1 History

Introduction

The history of radiolarian research begins in the mid-nineteenth century, with research activity continuing with widely varying intensity and focus up to the present day. Unlike large primary divisions of science which have their own internal dynamics, radiolarian studies have always been carried out by relatively small numbers of individuals. Their work has been very strongly shaped by the development of the larger scientific subjects within which radiolarian research has been embedded. It is thus not possible to understand the historical development of the field without also understanding something of the history of these larger fields within which radiolarian studies have been carried out. These include biology, both in general, and specifically protistan biology and marine biology (particularly plankton); and earth sciences: paleontology, stratigraphy, and paleoenvironmental studies – e.g. paleoclimatology and paleoceanography. All of these disciplines have significantly affected the type and intensity of radiolarian research. This chapter thus covers not only radiolarian research but, to the degree appropriate, developments in these other disciplines as they affected the development of radiolarian research.

Bibliographic summaries of radiolarian research provide an overview of activity in the field. Because different bibliographies,

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each with different degrees of completeness and detail, are available, it is best to look at data from multiple sources (Figures 1.1, 1.2). Species descriptions (Figure 1.1a) provide one measure of research activity as taxonomic work is a foundation for other types of research. After a modest degree of publication in initial period of study from ca. 1840–1870, there is a huge spike (due to Haeckel's Challenger monograph, described in "E. Haeckel and his disciples") in the late 1880s, followed by a period of moderate activity up to ca. 1910 or so, after which taxonomic research on radiolarians dropped to very low values until the late 1950s, other than a couple of "spikes" due to some monographic papers in the late 1920s and mid-1940s. Taxonomic work on radiolarians then, from ca. 1960 or so, increased gradually to levels higher than seen in earlier times, followed by a decline in annual species numbers from around 1980 on. Interestingly, a rather parallel pattern of initial interest up to the beginning of the twentieth century, then a period of decline until ca. the 1950s, is also seen in the history of diatom research (Stoermer and Smol, 2010).

If, instead of using numbers of species, one plots numbers of papers (Figures 1.1b, 1.2), a rather different picture emerges. Although there are still two peaks in publication activity, one in the late nineteenth century, and the other in the 1980s, the relative sizes of the peaks are now dramatically different, with many more papers being published in the twentieth, vs. nineteenth century. More papers with time reflects a general pattern in the history of science, where scientific activity and numbers of publications increase rapidly in the twentieth century – indeed, for academic publishing as a whole, the trend has been more or less one of continuous geometric increase with doubling times of 15–24 years since the early nineteenth century, measured either by publications (Larsen and von Ins, 2010) or numbers of journals (Jinha, 2010). Several aspects of the radiolarian publication history however differ from the general pattern of scientific publication.

First, the ratio between numbers of new species and numbers of papers has changed dramatically over time, with nineteenth-century work being dominated by many new species descriptions in a small number of papers, while twentieth-century studies published, per paper, many fewer species, even if due to the larger

total number of papers the total taxonomic output is similar. There is thus either a fundamental change in the style of taxonomic publishing, and/or a shift in publication to non-taxonomic research. Both are probably significant factors. It is possible even today for a student to encounter a nearly unknown radiolarian assemblage which needs to be sorted into species categories without the help of prior literature. This effort, vastly eased by modern imaging technology, can now be done for hundreds of species in a few months' work. However, without the need to reference prior literature, early workers could publish simple descriptions of large numbers of species relatively easily. There is of course also a shift toward applied work with radiolarians over time, so that, unlike in early years, more recent literature is dominated by papers that contain no new taxonomy.

Second, there is a substantial decline in outputs in both taxonomic description and general numbers of publications in the last ca. 20 years. Although this is in part due to incomplete recording in the last ca. 10 years, the similarity between different data sources, and in particular in the relatively comprehensive Paleotax data, suggests that the decline in output is real. This is not a general feature of science publication, which continues to grow rapidly (Larsen and von Ins, 2010; Jinha, 2010). Lastly, there are noticable differences in activity between subdisciplines. Subdisciplines in radiolarian research are, due to many differences in material and the research context that are linked to geologic age, conveniently expressed by the geologic time interval that individual studies examined (living; Cenozoic; Mesozoic; Paleozoic: Figure 1.2). Research on Cenozoic/living radiolarians dominates nineteenth-century studies, and increases relatively rapidly after WWII to a plateau by around 1970, before gradually declining in the 1990s to the present day. Mesozoic and Paleozoic studies by contrast begin to increase in the 1970s and 1980s, respectively, before declining in the beginning years of the twenty-first century. These differences create different time intervals of dominance, with Cenozoic/living being the dominant area of research up to ca. 1980, and Mesozoic research being the dominant activity after this time. The causes of these patterns will be described in our historical review.

These patterns suggest convenient time intervals in which to frame a review of radiolarian reseach: early studies up to around

1910, the low activity interval between 1910 and ca. 1950, the growth period of Cenozoic/living studies up to ca. 1970, and the "modern" phase of research beginning in the 1970s and continuing to the present day. The small (third) peak in publication seen in all data beginning in the late 2000s may represent a new phase of research, though this is more open to interpretation, and will be discussed together with "outlook – future developments" at the end of this chapter.

Within the field of radiolarian studies, the number of species descriptions by author (see Table 5.5) provides at least a rough guide to the importance of individual workers, particularly in earlier times when descriptive work dominated research activity.

Scientific Context

The first of the broader issues that influenced early studies of radiolarians are the basic framework ideas on the development of science itself, as early radiolarian research grew up during this period of general scientific development. Modern science, with its distinguishing characteristics of emphasis on non-metaphysical material mechanisms as the cause of the patterns and structure of the natural world, formal hypotheses, and testability, is generally agreed to have originally developed primarily in Europe over several centuries, but maturing in the eighteenth and nineteenth centuries (Wikipedia contributors, 21.6.2018). By the mid-1800s natural sciences were firmly established in western countries and divided into the major divisions we still use today, with numerous professional positions in universities, supported by professional societies and other coordinating organizations. Even the name was modern, with the term "scientist" (coined by W. Whewell in 1833) gradually replacing the earlier, less distinctive term "natural philosopher" (https://en.wikipedia.org/wiki/William_Whewell; accessed 3.9.2017). In other parts of the world descriptive and sometimes quite extensive studies of nature analogous to the descriptive studies of biodiversity in the western world were also developing, e.g. in Japan (Marcon, 2015). These activities were linked, as in western countries, to other interests (medicine, agriculture, hobby gardens, and others) but they were not systematically linked to developing formal paradigms of scientific hypotheses and testing as in the West. Nor, lacking widespread access to microscopes and other suitable technology, was the systematic study of microorganisms possible.

The development of science in Europe was gradual and not uniform between disciplines, with physical science developing more rapidly than biologic. At the beginning of the nineteenth century however, the transition in biology from a descriptive style to one where description was informed, and thus influenced by scientific theories of process, was already underway. Initial steps in this transformation included a re-examination of the "scala natura" description of the natural biologic world that had been inherited from antiquity (traceable back to Plato), and had been overlain with religious-metaphysical mechanisms (Mayr, 1982; https://en.wikipedia.org/wiki/Great_chain_of_being, accessed 21.6.2018). Observations of the diversity of life had been until then pressed into a

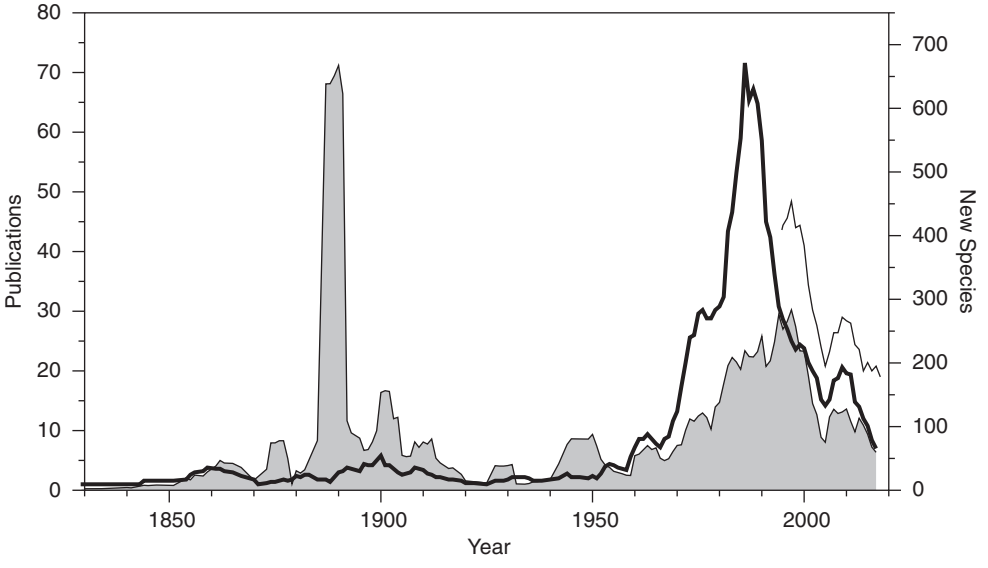


Figure 1.1 Publishing activity over time for radiolarian research. a) shaded – number of new species per year (3-point smoothing); b) bold line – number of publications per year (Suzuki database with 3-point smoothing); c) thin line – number of publications per year with "radiolaria" in the title in Google Scholar, 1988–2018 (searched August 2019). The Suzuki database primarily records taxonomic literature and thus underestimates applied radiolarian research where radiolarians are used but no new taxonomy is published. However, a simple Google Scholar search for radiolarian papers, not specifically taxonomy, gives a very similar trend, albeit with higher total numbers of papers.

description of a continuous chain of forms, from the simplest to the most complex, perfect forms (man, and above this the metaphysical beings of angels and god). The simplest forms at the base merged into and continuously arose from the inorganic world below via spontaneous generation – an idea which, although long under attack, was still present well into the early nineteenth century (https://en.wikipedia.org/wiki/Spontaneous_generation, accessed 22.6.18). More objective study showed numerous flaws in this description, weakening the metaphysical/religious explanations of mechanism tied to this description. Cuvier for example demonstrated in 1812 that there was not a continuous series of forms among metazoans (Mayr, 1982). A series of tests, culminating in Pasteur's 1859 experiment, finally disproved the idea of spontaneous generation. New scientific theories, based on these more objective descriptions of nature, and using materialistic mechanisms, were proposed in to replace the scala natura. Several theories of evolution were also developed, such as those of Lacépède and Lamarck, although these lacked an adequate mechanistic basis (Mayr, 1982). These earlier ideas were replaced later in the century by Darwin's evolutionary theory (Darwin, 1859).

The idea that all life was made of cells was published by Schleiden (1839) and Schwann (1839), and that all cells arise from other cells (and thus not, at the base of the chain, from the inorganic world) was proposed by Raspail in 1825 but only popularized by Virchow in 1858 (Enerson, 2018).

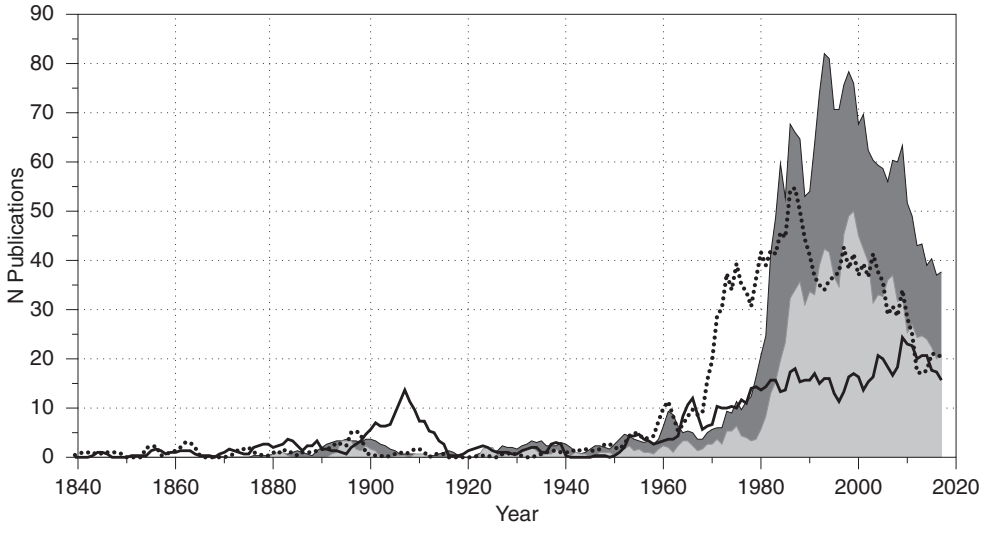


Figure 1.2 Numbers of papers published per year by geologic time interval, from reference database of radiolarian literature distributed at the Cadiz Interrad meeting (2012). Light grey: Paleozoic; Dark grey: Mesozoic; Dotted line: Cenozoic; Solid line: Living. Data smoothed (3-point moving average) for clarity. Cadiz literature database includes many applied papers and papers without the word "radiolaria" in the title but does not include as many titles per year for pure taxonomy as the Suzuki database.

Early studies in Europe using primitive microscopes had documented the existence of microscopic life forms, (e.g. J. Hill 1652, van Leeuwenhoek 1674: Corliss, 1975), and O.F. Müller (1770s and 1780s), but little was known about their biology or diversity even in the early nineteenth century (Corliss, 1978). Improved microscopes in the mid–late nineteenth century, however, were enabling new insights on microscopic life, in particular from various innovations in lens and illumination design in the 1830s to 1870s (Croft, 2006).

