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Fossil Focus: Acritarchs

by Heda Agić*[1]

Introduction:

The acritarchs are a major, long-ranging and successful group of small, capsule-like, organically preserved fossils, which are present in the rock record of most of Earth's history, dating back 1.8 billion year, or perhaps even as many as 3.4 billion years (Fig. 1). They include mostly single-celled microfossils ranging from a few micrometres (one-millionth of a metre) to one millimetre in size, and each is made up of a sac of organic tissue (vesicle). They are most commonly round, and can be either smooth or covered in spines (Fig. 2). Acritarchs are found in rock deposits that were once marine and terrestrial aquatic environments, and have been described from localities on all continents, as well as from all time periods from the Proterozoic eon (starting 2.5 billion years ago) to the present. Before the animals arose and began to diversify in the late Neoproterozoic era (around 545 million years ago), these cells had reigned for more than one billion years as the most complex organisms on the planet! That is a quarter of Earth's history and a longer record than any other fossil group, apart from bacterial microfossils and structures called stromatolites. More importantly, acritarchs played a role in increasing the amount of oxygen in the oceans during the Neoproterozoic era, which eventually paved the way for the rise of animals and other large and complex organisms.

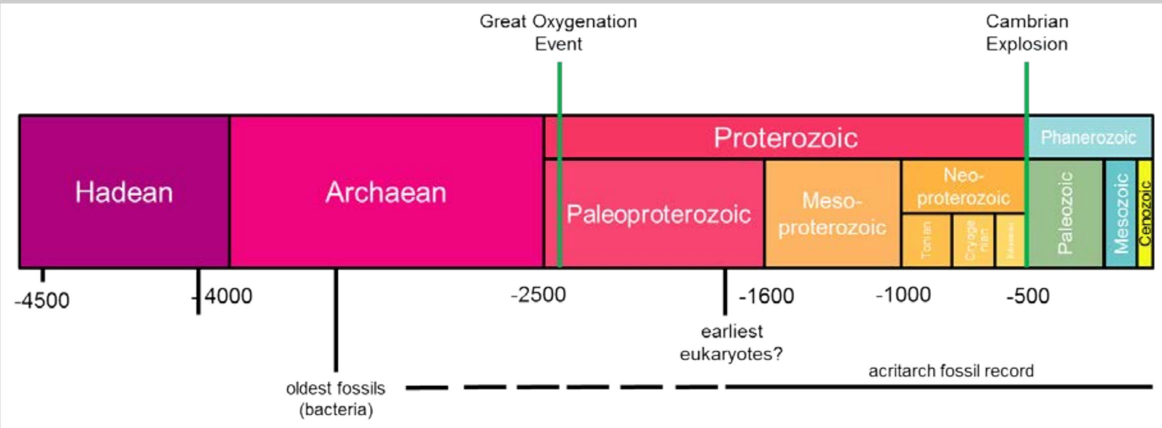

Figure 1 — Timeline showing the extent of the acritarch fossil record (numbers refer to age in millions of years). During most of Earth's history, life was microscopic and did not produce mineralized remains. The fossil record during this time comprises permineralized microfossils, trace fossils and stromatolites, and organic-walled microfossils. As a group, acritarchs have a very long stratigraphic range, dating back to 1.8 billion years ago. Credit: H. Agić.

No one knows for sure what kind of organisms acritarchs are. Acritarchs are what is known as a polyphyletic group, meaning that they probably include some organisms that are similar but not closely related to each other, such as phytoplankton (algae), animal egg cases and various early protists. Due to their simple shape, which has few distinguishing features, understanding the palaeobiology of the acritarchs and other organic-walled microfossils is not easy. Even though these microfossils have been studied from different places and time periods for a century, their evolutionary relationships are still not fully known.

