforation of their tests. The Radiolaria were then erected in 1854 by Christian Gottfried Ehrenberg, who originally named them 'Strahlentierchen' after the radial symmetry of their skeletons, likening them to 'small sunbeams'.

Their biomineralized skeletons give Retaria excellent preservation potential in the fossil record (e.g., [5, 6]), thus providing a continuous record of more than 500 million years unmatched by other microbial groups. Hundreds to thousands of specimens can be preserved in a few grams of sediment [7], facilitating their use as biostratigraphic markers for dating sedimentary rocks. This laid the foundation for industrial micropaleontology in the early 20th century in the search for oil. Consequently, Retaria have become instrumental tools for biostratigraphy and paleoclimate reconstruction across the last half billion years of Earth history [5, 8], offering outstanding resolution for the last 66 million years [9–11].

The profound geological and industrial interest in Retaria has generated an extensive body of research often overshadowing biological studies of these organisms. A bibliometric analysis of research over the past century reveals that more than 80% of publications focus on paleoclimate reconstruction, stratigraphy, or fossil-based taxonomy (Figure 2). This imbalance has resulted in

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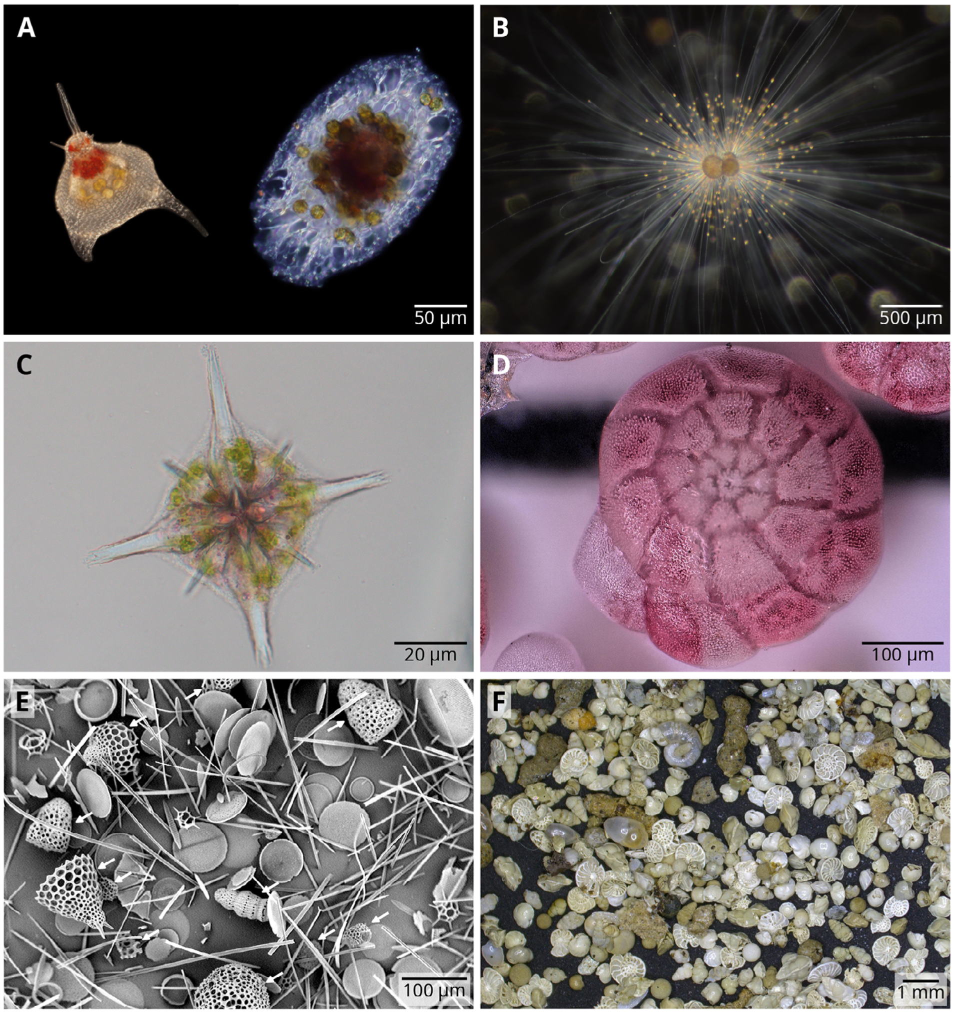