Increasing wealth and technologic power from the industrial revolution meant increased resources were available to more systematically explore remote environments, including the open oceans. Scientific studies of these had begun already in the 1700s, but the number of expeditions increased substantially in the later 1800s, most notably with the Challenger expedition of 1872–1876 (Lalli and Parsons, 1993; Figure 1.3). The Challenger Expedition grew out of the first systematic studies of marine organisms by E. Forbes and the discovery in 1860 of abundant life growing on a deep-sea telegraph cable. This disproved Forbes' 1843 Azoic Theory of no life in the deep oceans and stimulated new research on the vast, scientifically unknown biologic realm of the open oceans. Plankton studies would become a regular part of the research program on such expeditions, though "plankton" as a distinct concept was not coined until 1887 by V. Henson, who subsequently, in 1889, would lead the German "Plankton Expedition" – the first specifically devoted to study of planktonic organisms. (The study of the radiolarians from this expedition by Brandt were however mostly on the poorly fossilizing Collodaria.) This expedition's financing provides an example of the growing commercial interests in ocean environments, as a significant contribution to the costs was donated by the German

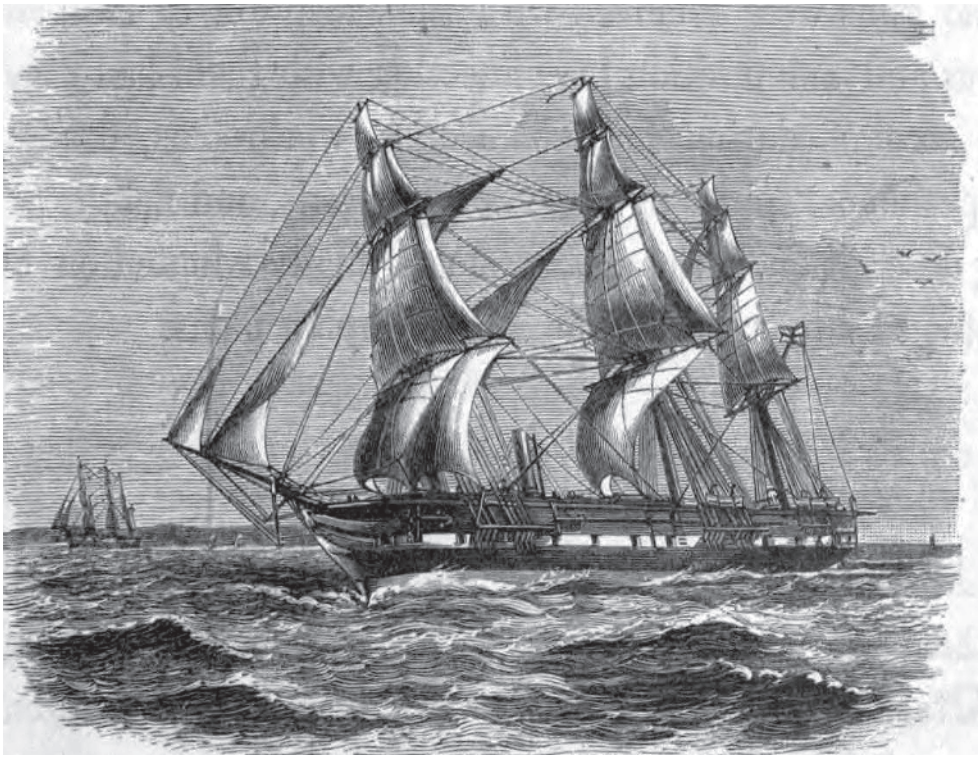


Figure 1.3 The H.M.S. Challenger. Primarily known for its seminal ocean research expedition (1872–1876) which circumnavigated the globe, covered 127,580 km, and explored all major ocean basins from the tropics to polar regions. A small shipboard staff of six scientists led by C.W. Thomson took physical oceanographic measurements, and collected water, plankton, and deep sea samples during the cruise which were distributed to numerous other scientists when the expedition ended, including E. Haeckel, for radiolarian studies. Source: Wikimedia Commons.

commercial industry's Fisheries Association (Deustcher Fischereiverein) (https://de.wikipedia.org/wiki/Deutscher_Fischerei-Verband, accessed 6.9.2017). In a parallel development, the late 1800s saw the establishment of several marine biology laboratories, e.g. the Naples laboratory in 1872, and the Marine Biologic Laboratory in the USA in 1873 (moved to Woods Hole in 1888; Lalli and Parsons, 1993). The Naples Zoological Station was particularly important to the development of marine biologic research. Founded by A. Dohrn, a zoologist and later evolutionist who had studied in part under the famous radiolarian researcher E. Haeckel in Jena, the Naples Station was an "open" facility, which could be used by visiting scientists from any country, who paid (an innovation itself) "bench fees" for using the facility (Cortese, 2014).

Geology in the first half of the nineteenth century was still primarily a practical, descriptive science, and considerable energy was devoted to stratigraphic categorization, mapping, and similar activities, though major debates on tectonics and other geologic themes were present (Gohau, 1990). Theoretical work was supported by the work of Lyell and others who had largely established the required basic

principles such as uniformitarianism (the geologic record is to be interpreted as resulting from processes known in recent times). Historical geology however was still hampered, despite the spread of Lyellian uniformitarianism, by religious requirements for a very young age for the earth. The basics of stratigraphy were well established, even if the number and names of stratigraphic divisions were still in a state of flux. Biostratigraphy was also an established tool, having been founded by W. Smith (e.g. "Strata Identified by Organized Fossils," published 1816–1819). A. d'Orbigny in 1840 introduced the use of microfossils (specifically foraminifera) for biostratigraphic purposes. Micropaleontology as a distinct field had however not developed – indeed, d'Orbigny himself at first saw foraminifera simply as very small cephalopods. This was corrected by Dujardin's 1835 observation that micro-organisms are unicellular (Corliss, 1978; Vénec-Peyré and Bartolini, 2013). Toward the end of the nineteenth century, geology became more closely allied to expanding industrial and national interests, with the founding of numerous geological surveys and extensive field geologic studies to map and identify natural resources. The United States Geological Survey, for example, was founded in 1879 (Rabbitt, 1975). These activities, along with the discovery and increasing use of oil deposits at the end of the century, would also have a major impact on radiolarian research, but not until well into the twentieth century.

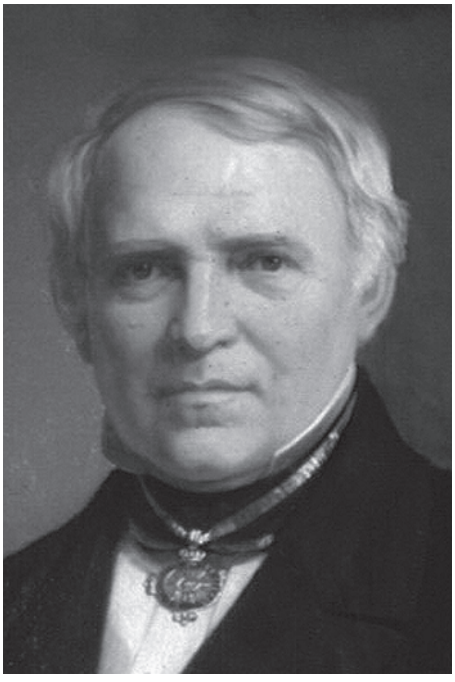


Figure 1.4 Christian Gottfried Ehrenberg (1795–1876). Source: Museum für Naturkunde historical document archives.

Early Studies (First Half of the Nineteenth Century)

C.G. Ehrenberg and J. Müller

Radiolarians during the first half of the nineteenth century were known only from relatively inconsequential, minor notes in early biologic surveys, e.g. Meyen (1834), and had not yet been studied in any significant way in fossil form. Radiolarian study (and micropaleontology in general) really began with the work of C.G. Ehrenberg, who systematically described numerous fossil forms (but very little living material), and J. Müller, who initiated study of living radiolarians in 1855 (Lazarus, 2014).

Christian Gottfried Ehrenberg (1795–1876, Figure 1.4) grew up in Delitzsch, Germany, and developed an interest in natural history while still a Gymnasium student. This led him to break off his initial study of theology and take his degree (1818) in medicine at the university in Berlin, as at this time the study of biology was still closely connected to the field of medicine (Wetzel, 1966; Mayr, 1982). Ehrenberg at first studied a variety of plant and animal species, and as a biologist took part in two expeditions: one to the Near East (1820–1826, under the leadership of the

Prussian general J.H. v. Minutoli), and a second to Russia (1829). The former expedition was in many ways disastrous, as it was underfunded and poorly planned, and the majority of the participants died of illness before it was completed (Siesser, 1981). For Ehrenberg, who lost his friend Hemprich to illness during the expedition and only narrowly survived himself, it was a double disaster. His painfully collected scientific materials (ca. 80,000 specimens that had been mailed to Berlin) had been mishandled. Many of the specimens had been sold to other scientists or collectors, and most of the labels on those still remaining had been lost. Ehrenberg soon turned to the study of microorganisms. Some he collected himself in Berlin or in Germany; many more were sent to him by other naturalists as his fame as "the" microorganism specialist grew with the years. Ehrenberg's exceptional knowledge of microorganisms was known as well beyond the realm of scientists and naturalists; he was not infrequently invited to meetings of high society (on one occasion the King of Prussia) to set up his microscope and show off his microorganisms to those assembled (Jahn and Landsberg, 2000).

Ehrenberg's fame was deserved. Although protists had been described sporadically for many decades, even the more detailed studies, e.g. by O.F. Müller (1730–1784, posthumous publication 1786), tended to mix protist and metazoans together. Initial definitions of them as a group, while recognizing their distinctiveness, also implied their primitive, simple nature, as the word "protozoa," coined by Goldfuss in 1817–1818 clearly suggests. Goldfuss placed Protozoa at the base of the scala natura, emerging from the "Urschleim" [primeval slime] (Entzeroth and Hausmann, 1993). Ehrenberg was the first to systematically study a broad range of living and fossil microorganisms and to document them as widespread, diverse, complex, highly developed forms of life. He thus can be considered the father of protozoology and, together with A. d'Orbigny, the cofather of micropaleontology (Corliss, 1978; Siesser, 1981). He described thousands of new species, including many of the type species for common genera in important groups of microorganisms, such as the diatoms (Jahn, 1998; Lazarus, 1998). Ehrenberg did not have the ability to understand the geologic aspect of the fossils he studied as most of the geologic age assignments at that time were still extremely imprecise (e.g. Tertiary vs. Cretaceous) and even these were frequently wrong (Zittel, 1876, p. 76). His importance is that, other than the short, one-page description of a single species (the collodarian colony *Sphaerozoum fuscum* by Meyen, 1834), he was the first to systematically study and describe radiolarians.

Ehrenberg's doctoral thesis on fungi had demonstrated that they developed by normal biologic means of reproduction, and not, as the still commonly believed medieval (or older) theory of scala natura (also known as "the great chain of being") suggested, by development from lower forms. Finding evidence to refute the scala natura theory remained important to Ehrenberg's later scientific development, as in his studies of microorganisms he stressed their complex nature and constancy in characters, both characteristics that he felt refuted the predictions of scala natura, which claimed that lower forms of life were ever simpler, less developed, and had a tendency to transform into other life forms along the "scale"; and at the base (where microorganisms were assigned), a seamless transition occurred to the inorganic realm (Mayr, 1982). The scala natura was however, regardless of popular belief, already largely disproven to many other contemporary biologists, e.g. from Cuvier's (1812–1817) studies of animal systematics (Mayr, 1982). Ehrenberg went so far in his effort to establish the complexity of microscopic life as to claim that the organelles of living protist cells were in fact miniature organs, fully homologous with those of macroscopic,

multicellular life forms. In this he rejected the discoveries of other biologists on the unicellular nature of microorganisms (e.g. Dujardin, 1835). His biases on the constancy of species (based in part on comparisons using broadly defined genera, e.g. Ehrenberg, 1839, p. 154 on *Haliomma*, which he found living in ocean water and in "Cretaceous" rocks from Greece) and gaps between forms similarly led him later to reject Darwin's evolution theory. These contrarian views resulted in much of his work being, if not rejected in its entirety, nonetheless being neglected by both contemporary and later generations of biologists (Wetzel, 1966; Siesser, 1981). T.H. Huxley, for example, described Ehrenberg's research (and before the publication of Darwin's *Origin*) as "wonderful monuments of intense and unremitting labour, but as least as wonderful illustrations of what zoological and physiological reasoning should *not* be" (Huxley, 1851, p. 436 – with several following pages rebutting Ehrenberg's ideas). Ehrenberg also persisted in using the same microscope throughout his career (Figure 1.5; pers. comm. T. Mappes, 6.8.19) even though it was technically increasingly obsolete, and did not yield the same quality images as newer models (Siesser, 1981).

Despite these weaknesses, Ehrenberg's strength lay in precise observation and documentation of the morphology of the organisms he was studying, including remarkably objective, nearly photographic drawings, and careful preservation and labeling of his source materials (Figures 1.6, 1.7), in which work he was aided by his longtime assistant, his daughter Clara. This documentation of his descriptive studies has permitted most of his taxonomic legacy to survive and be used in modern scientific work. It is possible that his care in documentation was rooted in his earlier, disastrous experience with the materials from his Near East expedition.