In 1963, US palaeontologist William Evitt introduced and coined the name Acritarcha, from the ancient Greek words *achritos* and *arché*, meaning 'uncertain' and 'origin', to serve as a catch-all phrase for marine plankton from the early Palaeozoic era (541 million to 252 million years ago). Because nobody was certain which groups of fossil or modern organisms these tiny monsters were most closely related to, everything small and organic was put into this one 'wastebasket' group, or taxon. The name Acritarcha is now becoming somewhat obsolete: more and more of its taxa are being assigned to known groups of microorganisms.

It's all in a name

Much like defining them, naming these organically preserved microfossils has proved challenging for scientists, and there are several technical terms that can be encountered while studying the acritarchs. The name Acritarcha itself is a traditional grouping that most commonly includes single-celled, organically preserved vesicles. Most of these vesicles are assumed to be eukaryotic — that is, their cell contained a nucleus and other organelles enclosed in membranes. Organic-walled microfossils are any small fossils without biomineralized components such as shells, teeth or bones. They can be single-celled, a chain or cluster of cells, filaments or carbonaceous remnants of animal body parts (called small carbonaceous fossils). A broader group of organically preserved, acid-extracted microfossils are called palynomorphs or palynoflora. These include acritarchs, dinoflagellates, pollen, spores, chitinozoans and fungi. The scientific discipline that studies these fossils, as well as their modern counterparts, is called palynology. It is an interdisciplinary science drawing from and applied to geology, botany, climate studies and forensics. The name comes from the Greek word *paluno* meaning 'strew' or 'dust', so palynology literally means the study of dust.

This article focuses on what were traditionally termed acritarchs, and how they can cast light on the early evolution of complex cells during the Proterozoic eon.

Defining features and their function:

Acritarch anatomy is fairly straightforward. Their morphology is plain and is similar in all members of the group, so it is difficult to identify specific characteristics for cladistic analysis to investigate their evolutionary relationships, but all acritarchs share some common features (Fig. 2). They consist of an organic-walled vesicle that is resistant to being dissolved in acid, and is usually rounded or elongate in shape. Some species possess additional surface elements such as spines, called ornamentation. Patterns on the surface of the vesicle wall (called 'sculpture') and ornamentation may be used to distinguish between species and even to work out what kind of environment the microorganism inhabited during life.