FIGURE 1 | Examples of Retaria specimens showing their diversity, symbiotic interactions, characteristic reticulopodia, and abundance in sediments. (A) Polycystine Radiolaria, Nassellaria (*Pterocanium* sp.; left), and Spumellaria (*Cypassis oblongus*; right), collected off the coast of Villefranche-sur-Mer (France), golden dots are identified as dinoflagellate symbionts (MMS). (B) Planktonic Foraminifera showing the extended net-like structure developed by the reticulopodia and the dinoflagellate symbionts (Howard Spero, taken during the Planktonic Foraminifera workshop funded by the US National Science Foundation). (C) Acantharia Radiolaria (*Phyllostaurus* sp.) collected off the coast of Bermuda showing the haptophyte symbionts (NLC). (D) Benthic Foraminifera (*Ammonia confertitesta*) collected on tidal mudflats in Friedrichskoog (Germany) stained with Rose Bengal in ethanol (NG). (E,F) sediment assemblages showing a diverse and abundant community of (E) Polycystine Radiolaria, indicated by white arrows, within South Atlantic sediment samples collected during the ACCLIMATE-2 cruise [162]; (3735m deep; NLM), and (F) benthic Foraminifera off the coast of Perú (640m deep; NG).

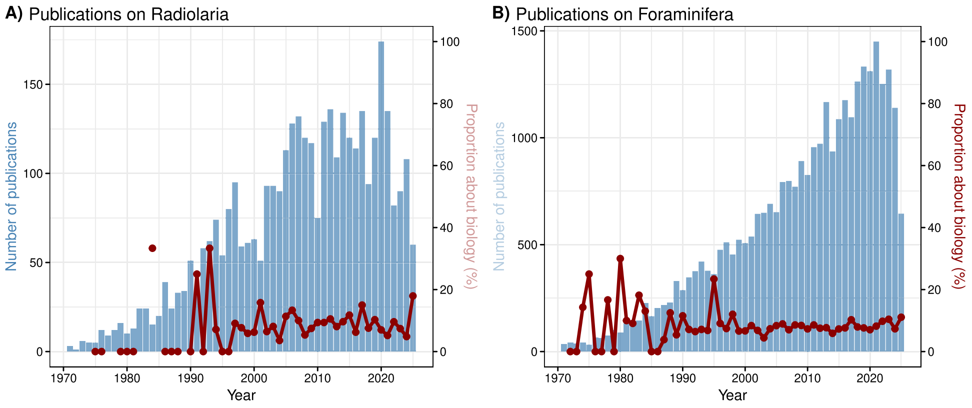

FIGURE 2 | Number of publications on Radiolaria (A), and Foraminifera (B), and the proportion of biological research compared to fossil/sediment research.