Figure 1.5 Microscope similar to that used by Ehrenberg. Made by the firm of Schieck in Berlin, they were considered to be of very good quality when first introduced. Note the long working distance to the specimen stage and round area for holding preparations. Ehrenberg's micas fit this type of instrument well. Source: Photo and instrument courtesy of Timo Mappes.

Ehrenberg defined several of the higher level categories of radiolarians (e.g. Polycystina, Spumellaria, Nassellaria) that are still used today. In all, Ehrenberg

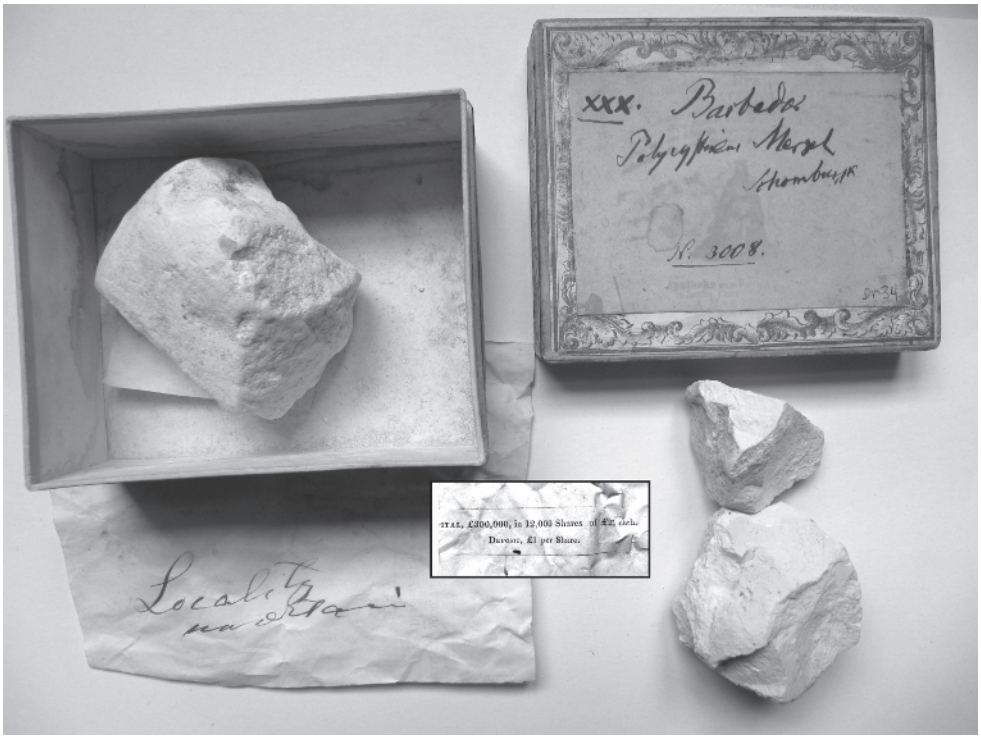


Figure 1.6 Ehrenberg Collection sample of Eocene radiolarian chalk, Barbados. One of several samples from Barbados in the Ehrenberg Collection. Determining the geologic context of historical material is challenging and requires historical research, as this sample illustrates. The material was given to Ehrenberg by Sir Robert Schomburgk (Ehrenberg, 1846, 1847), who like many naturalists explored the Americas in the early 1800s. Although Schomburgk was originally German he spent most of his career in English-speaking countries and he may well have personally collected the material even though the label in the box: "Locality uncertain" is in English, as is the scrap of paper it was written on (the back, shown in the inset, apparently refers to a stock offering in English Pounds). Schomburgk was at the time stationed on British government business in Barbados (Robert Hermann Schomburgk, Wikipedia, accessed 17.8.19) and may simply have failed to note precisely where the material was collected. No details are given in the Ehrenberg publications as to the extent of the material, other than stating that "several fist-sized" pieces were included. The presence of multiple individual geologic objects, sometimes with clearly different geologic characteristics in a single "sample," is common in such historic collections. Anna Jobst, the archivist who databased the collection, by matching different published sources and collection records suggested that the sample(s) can be assigned to the peak of Mount Hillaby (Ehrenberg Collection database, accessed 17.8.19). This would place them several km away from the better known material from modern studies of Barbados microfossils of the Bath Cliffs (Saunders et al., 1985), though still part of the Eocene nappes of pelagic sediments that are present in the island's geology (Donovan, 2005).

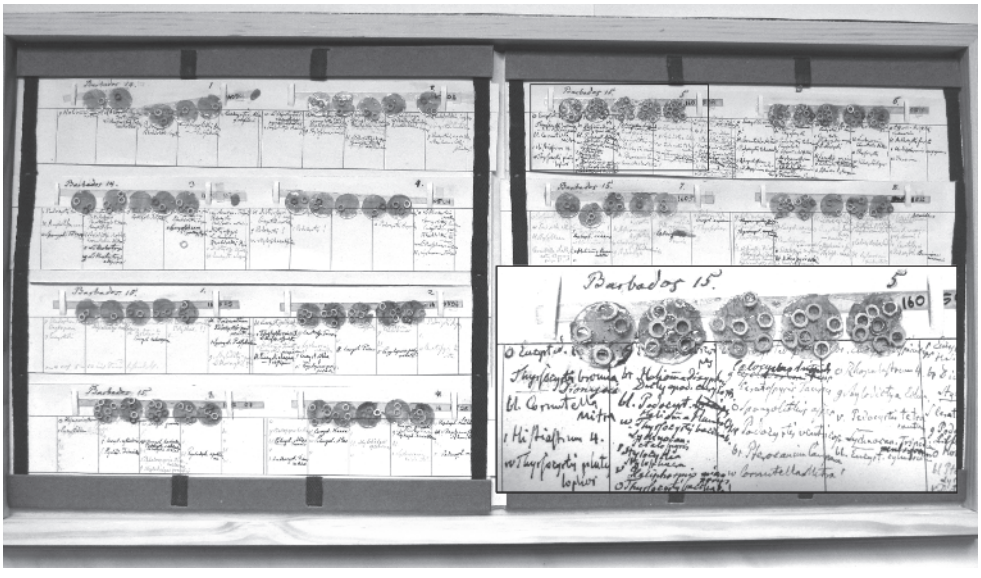


Figure 1.7 Ehrenberg mica microscopic preparations (here cabinet 15, tray 5). Ehrenberg made his preparations on small round discs of mica, on which he melted a thin layer of Canada Balsam then sprinkled the source material over. He generally made at least 5, and often more than 30 such discs from a single sample (though note that "sample" is somewhat ambiguous – see caption to Figure 1.6). For storage, groups of 5 discs were glued, using more balsam, onto a thin mica strip and inserted into slots cut into a broad paper mounting strip. Specimens of interest were marked by small colored paper rings on the micas and the taxonomic name noted with an abbreviation to the ring color on the strip of paper underneath, with blocked areas corresponding to the sequence of micas. Strips were bundled into cardboard folders, and in turn held in larger cardboard boxes resembling books. With the passing of years, the micas began to loosen from the mica strips, and break during opening or closing the folders. They were thus transferred to the tray system used today. Given the very limited space Ehrenberg's taxonomic names were often abbreviated and are frequently hard to read, even in close-up (see inset). As Ehrenberg worked prior to the development of the concept of type specimens, there is no indication in the collection which mica or ring holds the specimens used in his original species description publications. This makes finding the ca. 2,000 type specimens for his published species (all taxonomic groups included) challenging, as there are ca. 40,000 micas in the collection. Given the rough surface of the micas and the optical flaws of the mica backing, imaging the specimens once found is also sometimes difficult. After Lazarus (1998) and Lazarus and Jahn (1998).

described over 500 radiolarian species and more than 70 genera (Suzuki, 2009), and of these at least 159 species and most of his genera are known to be accepted and in current use (Lazarus et al., 2015). The taxonomic status of many more of his species are under revision, based on a foundational re-examination of Ehrenberg's original collections (individual chapters in Tanimura and Aita, 2009; see also Chapter 5: Taxonomy and Fossil Record).

Johannes Müller (1801–1858, Figure 1.8) was a very influential biologist (see, e.g. Otis, 2007) who carried out the first extensive

Figure 1.8 Johannes Müller. Source: Image archives of the Humboldt University, Berlin.

studies of living radiolarians, though the very first usable description is that of Huxley (1851), who briefly described (three text pages and a plate) collosphaerid colonies and the large solitary species *Thalassicolla nucleata* Huxley. Although Müller's interest in the diversity of nature was lifelong, for much of his early career he concentrated on medicine, where he substantially advanced the field of physiology (summarized in his multivolume *Handbuch der Physiologie des Menschen*, published between 1833–1840). Beginning in the 1840s and until his premature death in 1858, he studied many groups of invertebrates, ending with five published studies of living radiolarians from coastal seas in the Mediterranean (1855–1858). The last of these in particular introduced the word "radiolaria" for the group and gave detailed descriptions and illustrations of numerous living species (with dozens of new species and genera) of acantharians, spumellarians, nassellarians, and collodarians. His text discussed details of both cytoplasm and skeleton, and together with his illustrations provided a starting point for future biologic studies, particularly those of his student Ernst Haeckel.

Second Half of the Nineteenth Century to ca. 1920

E. Haeckel and his disciples

Ernst Haeckel (1834–1919, Figure 1.9) was without question the single most important individual ever to study radiolarians: measured both by his radiolarian studies, and by his general importance to human

Figure 1.9 Ernst Haeckel, ca. 1860. Source: Wikimedia Commons.

history, as Haeckel was also very active in other areas of biology, science popularization, and in politics (Gasman, 2004; Richards, 2008). Building on the foundations of shell morphologic descriptions by Ehrenberg and cell biology by his doctoral advisor J. Müller, Haeckel named (although often failed to adequately describe) literally thousands of radiolarian species, both fossil and living. He also popularized radiolarians (and other groups of organisms), and explicitly linked radiolarian taxonomy to Darwinian evolutionary theory. The only areas of radiolarian research he did not profoundly influence were the study of pre-Cenozoic forms, or the use of radiolarians in geologic research, e.g. for biostratigraphy.

Haeckel came from an upper middle-class family and initially studied medicine. He soon shifted to studying zoology under, among others, Karl Gegenbauer and J. Müller. During an extended trip to Italy, Haeckel began in 1859 to study radiolarians from the coastal waters off Messina, as Müller had done earlier. These studies were extended into his Habilitation work (formal qualification for a professorship in classical European academic systems), which was published (Haeckel, 1862) as his first major work on radiolarians. He was appointed to the first professorship in Germany dedicated to the new discipline of zoology in 1865 (Entzeroth and Hausmann, 1993). Haeckel carried out extensive studies of many types of organisms including vertebrates, sponges, and coelenterates over the next two decades and became very active in promoting, via talks and publications, Darwin's evolutionary theory. Based on his 1862 publication he was given the radiolarians from the recent Challenger Expedition to analyze. His report, published in 1887, was one of the largest published in the Challenger series, and remains to this day the most extensive single work ever published on radiolarians, with 2,750 pages and 140 plates in 3 large volumes. Haeckel concentrated more and more on political and popular science activities from around 1900 until his death in 1919.

Haeckel is primarily known both to scientists and to historians not for his radiolarian studies, massive though they were, but for his other scientific work, his popularization of biology including biodiversity and evolution, and his promotion of a political version of evolution. Haeckel was an important figure in biology in the second half of the nineteenth century, producing major syntheses of general metazoan morphology, developmental biology, and evolution, e.g. his *Generelle Morphologie* (Haeckel, 1866). He is famous in biology for, among other ideas, his theory that "ontogeny recapitulates phylogeny," as well as for coining many biologic terms, such as "ecology." Haeckel attempted to insert evolutionary biology into politics and sociology, promoting racial theories and eugenics. Haeckel also founded a new school of philosophy – Monism – many members of which also promoted his political views, and not a few became active members of the Nazi Party. Haeckel was however also cited by communist activists. Because of his major role not only in nineteenth-century biology but his complex, problematic contribution to political ideas in Germany, he is a controversial figure and a regular subject for historical study. See, for example, Gasman (2004) and Richards (2008) for decidedly different interpretations of his person and historical role. Haeckel's popular works e.g. *Kunstformen der Natur* (Haeckel, 1904) introduced radiolarians to the general public, played a role in linking the biology of form to the then-current Art Deco movement (Kockerbeck, 1986), and to this day remain popular and continue to inspire artists and students of biologic form.

Haeckel provided the first comprehensive description of all aspects of radiolarian

diversity – species descriptions, higher level taxonomic concepts, morphologic characteristics. His studies of living radiolarians were devoted approximately equally to all major groups of marine rhizarians, all of which at that time were called "radiolaria": Spumellaria and Nassellaria (Polycystina), Acantharia and Phaeodaria; the latter two groups today are no longer considered radiolarians in the modern sense of the word. Haeckel described in all over 3,000 new species, several hundred genera (counting subgenera, over 1,000), and dozens of families alone for the Polycystina (precise numbers are not available as current databases partially still mix information on Polycystina, Acantharia, and Phaeodaria together. See also Chapter 5: Taxonomy and Fossil Record). Haeckel's first major work on radiolarians in 1862 covered, in great detail, every aspect of radiolarian biology in over 200 text pages and 38 plates, including cellular morphology, behavior, biogeography, reproduction, and taxonomy – a quantum leap in our understanding of the group. One reason for this is that Haeckel, unlike Ehrenberg, who used the same early nineteenth-century model throughout his life, used then state-of-the-art microscopes (his first, custom-made for him in 1853 from the Berlin manufacturer Schieck; Otis, 2007) which allowed him to see much more cellular detail than earlier workers. After becoming professor, Haeckel could amplify his interest in radiolarians through his students and followers – notably Hertwig (1876, 1879); Bütschlii (1882); Dreyer (1889); Jorgensen (1905); Popofsky (1908); and Mast (1910) – protozoologists who continued his biologically oriented examination of the group. Many of these studies were, similar to Haeckel's (1887) work, connected to the exploratory marine research expeditions which characterized the latter nineteenth and early twentieth centuries. Haeckel's (1887) monograph however remains unique in the scope and detail of its results, although many of his described taxa are problematic, as discussed in Chapter 5 (Taxonomy and Fossil Record).

