Decoding the fossil record of early lophophorates

Systematics and phylogeny of problematic Cambrian Lophotrochozoa

AODHÁN D. BUTLER
The evolutionary origins of animal phyla are intimately linked with the Cambrian explosion, a period of radical ecological and evolutionary innovation that begins approximately 540 Mya and continues for some 20 million years, during which most major animal groups appear. Lophotrochozoa, a major group of protostome animals that includes molluscs, annelids and brachiopods, represent a significant component of the oldest known fossil records of biomineralised animals, as disclosed by the enigmatic ‘small shelly fossil’ faunas of the early Cambrian. Determining the affinities of these scleritome taxa is highly informative for examining Cambrian evolutionary patterns, since many are supposed stem-group Lophotrochozoa. The main focus of this thesis pertained to the stem-group of the Brachiopoda, a highly diverse and important clade of suspension feeding animals in the Palaeozoic era, which are still extant but with only a fraction of past diversity. Major findings include adding support for tommotiid affinity as stem-group lophophorates. Determining morphological character homologies vital to reconstructing the brachiopod stem-group was achieved by comparing Cambrian Lagerstätten with the widespread biomineralised record of Cambrian stem-brachiopods and small shelly fossils. Polarising character changes associated with the putative transition from scleritome organisms to crown-group brachiopods was furthered by the description of an enigmatic agglutinated tubular lophophorate Yuganotheca elegans from the Chengjiang Lagerstätte, China, which possesses an unusual combination of phoronid, brachiopod and tommotiid characters. These efforts were furthered by the use of X-ray tomographic techniques that revealed novel anatomical features, including exceptionally preserved setae in the tommotiid Micrina. The evidence for a common origin of columnar brachiopod shell structures in the tommotiids is suggested and critically examined. Enigmatic and problematic early and middle Cambrian lophotrochozoans are newly described or re-described in light of new evidence, namely: the stem-brachiopod Mickwitzia occidentes Walcott from the Indian Springs Lagerstätte, Nevada; a putative stem-group entoproct Cotyledion tyloides Luo and Hu from Chengjiang, China; a new enigmatic family of rhynchonelliform brachiopods exemplified by the newly described Tomteluva perturbata from the Stephen Formation, Canada; and the tommotiid Micrina etheridgei (Tate) from the Flinders Ranges, South Australia. Cladistic analyses of fossil morphological data supports a monophyletic Brachiopoda.

Keywords: Brachiopoda, Chengjiang, Lagerstätte, Cambrian Explosion, palaeobiology, stem-group, entoproct, phoronid, tommotiid, exceptional preservation

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For my family
This thesis is based on the following papers, which are referred to in the text by their Roman numerals.


The following popular science article was prepared during the PhD and is included in the kappa, but is not a part of the thesis.

Additionally, the following papers were prepared during the course of the PhD but not included in the thesis.


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**Statement of authorship**

- Paper I and Paper II: A. Butler analysed the material, interpreted the results and wrote the MS with input from all authors.
- Paper III: A. Butler produced, analysed the CT data and shared writing.
- Paper IV: A. Butler performed cladistic analyses of data, helped with interpretations of fossils and shared writing.
- Paper V: A. Butler assisted with discussion and analysis of these fossils and shared writing.

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Introduction

The Cambrian as a period of profound biological and geological change.

For the majority of geological time on Earth, biological processes have been in effect. The appearance of complex multicellular life that characterises the biosphere of the Phanerozoic Eon on the other hand, has a relatively recent origin. The first putatively metazoan fossils from the Ediacaran biota that appear approximately 580 Ma ago (Narbonne & Gehling, 2003) have remained enigmatic since their discovery and despite much speculation no convincing argument to link them with bilaterian or diploblastic metazoans sensu stricto has been forwarded to date. It is not until we search well into the Cambrian (Stage 2) that direct body fossil evidence for animals in a recognisable sense emerges, although signs of conspicuously metazoan activities much earlier than this are disclosed by the trace fossil record of trackways, burrows (Mángano & Buatois, 2014) and faecal pellets, in addition to inference of molecular clock estimates (e.g., Jensen et al., 2005; Marshall, 2006; Maloof et al., 2010). These findings imply the metazoan and bilaterian body plan had evolved, and was present before evidence of it was preserved in the body fossil record. This thesis focuses on the morphology, phylogeny and evolutionary significance of early lophotrochozoans, a major clade of bilaterian animals whose fossil record spans from the present to the earliest evidence of biomineralised animals in the early Cambrian.