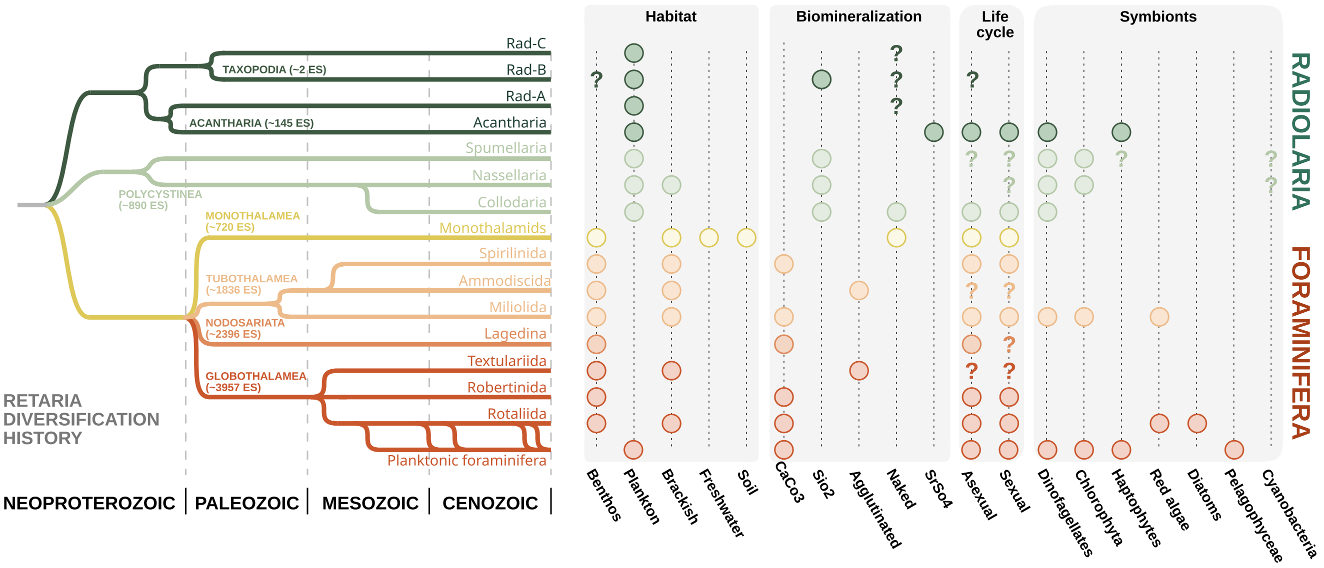

FIGURE 3 | Schematic representation of Retaria evolution, diversity, and classification. Note the absence of a dot indicates "not yet observed" rather than a definitive "absence" and the question mark indicates a hypothesis based on available data but not yet observed.

a scarcity of knowledge regarding fundamental biological aspects, leaving many open questions about their genetics, physiology, life cycles, and ecological interactions. In addition, biological research is not only comparatively scarce but also fragmented, as the Foraminifera and Radiolaria communities have historically worked independently of one another. Bridging these gaps is essential to place the fossil record in its full biological context and to understand how these organisms function, adapt, and respond to environmental changes, thereby contributing to their geological applications.

Here we highlight recent progress in our understanding of fundamental biological aspects of living Foraminifera and Radiolaria, focusing on shared patterns between the two lineages. We identify the "Big Five" disciplines of Retaria biological research to structure these shared patterns across the group: from their living diversity and evolution beyond rocks and sediments, to their ecology, life cycles, and roles in the ecosystem. We further identify major research gaps and point to potential future collaborative horizons. Through this synthesis, we argue that a unified Retaria framework will benefit both biologists and paleontologists to move the field forward. Altogether, we present the first synthesis supporting Retaria as an integrated and emerging model system.

2 | The "Big Five" Areas of Biological Research in Retaria

2.1 | High-Ranking Classification and Evolution

Foraminifera and Radiolaria were originally grouped as Retaria based on their characteristic net-like structure developed by their pseudopodial cytoplasmic extensions called reticulopodia (from the Latin "rete") [12]. This morphological connection was later supported by molecular data, confirming the phylogenetic monophyly of Retaria within the Rhizaria supergroup [13]. Retaria's high-ranking classification aligns closely with the chemical composition of their mineral skeletons (Figure 3). While Foraminifera typically build calcium carbonate ($CaCO_3$) tests, Radiolaria mineralize skeletons made of either strontium sulfate ($SrSO_4$) in Acantharia, or opaline silica (SiO_2) in Polycystinea and Taxopodida. These distinct chemical signatures suggest that convergent evolution of biomineralization occurred in each group after their divergence in the Neoproterozoic, more than 600 million years ago [14, 15]. However, not all specimens develop a skeleton, and a wide morphological spectrum exists across Retaria. This extends from fully mineralized skeletons to agglutinated tests (e.g., Textulariida; [16]), to the arrangement of spicules (e.g., Taxopodida and Acantharia clades A and B; [17]), or even skeleton-less forms (e.g., Collophidiidae within Collodaria or Allogromiids; [18, 19]).

Such convergent traits and shared variability in skeletal expression suggest common selective pressures, likely resulting from similar evolutionary trajectories and ecological niches. Indeed, Radiolaria, planktonic Foraminifera, and other large planktonic protists like Phaeodaria, were historically grouped together as Sarcodines due to their similar ecological niches (e.g., [20]). However, the advent of DNA sequencing challenged this grouping by prioritizing evolutionary relatedness. Phaeodaria are now part of the Cercozoa [21], still within the broader supergroup Rhizaria, to which Retaria belongs. And last the previously *incertae sedis* Helizoan Taxopodida has been placed within Radiolaria [22], establishing the Radiolaria group that we know today.