Roughly in parallel to the growth of these early biologic studies, other studies describing only fossil forms continued to be produced in Europe, often more similar in style to Ehrenberg than Haeckel, e.g. Stöhr (1880), Bütschli (1882), Dreyer (1889), and Tan (1927) on Cenozoic materials. An important extension to study of pre-Cenozoic materials also occurred, e.g. Pantanelli (1880), Hinde (1890; Fig. 1.10), Rüst (1892), and Squinabol (1904) on Mesozoic and Paleozoic materials. These latter studies,

Figure 1.10 George J. Hinde (1839–1918). Son of a factory owner in England, Hinde began his career as a farmer in England, then worked for several years as a sheep rancher in Argentina. After further years of wandering and doing geologic research in North America, Hinde returned to England in 1874 and was elected a Fellow of the Geological Society of London. From then on, he concentrated on studies of various invertebrate, mostly Paleozoic microfossil groups, including sponges, conodonts, and radiolaria (Woodward, 1918). He described in all 231 new radiolarian species (Suzuki Paleotax database) Source: illustration provided by M. Afanasieva.

although generally hindered by the difficulty in extracting and obtaining high-quality images of radiolarians from cherts and other lithified rock, nonetheless demonstrated the great geologic range of radiolarians and documented that the forms of the individual shells were at least in part clearly different from those in the Cenozoic. It should be noted though that these early studies primarily documented the faunas, but did not significantly develop them as applied tools for geologic research.

Another significant development was the gradual spread of radiolarian studies outside of Western Europe. Brief mentions of radiolarians began to appear from authors based in, e.g. North America (Dana, 1863 – cited in Mivart, 1878; Baker and Bowman 1917; Aberdeen, 1940) and more detailed studies eventually also began to appear, e.g. a biologic study by the Russia-based Cienkowski (1871), and geologic papers by the Hungarian worker Hojnos (1916, and subsequent papers). A first mention of radiolaria in Japan comes from geologic papers by S. Yamane (1924) and more detailed radiolarian reports from Mesozoic cherts in Japan by S. Yehara appeared in 1926 and 1927. J. Khudyaev (1931) published the first Russian [soviet] paper, on fossils. The spread of radiolarian research around the globe was due in part to the growth in the use of modern scientific methods in many non-western countries, e.g. in Japan as part of the Meiji Restoration and subsequent industrialization. Western Europe, however, remained overwhelmingly the center of radiolarian research.

Legacy of Early Studies

The first phase of radiolarian research in the nineteenth century laid the foundations for later work, and in particular provided a broad, detailed set of studies of living radiolarian morphology, the extent of which has not since been duplicated. The taxonomic legacy is decidedly more mixed. As noted in Lazarus (2014) much of the taxonomic legacy of early workers is difficult to use. This is particularly true for German studies, but also true for most other early studies. There are a variety of reasons for this, including artificial, overly elaborate higher level taxonomy; inadequate species descriptions and illustrations; failure to designate or deposit type specimens or other reference material; and loss of many German collections in World War II (see this section and also Chapter 5: Taxonomy and Fossil Record). These problems affect Cenozoic and living material much more than older geologic materials, simply due to the much greater number of Cenozoic-living taxa named in early research. The confused nature of radiolarian taxonomy made it much more difficult to use radiolarian species (or other taxa) in applied research. Generic names were so poorly delineated or documented according to the Rules of Nomenclature that generic name use was for most species almost arbitrary, with several equally unclear choices available for any given species. The artificial nature of taxa definitions extended ranges artificially over great intervals of geologic time, hindering the development of stratigraphy (see also "The origins of radiolarian biostratigraphy: 1940s to 1950s"). Furthermore, the failure to deposit type materials, or their subsequent loss, meant that many of these issues could only be resolved with great difficulty. As discussed in Chapter 5, despite a great deal of recent progress, there is still much further work to do, and taxonomic problems with early studies remain a barrier to modern research. Lastly, nineteenth-century studies demonstrated the great geologic range of radiolarians and documented that the forms of the individual shells were at least in part clearly different from each other on the scale of geologic periods, even if the taxonomy did not yet adequately reflect these differences.

Early Twentieth Century (ca. 1920–1940)

In the early decades of the twentieth century there was a gradual shift in the development of scientific research on living and fossil protists. The growth of scientific medicine led to a more focused interest on microorganisms (bacterial and eukaryotic) responsible for disease, with relatively fewer resources being devoted to general field-based surveys of protist diversity (Corliss, 1978). Presaged by the shift in the latter part of the nineteenth century from "natural history" toward physiology, biology in general was in the early twentieth century becoming more experimental, quantitative, and laboratory-based, with a greater focus on cellular and subcellular research (Mayr, 1982; https://en.wikipedia.org/wiki/History_of_biology, accessed 6.7.2018). In the ocean sciences, marine laboratories were gradually shifting from an early focus on biodiversity and organismal research to a broader range of more quantitative studies of physical and chemical oceanography (a trend that, particularly after WWII, in part was driven by increased military interest in the oceans: Ocean Studies Board NRC, 2000), or to more focused studies of fisheries science (Lalli and Parsons, 1993). In the USA for example, the Scripps Institution for Biological Research, originally founded in 1903 by marine biologists as the Marine Biological Association of San Diego, was renamed the Scripps Institution of Oceanography in 1925 to reflect the changing focus of its research (https://scripps.ucsd.edu/about/timeline; https://en.wikipedia.org/wiki/Scripps_Institution_of_Oceanography, both accessed 6.7.2018); while on the US East Coast, the older (established 1888) Marine Biological Laboratory on Cape Cod was supplemented, and eventually overshadowed by the new Woods Hole Oceanographic Institution, established in 1930 explicitly, in the words of the National Academy Of Sciences, to "prosecute oceanography in all its branches" (http://www.whoi.edu/main/history-legacy, accessed 6.7.2018). The growth of ecology in the early twentieth century assisted the development of biological oceanography as a field distinct from marine biology. Biological oceanography shifted plankton studies more toward understanding general patterns of plankton such as abundance and productivity, dominated by phytoplankton, and their relationship to physical oceanography; descriptive studies of individual taxa by contrast declined in importance. These changes were in part due to the need by fisheries scientists to understand the food chains of fish that began with patterns of plankton productivity (Lalli and Parsons, 1993). This shift towards medical and applied economic research affected the biologic study of many groups of organisms. Diatom research, despite having a connection to plankton productivity and ecology, became increasingly marginalized, particularly for freshwater diatoms. Even in the late 1950s there were no university-based researchers in the USA specializing in freshwater diatoms (Stoermer and Smol, 2010). Experimental, laboratory-based research on open-ocean, unculturable zooplankton such as radiolarians, which in addition were of no known significance for applied biological oceanographic research (e.g. fisheries) was even less attractive. Radiolarians thus, by not being optimal material to study the priority questions of early twentieth-century biology, became relatively neglected by biologists. Biologic studies of radiolarians in the early twentieth century were published, but had relatively little impact on the main trend of development in the field. In addition to workers such as Popofsky (see "E. Haeckel and his disciples"), others such as Hertwig (1932) and Bernstein (1932) continued the tradition of plankton studies established by Haeckel.

Sugano (1937) described many species of radiolarians in the plankton near Japan, also using the artificial nomenclature and concepts of Haeckel. Enriques (1919 and subsequent papers) began a more modern, biologically based taxonomic revision of living radiolarians which would have been influential, but unfortunately died early in a traffic accident and his work was largely unknown (Cortese, 2014).

While biological research on radiolarians gradually declined, changes in geology and paleontology were taking place, equally gradually, that would eventually lead to a resurgence in radiolarian research, though primarily on fossil forms. This took place as part of the gradual growth of the discipline of micropaleontology.

The study of microfossils is nearly as old as the study of microorganisms, as they were extensively described by Ehrenberg, d'Orbigny, and others already in the early nineteenth century. Micropaleontology however only began to develop as an independent discipline when microfossils were understood not just as biologic remains, as had been largely done by e.g. Ehrenberg, but as material that could be used to study geologic questions. The main focus, at least initially, was as a means to correlate between geologic sections (biostratigraphy), an idea originally introduced by William Smith in 1816 (Hay and Southam, 1978). d'Orbigny was certainly the first to use microfossils (foraminifera) this way, although microfossils were simply one of many fossil groups used for his stratigraphic work. In the latter part of the nineteenth century, although still partially based on concepts of catastrophism, biostratigraphy developed rapidly. During this time period it was first used primarily as a way to distinguish the major geologic periods, but increasingly to assist basin level correlations by using refinements in concepts, such as stages (d'Orbigny) or zones (Oppel), developments that were fully in line with Smith's original use in local to regional correlations (Hancock, 1977; Hay and Southam, 1978; Balini et al., 2017). Microfossils however only began to be used extensively for biostratigraphic work at the end of the nineteenth and beginning of the twentieth century, when improved technology allowed numerous wells to be drilled, resulting in the recovery of rock samples much too small to contain useful amounts of larger fossil organisms (Martin, 2013). European workers such as Grzybowski discovered their utility in oil wells in the 1890s (Czarniecki, 1993; Martin, 2013), and somewhat later, in the early 1920s, micropaleontologists (mostly young women, particularly E. Applin, A. Ellisor, and H. Kniker) demonstrated this in the USA (Gries, 2017). Joseph Cushman's 1928 book on foraminifera established and spread this new type of microfossil use worldwide (Cushman, 1928; Huber et al., 2013). By the 1930s the dramatic increase in demand for oil supported the rapid expansion of the new applied science field of micropaleontology, with micropaleontology laboratories being established by many oil companies, universities, and government agencies worldwide (Russell, 1970; Yakovleva-O'Neill and Kozlova, 2013; Martin, 2013), courses in micropaleontology being added to university curricula (Martin, 2013), and even popular articles on micropaleontology being published (Figure 1.11: *Popular Mechanics*, 1932). Initial studies on foraminifera spread quickly by the 1930s to other fossil groups such as dinoflagellates, which were studied by European workers e.g. Deflandre, O. and W. Wetzel (Dietz et al., 1999). While these developments established the importance of, and general financial support for, micropaleontology, studies of several other fossil groups did not initially benefit. Radiolarians were not initially targets of study, and diatoms were only marginally involved. As was also true for radiolarians, initial studies of fossil diatoms in the nineteenth century primarily documented their diversity and morphology. Biostratigraphically oriented

Figure 1.11 An early popular science article portrayal of micropaleontologists. The tendency of industrial micropaleontologists to refer to their microfossils as "bugs" persists to this day Source: *Popular Mechanics*, 1932. Reproduced with permission of *Popular Mechanics*.

studies, in connection to oil exploration, developed gradually in the 1920s, particularly in papers on Cenozoic California sections by G.D. Hanna (Burckle, 1978). An even slower start is seen to the study of fossil coccoliths, with limited morphologic studies in the nineteenth century, and biostratigraphic work appearing, in this case, only well into the twentieth century, with the landmark study of Bramlette and Riedel (1954) (Olney, 2002: www.ucl.ac.uk/GeolSci/micropal/calcnanno.html, accessed 8.2017; Agnini et al., 2017).

One major change in the scientific context of radiolarian research that occurred between ca. 1930 and 1950 was the shift from Europe to America as the main center of both academic and applied scientific research. As a consequence, after World War II English gradually became the global standard for publication in the sciences. Scientists whose native language was English were increasingly likely not to learn other scientific languages (which could fairly be argued was for these workers at least culturally a trend towards provincialism, not globalization), and for non-native speakers of English, the only scientific foreign language learned would be English. In practice however, this meant that, unlike the situation in the late nineteenth century and earliest twentieth century, scientists could not publish in one of several other languages (particularly French or German) and expect their work to be fully known. In Western Europe, most workers soon adapted to this new communication standard. In countries such as Japan or in the Soviet Bloc, the large number of radiolarian co-workers led to several large bodies of "own language" literature, particularly Russian and Japanese. This development certainly made it easier for workers in these countries to publish and read research papers in their field, and thus helped radiolarian research to develop in these countries. However, these papers were not widely read outside of their home countries. These new barriers to communication increasingly affected the flow of ideas, and even the awareness of taxonomic publications between countries.

The Early New Period (ca. 1940–1970)

The Second World War period was a disaster for radiolarian research in that many of the most important collections of radiolarian materials, all in Germany, were destroyed by bombing or fires (Lazarus, 2014). This includes those of Rüst and Popofsky. Further, both the surviving material from Haeckel and Ehrenberg soon became inaccessible to almost all radiolarian researchers as they were located in East German cites – behind the Iron Curtain for western workers, and not easily accessible even for many workers inside the Soviet system. However, the massive technological changes that WWII triggered soon led in the post-war years to major changes in science and radiolarian research. In the years during and following WWII many of these developments occurred in parallel, so that it is easier to treat them thematically. Themes include biostratigraphy, the deep sea fossil record, taxonomy, biogeography and ecology, and cell biology.