The most conspicuous evidence of the Cambrian explosion is apparent in the rapid appearance of almost all known animal phyla (Conway Morris, 1989) and the diversification of biomineralised organisms and their easily fossilisable skeletal remains that dominate the subsequent fossil record of the Phanerozoic. An almost-simultaneous appearance of predatory (i.e. mineralized mouthparts such as teeth) and defensive hard tissues (i.e. spines and armoured shells) is evident across a broad range of animal groups (Murdock et al., 2011). Further evidence of the Cambrian radiation is disclosed by fossil Konservat-Lagerstätten that retain exquisitely preserved soft-tissues and provide a window into the ecology and detailed anatomy normally absent from the fossil record resulting from the normal processes of death, decay and biological recycling. Precisely why the Cambrian explosion occurred is a topic of seemingly endless debate within paleontological research. Explanatory processes for the onset of the Cambrian explosion are
manifold and are roughly divided between the camps suggesting abiotic physical drivers and on the other hand those highlighting biological innovation as the main driver. Physical mechanisms suggested have ranged from: rising oxygen levels (Chen et al., 2015), shifts in ocean chemistry from weathering (Peters & Gaines, 2012), to transgressive sea level changes providing suitable habitats (Dalziel, 2014). Biological explanations have included: increases in genome size (Li & Zhang, 2010), the onset of predator/prey interactions (Bengtson, 2002) which in turn were facilitated by morphological innovations such as vision, brains and the through gut (Nielsen & Parker, 2010).

A further possibility is raised that the Cambrian explosion is an artefact of reading the imperfect fossil record (an inherently biased source of data) in a literal sense. Runnegar (1982) posed the question whether the Cambrian explosion was an explosive event of metazoan evolution (representing a real diversification event), or rather an explosion of fossilisation potential driven by the innovation of biomineralised skeletons. As of yet, no single causative factor provides a satisfactory explanation as a triggering event for the ‘Cambrian explosion’, rather, it is likely that a complex series of related biotic and abiotic interacting processes and feedback loops are in effect at this time (Smith & Harper, 2013).
Figure 1. Diagrammatic timescale illustrating fossil record of early complex and skeletonised metazoan animals, in addition to proxy measures (i.e. trace fossils) after Marshal (2006)

A further caveat to interpreting patterns of evolution associated with the earliest Cambrian is that the fundamental basis of stratigraphic correlation has as of yet not been agreed upon by the ISCS (International sub-commission for Cambrian stratigraphy). This is a consequence of long standing issues with satisfactorily correlating and designating type sections for regional stratigraphic sub-divisions into a global timescale, thus the precise chronological position of many faunas of palaeobiological significance remains uncertain. The timescale in Fig. 1 refers to the Siberian nomenclature (from which a significant body of SSF’s have been described) and provisional subdivisions as proposed by the ISCS (see also Fig. 5).

Lee et al. (2013) inferred relatively rapid rates of molecular and morphological evolution for arthropods during the Cambrian as compared with later times, regardless of whether the length of the diversification event was re-
stricted to the early Cambrian or telescoped back into the late Ediacaran with
a large missing fossil record sensu Erwin et al. (2011) as has been inferred
from molecular clock estimations. This pattern of rapid evolution associated
with the Cambrian radiation remains to be tested in a similar fashion for
other clades. Although the diversification and biomineralisation of lopho-
trochozoans is seemingly earlier than that of arthropods (Kouchinsky et al.,
2012), if this is indeed demonstrably the case, this places a constraint on
simultaneous common causative mechanisms as synchronous drivers of the
Cambrian explosion (Lee et al., 2013).

Introduction to Lophotrochozoa/Spiralia

Lophotrochozoa (or Spiralia) represents one of the major clades of bilaterian
protostome animals encompassing many familiar animal groups such as
annelids, molluscs and brachiopods and many less well recognised ‘minor’
phyla, i.e. Platyhelminthes, Cycliophora, Rotifera and Gnathostomulida (Fig.
2). Despite the myriad advances in phylogenetic reconstruction enabled by
the advent of molecular systematics the relationships of Spiralia are among
the most-problematic and least well resolved groupings within the animal
tree (Dunn et al., 2014). Indeed even the name of the clade is debated, de-
pending on the placement of taxa within the tree of spiralian, Lophotrocho-
zoa, defined as a clade composed of Mollusca, Annelida, and Lophophorata
(Halanych et al., 1995), is either a subclade of Spiralia (Nesnidal et al.,
2013; Fig. 2 right) or a synonym of Spiralia (Dunn et al., 2014) (Fig. 2 left).