While the different subgroups of Retaria are relatively well established by both morphological and molecular data, their phylogenetic relationships remain poorly supported and challenge the monophyly of Radiolaria. Several independent phylogenomic and transcriptomic analyses have placed Foraminifera as the sister group to either monophyletic Radiolaria [23], Acantharia [24], or Polycystinea [25, 26]. This ongoing uncertainty is often attributed to both the fast rates of evolution in Foraminifera and Polycystinea (specifically Nassellaria and Collodaria), and the lack of comprehensive genomic markers in phylogenomic studies, which rely mostly on ribosomal genes (rDNA; [15, 27]). Although ribosomal genes offer extensive taxon sampling, their accelerated evolutionary rates can generate phylogenetic artifacts, such as long-branch attraction, resulting in spurious evolutionary relationships. Despite the mitochondrial genome has been sequenced [28] and barcoding at the COI marker is underway [29, 30], complete genomes are still missing and are expected to be highly dynamic [31, 32]. Resolving these questions will require expanding taxon sampling in phylogenomic studies and ultimately assembling Retaria genomes, an endeavor that has only just begun. Retaria genomes will not only contribute to resolving the monophyly of Radiolaria, but high-resolution genomic data will allow reconstruct ancestral metabolic and functional patterns that have only been hypothesized through phylogenetics (e.g., [15, 33]).

2.2 | The Breadth of Modern Diversity

Taxonomic diversity is arguably the most studied facet of Retaria. To date, approximately 1000 and 5000 living species of Radiolaria and Foraminifera, respectively, have been morphologically described (Figure 3). More recently, the advent of molecular approaches has challenged previous knowledge based purely on morphological observations, providing a distinct and independent perspective. DNA barcoding is the technique for the combined morphological and molecular characterization of single-cells, and while it largely confirms the validity of morphological traits used to delineate morphological orders and families (e.g., [34, 35, 3]), it can also lead to re-interpretation of some morphological traits used in fossil or morphology-based phylogenies (e.g., [17, 36, 37]). In addition, single-cell barcoding has revealed unseen “cryptic” diversity within morphological species [38], demonstrating that the classical morphospecies concept frequently underestimates the extent of genetic diversity.

A major reassessment of extant Retaria diversity and their ecological roles has resulted from the high-throughput sequencing of environmental samples, an approach known as metabarcoding. This approach has revealed the dominance and extensive diversity of groups previously underestimated across Retaria, such as Monothalamea [39] and Taxopodida [15], particularly in deep-sea environments [40]. However, relating molecular diversity of environmental rDNA to morphospecies remains challenging, primarily because high intragenomic copy number and sequence variability can inflate the number of molecular operational units [41–44]. While ribosomal gene copy number scales with cell size and count in most Radiolaria [45, 46], no such relationship has been identified in Foraminifera [47] or solitary Nassellaria (i.e., excluding Collodaria; [42, 46]). Notably, solitary Nassellaria show a lower representation of genetic signatures compared to morphological species, even when using specific primers [44]. This suggests the existence of yet-to-be-understood cytological barriers that may affect DNA extraction efficiency.

Although molecular methods have re-evaluated the extent of Retaria diversity, linking molecular, and morphological data remains challenging due to the necessity for comprehensive and well-curated databases [48–51]. However, the development of such resources is hindered by the limitations in relating molecular diversity to morphospecies. To overcome these hurdles, it is necessary to: (i) barcode an extensive diversity of morphospecies across different localities, (ii) constrain biological biases that may inflate diversity estimates [50], (iii) calibrate the relationship between gene copy number and biovolume [30, 45], and (iv) establish a link between the well-documented diversity of the fossil record and extant species. Nevertheless, despite the divergent perspectives provided by molecules and morphology, metabarcoding has become a fast and relatively inexpensive method for collecting Retaria data and will likely continue to generate datasets valuable for paleontological, biogeochemical, and ecological research. Therefore, the apparent disagreement between molecular and morphological data only opens opportunities for a better integration of disciplines needed for a comprehensive diversity assessment of both extant and fossil taxa.