The Origins of Radiolarian Biostratigraphy: 1940s to 1950s

The development of radiolarians for stratigraphic studies occurred gradually. It was clear at the beginning of the twentieth century from the many individual studies of faunas from widely different age intervals e.g. Stöhr, Rüst, Yehara, Hinde, Khabakov, and others (see "E. Haeckel and his disciples") that radiolarian species compositions were not constant over time, and thus they had stratigraphic potential. Individual authors, though noting these differences (e.g. a summary for the entire Phanerozoic by Lipman, 1959) did not however develop this into practical biostratigraphic use. The stratigraphic utility of radiolarians was obscured by the inappropriate use of Haeckelian generic taxonomy (and the artificial nature of this taxonomy) which, together with the poor preservation, technical limits to specimen extraction (thin sections were often used on older material), and poor quality imagery of the material, sedimentary reworking, geologic age misidentifications, and other issues, led many to think that at least at the generic level, little change had occurred in radiolarians over the entire span of the Phanerozoic (Moore et al., 1952; Campbell, 1954; Sanfilippo and Riedel, 1985; Sanfilippo et al., 1985). Aberdeen (1940) for example used Haeckelian genera defined from living material to assign all species found in the Devonian material she studied. Similarly, in a dispute over the age of carbonate nodules embedded in Japanese "pre-Cambrian" metamorphic rocks, a revised age estimate of Mesozoic by use of a Lyellian percent similarity to modern taxa (Fujimoto, 1938) was debunked by the assertion that most radiolarian genera and even species had already appeared by the Paleozoic (Ichikawa, 1946). Even at the level of gross comparisons of taxonomic composition between major geologic intervals, there were also doubts as to the validity of taxonomic differences in lists created by different authors, as published illustrations were often inadequate. More careful, high stratigraphic resolution studies of radiolarians in series of samples from more continuous stratigraphic successions in single studies, e.g. Clark and Campbell (1942), had by the mid-twentieth century reported substantial differences even over short periods of geologic time, which led them to suggest that more comprehensive studies might yield a very useful stratigraphic tool. This would only be realized by the availability of new material, obtained due to new political and economic developments in marine science.

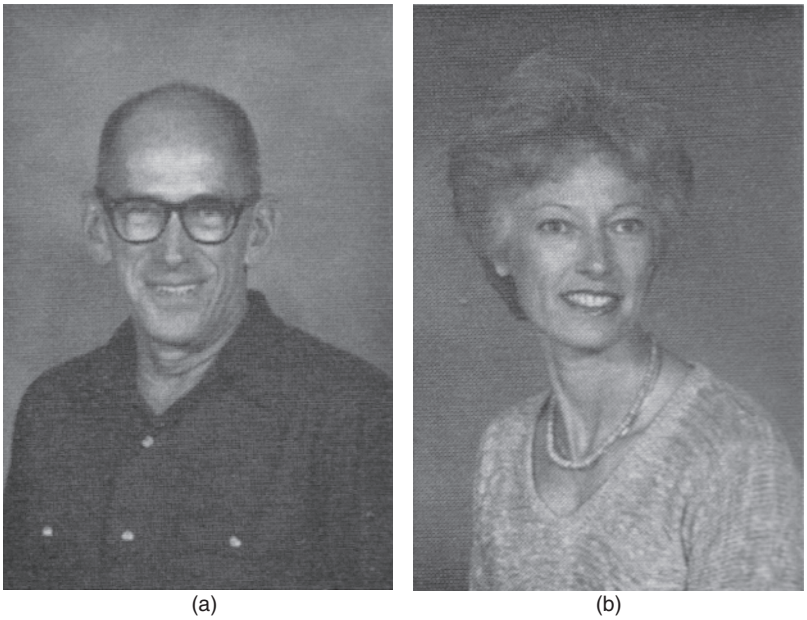
The scientific and technical resources invested by the militaries of all nations during World War II rapidly increased the technical capabilities available for marine research. Ships became more capable of

longer voyages and supporting heavier marine sampling equipment; radar, sonar, and satellites (the latter initially only for the military, but by the 1960s openly available) improved navigation; and new or improved technologies (e.g. seismic profiling of the sea bottom) were developed which would assist in detailed sampling of ocean sediments (Lalli and Parsons, 1993; Ocean Studies Board, 2000). The military presence in ocean research remained strong after the war ended, and continued throughout the decades of the Cold War (Ocean Studies Board, 2000; Hamblin, 2005): "The current format of oceanography, which involves an interdisciplinary grouping of marine physicists, biologists, engineers, chemists, and geologists, was largely an invention of the [US] Navy [in World War II] to meet its specific needs" (McNutt, p. 52 in Ocean Studies Board, 2000). Parallel to this, commercial interests increased in offshore and open ocean regions, in particular from the oil industry. The resultant dramatic increases in resources available transformed ocean science from small-scale, individual research with episodic expeditions into a systematic, global, "big-science" activity. This large enterprise would provide the materials needed to develop the first major phase of radiolarian biostratigraphic research.

After WWII W.R. Riedel (Figure 1.12) in 1950s studied deep-sea sediments recovered with the aid of the new piston core technology (Kullenberg, 1947), as large numbers of these cores were being collected by newly empowered oceanographic institutions. He realized that detailed species-level stratigraphy was possible; also that one reason for the belief of "no change" in radiolarians over time was due to reworking in surface sediments in some ocean basins, particularly in the tropical Pacific (e.g. Riedel (1951) where he compared the largely not reworked tropical Indian Ocean record to the more reworked record in the tropical Pacific). He also corrected key older mis-interpreted publications by redescribing the "Pliocene" fauna of Tan (1927) from Rotti as being actually two different assemblages, originally from different samples – one Cretaceous, the other Pliocene-Pleistocene (Riedel, 1953). By 1957, Riedel (working with U.S. Navy funding) was able to use a combination of land section samples and deep-sea piston cores to establish the first outline of a Cenozoic biostratigraphy (Riedel, 1957); by 1959, related species could in some cases be assigned to evolutionary lineages, many extending over large parts of the Cenozoic (Riedel, 1959). In parallel, Lipman (1948 and many subsequent papers, Figure 1.13) in Soviet Russia, and Nakaseko (1954 and numerous subsequent papers; Figure 1.14) worked on the rich, if complex record of radiolarians in land sections. Nakaseko established a regional Cenozoic stratigraphy for Japan. He particularly focused on robust taxa (e.g. the thick-shelled species of the spherical spumellarian *Thecosphaera*) which were common even in poorly preserved, highly diagenetically altered Neogene rocks studied in the – successful – search for oil deposits.

Deep-Sea Drilling

By the late 1950s the oil industry had developed technologies capable of drilling far offshore, using drill ships and other platforms that did not require anchoring to the seabed (Bascom, 1961). As scientists became aware of these capabilities they were employed to examine major scientific questions. Project Mohole, for example, tried to drill through the thin crust of the ocean floor to determine the nature of the mantle beneath (Bascom, 1961). This project failed, primarily due to management problems, but also as drilling a crust-penetrating hole through ocean basalts was effectively beyond the technology of the time (Winterer, 2000). Other scientists however saw that, employed as designed to penetrate extended



(a) (b)

Figure 1.12 a) William R. (Bill) Riedel (1927–) and b) Annika Sanfilippo. Riedel began working with radiolarians in the early 1950s in his native Australia as assistant paleontologist at the South Australia Museum, and continued his work with early piston cores taken by Swedish and U.S. expeditions, in particular those collected by Scripps Institution of Oceanography where he became curator of the core collection in 1955. Riedel co-authored the proposal to start the Deep Sea Drilling Program and remained deeply involved with deep-sea drilling throughout his career. Riedel also helped found the Interrad radiolarian society and the first fully online paleontologic journal *Paleontologica Electronica*. He carried out research not only on radiolarians but also fossil fish teeth (ichthyoliths). Riedel largely rekindled interest in radiolarians as important microfossils in applied research after WWII. In collaboration with his longtime co-worker at Scripps, Annika Sanfilippo, he described numerous lineages of Cenozoic radiolarian species, which provided the biostratigraphic events for the now-standard low-latitude Cenozoic radiolarian zonation. Riedel retired to Australia in 2000, while Sanfilippo is still active and associated with Scripps. Source: Courtesy of Annika Sanfilippo.

sediment sections in deep water, such tools could recover what was increasingly being realized was an unprecedented archive of high-resolution climate and ocean change held in deep-sea sediments. Emiliani's 1963 pilot deep-sea drilling project "LOCO" (Winterer, 2000) provided an example of the technical possibilities. Seismic studies had shown that deep-sea sediments were in some cases more than 1 km thick, while studies of the uppermost layers from piston cores had made clear their rich content of fossils and geochemical indicators could be used to understand the history of the earth's climate with unparalled detail. These piston core studies included those of Riedel and particularly research by Emiliani, who obtained paleoclimate data from the geochemistry of foraminiferal carbonate (Emiliani, 1955). It was clear that it would also be possible to use the fossils to date the sediments directly overlying the

Figure 1.13 R. Kh. Lipman. Source: courtesy of Marina Afanasieva.

ocean crust at different locations, and thus provide a definitive test of the newly developing but extremely controversial paradigm in the earth sciences of plate tectonics and continental drift (see also "Mid New Period 1970s–2000s").

The Deep Sea Drilling Project (DSDP) began recovering deep-sea sediments in 1968, after a few years of planning and preparation. In order to reliably recover sediments at depth, and in all ocean basins, a large, dedicated drilling ship was commissioned – the Glomar Challenger (Figure 1.15). This was a major investment and moved studies of marine sediments into the realm of large, well-funded science activities. From the outset, DSDP studies relied extensively on planktonic marine microfossils to provide geologic age estimates for the recovered sediments, and more material accumulated, as probes into past climate conditions via their distinctive, climate-sensitive compositions of species in the sediments. DSDP had been initiated and was managed by a small group of oceanographic institutions, and as Riedel at Scripps was actively involved (e.g. Riedel, 1963), radiolarian research was further linked to the rapidly developing study of deep-sea sediments using interdisciplinary, big-science methods. Within a few years at least 15–20 radiolarian papers were being published annually based on study of the new materials from the drilling ship by a new generation of marine micropaleontologists at several institutions, an output level that would continue until the 1990s. The DSDP, and its successor programs ODP and IODP, significantly affected radiolarian research in other ways. Because the large majority of recovered sediments were Cenozoic in age, study of this time interval became relatively more important. Secondly, as both the (then) Soviet Union and Japan were participating members in the international DSDP program, at least some level of contact was maintained between these – based on language, training, and political barriers – very different groups of workers. Research done on DSDP, and piston core sediments, also furthered the highly interdisciplinary approach to science that originated during WWII. Biostratigraphy in particular was normally integrated for individual drilled sections, with multiple microfossil groups. Radiolarian workers thus shared methods and data intensively with specialists working on other groups, and with many other types of geologic specialists working, on or off the drilling ship, on the same sections – sedimentologists, geochemists, geophysicists, and others.

Biostratigraphy from land sections also developed between ca. 1950 and 1970. Workers in several countries began to develop initial zonations based on what were still dominantly taxonomic studies

Figure 1.14 Kojiro Nakaseko (1925–2011). After studies in Kyoto, Nakaseko took a position at the University of Osaka (his hometown) and studied Neogene geology in Japan and, beginning in the 1950s, increasingly studied radiolarians. He later introduced the HF method for preparing radiolarians from indurated rocks into Japan, founded radiolarian meetings in Japan, contributed to the replacement of geosyncline theory by modern plate tectonic theory via radiolarian biostratigraphy and paleobiogeography, and was a successful geologic consultant to the oil and engineering professions Source: Takemura and Hori, 2015. Reproduced with permission of Elsevier.

describing assemblages of species, e.g. Clark and Campbell (1942; Campbell and Clark, 1944a, b) in the USA, Lipman (1960a, b)in the Soviet Union, and Nakaseko (1959, 1960) in Japan. Although the median number of papers published per year in Japan in the 1950s–1970s was still only about 1 (Yao et al., 2001), Nakaseko's work was particularly important in that he trained a large number of students who would contribute to the expansion of radiolarian research in Japan in the subsequent decades. Most importantly however, many workers were active in biostratigraphic research in the Soviet Union, and indeed, other than the substantial, more biologically oriented output from French workers, Soviet biostratigraphic publications dominated the radiolarian literature from the 1950s until the mid-1960s, when North American research became more active.

Figure 1.15 The Glomar Challenger (1968–1983). Named after the original nineteenth-century Challenger expedition ship, prefixed by the portmanteau word Glomar, for global marine, the Glomar Challenger was used in the Deep Sea Drilling Project – the first phase of what became a series of deep-sea drilling programs. Built by the Levingston Shipbuilding Company for the DSDP in Texas, it was operated by the Scripps Institute of Oceanography for the U.S. National Science Foundation. It eventually recovered nearly 100 km of deep-sea sediment cores from 624 sites, covering over 375,000 nm. Material recovered by the program provided the abundant material for studies by dozens of marine micropaleontologists, including many early radiolarian workers such as Riedel, Sanfilippo, Nigrini, and Moore. The Glomar Challenger was replaced with the larger, more capable Joides Resolution with the onset of the Ocean Drilling Program, the successor to DSDP. Source: Peterson et al. 1970. Photo from Peterson et al. (1970).