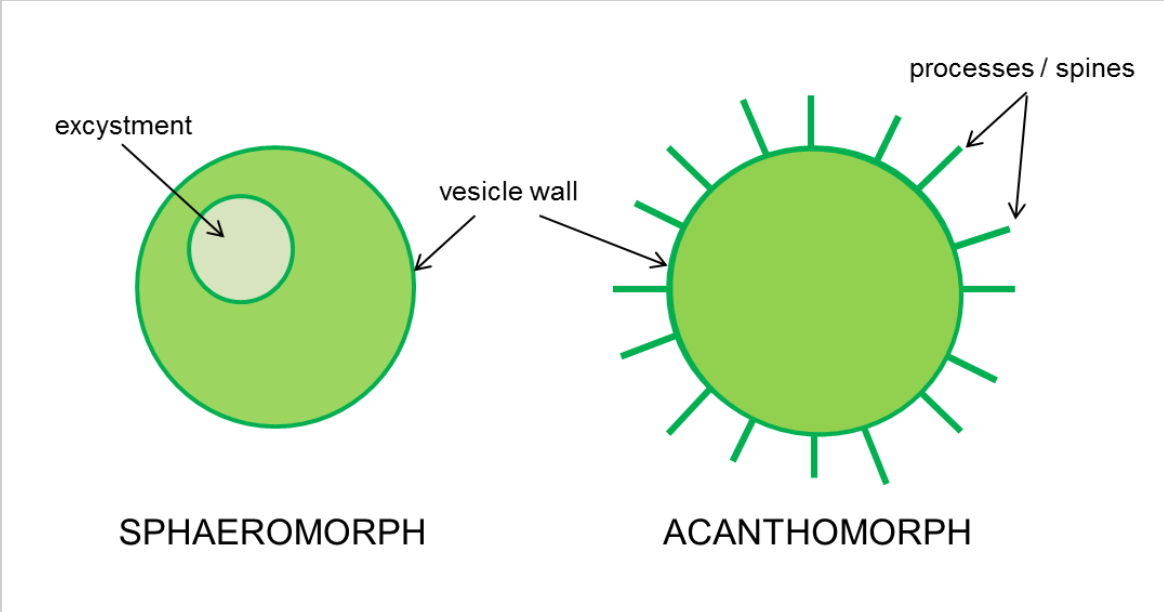

Figure 2 — Basic acritarch anatomy. These are the two most common morphotypes encountered in the Precambrian fossil record. Microfossils without ornamentation (spines) are called sphaeromorphs, and spine-bearing ones are called acanthomorphs. Some acritarchs may also bear an opening (excystment). All acritarchs are vesicles made by an organic wall that varies in thickness and ultrastructure. Credit: H. Agić.

Unornamented spherical acritarchs are known as sphaeromorphs, and they are the oldest acritarch group (1.8 billion years old). They may be smooth (group leiosphaerids), or bear a variety of surface sculpture, such as meshwork (Figs. 3A, 9B), pores (Fig. 3D) or corrugation (Fig. 8A). Acritarchs ornamented with spiny protrusions ('processes') are called acanthomorphs (Figs. 3B, 3E–F). Processes may vary in size, shape and distribution along the vesicle surface. Their function in life is uncertain. They increased the microorganism's surface area — especially if they had hair-like extensions, which some suggest may have increased buoyancy and prevented the microorganism from sinking down the water column, allowing it to remain in the photic zone, the layer of water that receives sunlight. Alternatively, processes might be caused by the formation of a reproductive cyst, similar to a phenomenon in living unicellular algae (dinoflagellates and chlorophytes, such as *Staurastrum*). As the cell prepares to reproduce, it starts generating a sturdy protective outer layer, and contracting inwards. Contractions cause processes to form on the surface. This suggests a probable cyst-like function for acritarchs' processes. Spiny ornament also occurs on resting-egg cases of living arthropods, prompting the interpretation of some large acritarchs from the Ediacaran period (635 million to 541 million years ago) to be resting-egg stages of the earliest animals.

The oldest acanthomorphs in the rock record come from the late Palaeoproterozoic era to the early Mesoproterozoic era (around 1.6 billion years ago), but they remain rare, with simple processes, until the Ediacaran period, which saw a diversification of large spine-bearing microfossils. Processes become exceptionally complex and diverse in shape at the boundary between the Cambrian period and the Ordovician period (around 490 million years ago), for example in the acritarchs with polar symmetry that are called diacromorphs (Fig. 3F).