2.3 | Ecology and Symbiosis

Nowadays, Retaria are ubiquitous aquatic organisms, ranging from the surface to the deep sea and occupying both pelagic and benthic ecosystems. Foraminifera occur mostly in the benthos, from shallow mudflat to the deepest oceanic waters, but are nevertheless broadly distributed in aquatic environments [52] from the oceanic plankton, to brackish and freshwater, and even soil environments [53, 54]. Radiolaria, while more biogeographically restricted to marine or brackish environments, reach substantial abundances in the oceanic plankton realm and show marked differences among groups in their vertical and latitudinal distribution [55, 56]. In the plankton where both Foraminifera and Radiolaria co-occur, different lineages show clear biogeographic preferences. For example, some Radiolaria groups develop an organic gelatinous matrix that has been hypothesized to be an adaptation to oligotrophic waters [57], Acantharia tend to be very abundant at high latitudinal surface waters [58], and Foraminifera tend to be more abundant in coastal (for benthic specimens) and shallow (first hundred meters) waters [59].

From all ecological patterns, Retaria stand out for their diverse and active biotic interactions, encompassing predation, parasitism, and photosymbiosis. Nearly 25% of all recorded protist biotic interactions involve a Retaria, of which 76% are photosymbiotic relationships [60]. Photosymbiosis is widespread across Retaria in nearly all planktonic and some benthic lineages [61–64]. This trait likely emerged during the Late Mesozoic, triggered by prolonged periods of oceanic oligotrophy and anoxia [65, 66]. Subsequently, several extinction-speciation events have shaped specific host-symbiont interactions, favoring a few ecologically abundant partners over novel, scarce ones [64, 15]. These partners comprise a wide diversity of microalgae and bacteria, including diatoms [67], chlorophytes [68, 69], haptophytes [66, 70, 71], rhodophytes [72], prasinophytes [73], and chrysophytes [74], as well as several bacterial lineages [75–77] (Figure 3). Despite this variety, dinoflagellates are probably the most common photosymbiont found in Retaria [78–80]. Sometimes, different lineages of symbionts are hosted within the same cell, characterizing Retaria as rich and complex holobionts [81, 82]. While it is a common assumption that these relationships are mutualistic [83], haptophyte symbionts of Acantharia (Phaeocystis) exhibit up to a 38-fold increase in plastids compared to their free-living state, suggesting that the host can significantly alter symbiont ultrastructure to increase photosynthetic efficiency [84]. Because these alterations permanently prevent the symbiont from surviving outside of the host environment, this phenomenon has been interpreted as kleptoplastidy-like behavior by the host [85]. Similarly, benthic Foraminifera are known to sequester chloroplasts through true kleptoplastidy [86, 87], questioning the conventionally assumed mutualism and suggesting instead that the Retaria host is actively "farming" (or exploiting) their symbiotic microalgae [84].

While photosymbiosis is a particularly prominent area of Retaria research, other symbiotic interactions are much less documented yet may be as ecologically significant. This scarcity of data stems from the challenges of studying Retaria in culture, meaning most of our knowledge is derived from direct observations in the natural environment. Still, Retaria have been observed actively feeding on diatoms [88, 89], ciliate tintinnids [90], nauplii larvae [91], copepods [57] or other Retaria [20, 92]. Benthic Foraminifera have been observed preying on gastropods, nematodes, juvenile crustaceans, and echinoderms up to 12 mm long [93–95]. When it comes to parasitism, there are next to no documented examples of virus-like particles infecting Retaria, and the marine alveolate Syndiniales represent nearly the only documented example of a eukaryotic parasite to Retaria. Despite the paucity of documented parasitic relationships, interactions between Retaria and Syndiniales have been described multiple times (e.g., Refs. [96–100]). Metabarcoding co-occurrence networks suggest that Syndiniales might parasitize even the large, morphologically undescribed molecular diversity of Retaria [101]. Given the widespread distribution of Retaria, their broad range of cell sizes, and high relative abundances, such parasitic interactions may play crucial roles in structuring planktonic communities [101, 102], exerting a direct influence on carbon and other biogeochemical fluxes [103].