Taxonomy

Although monographs on radiolarian taxonomy were published in the 1950s (Deflandre, 1953; Campbell, 1954, and similar volumes in the Soviet Union), these were still largely summaries of the highly artificial genus and higher level taxonomy inherited from Haeckel, and contributed little to advancement of the field. Campbell's (1954) volume in fact was a step backward – it introduced so many problematic changes that it was soon heavily criticized by Riedel and others (Deflandre, 1960), and has in fact virtually never been cited since. Most activity instead was in the description of new species and genera, as new material

from deep-sea sediments, and ever more studies of land sections around the world, yielded enormous diversities of undescribed forms. As it became increasingly apparent that much of the diversity of form in the Mesozoic and Paleozoic could not easily be fit into Haeckelian concepts, a new taxonomy began to be created for older materials, both at genus and family level (e.g. Deflandre, 1953; Foreman, 1968; Pessagno, 1969; Dumitrica, 1970: Figure 1.16). Haeckelian taxonomy was retained for Cenozoic forms but substantially modified as more material data on natural variation, biology, and stratigraphic change accumulated. Riedel (1967a, b) revised many of the Haeckelian families and introduced new ones. At lower taxonomic levels the study of lineages in longer sections from DSDP led in the 1960s and 1970s to the revision of many artificial Haeckelian generic concepts and rejection of the idea of extremely long generic ranges in radiolarians (Sanfilippo et al., 1985). Unfortunately, the great diversity of material, limited manpower, and pre-digital technical resources (no databases, digital literature, etc.) hindered the development of new catalogs to replace those of the Haeckelian era (e.g. Campbell, 1954). Lack of comprehensive taxonomic reference sources continues to dog the field even today (see Chapter 5: Taxonomy and Fossil Record). Crucial groundwork however was being laid for future taxonomic revision via the collection of much of the scattered literature into private libraries, which in turn were to be the foundation that many subsequent students of radiolarians used to learn the subject. Most important were the efforts of Riedel and his coworker Sanfilippo, who, often in collaboration with Nigrini in the 1950s to 1980s collated much of the older radiolarian literature, funded translation of much of the Russian language literature into English, and made this library available in the form of microfiche, which until the advent of graphical personal computers in the 1980s was the most sophisticated technology available. A copy of the Riedel Microfiche was a hallmark of most of the major radiolarian research groups. Unfortunately, the microfiche technology was not able to reproduce grayscale photographs, so only the text and illustrations done with line drawings could be effectively disseminated. A first volume including line drawings of the type species for each genus in literature up to 1900 was published (Foreman and Riedel, 1972), but due to lack of manpower not continued.

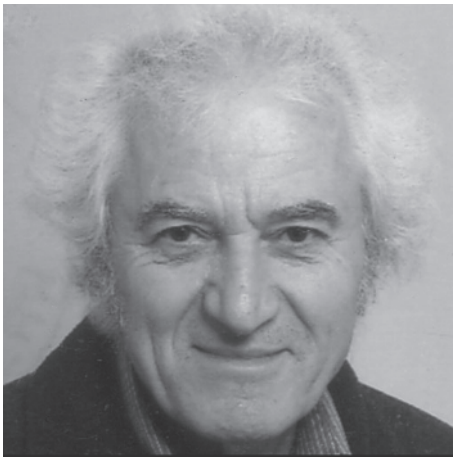


Figure 1.16 Paulian Dumitrica (1937–) Dumitrica grew up and obtained a Masters' degree in 1960 in Romania, where he began his studies of radiolarians. He completed his doctoral studies in 1974 (on silicoflagellates) and has been based at the University of Lausanne since 1993 (Cortese, 2014). Dumitricia has worked for decades to provide a consistent framework for the higher-level systematics of all Phanerozoic radiolarians, which culminated in the extensive (>200 page-long, plus index) chapter on radiolarian taxonomy in De Wever et al. (2001). He is also, with 461 new species in the Suzuki database, among the 10 most prolific authors of descriptive radiolarian taxonomy in the history of the field. Source: Courtesy of Paulian Dumitrica.

Biology

In the years following WWII and into the mid-1970s, research on the cellular biology of living polycystines was largely done by a single team in France – Hollande (Figure 1.17), J. Cachon, and M. Cachon-Enjumet (the latter also published as just Cachon or Enjumet) (e.g. Hollande, 1953; Hollande and Enjumet, 1960). Using a combination of detailed drawings and observations of whole, living cells and carefully stained thin sections, they discovered a wealth of new morphologic details of radiolarian cells, including details of the nucleus, capsular wall, axopods, and other organelles. Substantial new observations and amplifications of earlier reports on asexual reproduction were done, and several studies of symbionts and parasites as well. Although some observations of shells and shell growth were reported, these were fairly limited in scope, other than as characters for classical species and higher level taxonomy. In general the cellular biology was not integrated into the structure and possible functions of the shell, which, being the only part of the organism available to paleontologists, meant that most of the biologic details observed could not be directly used in paleontologic research. Indirect use, via linking of cellular morphology to cell ecology and function in the environment were also very limited, as it was, then as now, not possible to maintain most radiolarians for long in culture, or to observe individuals "in the wild" due to size and logistic limitations. Lastly, as virtually all the studies were published French, which was, as noted above, in the post-war years rapidly losing importance as a major scientific language, many scientists, particularly younger ones, did not read the studies in any detail. The difficulties of linking biologic observations in a meaningful way to the fossil record continues to be a challenge for radiolarian research even today.

Studies of radiolarian geographic distributions have been published since the earliest studies of Ehrenberg, who went to

Figure 1.17 André Hollande (left, talking to colleague J.B. Jadin; ca. 1998). Biologist who, working with colleagues Monique Enjumet-Cachon (also with last names used singly) and Jean Cachon, carried out extensive studies of radiolarian cellular biology in the 1950s to 1970s. He began his career in Algiers but in later years worked in Paris. Source: Mignot, 1998. Reproduced with permission of Elsevier.

considerable lengths in his many papers on microorganisms to compile tables of individual species distributions in different types of samples, as well as those from different geographic regions. Studies of modern species distributions date back at least to Haeckel, Cleve (1899 and subsequent papers), and Popofsky, who also recorded distributions in both sediment and plankton samples. Nonetheless, the very patchy nature of sampling meant that biogeographic patterns were not very discernable. With the availability after WWII of a rapidly expanding archive of both surface sediments samples from coring, and water plankton samples from net tows, it became possible to produce a much clearer picture of radiolarian biogeography. The work was carried out in parallel to numerous other studies of components in ocean plankton: sediment geographic distributions, e.g. phytoplankton in water samples, bulk lithologies, and other fossil groups such as foraminifera in sediments. Workers such as Petrushevskaya (1967, 1971a; Figure 1.18) described many new species from extensive sampling of ocean regions, using both plankton and ocean surface sediments. Hays (1965) and Nigrini (1967) published the first regional distribution maps for species (Southern and Indian Oceans, respectively). Numerous other studies followed in the 1970s, including statistical methods to define coherent assemblages that could be correlated to surface water masses (Nigrini, 1970; Sachs, 1973a,b) which were later used to develop paleoceanographic studies, as well as conceptual interpretations of these interrelated patterns (Casey, 1971).

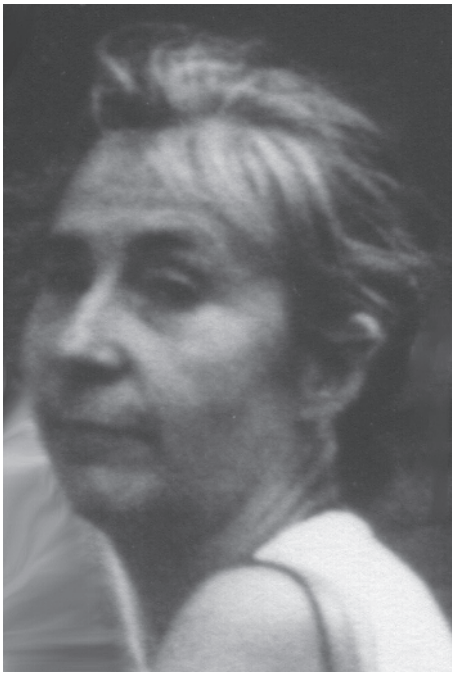


Figure 1.18 Maria G. Petrushevska. Productive researcher working in Soviet Russia who in the 1960s to 1980s studied Recent and Cenozoic radiolarian taxonomy, biogeography, and distribution in the water column. In addition to over 90 new species descriptions she revised numerous species and genera and proposed a variety of higher-level taxonomic systems. She also published two books on radiolaria (Petrushevskaya, 1981, 1986) and other monographic studies. Source: courtesy of Marina Afanasieva.

Mid New Period (1970–2000)

The ca. 30-year period between 1970 and 2000 yielded more radiolarian papers than all other time intervals before or since – more than two-thirds of the known literature, as well as peak rates of publication, reaching rates of more than 200 papers/year, particularly between 1980 and 2000 (Figure 1.1). This period can be divided into a shorter interval between 1970 and 1980 in which the field was dominated by Cenozoic studies, and the subsequent 20-year-long interval in which Mesozoic research predominated, with, particularly since the late 1980s, a substantial number of studies on Paleozoic radiolarians.

The field of marine micropaleontology, with a focus on the (mostly Cenozoic)

microfossil content of deep-sea sediments, became a distinct discipline in the early 1970s, with the landmark volume *The Micropaleontology of Oceans* (Funnell and Riedel, 1971), and the founding of the field-specific journal *Marine Micropaleontology* in 1976. Over 50 radiolarian papers, mostly on Cenozoic or Recent/living materials appeared in this journal in the initial 10-year period of publication. The first deep-sea drilling sections with radiolarian-rich sections were recovered by the Deep Sea Drilling Program in the late 1960s (e.g. Riedel and Sanfilippo, 1970). These reports marked the beginning of three decades of intense study of radiolarians from Cenozoic deep sea sediments. Numerous researchers were also continuing to work on the materials initially studied by Lipman in the 1950s, i.e. radiolarian bearing sedimentary rocks in the Soviet Union, both from Paleogene siliceous deposits in the continental interior, and radiolarians of all ages from accreted deep-sea sediments along the eastern Pacific margin. Nearly 300 papers on radiolarians, including also studies of living materials, were published by Soviet authors from 1970 until the collapse of the USSR beginning in 1989. Particularly noteworthy were researchers such as Petrushevskaya (e.g. 1967, 1971, 1981, 1986) who used plankton materials, surface sediments, and Cenozoic assemblages to extend knowledge of radiolarian morphology and taxonomy.

Radiolarians played an important role in the development of the new field of paleoceanography in the 1970s and 1980s. This field had developed gradually from the integrated, interdisciplinary research efforts of marine science teams initially assembled for military purposes during and after WWII (see "The origins of radiolarian biostratigraphy: 1940s to 1950s"). Piston coring of the oceans had become so extensive that literally thousands of locations in the oceans had been sampled, so that, despite problems with sediment disturbance, variable preservation of microfossils, and other issues, it became possible by the 1960s to create detailed geographic distribution maps of individual species of microfossils in surface sediments, which confirmed, but provided much more complete data than similar biogeographic studies of microorganisms in the water column. Early workers on these radiolarian faunas such as Hays (1965; Figure 1.19) and Nigrini (1967) teamed up with researchers working on other microfossil groups in the CLIMAP project (Imbrie and Imbrie, 1979). They used Imbrie's newly developed method of combining factor analysis with multiple regression (Imbrie and Kipp, 1971) to convert quantitative counts of relative species abundances in samples into ocean surface water temperature estimates, then applied the regression functions to glacial aged microfossil assemblages to reconstruct ocean water temperatures globally during the last glaciation. Similar quantitative methods with microfossils, when combined with geochemical data, were used to demonstrate the validity of the Milankovitch theory that the ice ages were regulated by orbital variation in the earth's absorption of solar radiation (Hays et al., 1976a). The motivation for this early work on climate change was mostly academic. In the early 1970s there was some concern among these research groups that the earth might, in a few thousand years, descend into a new ice age. There was awareness also of rising CO_2 concentrations and global warming, but only as a possibility; the first expert assessment of the climate consequences of continued CO_2 release, the Charney report, was only created (from a workshop held at the Woods Hole Oceanographic Institution) in 1979 (McNutt, 2019). In the early 1970s many other environmental issues such as ozone layer destruction attracted more attention. That changing atmospheric CO_2 concentrations would soon lead to severe global warming only became the dominant environmental concern among scientists in the 1980s.