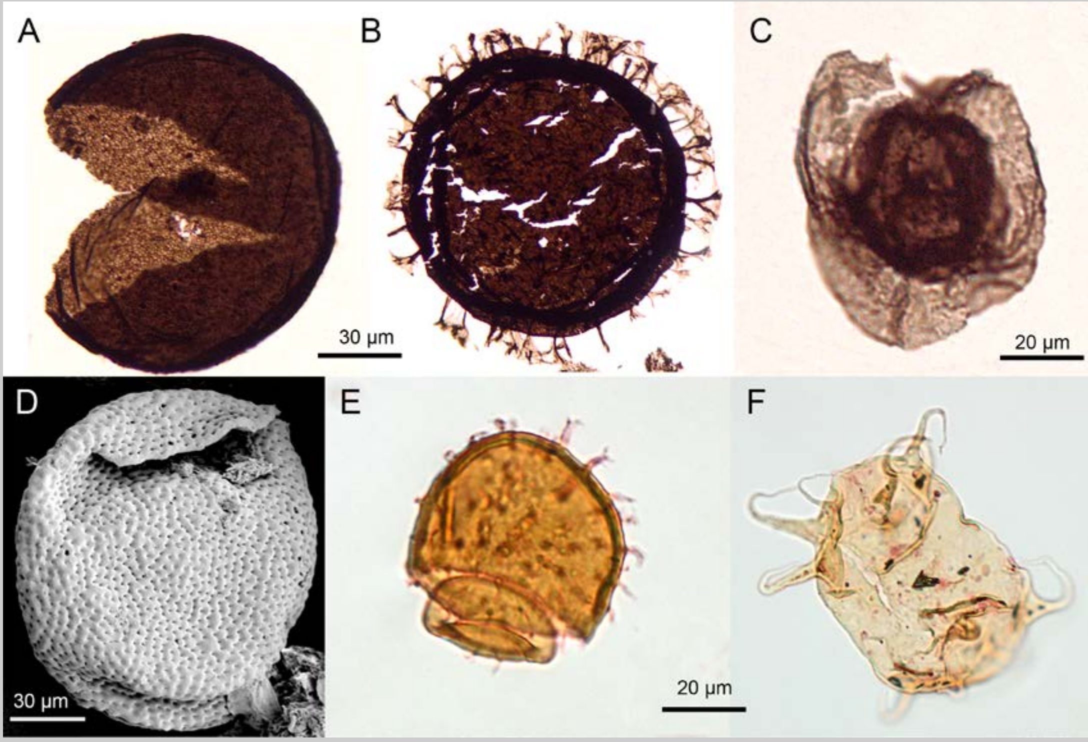

Figure 3 — Some acritarchs representing characteristic morphologies from the Proterozoic and the early Phanerozoic eras. A–C, Mesoproterozoic (1.7 billion to 1.4 billion years old) fossils from the Ruyang Group, China. A, *Dictyosphaera macroreticulata* is a sphaeromorph with a distinct surface pattern. B, Spine-bearing taxon *Shuiyousphaeridium macroreticulatum*. C, Double-walled acritarch *Pterospermopsimorpha insolita*, consisting of a central body and an outer envelope. D, Prasinophyte *Tasmanites volkovae* from the lower Cambrian (around 555 million years old) Lükati Formation in Estonia, imaged by scanning electron microscope and exhibiting porate surface. E–F, Early Ordovician (about 490 million years old) species from the Varangu Formation, Estonia. E, *Priscogalea distincta* with a large opening structure that was once covered by an operculum. F, An acritarch with polar symmetry (also known as diacromorph) and a slit-like opening, *Actinotodissus achrasii*. Credit: H. Agić.

Some acritarchs have an opening in their vesicle wall, called the excystment or a pylome. It may be rounded or look like a rupture or a slit. Unlike sculpture or ornamentation, the presence of an excystment does not help to identify the species, because there are members of the same species with and without an opening. Moreover, both sphaeromorphs and acanthomorphs can have an opening. Similar to the processes of acanthomorphs, this opening is thought to have been involved in reproduction. Various modern protists such as algae or ciliates form a protective cyst through which they eventually release their reproductive, or germ, cells (gametes). Ordovician acritarchs have more complex excystments, covered with lids (opercula; Fig. 3E). Based on analogy with the modern alga *Acetabularia*, it can be inferred that this allowed for more controlled and effective gamete release.

Organic-walled microfossils with outer membranes (Fig. 3C) are known as disphaeromorphs and occasionally pteromorphs, and have changed very little since the Mesoproterozoic. They have traditionally been identified as prasinophyte algae, because they look remarkably similar to the prasinophyte reproductive cyst, called a phycoma. Prasinophytes are a class of simple single-celled organisms with a single chloroplast and a single mitochondrion, at the base of the green algal lineage (Chlorophyta).

Owing to their widespread distribution, the variety of types of rock they are recovered from and the similarity of their body plan to present-day non-skeletal plankton, acritarchs were probably the earliest eukaryotic phytoplankton — primary producers in the Proterozoic oceans.

Where can you find acritarchs?

Most acritarchs were presumably free-floating in the water column, like modern plankton. Dead vesicles would have settled on the ocean floor, where they were covered in sediment. Organic-walled microfossils can be permineralized in rocks called cherts or phosphates, or preserved in fine-grained shales and siltstones (Fig. 4), and less commonly in other rocks such as limestone. Due to their minute size, it is impossible to spot acritarchs in the field. Instead, shales rich in organic matter, of a tell-tale olive-green, dark grey or blue colour, are sampled in batches of at least 25 grams and then sent to a palynological laboratory for processing. This normally yields hundreds of microfossils. (Sometimes, a few hundred grams of shale will suffice for a whole PhD thesis!)

