

Fossil Focus: The place of small shelly fossils in the Cambrian explosion, and the origin of Animals

Author(s): Aodhán Butler*¹

Volume: 5

Article: 7

Page(s): 1-14

Published Date: 01/07/2015

PermaLink:

<http://www.palaeontologyonline.com/articles/2015/fossil-focus-place-small-shelly-fossils-cambrian-explosion-origin-animals/>

IMPORTANT

Your use of the Palaeontology [online] archive indicates your acceptance of Palaeontology [online]'s Terms and Conditions of Use, available at <http://www.palaeontologyonline.com/site-information/terms-and-conditions/>.

COPYRIGHT

Palaeontology [online] (www.palaeontologyonline.com) publishes all work, unless otherwise stated, under the Creative Commons Attribution 3.0 Unported (CC BY 3.0) license.



This license lets others distribute, remix, tweak, and build upon the published work, even commercially, as long as they credit Palaeontology[online] for the original creation. This is the most accommodating of licenses offered by Creative Commons and is recommended for maximum dissemination of published material.

Further details are available at <http://www.palaeontologyonline.com/site-information/copyright/>.

CITATION OF ARTICLE

Please cite the following published work as:

Butler, A. 2015. Fossil Focus: The place of small shelly fossils in the Cambrian explosion, and the origin of Animals. Palaeontology Online, Volume 5, Article 7, 1-14.

Fossil Focus: The place of small shelly fossils in the Cambrian explosion, and the origin of Animals.

by [Aodhan Butler](#)*¹

Introduction: Darwin, the Cambrian explosion and the origin of animals.

The small shelly fossils (or SSFs) of the early Cambrian period (approximately 541 million to 509 million years ago) could in many ways be described as the world's worst jigsaw puzzle. This article will attempt to give a brief tour of the significance, history and biology of this humble yet potentially hugely important group of fossil organisms and how they may help in answering fundamental questions about how and when the major groups of animals evolved on Earth.

A palaeontological mystery...

"To the question why we do not find rich fossiliferous deposits belonging to these assumed earliest periods prior to the Cambrian system, I can give no satisfactory answer." Charles Darwin, *On the Origin of Species*, (1859)

A striking observation made by Victorian geologists and naturalists, including Charles Darwin, was that rocks from the [Cambrian](#), [Silurian](#), [Ordovician](#) and later periods (the [Phanerozoic Eon](#) as it would later come to be known, starting approximately 541 million years ago, to the present) were to a greater or lesser degree filled with the remains of bones, shells, animal teeth and plant fossils ranging from leaves to entire fossilized forests. However, in rocks laid down before the Cambrian strata (in the Precambrian Eon), no trace of macroscopic life as we knew it could be found. Geologists had hit on an apparently huge problem with their understanding of geology and the fossil record at the time. Quite simply, where were the plants, animals and other evidence of life?

So where are all the fossils ?

Charles Walcott (who discovered the [Burgess shale](#) fossil field in Canada) proposed the name Liplian for an interval of time that he thought had come before the Cambrian and was somehow not represented in the fossil record or simply did not preserve any fossilized remains. A few reasons were suggested: there were no animals around, they were soft bodied (non-biomineralized) and so did not preserve well or at all, or conditions were not suited to fossilization until the 'Lagerstätte windows' (for more information, you can read [this](#) article). On closer inspection, however, it turned out that the devil is in the details. There is, as it turns out, a rich record of [trace fossils](#) — burrows or trackways in early Cambrian rocks — which amounts to indirect evidence of the presence of some kind of complex organisms. Indeed, the start of the Cambrian is defined by the appearance of the trace fossil *Treptichnus pedum*, thought to be made by an organism similar to modern priapulids, a kind of marine worm.

In the latter half of the twentieth century, the discovery of mysterious faunas, or collections of animals, from the [Ediacaran](#) period (635 million to 541 million years ago) showed that complex multicellular life predates the Cambrian. Organisms from these faunas may be related to modern animals in some way, but how they fit into the bigger picture of animal evolution is still controversial. They were almost universally soft-bodied. More recently, the presence of small, weakly [mineralized](#) fossils was recognized from the rocks in Siberia and other locations earlier than the rocks that contain trilobite fossils. These are ‘small shelly fossils’, an informal term coined by palaeontologists Samuel Matthews and Vladimir V. Missarzhevsky in 1975 (see further reading) as a catch-all classification for a vast array of skeletal fossils, some of which appear in the late Precambrian, but most of which are found in the earliest Cambrian period (Fig. 1). These represent some of the first evidence of biomineralization and formation of skeletons by metazoans (animals and their close relatives), and pre-date by some time the sudden appearance of large fossils so often associated with the ‘Cambrian explosion’.