Figure 2. Patterns of conflicting phylogenetic signal within spiralians in phylo-
genomic and molecular systematic analyses (Dunn et al. 2014, fig. 2d).

The main focus of investigation within this thesis centres on the spiralian
sub-clade Lophophorata (Hyman, 1959), organisms united by the synapo-
morphies of a horseshoe shaped tentacular ciliated feeding apparatus, the
lophophore that surrounds the oral opening and the epistome, a lobe-shaped structure covering the mouth. Although this clade is contradicted in a number of molecular analyses (Fig. 2 left; Hejnol et al., 2009) a monophyletic Lophophorata is recovered in later analyses (Nesnidal et al., 2013) and the conflict between morphology and the molecular data is apparently an artefact of systematic error related to nucleotide compositional bias, thus rejecting the ‘polyzoa’ hypothesis. With the implication from this that phoronids are not derived from brachiopods and have not secondarily reduced their shell contra Cohen (2000) and Balthasar & Butterfield (2009)

While the indications are that lophophorates are a monophyletic clade (Nesnidal et al., 2013; Laumer et al., 2015) constituent lineages of Lophophorata, namely Phoronida, Brachiopoda and Ectoprocta (Bryozoa) as of yet remain unresolved in their phylogenetic position with regard to each other. As a further complication whilst Brachiopoda possess an extremely abundant fossil record tracing back to the early Cambrian, a consequence of both their biomineralised skeleton and ecological success through the Phanerozoic, ectoprocts and phoronids have a much sparser appearance in the fossil record with large ghost ranges and only recently a prospective Cambrian occurrence of both groups being suggested (Landing et al., 2015; Zhang et al., 2014; Zhang & Homer, 2015) and not without controversy in the case of the Bryozoa (Ma et al., 2015; Taylor et al., 2013) with the oldest non-disputed occurrence of bryozoans dating from the lower Ordovician.

A primary focus of this thesis, brachiopods, were among the most bio-diverse and abundant Palaeozoic groups of animals and were a major component of benthic marine ecosystems. The dramatic disappearance of many major brachiopod clades at the end-Permian extinction event however ended their dominance, they never fully recover in terms of diversity in later periods of earth history. A pattern still evident today, since their extant diversity is a highly pruned remnant when compared with extinct clades. As a result of their past abundance, biomineralised shell with high fossilisation potential and cosmopolitan distribution, brachiopods possess one of the highest fidelity fossil records in terms of completeness and stratigraphic congruence of any major fossil animal group (Foote and Sepkoski, 1999).

Morphology and the pattern of relationships derived from it in the form of cladistic analyses, have found brachiopods to be monophyletic in an almost universal fashion (Hennig et al., 1966; Rowell, 1982; Carlson, 1995; Holmer et al., 1995; Williams et al., 1996). The exact nature of internal relationships remains much debated however, for example, the monophyly, or not, of craniids plus linguliforms (‘Inarticulata’) and their relationship with articulated brachiopods (Rhynchonelliformea) (Fig. 3). Molecular analyses however, have been in conflict with the signal from morphology, Housekeeping gene based phylogeny found phoronids, non-biomineralised lophophorates usually considered a sister group of lophophorates with regard to brachiopods, in fact belong within the Brachiopoda as sister group to the inarticulates (Fig.
Sperling et al. (2011) made the observation that a paraphyletic brachiopod tree is consistent with the same unrooted dendrogram as for a monophyletic Brachiopoda. Recovering paraphyly of brachiopods in ribosomal trees was inferred to be the result of a long-branch attraction artefact caused by rapid rates of evolution in Rhynchonelliformea when compared with other brachiopod clades. The main issue with resolving brachiopod (and lophophorate) phylogeny is therefore likely a rooting problem (Fig. 3A-B).