Figure 4 — Lower Cambrian shales exposed along the shore of the Digermulen peninsula in Finnmark, Arctic Norway. Olive-green and blue-green fine-grained shales are excellent for preserving organic matter and organic-walled microfossils. Credit: H. Agić.

How can you study acritarchs?

Because acritarchs are embedded in sediment, they may be studied either by polishing the rock into petrographical thin sections (usually used by geologists to study individual minerals in a rock) and observing them *in situ*, or by extracting them from the rock matrix with the help of strong acids.

Thin sections

Petrographical thin sections reveal the acritarchs in cross section, which often provides information about how they were preserved. Microfossil cross sections are also useful to show extra details about the fossils' anatomy, such as the nature of the processes or the internal structures (presumably reproductive bodies) that may occasionally be preserved inside the vesicle. This method also means that the samples cannot be contaminated by recent palynomorphs such as pollen that might have found their way into the lab ventilation.

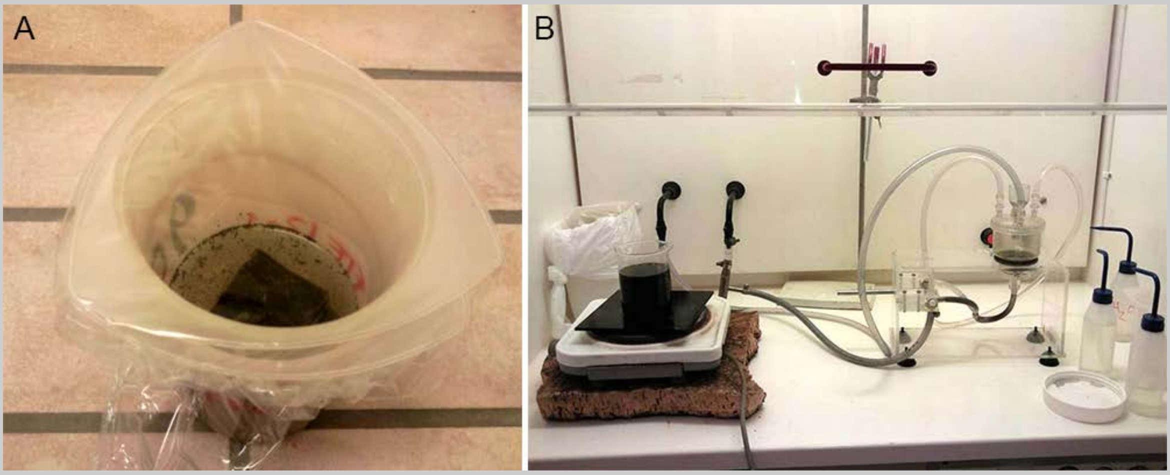

Figure 5 — Acritarchs are extracted from the host rock for study by macerating the rocks in acid. The leftover organic residue is filtered through mesh, usually with holes 10 µm across. Credit: H. Agić.

Palynological acid maceration

Carbonate rocks can be dissolved in hydrochloric acid (HCl), whereas rocks made of silica are dissolved in hydrofluoric acid (HF), usually for a few days (Fig. 5). Since this procedure uses some of the most dangerous (and potentially lethal!) acids, it must be performed in a controlled laboratory, and with protective equipment (Fig. 6). Acids dissolve the minerals, leaving a gooey residue of organic matter (kerogen and sturdy, insoluble vesicles of organic-walled microfossils). The residue needs to be carefully decanted (Fig. 6), and then filtered through several mesh sizes, commonly around 10 and 25 micrometres. The filtrate may be stored in ethanol or acetone to prevent bacterial or fungal growth that would contaminate the fossil material. The residue is then picked out carefully with a pipette and strewn onto the glass slides and/or stubs to be examined with a light microscope or a scanning electron microscope. A single drop may contain tens of microfossils.