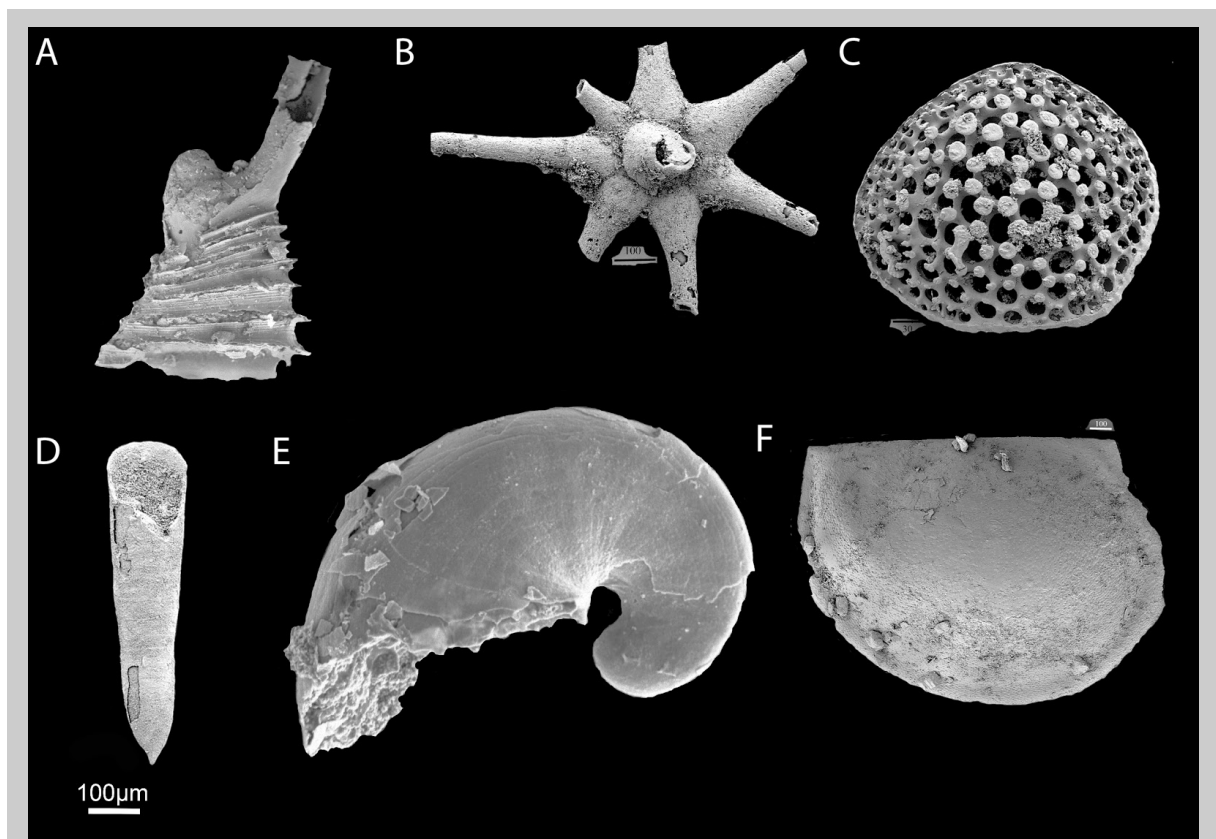


Figure 1 — A typical assemblage of diverse small shelly fossils from the Cambrian of Greenland. Images from scanning electron microscopy. A. *Yochelcionella*, a stem-group [mollusc](#) with a ‘snorkel’. B. *Chancelloria*, mysterious fossil organisms thought to be related to molluscs or sponges. C. *Microdictyon* plate, an armoured ‘worm’. D. Hyolith, small conical shell probably related to molluscs and [annelids](#). E. *Pelagiella*, a stem-[gastropod](#). F. A small bivalved [arthropod](#) or bradoriid. Images courtesy of John S. Peel.

Timing of the SSF appearance

Small shelly fossils near the start of the Cambrian mark a key transition from a world of [microbial mats](#), single-celled organisms and simple soft-bodied forms, to one dominated by animals with skeletons, burrowing organisms and other metazoans. This transition happened in an epoch dubbed the Terreneuvian: the oldest part of the Cambrian, between the start of the Cambrian period and the appearance of trilobites (around 20 million years, including the Fortunian and Tommotian stages in Fig. 2).

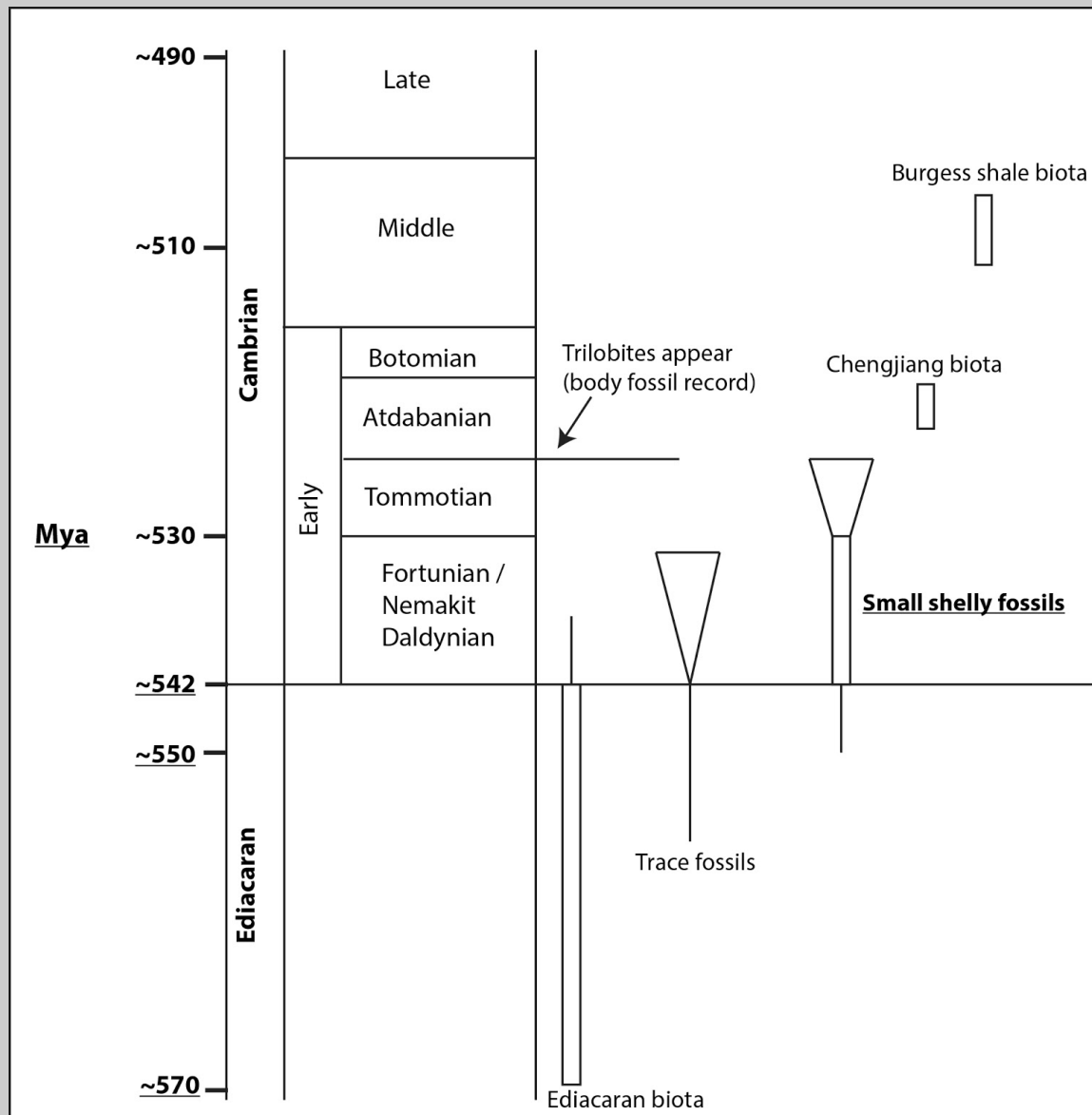


Figure 2 — An approximate timeline of the Cambrian period and late Ediacaran period.

One of the first small shelly forms to appear is *Cloudina* (Fig. 3A), which is made up of stacked conical fossils found initially in the late Precambrian and persisting into the Cambrian. Other early 'weakly mineralizing' forms include *Namacalathus* (Fig. 3B) and *Namapoikia* from Namibia. Interestingly, Ediacaran organisms and these early shelly organisms are never found together, but they can be found in alternating layers, perhaps indicating that they preferred different environments.