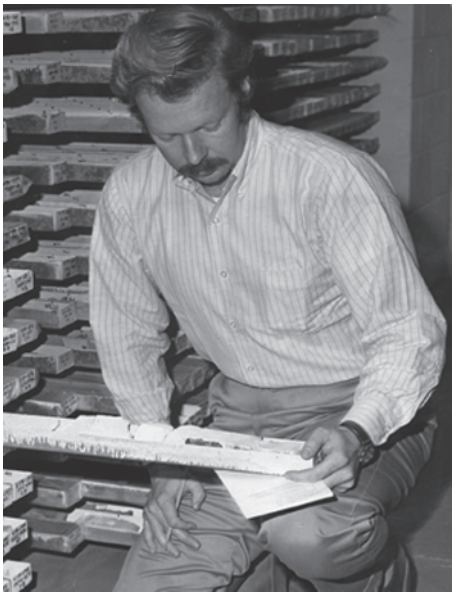


Figure 1.19 James D. Hays. Although his radiolarian training was done partially with Riedel, Hays' career was centered at the Lamont Observatory of Columbia University. Early work on Antarctic radiolarian biogeography and stratigraphy was soon extended into other ocean regions though mostly with a focus on late Neogene polar assemblages. Hays worked with John Imbrie to pioneer the use of quantitative analysis of microfossil assemblages to reconstruct ocean temperatures over glacial-interglacial cycles, and together with Nick Shackleton confirmed the Milankovitch hypothesis of orbital control over the timing of ice ages (Hays et al., 1976a). Orbital variations in sediment archives would become a key method to develop high-resolution paleoceanographic studies in Cenozoic and older time intervals in the 1990s and beyond. He also maintained an interest in radiolarian evolution, working with evolutionary biologists at Columbia, and paleobiologists such as Niles Eldredge at the American Museum of Natural History, to train students such as Kellogg and Lazarus in evolutionary studies. Source: Lamont-Doherty Earth Observatory. Reproduced with permission of Lamont-Doherty Earth Observatory

Another aspect of CLIMAP and a series of follow-up projects (SPECMAP, CENOP, etc.) was to focus the training of Quaternary radiolarian workers on quantitative applications to earth science questions. Taxonomic work was relegated to designated team specialists (often C. Nigrini and J.P. Caulet, Figure 1.20) with the goal of standardizing a small but sufficient number of species concepts to allow quantitative analysis of common species in Quaternary radiolarian assemblages. Given the vast amount of work needed to untangle the legacy of artificial taxonomy from late nineteenth-century workers this was practical, but also limited both the usable taxonomic foundation for future applied research, and the number of taxonomically oriented workers who would in the future work to improve the situation. This problem of allocating human resources between foundational taxonomy and the application to other hypothesis testing is a common one in biodiversity-based sciences. For example, an analogous situation developed in invertebrate paleontology much later in the 1990s, as growth in fundable, high-profile research in quantitative paleobiology to some extent came at the expense of primary taxonomic work. The consequences however can be very long lasting – there is still, four decades later, no accepted catalog or even numerical value for living/Quaternary radiolarian species diversity, despite that the number of species (certainly <1,000) is in principle of manageable size.

Studies of living radiolarians in this time period included both study of their biogeographic and ecologic setting in ocean waters, and laboratory study of living and dead individual specimens. Particularly important was the work of Anderson, who largely took over the study from the earlier work of Hollande, Cachon, and Cachon. Between the 1970s and 2000s he extensively studied the biology of the living radiolarian cell, and used TEM images of

Figure 1.20 Jean Pierre Caulet (?–) and Catherine Nigrini (1939–2005). Caulet's early years were spent in French colonial North Africa. He completed his studies at the National Museum of Natural History in Paris and began working there on radiolarians by the beginning of the 1970s. Initial work was based mostly on deep-sea sediments collected by French research ships (Caulet had become curator of these cores at the Paris Museum) but by the 1980s he was also working with deep-sea drilling sediment materials and publishing in the drilling program reports, while working on Cenozoic radiolarian taxonomy (author or co-author of 68 species) and biostratigraphy with several colleagues around the world. In the 1990s he developed, in collaboration with Nigrini and others, the URI method for estimating paleoproductivity from radiolarian assemblages. With Nigrini he began, and continues to develop in retirement, the Radworld catalog database of radiolarian taxonomy. Cathy Nigrini grew up in Canada and completed her doctoral studies at Cambridge, UK, in 1966. She worked on radiolarians from surface and Cenozoic sediments, describing new species (42 species in the Suzuki database) and revising several genera, and participated on several deep-sea drilling legs. She also helped define and calibrate Cenozoic radiolarian event biostratigraphy and led the radiolarian taxonomic catalog development needed for major paleoceanographic research projects such as CLIMAP. Nigrini worked with others to build comprehensive taxonomic catalogs such as Radworld. Nigrini held many short-term associate appointments but mostly worked from home locations in the USA, tracking her husband's career in the oil industry. (Lyle and Moore, 2002). Caulet and Nigrini are both co-authors of the most recent prior reference book on radiolarians (De Wever et al., 2001).

microtome section cells to describe the structure of cell organelles. He also carried out basic observations of feeding, shell formation, and other aspects of radiolarian biology. Anderson's (1983) book synthesized the available biologic knowledge of radiolarians and included, albeit somewhat sketchily, an overview of their taxonomy and fossil record. Although Petrushevskaya (1981) had recently published (in Russian) a monographic treatment of nassellarians, one of the two main groups of living radiolarians, Anderson's book was the first modern volume on radiolarians in the English language since Haeckel's Challenger report and was widely read by radiolarian workers. Anderson also trained A. Matsuoka in radiolarian biologic research and Matsuoka in turn developed such studies on his return to Japan.

Rapid expansion of both plankton and marine micropaleontologic research in the late 1960s and 1970s had made clear that the biogeographic patterns of living plankton and fossil plankton were remarkably similar, which was an essential piece of information needed to use the microfossil record to study paleoceanography. But how the living plankton assemblage was transferred into marine sediments was unclear, and indeed, simple calculations of how long single cells would take to sink to the ocean bottom suggested that the patterns should not match nearly as well as they did. At the same time, geochemists were beginning to explore how biologically active elements such as carbon and nitrogen were cycled within the oceans. Both groups converged in the late 1970s on the use of newly developed sediment traps (e.g. Honjo et al., 1980) to document and quantify how surface particles (mostly plankton) sank through the water column and were altered by dissolution, consumption, and other processes, transferring elemental material to deep waters, and both organisms and their chemical contents into the deep-sea sedimentary record. This work yielded the first quantitative understanding of the ocean's role in carbon cycling (the term "carbon pump" was coined, based on this early research, by Volk and Hoffert in 1985), and explained how single cells were bundled into larger objects (fecal pellets, marine snow) which sank much more rapidly, thus preserving the biogeographic patterns of the living assemblages. Takahashi (1981) in particular studied the sinking processes of radiolarians, documenting the relatively rapid transport of radiolarian shells to great depths, which contributed to a modern understanding of how biologically active elements are cycled in the oceans. Some elements, particularly carbon, are largely recycled in the upper water column, but others, including silica, are mostly exported to the ocean floor, where dissolution in the upper sediment surface occurs (Tréguer and De La Rocha, 2013). By use of newer sediment trap models with separate holders for each month, it also became possible to study how the flux of particles varied with time. This was used by Takahashi and other plankton biologists to document for the first time with reasonably complete time series data the seasonal patterns of plankton groups, and even that of individual species, which until then had only been known very vaguely from highly irregular, time-limited plankton tow data. Takahashi also created what was at the time the most comprehensive taxonomic catalog for the living assemblage, using advances in scanning electron microscope technology to extensively illustrate the shells of numerous species. His monograph (Takahashi, 1981) became for many years a key reference for study of living or late Neogene radiolarians.

Mesozoic research increased dramatically in the 1980s and 1990s both as the use of better preparation methods (hydrofluoric [HF] acid to extract radiolarians from silicified rocks and even cherts: Pessagno and Newport, 1972) became standard, and with more understanding of concretions and other special facies where better preserved

radiolarians could be found. A further impetus was the dramatic change in earth science research resulting from the development of plate tectonic theory. This new way of thinking about the earth essentially created a fundamentally new modern earth sciences, transforming geology from a semi-descriptive field to one based on quantifiable mechanisms fully based in the primary physical sciences (Oreskes and Le Grand, 2003). The theory was developed by the same style of research that grew out of WWII military management of science: international, multidisciplinary teams, frequently funded by the U.S. Navy research system, and largely based at the oceanographic institutions that also gave birth to marine micropaleontology (Oreskes and Le Grand, 2003). Plate tectonics helped explain many otherwise unexplainable empirical patterns, such as the occurrence of deep-sea sediments, particularly radiolarian-bearing cherty rocks, in specific geologic settings in mountain belts, often at considerable elevation (Figure 1.21; Bernoulli and Jenkyns, 2009a, b). Workers such as Baumgartner and De Wever, and their many students, in the 1980s and 1990s used radiolarians to decipher the history of the Alps and other areas of the "Tethyan" Mediterranean (e.g. Baumgartner et al., 1995). Another idea derived from this new paradigm of plate

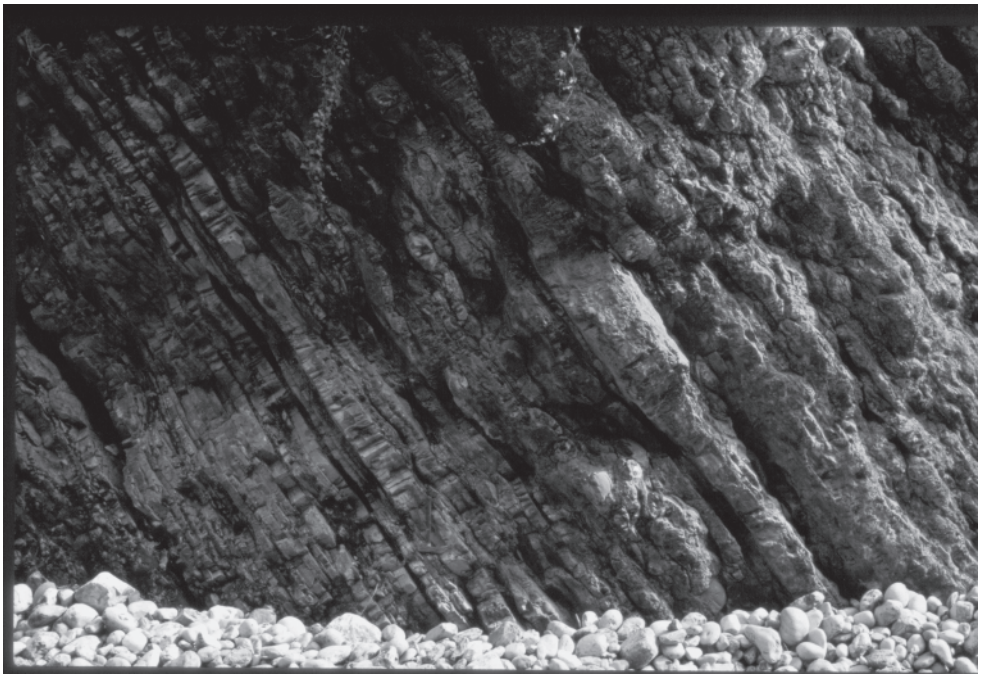


Figure 1.21 Radiolarites in the Alps. Thin-bedded cherty rocks containing radiolarians and associated with relatively rare rock types (for land sections) such as sepentinites and pillow lavas are widespread in mountain belts around the world, and this association (the "Steinmann trinity"), as well as their position in other "geosynclinal" facies such as greywackes had puzzled geologists since at least the 1930s (Bailey and McCallien, 1950; Bernoulli and Jenkyns, 2009a,b). New radiolarian extraction methods such as HF permitted taxonomic and biostratigraphic study of the assemblages, which helped clarify the genesis of these rocks and how such geologic environments fit into plate tectonic theory. Source: courtesy of Daniel Bernouilli.

tectonics was that many geologic terranes (the tectonic blocks that make up large parts of the continents' mountain belts) were now recognized as wandering plate fragments, with distinct geographic and temporal origins. Mountain belt lands thus had complex, composite geologic histories, which could in many cases best be resolved with radiolarian assemblages, as these were one of the very few fossils still preserved in the often highly altered metamorphic rocks that these terranes were composed of, and could provide information on the ages, and even, via the species composition, the approximate paleolatitude (tropical, temperate, or polar) of each distinct tectonic block. New analytic methods such as the unitary association method (Guex, late 1970s, summarized in Guex, 1991) were developed to extract robust stratigraphic information from these assemblages, where preservation was often poor and, due to the highly complex tectonic setting, even basic principles of stratigraphy such as superposition of younger on top of older rocks could not be safely assumed. International cooperation on Mesozoic taxonomy also yielded at least partial catalogs of both genera and species, e.g. Baumgartner et al. (1995). One consequence of the growth of Mesozoic, and later Paleozoic studies was however a degree of decoupling of the methods, goals and research style from those developed in Cenozoic and living radiolarian research. Pre-Cenozoic workers generally worked on field geologic problems, in geology departments or geologic surveys. They had comparatively little training in biology or oceanography, or opportunity to address research questions in these fields. The taxonomy also was largely new. Higher level systematics in particular was not only different, but built in a different style than for the Cenozoic, where reference to living materials and the legacy of early biologic studies were important constraints.

Although the initial growth in radiolarian studies using these new methods was in Mesozoic work, studies of Paleozoic rocks soon followed. Early workers included Holdsworth (e.g. 1977), Nazarov (1975, and many subsequent papers; Figure 1.22), and Kozur (numerous articles beginning in the 1970s, Figure 1.23), who worked on both late Paleozoic and early Mesozoic rocks. Although at first it was uncertain if enough radiolarian material could be found to be stratigraphically useful, it soon became clear that, albeit with lower resolution, radiolarian zonations could indeed be established and used in applied geologic studies (Holdsworth and Jones, 1980).