The ability of acritarchs to withstand rigorous acid maceration is a diagnostic feature of the group itself. Chemical analysis of the acritarchs' walls has shown that they are made of complex molecules similar to sporopollenin — a tough compound that helps to protect modern plant spores and pollen against hazards such as desiccation.

Figure 6 — Working with strong acids such as HF and HCl requires proper lab safety and protective equipment. A palynologist normally wears a collared lab coat, gloves (sometimes a double pair), rubber cuffs, apron, boots and eye protection. Credit: W. Taylor.

Microscopy

Transmitted light microscopy (LM) reveals the main features of microfossils. It useful for getting an overview of large numbers of fossils, and it is excellent for counting specimens for quantitative analysis.

Figure 7 — Filtered residue containing the microfossils is mounted onto glass slides and studied by transmitted light microscope (left, credit: W. Taylor) and scanning electron microscope (right, credit: H. Agić.).

Scanning electron microscopy (SEM) reveals details of the wall structure and patterning that are invisible in LM. This aids in identifying species and sorting them into groups (taxonomy). Transmitted electron microscopy (TEM) is valuable in studies of acritarchs' ultrastructure (also useful in taxonomy), and has provided another character for working out their biological affinities.

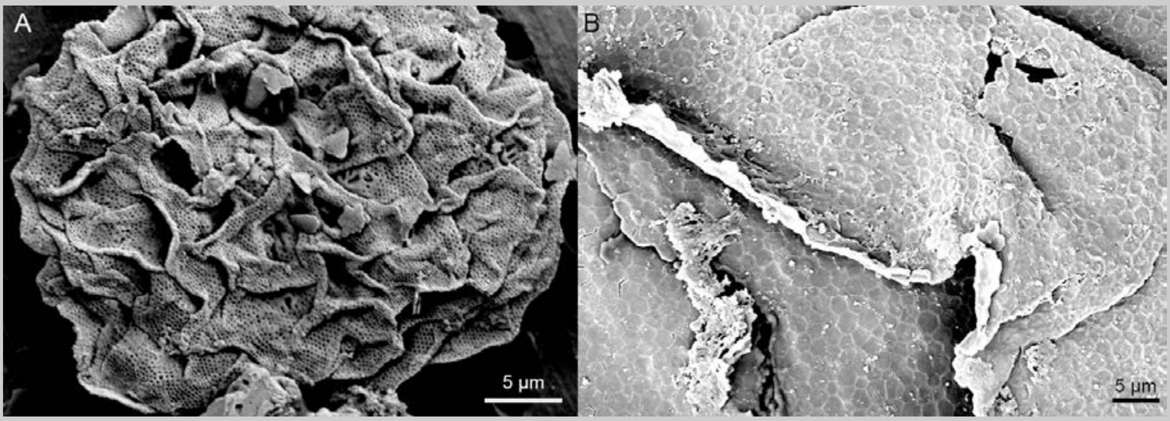

Figure 8 — Scanning electron microscopy provides fine-scale details of microfossils' morphology that would have been missed in traditional light microscopy. A, Tiny Cambrian acritarch *Reticella corrugata*. B, Detail of the wall structure of the 1.7-billion-to-1.4-billion-year-old *Dictyosphaera macroreticulata*. Credit: H. Agić.

Significance of acritarch research:

Although they are small in size, organic-walled microfossils have made a great contribution to several areas of palaeontological research.

Biostratigraphy

Due to their abundance, wide distribution independent of local environments and rapid morphological evolution (at least for the Palaeozoic species), acritarchs make great index fossils. Index taxa are used to define geological time intervals, and they help geologists to pinpoint exactly where in the geological column a specific rock sample comes from, and thus how old it is. This makes organic-walled microfossils a great asset for stratigraphy — the study of rock layers — and, by proxy, very useful for the oil and gas industry. Stratigraphic units defined by acritarchs (called biozones) are common for the Palaeozoic, and were helpful in resolving the earliest stages of the Cambrian, when animal body fossils are scarce. Proterozoic stratigraphy is still in its infancy, yet a lot of progress has been in made in the past decade and there are now suitable index-fossil candidates for defining several time intervals in the Neoproterozoic (Fig. 9).