As we move to younger rocks, into the Cambrian itself (rocks from the Fortunian epoch), we begin to see small shelly fossils called halwaxiids, made of a mineral called [aragonite](#); mollusc-like forms; and hyoliths (similar to those in Fig. 1).

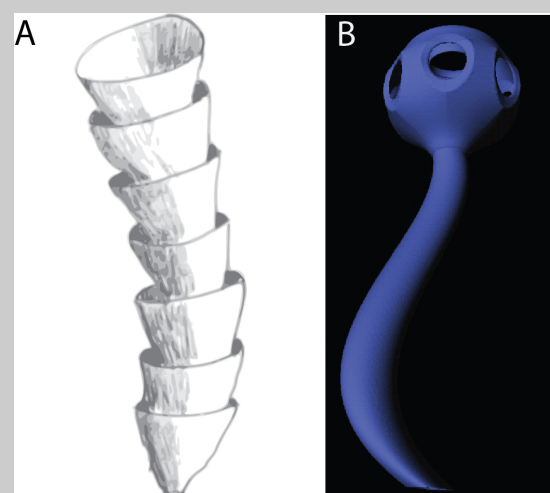


Figure 3 — Weakly mineralized fossils of uncertain origin from the late Ediacaran period. A. *Cloudina* reconstruction ([Source](#)). B. *Namacalathus* reconstruction.

The hey-day of small shelly fossil abundance is in 'Stage 2' of the Cambrian, also known as the Tommotian epoch (Fig. 2). This name comes from the strata of Siberia, which contain a large assemblage of SSFs called the tommotiids. The appearance of these fossils has been suggested as the indicator for the onset of this period of geological time. They are found alongside extensive early reef-like deposits of cup-shaped archaeocyaths, organisms thought to be sponges. This is directly before the appearance of trilobites and most of the famous Cambrian exceptional fossil sites such as the Burgess Shale and Chengjiang biotas (Fig. 2).

Globally, small shelly fossils have occurred widely, turning up in Cambrian rocks corresponding to shallow marine environments in many places around the globe, including China, Morocco, Australia (Fig. 4), Estonia, Sweden, the United Kingdom, Russia, Mongolia and even Antarctica.

Types and preservation of SSFs

The vast majority of small shelly fossils had skeletons built from a mineral known as apatite (a form of calcium phosphate, the same material as bones and teeth); other forms, particularly the early examples, were made from calcium carbonate, like modern bivalves or snails.

Phosphate is relatively rare in the oceans today. It is one of the main nutrients that support photosynthesis in plants and algae, so it is in constant short supply. Cambrian oceans, however, are thought to have had a much higher phosphate content, enabling early animals to make extensive use of this mineral for their skeletons. Indeed, many SSFs are casts of the original animal that have been preserved by a phosphatic coating that grew on or inside the animals remains after death, rather than being an originally phosphatic skeleton. Fossils preserved this way are called steinkerns. In this way, skeletons originally made of calcium carbonate can end up in the rock record as a phosphatic fossil.



Figure 4 — Flinders Ranges, South Australia. Prime hunting grounds for Cambrian SSFs.

Why did hard parts evolve?

“Now, *here*, you see, it takes all the running you can do, to keep in the same place.” Lewis Carroll, *Through the Looking-Glass, and What Alice Found There* (1871)

Many types of hard tissue with a huge range of functions can be seen in living animals. These act as internal supports (like the vertebrate skeleton inside you!), teeth for feeding, external supports or exoskeletons (snail shells for example) and dermal sclerites, or scales, for protection and to help swimming. The origin of hard parts is thought to be an example of an evolutionary arms race between predator and prey, constantly trying to gain advantage over, and out-compete, each other. Prey animals tried to build better hard defences (shells and spines) and predators developed mineralized mouthparts and other strategies (such as behaviour) to defeat this armour.

This concept in biology has been called the Red Queen hypothesis (after the character from *Through the Looking-Glass*). Other ideas have suggested that building skeletons was a way for animals to dispose of excess metabolic wastes or to store minerals such as calcium; the use for defence, support, feeding and so on was a side effect.

Research methods

The usual method of collecting these phosphatic fossils is taking large blocks of limestone and dissolving them in acetic acid (essentially concentrated vinegar, leading to some people calling these fossils ‘small smellies’!), then picking through the dried residues to recover whatever fossil remains are left. Skeletons made of calcium phosphate will not dissolve in the mild acid bath (Fig. 5).



Figure 5 — A typical set up in an acid-processing lab. Samples are sorted, weighed and split mechanically. Carbonate rocks are left in the acid bath until the rock has fully dissolved. The remaining shelly fragments are sieved, washed and then sorted under a microscope.

Traditionally, SSFs were studied using a conventional light microscope to observe thin-sections of rock or whole specimens picked out of the acid residues. The invention of the electron microscope has allowed researchers to analyse the surface features of these animals in much higher detail, enabling them to find exquisitely preserved details such as cellular imprints and impressions of [microvilli](#), extremely small features ranging from a few microns to nanometres in size. These are very useful for unravelling the mystery of the relationships of SSFs to more well-known fossil animals.