2.4 | Biogeochemical Cycles

Retaria are essential to marine biogeochemical cycling. Their broad distribution allows Foraminifera and Radiolaria to shape key processes in both planktonic and benthic environments. Together with other large rhizarian protists (i.e., Phaeodaria), Foraminifera and Radiolaria account for an estimated 5.2% of global marine biomass within the sunlit layer of the ocean (0–200 m) [104]. Regarding the biological carbon pump, planktonic Foraminifera contribute about 42% of global inorganic carbon fluxes in the mesopelagic (200 to 1000 m) and 50% of the flux reaching the seafloor [105, 106]. Beyond inorganic export, Foraminifera may represent an overlooked source of organic carbon export due to their large cell volumes. Radiolaria also contribute significantly to the export of organic carbon, reaching up to 60% of the organic flux to 3000 meters [107–109]. Through their mineralized siliceous skeletons, Radiolaria also contribute to other biogeochemical cycles. Together with Phaeodaria, they account for up to 19% of global oceanic biogenic silica production, acting as major mediators of the marine silicon cycle [110] and vectors of silica transport to the deep ocean [111]. In addition, Acantharia possess the unique ability to precipitate pure strontium sulfate ($SrSO_4$) skeletons [112, 113]. Despite the high solubility of $SrSO_4$ in seawater, their rapid sinking speed and high density [114] make Acantharia critical contributors to marine strontium cycling.

In deep environments, Foraminifera constitute a dominant proportion of the benthic biomass, particularly below 1000 m [115], often exceeding 50% in some regions [116, 117]. Compared to metazoan meiobenthos, Foraminifera exhibit high rates of organic carbon assimilation [118], serving as crucial links between phytodetritus and meiofauna [119]. Beyond carbon processing, Foraminifera contribute significantly to nitrogen and phosphorus cycling [120]. Notably, several species can denitrify under oxygen-depleted conditions, acting as an important marine nitrate sink and a potential source of the greenhouse gas nitrous oxide (N_2O) [121–125]. While eukaryotic steps in the denitrification pathway have been identified [126–129], denitrifying Foraminifera can account for up to 100% of benthic denitrification in certain marine environments such as the Peruvian oxygen minimum zones, the Gellmar Fjord or the Bedford Basin [130–132]. Foraminifera can also accumulate intracellular phosphate at concentrations 100—1000 times higher than surrounding waters [133, 134]. In areas such as the southern North Sea and the Peruvian continental margin, phosphate stored in Foraminifera is equivalent to one month's worth of riverine phosphorus input, providing a potential buffer for coastal systems against anthropogenic eutrophication [134].

While research on Foraminifera has progressed significantly in recent decades, little is known about the role of Radiolaria in the deep ocean or even in sediments, where metabarcoding has reported an unexpected diversity and abundance of Radiolaria reads [40]. In regions such as the Southern Ocean, the sedimentation of silicifying Radiolaria leads to extensive siliceous deposits, composed primarily of diatomaceous oozes but often including abundant Radiolaria skeletons [135]. Both Foraminifera and Radiolaria are likely central drivers in ocean biogeochemistry, shaping the cycling and redistribution of key elements. Altogether, Foraminifera research provides a promising foundation for uncovering the biogeochemical roles of Retaria and their contribution to the ocean's chemical equilibrium.

2.5 | Life Cycle

Of all research areas regarding Retaria, their life cycle remains perhaps the most elusive facet. Consistent with many protist lineages, the wide range of reproductive strategies observed across Retaria makes it difficult to define a canonical life cycle. In Foraminifera, extensive records show an alternation between haploid (single set of chromosomes) and diploid/polyploid (two or more sets of chromosomes) stages; by contrast, data on changing ploidy within Radiolaria life cycles remain scarce [136]. However, both groups release flagellated swarmer cells, which are presumed to be gametes, suggesting the presence of sexual reproduction (e.g., [137–140]). This process typically involves the release of thousands of swarmer cells in Foraminifera and from a vegetative cell in some Acantharia, or a cyst in other Acantharia species [141–143]. While gamete release has been observed repeatedly in both groups (e.g., [66, 138, 144–147]), nuclear fusion or karyogamy has never been documented. Numerical models suggest that successful encounters require precise temporal and spatial coordination, potentially synchronized with lunar cycles [148]. The absence of gamete fusion in laboratory settings may stem from biological incompatibility between the released gametes (of the same parent cell) or the lack of specific environmental triggers. Furthermore, as Retaria are often complex holobionts, the lack of knowledge regarding their potentially mandatory interactions with other organisms may further hinder observations in vitro.