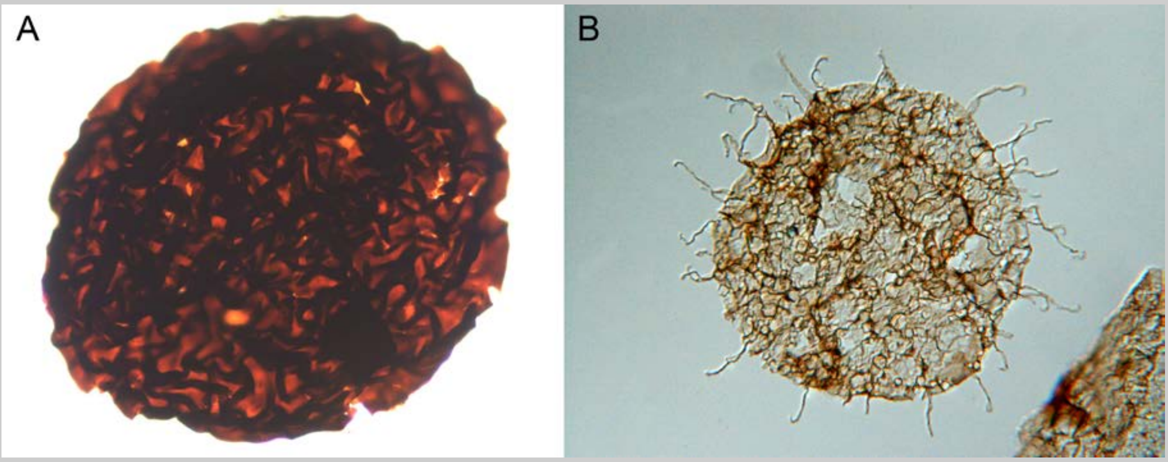

Figure 9 — Acritarchs have been a useful tool in resolving the Neoproterozoic stratigraphy. A, *Cerebrosphaera buickii* is a microfossil with a peculiar brain-like appearance. It is common in the Tonian–Cryogenian age rocks in Australia, Svalbard (Norway), Sweden and the United States. Image courtesy of Kath Grey. B, A candidate for an Ediacaran index fossil, *Tanarium anozos* from Officer Basin, Australia. Credit: S. Willman.

Environmental studies

Different types of acritarch tend to occur in distinct palaeoenvironments. Acanthomorphs are common in shallow waters, and thin-walled leiosphaerids normally prevail in deeper, low-energy environments — their thin vesicles otherwise get broken up by sediment abrasion. Consequently, quantitative data of acritarch assemblages from a given locality will provide geologists with another tool for inferring past environmental conditions.

Palaeobiology and evolution

As the only complex fossils around for a few billion years of Earth's history, acritarchs help us to understand evolutionary and ecological patterns of early life. Analysis of the wall ultrastructure of a handful of species (for example, *Leiosphaeridia* and *Tanarium*) has enabled morphological comparison with living groups of microorganisms, bringing us closer to pinpointing the time of origin and mode of life of some protists. Recently, several species of Neoproterozoic acritarchs were found to bear marks of micropredation, giving us a glimpse of a food web in the pre-animal world.

A window into early eukaryotic evolution:

Interpretations of the biological affinities of acritarchs differ, but most scientists agree that they are eukaryotic microorganisms, probably various kinds of single-celled protist. Therefore, due to their complex cell morphology and long fossil record, acritarchs offer handy information about patterns of eukaryotic evolution and diversification through time.

Eukaryotes are one of the three domains of life (alongside Bacteria and Archaea), and include organisms such as animals, plants, fungi, algae, amoebae and various other protists. The evolution of the eukaryotic cell was one of the key transitions in the history of life. Complex cells that were able to tap into more energy (provided by oxygen-respiring organelles called mitochondria) eventually evolved multicellularity, which in turn gave rise to the large organisms that we are familiar with today.