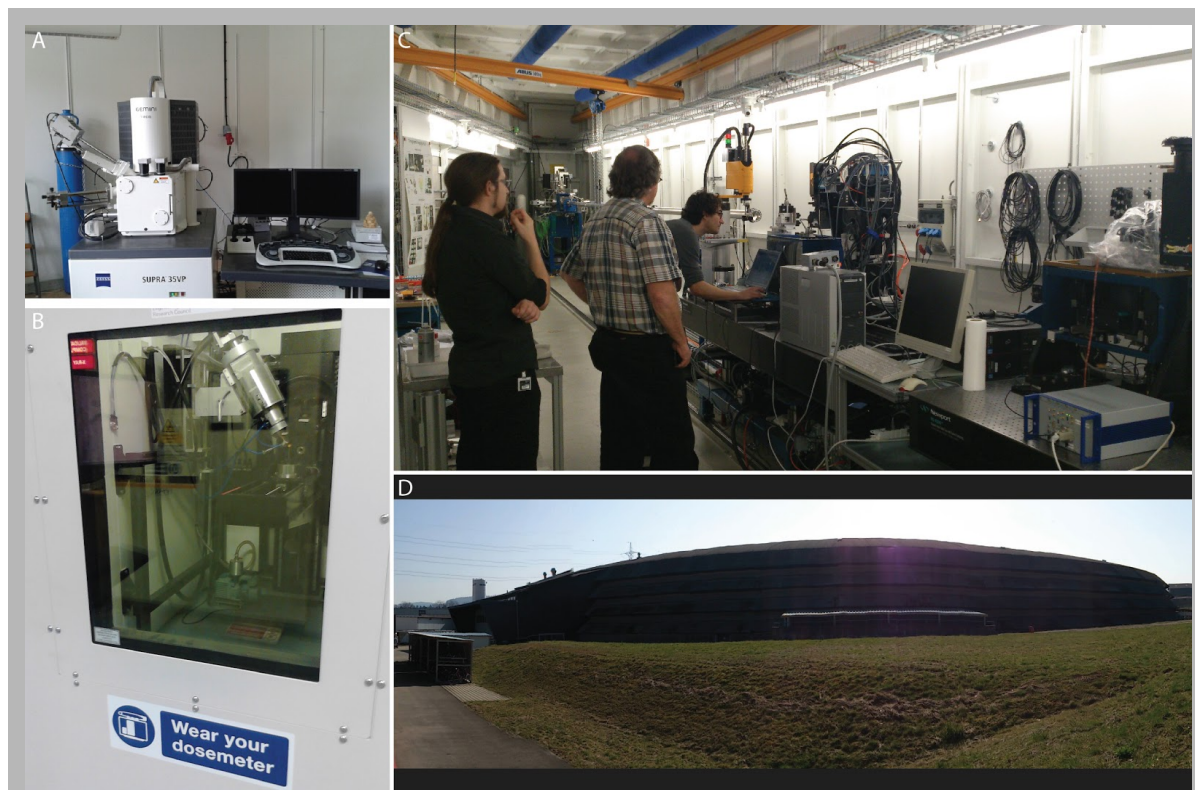


Figure 6 — Research techniques used to investigate small shelly fossils. A. Scanning electron microscope, Uppsala University, Sweden. B. CT scanner at the University of Manchester, UK. C. TOMCAT beam line at the Swiss Light Source for synchrotron tomography. D. Outside panorama of the accelerator-ring building at the Swiss Light Source.

Electron and light microscopy provided a basis of knowledge about SSFs, but until recent years researchers had literally only scratched the surface of SSF anatomy. Little was known about the internal structure and anatomy of most small shelly fossils, and what little was understood had been gathered through random breakage of the fossil, exposing an occasional surface, or by destructively grinding it into thin sections.

This all changed with the advent of 3D virtual-palaeontological techniques that allowed researchers to scan the fossils (Fig. 6) and peel away the skeleton, layer by layer, on a computer screen, exploring the creatures' internal structure in great detail (Fig. 7).

To produce such a model, researchers first need to scan the fossil. The most common technique is [X-ray computed tomography](#), or CT scanning — similar to what you might find in a hospital or dentist surgery. The fossil is placed into the scanner and X-rayed from up to 4,000 positions on a spinning platform. A computer program is then used to reconstruct a detailed 3D model that can help the researcher to investigate the structure of the fossil.

For higher-resolution models, researchers have generated X-rays using a particle accelerator called a synchrotron. The X-ray source from the synchrotron is much more intense than a standard source,

and it produces radiation of a single wavelength, similar to a laser. The end result is a much faster scan than with smaller machines, at higher levels of detail. However, machine time on such equipment comes at a premium! It is expensive and much sought-after. With these tools at their disposal, researchers move a large step closer to solving the enigma of just what small shelly fossils represent, and how they relate to living animals.

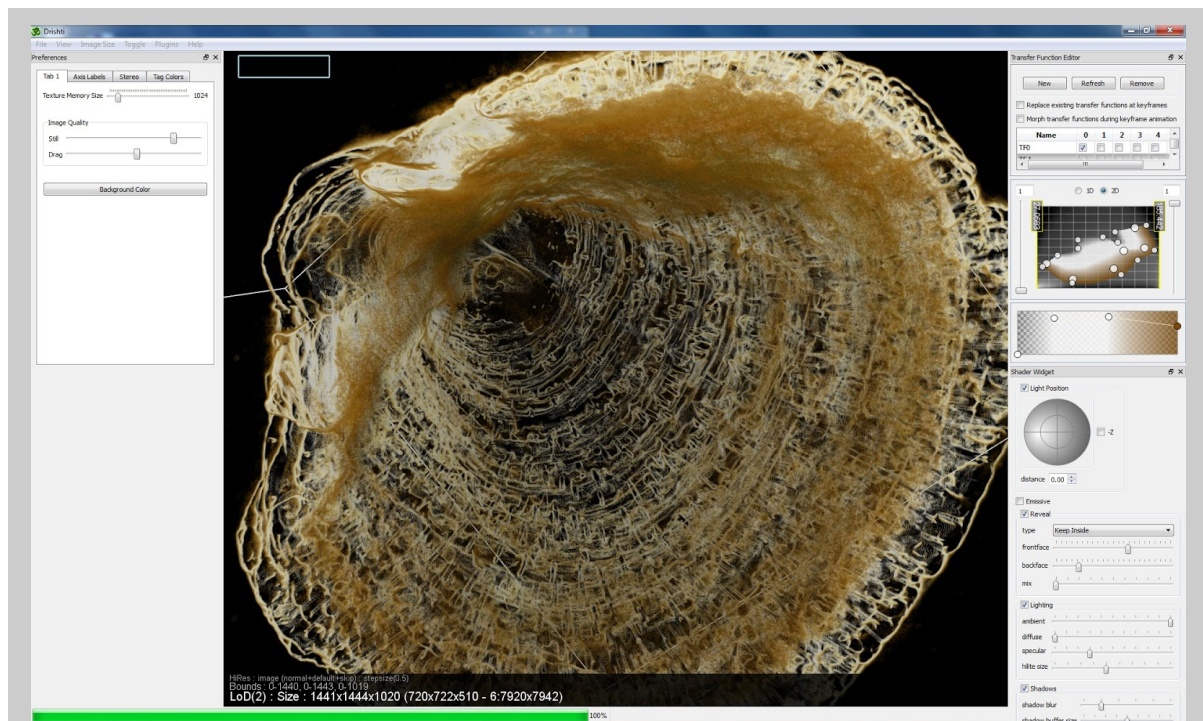


Figure 7 — Example of CT reconstruction in progress, for the tomotioid *Micrina*. Internal structures are clearly visible when the surface layers are removed.

What then are the SSFs?

Putting together the evidence gained so far from such studies, I have outlined a few examples of how some SSFs have found a home in more recognizable animal groups.

Mysterious isolated skeletal plates — or sclerites — had long been known from acid residues of an animal dubbed *Halkieria*. Nearly all known species of this genus were known from such fragments, and reconstructions of the host organism remained elusive for a long time. That was, until the amazing discovery of exceptionally preserved articulated examples from the Sirius Passet Lagerstätte in Greenland. These showed a truly remarkable slug-like animal covered in armoured plates, with bivalved ‘shells’ at either end (Fig. 8).