Current models for both planktonic Foraminifera and Radiolaria suggest similar reproductive strategies characterized by vertical migration, or rather, sinking in the water column because of their skeleton growth and density change. In Foraminifera, the model posits that individuals sink through the water column as their mass increases, eventually aggregating in deep, chlorophyll-rich layers for gamete production and release [59]. Similar patterns have been suggested for symbiont-bearing Acantharia, whereas gametogenesis in cyst-forming Acantharia is proposed to occur in the dark ocean, possibly within a cyst stage, with vegetative stages developing in the upper ocean [141]. These vertical trajectories likely increase the probability of gamete encounters and provide resulting zygotes with a favorable environment across the water column to secure high initial levels of energy. Although the details of gametogenesis vary among taxa, a specific nuclear process termed “Zerfall” (German for “disintegration”) or “Zerfall-like” has been observed prior to gamete formation in members of both Acantharia and Foraminifera [32, 149, 150]. During Zerfall, the nuclear envelope breaks down, and nuclear contents, predominantly nucleoli and nucleic acids, are extruded into the cytoplasm. Information about the reproduction of Polycystinea is however limited, and we can only infer similar patterns based on similar biogeographic patterns.

Asexual reproduction has also been documented in several species of Foraminifera and Radiolaria, employing strategies such as binary and multiple division [151, 152]. In planktonic Foraminifera, multiple division appears to be rare, recently estimated to account for approximately 5% of the in situ population [92]; by contrast, it is more frequent in benthic specimens [153–155] with reasons so far beyond our understanding. This reproductive mode is the only observed under laboratory conditions to date, having led to the production of multiple generations in Foraminifera cultures [89]. The evolutionary success of Retaria may reside in its potential capacity to use different modes of reproduction, allowing them to respond rapidly to environmental fluctuations. Specifically, sexual reproduction facilitates genetic recombination to drive adaptation, while asexual reproduction enables rapid population growth. While Radiolaria have not yet reproduced in the laboratory, future experimental work on Retaria will likely build upon the recent advances in Foraminifera culturing [92, 89]. In the last decade, culturing approaches have become increasingly interdisciplinary, integrating single-cell high-throughput manipulation, omics, and advanced imaging techniques [156]. We therefore hope to see dedicated efforts toward Radiolaria cultivation in the coming years to establish Retaria as a comprehensive model lineage.

2.6 | Emerging Aspects in Retaria Research

Despite previously described limitations, including elusive genomes, complex holobiont dynamics, and culturing challenges, Retaria are emerging as ecological models thanks to their ubiquitous presence in global oceans [157]. Their wide size range further allows them to serve as biological models bridging the physical and functional scales between microbes and mesozooplankton. Their vast diversity, divergent biogeography, and exceptional fossil record make Retaria excellent candidates for studying functional traits and predicting climate change responses, among other applications. For example, both morphological and metabarcoding surveys have highlighted the wide distribution and dominance of photosymbiotic Retaria [61, 58], while recent initiatives are unifying functional trait research among protists [158]. In addition, recent studies have focused on physiological responses to climate change, such as thermal-stress [159], and have modelled their migration patterns under different ocean warming scenarios [160, 161]. In this context, we expect that Retaria research will expand beyond the “Big Five” disciplines discussed here in the coming years.

3 | An Unified Retaria Framework

Building upon a solid legacy from fossil and sediment records, biological research on extant Retaria has proven that these protists are unique emerging models for a variety of research fields. Despite the relatively low proportion of biological studies on Retaria, the last decade alone has witnessed significant advances, from expanding our understanding of Retaria diversity beyond that preserved in sediments and rocks to the successful reproduction of planktonic Foraminifera in culture. As a community, we can begin by actively exchanging knowledge, establishing unified morpho-molecular databases, developing standardized protocols, and creating joint funding initiatives. We should additionally welcome each other on field campaigns and provide unified Retaria training to the next generation of scientists. With this synthesis, we propose Retaria as an integrated and emerging model system across different research fields.