How can you recognize eukaryotes in the fossil record?

The most recognizable eukaryotes, including animals and higher plants, did not evolve until the Palaeozoic era, yet the diversity of microscopic eukaryotes outside those groups was significant before this time and remains considerably high at present. Being tiny and soft-bodied, such organisms don't have a lot of morphological characters that can easily enter the fossil record. For a microfossil to be considered eukaryotic rather than prokaryotic (simple small cells and filaments of bacteria), it needs to fulfil a few criteria.

The cell ought to be large (>20 micrometres). Bacteria tend to have small cells (about 0.2–10 µm), although there are exceptions to this rule. Purple sulphur bacteria may grow up to about 600 µm, and the smallest living eukaryote, the prasinophyte *Ostreococcus taurii*, is only 0.8 µm in diameter. So the size alone is not sufficient to prove that an organism is of eukaryotic affinity. A eukaryotic microfossil should also have a cell with complex morphological elements (such as spines), which are never produced by bacteria. Lastly, vesicles resilient enough to withstand acid extraction are produced solely by eukaryotes. Most acritarchs fulfil these criteria.

Geological history of the acritarchs

The oldest sphaeromorphs are preserved in roughly 1.8-billion-year-old shales from the North China Craton. The first acanthomorphs, including *Tappania* and *Shuiyousphaeridium* (Fig. 3B), appeared shortly afterwards, in Mesoproterozoic deposits from Australia, China, Siberia and USA, but remained relatively low in diversity until about one billion years ago. Nevertheless, this period encompassed the initial diversification of acritarchs, seen in the appearance of microfossils with various sculpture patterns (for example, *Dictyosphaera* and *Valeria*), protrusions from the vesicle (as in *Germinosphaera*) and outer envelopes (seen in *Pterospermopsimorpha* and *Simia*).

The early Neoproterozoic saw an increase in the preserved morphologies of organic-walled microfossils, nicely documented from various localities in Russia and Arctic Canada. Because of their low initial diversity and lengthy period of evolutionary stasis, early eukaryotes were probably not ecologically significant until the middle or end of the Neoproterozoic or the Palaeozoic, when the fossil record shows several diversification stages. The first of these took place in the late Tonian period (800 million to 700 million years ago), before the global Snowball Earth glaciation events, when the envelope-bearing and ornamented forms became more common. The latter followed the glaciations, in the Ediacaran, which included the diversification of large, spine-bearing forms (such as *Tanarium*, Fig. 9B).

Large acritarchs perished after the Proterozoic–Cambrian transition (541 million years ago), presumably because of increased predation pressure from the newly evolved zooplankton. Cambrian acritarchs (including *Skiagia* and *Asteridium*) show a trend towards decreased body size (Fig. 8A), which continued into the Ordovician. Drastically different cell morphologies appeared in the Ordovician and the Silurian period (485 million to 419 million years ago), including polygonal and triangular vesicles (*Arkonia*), polar distribution of processes (*Actinotodissus*, Fig. 3F) and an assortment of opening structures (galeate acritarchs).

Acritarchs diversified parallel to the Cambrian and Ordovician radiations of marine invertebrates. By the end of the Devonian period (around 360 million years ago), however, the group was declining in diversity, with only basic body plans such as those of leiosphaerids still present, eventually leading to a wane after the end-Permian mass extinction 252 million years ago and the ecosystem transition that followed. This was the start of the Mesozoic era; from then onwards, the acritarchs ceased to be the dominant eukaryotic phytoplankton, and were replaced by dinoflagellates and biomineralizing coccolitophores and diatoms — the 'red algal lineages'. Acritarchs were still present through the Mesozoic and the Cenozoic era that followed it, although they were not as abundant as before, and generally include organically preserved unicellular organisms that have not been identified. These are known as problematica.

Suggestions for further reading:

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