The isolated sclerites of *Microdictyon* (Fig. 1C and Fig. 9F) are well known from lower Cambrian small shelly deposits, and are thought to have been shed during moulting. Exceptionally preserved specimens from the Chengjiang locality clearly show the sclerites inside the soft-bodied animal, as muscle supports. It was only when these exceptional fossils were discovered that the nature and source of the isolated sclerites became clear — they belonged to an early worm-like [arthropod](#).

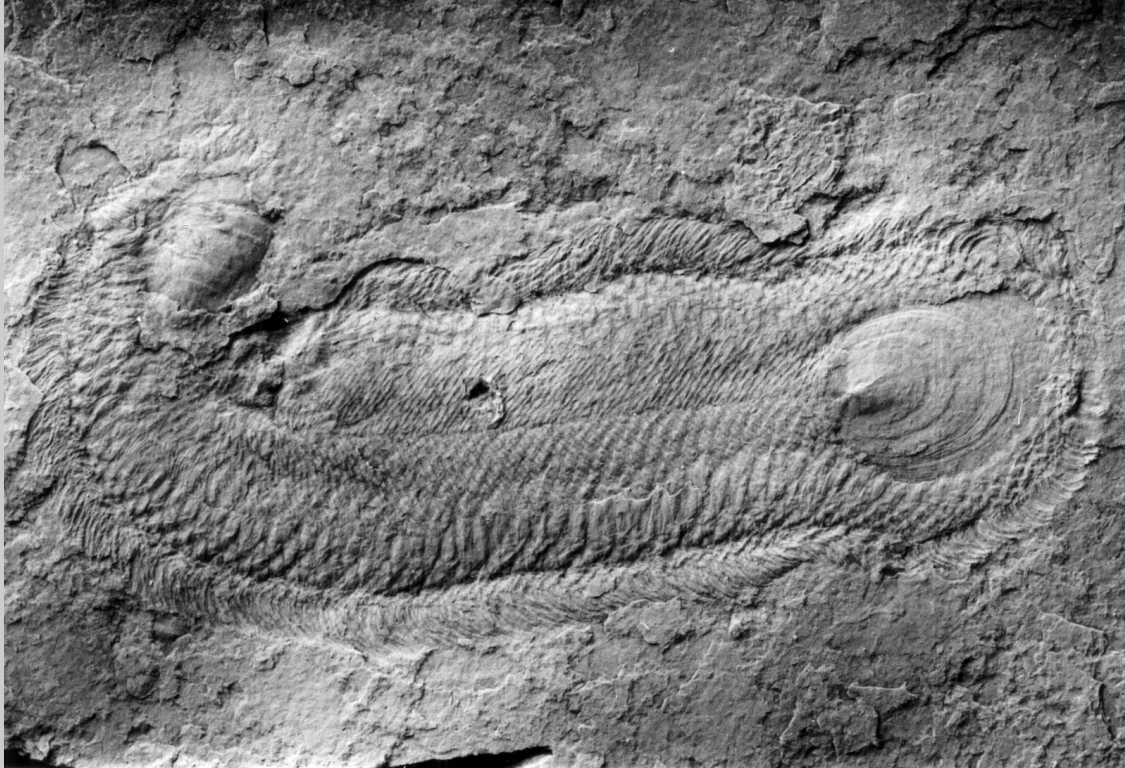


Figure 8 — Fully articulated *Halkieria evangelista* from the Lower Cambrian of Greenland (Sirius Passet Formation). Image courtesy John S. Peel.

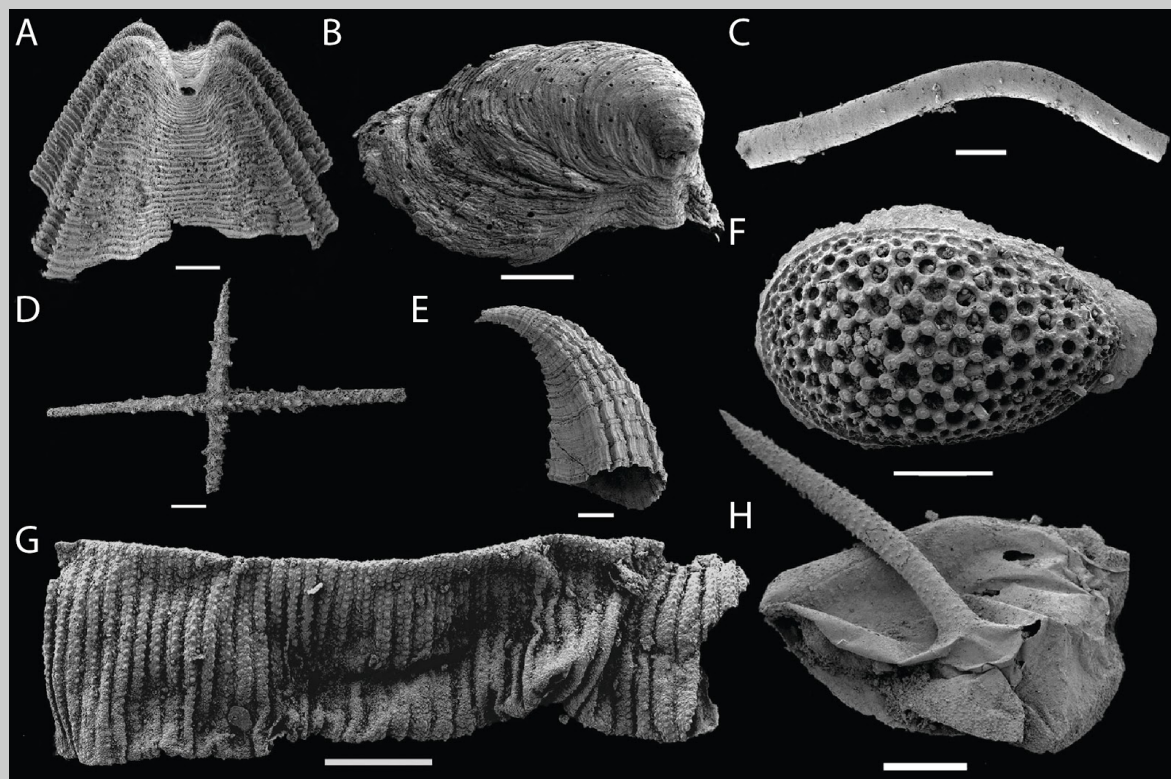


Figure 9 — Scanning electron microscopy of tomotioids and other Cambrian small shelly fossils from South Australia. A. *Daliyatia*, a tomotioid 'problematica'. Relationship to other animals and biology not yet clear. B. *Micrina*, thought to be a stem-group brachiopod. C. *Hyolithellus*, a probable annelid tube. D. Sponge spicule. E. *Lapworthella*, an enigmatic tomotioid of unknown origin. F. *Microdictyon* 'armoured worm' sclerite. G. Palaeoscolecid worm. H. A bradoriid spine from a species called *Mongolitubulus unispinosa*. Scale bars = 200 μ m. Images courtesy Tim Topper.