Although Foraminifera and Radiolaria were historically studied independently, here we show that all lines of research call for a synergistic approach. Both groups have independently developed biomineralization strategies, established complex photosymbiotic relationships with diverse microalgae, and employ similar reproductive modes, including multiple fission and the release of biflagellated dispersal stages. These patterns, arising from over 600 million years of evolution and supported by direct fossil evidence from over 500 million years ago, suggest fundamental biological principles that can only be fully understood through a unified study. Yet, the communities studying these organisms have largely worked in isolation with separate conferences, journals, and research networks, limiting the exchange of methods, insights, and conceptual frameworks.

A unified Retaria framework opens first and foremost hypotheses and research priorities in one group that are already evidenced in the other, providing independent tests of evolutionary and ecological theories. Methodological advances pioneered in one group can be rapidly adapted to the other, for example, recent success in culturing planktonic Foraminifera across generations provides a roadmap for achieving similar breakthroughs with Radiolaria. Molecular techniques, such as single-cell barcoding, metabarcoding protocols, and phylogenomic approaches, face similar challenges in both groups, including intragenomic variability, a lack of reference genomes, and database curation, meaning solutions developed for one community will immediately benefit the other. Practically, a unified approach enables resource sharing and infrastructure development, reducing duplicative efforts and consolidating a wider set of expertise.

The benefits of a unified Retaria framework extend to biologists, paleontologists and all scientists working on the lineage. For biologists, the exceptional fossil record of Retaria provides a continuous evolutionary context of over 600 million years unmatched in other protist groups. This offers calibration points for molecular clocks, temporal frameworks for understanding trait evolution, and empirical tests of diversification dynamics. Fossil occurrences constrain biogeographic hypotheses and reveal how modern diversity patterns may reflect deep-time processes. For paleontologists, modern biological research acts as a ground-truth for the ecological and physiological assumptions underlying paleoenvironmental analyses. Understanding life cycles, trophic strategies, symbiotic relationships, and biogeographical preferences clarifies taphonomic biases and abundance patterns in the fossil record. While molecular phylogenies reinterpret morphological character evolution, fossils provide direct evidence of absolute timing, and both together Retaria represents a continuous evolutionary history of life spanning more than 600 million years. An integrative framework additionally enhances predictive power, for example modern ecological responses combined with evolutionary baselines may improve forecasting of biotic responses to ongoing climate change, while biological knowledge of cryptic diversity and functional traits enriches paleodiversity assessments and ecosystem reconstructions.

Probably most importantly, a unified Retaria framework will facilitate rapid knowledge transfer. Methodological innovations in paleontology (e.g., high-throughput imaging, geochemical analysis) find applications in modern biology, while biological techniques (e.g., single-cell genomics, culture protocols) open new avenues for analyzing fossil and subfossil material. Integrating paleontology and biology (e.g., paleogenomics) represents a promising and certainly fruitful avenue for future research. Extracting ancient DNA from old fossils (i.e. older than ~1 million years) is so far unattainable, but linking the last ~1 million year record with extant diversity is reachable today. This bidirectional exchange will accelerate progress in both fields, create training opportunities for researchers fluent in both biological and geological perspectives, and position the integrated Retaria community to address grand challenges that neither discipline could tackle alone. Such integration strengthens our understanding of Earth system responses to past climate change and refines projections of ecosystem trajectories under anthropogenic forcing. Advancing this work requires a unified Retaria framework that encourages collaboration and seeks consensus among independent lines of evidence that may appear contradictory at first glance. Retaria is therefore a unique and ideal lineage for studying biodiversity dynamics amidst climate change and across deep time, offering a large diversity of cell sizes, ecological interactions, and biomineralization strategies that can only be achieved unifying Retaria research.

Author Contributions

All authors contributed equally to the conceptualization. **M. M. S.** and **R. M.** wrote the original draft. **J. M.**, **N. G.**, **N. L. C.**, **N. L. M.**, and **M. G.** contributed equally in the writing, review, and editing of the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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