Figure 1.22 Boris B. Nazarov. Source: courtesy of Marina Afanasieva.

While the above changes that expanded Mesozoic and Paleozoic research affected most countries, the impact on research in Japan was particularly profound (Ichikawa, 1982). The tectonic terranes where much of the research was concentrated made up only the border regions in larger continental blocks like North America, but were the dominant type of

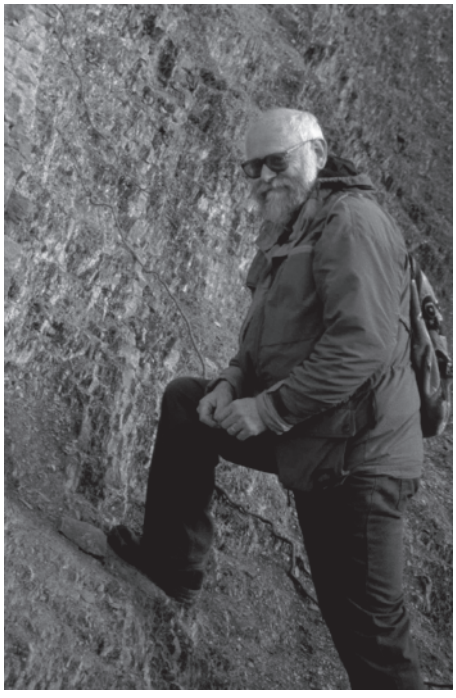


Figure 1.23 Heinz W. Kozur (1942–2013). After starting his career in East Germany, Kozur moved to Hungary to evade political harassment, but again for political reasons lost his position there in 1984. He continued to work independently, and in cooperation with other universities, particularly in Halle. Kozur worked mostly on late Paleozoic and early Mesozoic materials and studied both conodonts and radiolarians. An extremely prolific author with approximately 600 publications, he described, usually with co-author Mostler, 884 radiolarian species, second only to Haeckel. Source: Bachmann, 2014. Reproduced with permission of Mertmann.

rock formations in Japan, which consists largely of a complex of accreted terranes and oceanic material formed by Mesozoic-Recent subduction of the margin of the Pacific Plate. With the spread of plate tectonic theory, more detailed studies of many sections were done in Japan, revealing the complex history of the rocks. Radiolarians were noted to occur frequently in these samples, and began to be used for geologic dating (Nakagawa and Nakaseko, 1977). Many formations previously thought to be Paleozoic were recognized, primarily from radiolarians, to be Mesozoic. This had such a dramatic impact on the geologic study of Japan that it is locally referred to as the "radiolarian revolution" (Takemura and Hori, 2015). Radiolarian biostratigraphic work increased substantially in Japan in the subsequent years, going from an average of just a few papers per year through most of the 1970s to nearly 100 papers per year in the 1980s (Yao et al., 2001). Japanese radiolarian workers also played an larger role beginning in the 1980s in international meetings such as the Interrad Congresses. These meetings had initially been dominated by workers from the USA, Europe, and the USSR, and had developed in the 1980s out of a merger of more regional meetings that had been held during the 1970s, such as the Eurorrad meetings, and meetings associated with Nakaseko and his Osaka home institution in Japan.

Radiolarian research began in China gradually in the 1980s to increase in intensity, with the number of papers published per decade essentially doubling each decade from ca. 30 papers in the 1980s into the 2000s with nearly 140 papers (based on data from radiolarian community literature archives). Studies of surface sediments in the seas bordering China were an early focus but with time the large majority of studies were on the biostratigraphy and paleogeography of Paleozoic and early Mesozoic faunas.

While Mesozoic, and later Paleozoic research expanded, by the mid-1980s the study of deep-sea sediments, the primary focus of Cenozoic workers, had become dominated by geochemical methods. Although at first geochemistry had complemented, it soon increasingly displaced micropaleontologic-based estimates of paleoenvironmental conditions, using stable isotope ratios of oxygen and carbon, followed by an ever-increasing suite of other

geochemical proxies. The large majority of these geochemical signals were extracted from the calcite of foraminiferal shells, and as a result, carbonate sediments and the carbonate of fossils were increasingly the primary focus of deep-sea sediment research. Studies of siliceous microfossil groups such as radiolarians and diatoms became more marginal. It also did not help that the taxonomy of the highly diverse Cenozoic radiolarian assemblages was still burdened by Haeckel's inadequate nomenclature system, with the type materials largely inaccessible in East Germany behind the "Iron Curtain." Studies of Mesozoic and Paleozoic radiolarians by contrast could largely start with a clean slate, so that taxonomic progress with the older materials was much more rapid. Cenozoic research thus declined gradually but substantially in the 1990s (from ca. 60 papers to only 20 papers/year).

One of the more significant developments in radiolarian research during this period of growth was the failure in many, though not all, countries to establish a strong presence in regular university positions, as these offer the best opportunities to teach students who then go on to broaden the field and increase its importance in the research landscape. In both the USA and Europe, although a few important workers during this time period were university based and indeed trained a new generation of workers (e.g. Hays and Anderson, at Columbia University, NY; Pessagno, U. Texas, Dallas), many workers, and also the next generation of their students, worked instead in organizations such as oceanographic institutions and geologic surveys, where teaching and student training, although also done, were less important. The reasons for this are multiple. Paleontology in general was generally seen by the 1970s as a somewhat marginal specialty in both the earth sciences and in biology. These fields had become more quantitative and reductionist in style after WWII (i.e. molecular biology, which rapidly displaced organismal biology in the late twentieth century). Both the primary data – subjective observations of morphology – and the classical style of analysis that characterized much of paleontology did not fit well with the newer paradigm. Most universities hired at best only one paleontologist, who usually was either an invertebrate or vertebrate paleontologist, both specialties with a large established base (and lobby) and who had developed a more modern, analytic research program with paleobiology – a subject that micropaleontologists had largely avoided. Invertebrate and vertebrate paleontologists were also well suited to teaching general courses within the undergraduate earth science or biology curricula, and vertebrate paleontologists could provide useful publicity for their departments. When micropaleontologists were hired they were usually foraminiferal specialists who could integrate with geochemists in paleoceanographic research, or, in universities with the specialty, contribute to training programs for oil industry research needs. Establishment of substantial numbers of academic positions for radiolarian specialists only occurred in Japan, where the unique geology of the country supported a substantial number of professorships in radiolarian research, and in consequence, the training of large numbers of students. Indeed in Japan, so many students were trained that they are informally referred to in Japan according to approximate wave of study – first (1940s–1960s: Ichikawa, Nakeseko), second, and third generation. With rare exceptions (e.g. Caulet and later Lazarus) radiolarian workers also did not hold natural history museum curatorships, and large new collections of radiolarian materials were not created. Combined with the loss of older collections this has hindered developing the taxonomic foundations of the field, both by lack of reference material, and lack of dedicated taxonomist positions.

Current Period (2000-Present)

Radiolarian research in the first two decades of the twenty-first century is largely a continuation of the themes and trends established in prior decades. For example, taxonomic and biostratigraphic work still makes up the large majority of research. A major advance in radiolarian taxonomy was marked by the first comprehensive, documented synthesis of higher level radiolarian taxonomy by Dumitrica in De Wever et al. (2001). In addition to these well-established themes, there are a few new developments worth noting.

The most important is that molecular biologic studies of radiolarians are becoming increasingly common and are beginning to cover enough taxa to have a real impact on our understanding of systematics of the group (e.g. Sandin et al., 2019; 2020), and thus taxonomic practice by radiolarian specialists. Early molecular biologic studies of radiolarians, e.g. Amaral-Zettler (1997), were not aimed at understanding the taxonomy of the group as much as determining if the main higher level categories (Polycystina, Acantharia, Phaeodaria) were part of the same high-level clade, and what the relationships of these main groups were to other similar groups of protists such as the Foraminifera. This focus on the relationships *between* radiolarians and other groups of protists has been common in most molecular research on protists as the broader picture – and the possibility to discover new, high-level clades of organisms – is much more attractive to most researchers than resolving systematic details within a single clade, particularly one with already well-established, morphologically based systematics. The improved detail and breadth of molecular studies in recent years, mostly by research groups at oceanographic institutions in France and Japan, reflects improved methodologies, such as primers that specifically work with protistan genetic material, and vastly improved computing capabilities that allow both more automation, and the ability to analyze much larger data sets. In addition, it also is part of a broader trend towards understanding the vast, and until the advent of molecular methods, poorly understood diversity of the protists, and in particular, the marine plankton, as it is becoming clearer that these ecosystems are central to understanding global geochemical cycles and how the earth will respond to future climate change.

A second new development is the increasing availability of larger databases for radiolarian taxonomy and radiolarian occurrences. Several groups of workers have over the years compiled large digital catalogs of radiolarian taxonomy (each with >10,000 species), including Radworld (Caulet, Sanfilippo and Nigrini, begun in the late 1990s using Microsoft's "Access" database: Nigrini et al., 1998) and a parallel effort by Suzuki (Suzuki, 2016), also over many years, using the custom DBase Paleotax application (Löser, 2004). These databases have concentrated on capturing the original descriptions, with only a modest effort to synonymize names. Other much smaller catalogs for genus taxonomy have been made public via regular journal publishing (Paleozoic genera: Danelian et al., 2017; Mesozoic genera: O'Dogherty et al., 2009), and are thereby digitally accessible, albeit only in pdf format. However the larger, relational databases for species taxonomy are single-user, offline systems and thus have not become widely available to the research community. An exception (was) the Baumgartner et al. (1995) catalog of selected mid-Mesozic Tethyan species which was published as a web database in the 1990s and was accessible through the 2000s, but is, as of July 2019, no longer online. The community website (www.radiolaria.org: Dolven, 2001), which was started in late 2000 is another exception as the catalog section has always been an online system.

The content however has always depended on community contributions. Lack of funding, declining numbers of taxonomic specialists, and decisions by the authors of the offline database systems not to merge with the community site meant that content at radiolaria.org stalled in the late 2000s at just several hundred species, almost entirely of Cenozoic age.

Radiolarian occurrence data is also becoming available online. Major compilations of occurrence data include WoRRAD (Boltovskoy et al., 2010), currently available online (via direct sql query) to the NSB system, NSB/Neptune: (www.nsb-mfn-berlin.de: Lazarus, 1994; Spencer-Cervato, 1999; Renaudie et. al., 2020) which covers deep-sea data, mostly for the Cenozoic, and part of the Mesozoic land record in the Paleobiology Database (www.pbdb.org: Alroy et al., 2001, with much of the entry work by Kiessling and coworkers). As NSB and PBDB are still actively being developed and are widely used, more data will presumably be added to them in the future. There is also a database by Russian workers (Agarkov et al., 2019) which is not widely used and appears to hold data resolved only to geologic stages. As important as catalogs are to supporting better taxonomy, the availability of radiolarian occurrence data is perhaps even more significant. One of the striking aspects of radiolarian research in the last decades is the relative rarity of paleobiologic studies, even though paleobiology has been the single most important theme in the rest of paleontologic research in this time period (and as noted, has been important to securing university positions); and paleobiologic studies are, if not common, represented by dozens of publications for other microfossil groups such as foraminifera. Occurrence data for radiolarians allows, for the first time, larger-scale paleobiologic syntheses of patterns of radiolarian occurrence and evolutionary dynamics over geologic time. Importantly, these occurrence databases, unlike the offline species catalogs, include synonym information in the form of curated taxonomic name lists as these are essential to interpret the published data without creating substantially inflated diversity estimates. Merging these two aspects of taxonomic information is thus essential.

Work is currently underway which should soon make at least part of the broad range of offline taxonomic catalog data generally available, and link this to the existing online catalog and occurrence data. The Cenozoic taxa are being put online at mikrotax.org (Suzuki, Caulet, Lazarus, and Young, in prep.), and interest is growing in converting all the catalogs into generally accessible resources. Community developed and supported catalogs, linked to the occurrence data, should go a long way to resolving the perennial problem of inadequate radiolarian taxonomy. These developments reflect the increasing power of the internet, and increasing technical skills among radiolarian specialists. In a related development that particularly affects Cenozoic and living radiolarian taxonomy, the taxonomic legacy of Ehrenberg and Haeckel were finally addressed by a team of Japanese and German taxonomists who, making use of the new accessibility of the Ehrenberg and Haeckel collections resulting from the reunification of Germany, reimaged hundreds of original specimens in the collections left behind by these early workers (Tanimura and Aita, 2009). This information should make possible a stable revision of the confusing species, and particularly genus level taxonomy of Cenozoic-Recent radiolarians.

A last feature of the last two decades is an overall decline in research activity, at least as measured by the annual numbers of publications (Figure 1.1). The extent of decline in activity shown in this figure is

certainly exaggerated by the, normal for literature databases, failure to capture all of the most recently published literature, but the very large magnitude in decline is also too much to ascribe solely to database errors, and also reflects real-world changes in the radiolarian community. After many years of growth, or at least stability, academic positions for radiolarian workers are in decline in Japan, and fewer radiolarian workers, or micropaleontologists of any sort, are still working in other organizations such as oceanographic institutions that used to be major employers of radiolarian specialists. The one bright spot in these data is the steady increase in the numbers of papers on radiolarian biology, to the extent that in the last few years biology research output is equal to that of the more traditional, biostratigraphically oriented work on Paleozoic and Mesozoic material. These newer trends have implications for the future development of the field, but a discussion is deferred until the end of this book, where it is integrated into a summary of the main themes of the volume.