Another example is the origin of brachiopods (lamp shells), one of the most common fossil groups of the Palaeozoic era (541 million to 252 million years ago). It has been suggested that these animals can be traced back to a certain group of tommotiid small shelly fossils. The primary evidence for this comes from genera called *Eccentrotheca*, *Micrina* and *Tannuolina*, and a few other examples, the so-called Eccentrothecomorphs. These were initially known only from isolated sclerites. When researchers were lucky enough to find a number of well-preserved articulated examples, it became clear that they came from [stem group](#) animals probably related to brachiopods. The tommotiid *Micrina* (Fig. 7, 9B) also has a set of features characteristic to brachiopods, including their mode of growth, overall morphology, shell microstructure, presence of two articulated shell valves and phosphatic shell chemistry. It has been suggested that by studying the SSFs we can begin to reconstruct the evolutionary origins of the brachiopod body plan — albeit in stages, because there seem to be many intermediate forms between tommotiids and brachiopods. Although this view is far from universally accepted, it offers a tantalizing possibility to investigate the origin of a phylum from within the radiation of the small shelly fossils.

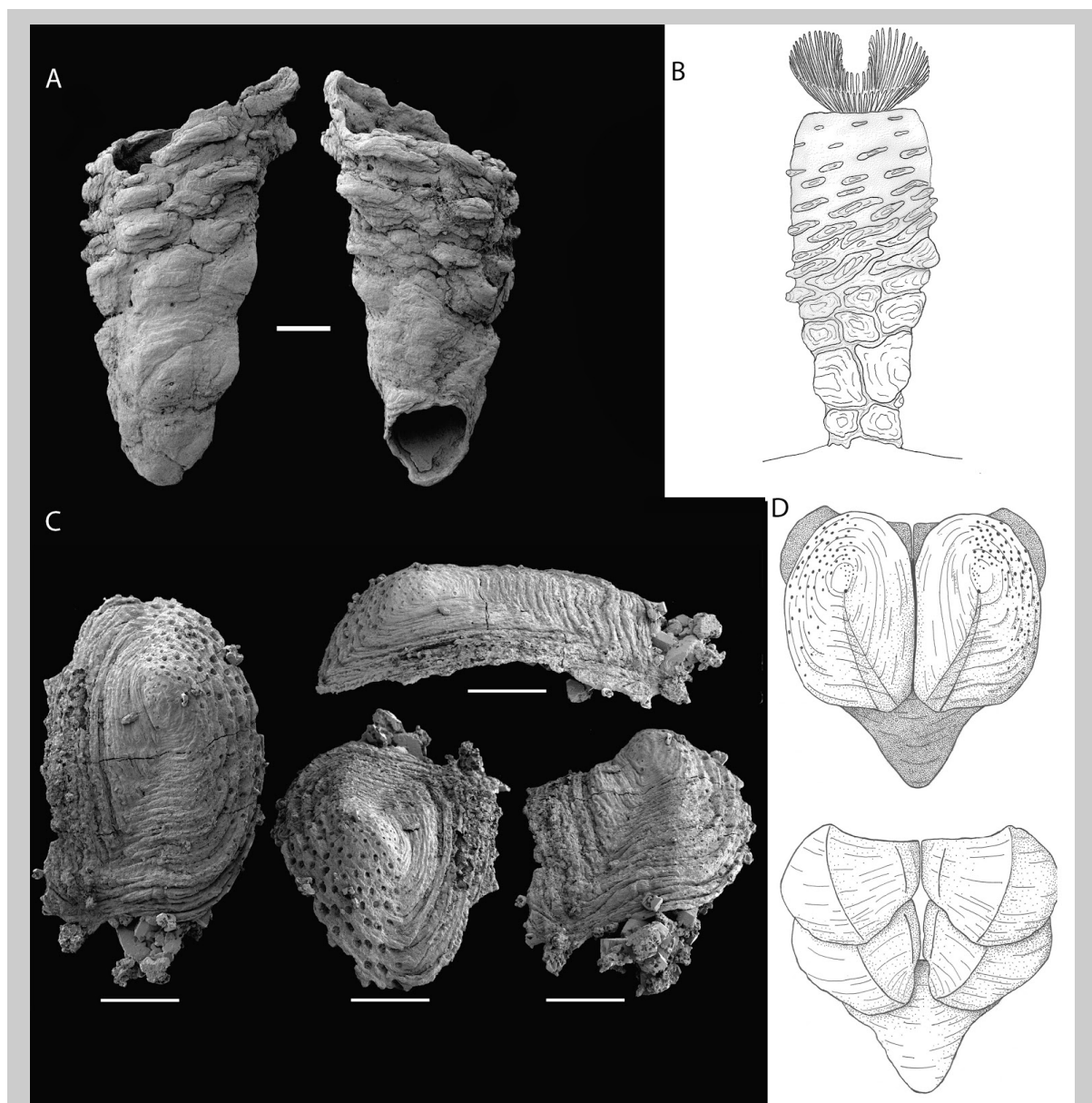


Figure 10 — *Tannuolina* from the Cambrian of Morocco and *Eccentrotheca* from South Australia. A. Rare articulated scleritome of *Eccentrotheca* consisting of many sclerites. B. Reconstruction of whole animal with feeding organ, or lophophore. C. Isolated sclerites of *Tannuolina*. D. Reconstruction of *Tannuolina* based on careful observations of how the sclerites fit together. Images courtesy Christian Skovsted.

One further alternative model has raised the possibility that brachiopods may have evolved through the ‘folding up’ of a slug-like animal similar to *Halkieria*, with opposed shell plates overlapping to form a closed filtration chamber, or in other words the bivalved shell (see Cohen *et al.* in further reading).

A recently described Cambrian filter-feeding animal, *Cotyledion tylodes*, is covered with an outer armour of relatively sparse oval plates (known as sclerites) that also resemble some tomotioid small shelly fossils (Fig. 11). The presence of a scleritome, a skeleton made of isolated elements or sclerites joined somewhat like medieval chainmail, seems to be a common uniting feature of many animal [stem groups](#). The scleritome of *Cotyledion* is most comparable to that of the tomotioid *Eccentrotheca*, but the sclerites differ in structure enough that it is thought not to be a tomotioid. However, the parallel in form and function is striking, and there is probably a close relationship between these fossils.

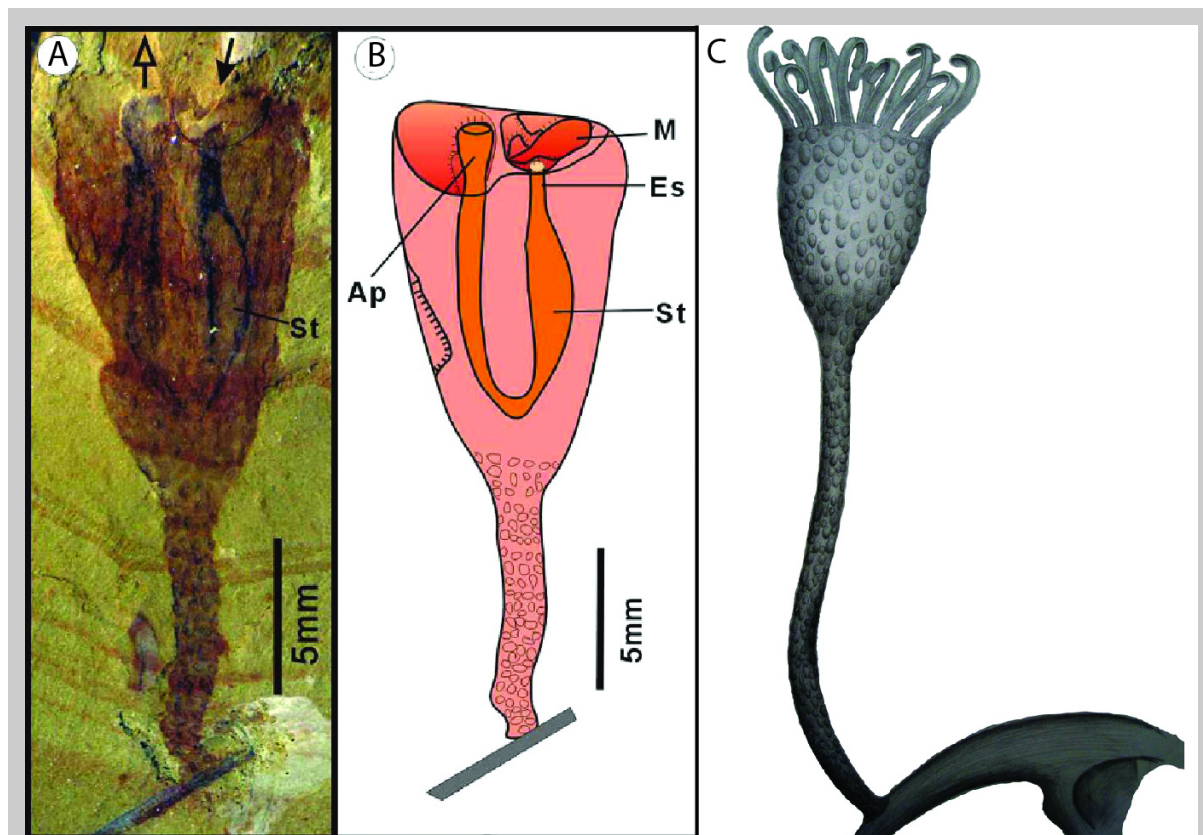


Figure 11 — *Cotyledion tylodes* fossil (A) and reconstructions (B–C) Adapted from Zhang *et al.* (2013). Ap, anal papilla; M, mouth; Es, esophagus; St, distended stomach. Note that the entire body is covered in oval sclerites, like that of *Eccentrotheca* (Fig. 10A).

Some additional SSFs, such as the rather beautiful but problematic *Daliyatia* (Fig. 9A), continue to defy classification, with the scleritome having been reconstructed in contrasting ways. One model suggests that the animal was slug-like, similar to *Halkieria*; another makes it a tube-dweller with a tightly packed scleritome, like *Eccentrotheca* (Fig. 10A, B). Pending the discovery of a complete scleritome or of an exceptionally preserved host animal, the jury is still out as to which of these reconstruction models is correct, if indeed either of them is!

What happens to the SSFs?

The occurrence and diversity of SSFs declines as we move later into the Cambrian. The SSFs are not a [clade](#) or natural grouping, so we cannot say that they became extinct in any meaningful sense. Rather, it seems that they evolved into, and were eventually replaced by, more recognizable forms of the 'Palaeozoic evolutionary fauna' such as brachiopods, bivalves, arthropods and gastropods. As we approach the Ordovician period, most of the remaining small shelly components of the fossil record turn out to be larval gastropods.

What does the future hold?

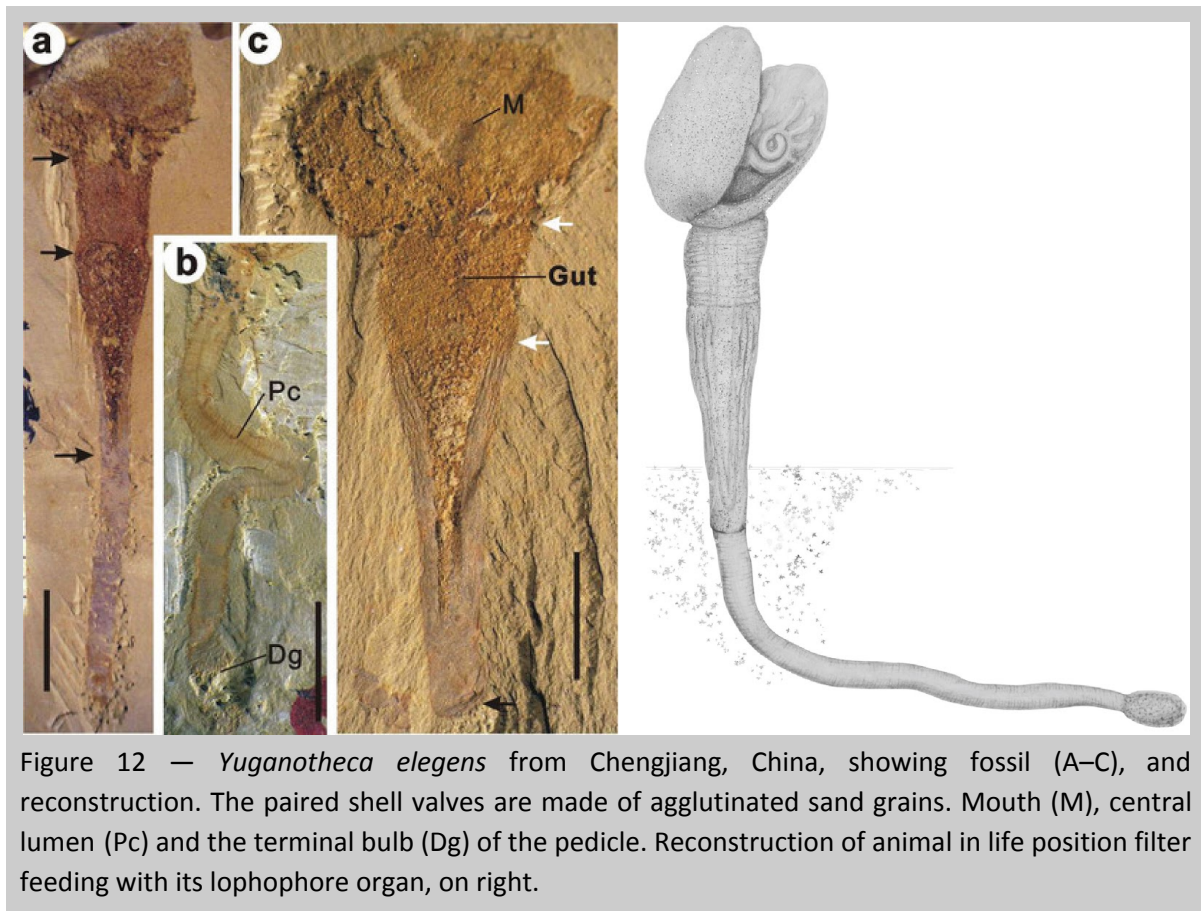
Some SSFs, as we have seen, are identifiable as stem-group animals such as arthropods; others correspond to primitive mollusc shells, brachiopod valves and [annelid](#) tubes or spines. Many more forms remain enigmatic, and for the moment are considered 'problematica', or fossils with an uncertain relationship to other organisms.

Organic parallels to the SSFs have emerged in the record of small carbonaceous fossils, or SCFs. These are another suite of small mysterious fossils, recovered by hydrofluoric-acid processing of shales and mudrocks. The recovered bits of organic material, made from [chitin](#) and other structural polymers, give us further insight into hidden Cambrian diversity. For example, they push back the earliest known mouthparts of some crustaceans by millions of years. These complementary fossil records of early animals help us to flesh out what sort of diversity may have been present early in the history of animal evolution, especially given that SCFs and SSFs preserve in very different environments (deep marine mudstones vs. shallow carbonate rocks, respectively).

New relatives of SSFs may also be discovered in the future, in animals that rely on agglutination (that is, their shells are made from grains of sediment stuck together much like a sandcastle). This is a strategy used by modern annelid worms and Phoronida (horseshoe worms) to build their protective outer living tubes. It may represent an ancient life strategy in some of the earliest animals, including the agglutinated fossils *Salterella* and *Volborthella*. A recently discovered unusual agglutinating fossil organism shows some brachiopod characteristics as well as features of their nearest relatives, the phoronids or horseshoe worms. This organism, *Yuganotheca elegans* from the Chengjiang site of exceptional fossil preservation, suggests that agglutination may have been more widespread in early animals than has been recognized, but this remains very much an open question (Fig. 12).

My personal view of what we can tell from this rich record of seemingly insignificant small fossils is that the appearance of animals happened in a more gradual way than was first thought, with an explosion of fossilization potential happening alongside the huge diversification of life in the Cambrian, a direct result of the evolution of hard parts. Subtle hints from sources such as SSFs, trace fossils and SCFs give us an idea that complex animal life had gained a foothold in the earliest Cambrian and possibly even extended to the late Ediacaran in some more controversial cases (Fig. 2).

In conclusion, the hardest jigsaws are usually the most satisfying to finish. It seems likely that further investigation of the hidden diversity within SSFs will turn up a few surprises and — who knows — perhaps the evolutionary roots of a phylum or two along the way!



Further reading

Cohen, B. L., Holmer, L. E. & Lüter, C. 2003. The brachiopod fold: a neglected body plan hypothesis. *Palaeontology* **46**, 59–65. doi:[10.1111/1475-4983.00287](https://doi.org/10.1111/1475-4983.00287)

Marshall, C. R. 2006. Explaining the Cambrian “explosion” of animals. *The Annual Review of Earth and Planetary Sciences* **34**, 355–384. doi:[10.1146/annurev.earth.33.031504.103001](https://doi.org/10.1146/annurev.earth.33.031504.103001)

Matthews, S. T. & Missarzhevsky, V. V. 1975. Small shelly fossils of late Precambrian and early Cambrian age: A review of recent work. *Journal of the Geological Society* **131**, 289–303. doi:[10.1144/gsjgs.131.3.0289](https://doi.org/10.1144/gsjgs.131.3.0289)

Murdock, D. J. E., Bengtson, S., Marone, F., Greenwood, J. M. & Donoghue, P. C. 2014. Evaluating scenarios for the evolutionary assembly of the brachiopod body plan. *Evolution & Development* **16**, 13–24. doi:[10.1111/ede.12059](https://doi.org/10.1111/ede.12059)

Skovsted, C. B., Clausen, S., Álvaro, J. J. & Ponlevé, D. 2014. Tommotiids from the early Cambrian (Series 2, Stage 3) of Morocco and the evolution of the tannuolinid scleritome and setigerous shell structures in stem group brachiopods. *Palaeontology* **57**, 171–192. doi:[10.1111/pala.12060](https://doi.org/10.1111/pala.12060)

Skovsted, C. B., Brock, G. A., Topper, T. P., Paterson, J. R. & Holmer, L. E. 2011. Scleritome construction, biofacies, biostratigraphy and systematics of the tommotiid *Eccentrotheca helenia* sp. nov. from the Early Cambrian of South Australia. *Palaeontology* **54**, 253–286. doi:[10.1111/j.1475-4983.2010.01031.x](https://doi.org/10.1111/j.1475-4983.2010.01031.x)

Zhang, Z. *et al.* 2013. A sclerite-bearing stem group entoproct from the early Cambrian and its implications. *Scientific Reports* **3**, 1066. doi:[10.1038/srep01066](https://doi.org/10.1038/srep01066)

Zhang, Z-F. *et al.* 2014. An early Cambrian agglutinated tubular lophophorate with brachiopod characters. *Scientific Reports* **4**, 4682. doi:[10.1038/srep04682](https://doi.org/10.1038/srep04682)

¹Uppsala University, Department of Earth Sciences, Palaeobiology, Villavägen 16, SE-752 36, Uppsala, Sweden.