Evolution of the Lophophorata: brachiopod origins

Brachiopods are unique in that they are one of the few clades of bilaterian animals in which higher-level relationships are characterised by biomineralised shells of differing biomineral types i.e. calcium carbonate as calcite or calcium phosphate in the form of apatite. However, the myriad patterns of relationships proposed for the major lophophorate groups consequently imply a number of significant evolutionary events relating to, for example, the evolution of the biomineralised shell. Some of these include: the independent evolution of the bivalved shell in sister linguliform and rhynchonelliform brachiopod clades i.e. convergence on the brachiopod body plan (Wright, 1979; Valentine, 1973; Gorjansky & Popov, 1986; Skovsted et al., 2009a; 2011), transitions between biomineralised shell chemistries (Balthasar et al., 2009; Carlson, 1995; Williams & Carlson, 2007) (Fig. 3), or secondary loss of the brachiopod shell and biomineralisation in the phoronid stem-lineage, thus making phoronids, in effect, ‘naked’ brachiopods (Cohen, 2000; Balthasar & Butterfield, 2009) (Fig. 3B).

An enigmatic group of phosphatic early Cambrian fossils known as tommotiids have been proposed as a stem-lineage to Brachiopoda, if this is indeed the case, then an ancestral phosphatic shell for brachiopods is therefore implied. Although phosphatic brachiopods were thought to have appeared first (Williams & Rowell, 1965) both phosphatic and calcitic early stem-brachiopods are now known from essentially coeval strata, corresponding to Cambrian Stage 2, (Kouchinsky et al. 2012) or possibly even older strata. A tommotiid origin then also presents the evolutionary scenario of the bivalved crown-brachiopod body plan emerging from early Cambrian tube-dwelling scleritome animals (Holmer et al., 2002; 2008a; 2011; Williams & Holmer, 2002; Skovsted et al., 2008, 2009a, 2011; Balthasar et al., 2009) (Fig. 4).

A ‘tommotiid origin’ model would suggest that these lower Cambrian phosphatic fossils form a paraphyletic stem-lineage to Brachiopoda, with calcitic mineralogy evolving convergently in Rhynchonelliformea and Craniiformea (Holmer et al., 2002, 2008a, 2008b, 2011; Williams & Holmer, 2002; Skovsted et al., 2008, 2009a, 2011; Balthasar et al., 2009). A number of morphological investigations in a cladistic framework have suggested
however, that the tommotiids may be a stem-group of the inarticulate phos-
phatic clades, rather than a stem-group to all brachiopods (Carlson, 2009) 
(see also Fig. 9) although it should be stressed that these findings are prelimi-
inary at best.

One potential avenue for a resolution of brachiopod and lophophorate rel-
lationships comes from fossil evidence that can detail the sequence of char-
acter acquisition and correctly determine the polarisation of crown and stem-
group characters (Smith, 2005; Edgecombe, 2010). Stem-group fossil taxa, 
have proven vital in constructing the evolutionary history of many clades 
due to the presence of novel character combinations not seen in extant repre-
sentatives, thus are vital when homology assessments are evaluated (Patter-
son, 1981; Budd & Jensen, 2000; Gauthier, 1988; Edgecombe 2010).

A prime example described in this thesis is of the enigmatic organism 
Yuganotheca elegans (paper IV) as it seemingly possesses characters of 
both brachiopods and phoronids.
Small shelly fossils and their phylogenetic implications for lophophorate origins

The first evidence of skeletal putative bilaterians are recovered from the extensive variety of phosphatised problematic sclerite-bearing taxa so called ‘small shelly fossils’ (Matthews & Missarzhevsky, 1975), a major component of the early biomineralised fossil record of the ‘Cambrian explosion’. The first reported occurrences of tommotids predate the estimated base of the Cambrian Stage 2 (Fig.1) (c. 530 Ma) in Avalonia (Landing et al., 2007; Kouchinsky et al., 2012). Sepkoski (1992) recognised “Tommotian” organ-
isms as an evolutionary group distinct from his Cambrian fauna *sensu stricto*. The disappearance of many tommotiid taxa during the end-Botoman extinction event marks the transition from fossil biodiversity dominated by biomineralised small shelly ‘problematica’ to the more recognisable (i.e. crown-ward) Cambrian organisms such as brachiopods, trilobites and molluscs.

To date these have remained chronically understudied in terms of the evolutionary significance of constituent organisms of these small shelly faunas. Although their relationships are beginning to be understood by the use of the stem and crown-group distinction (Budd & Jensen, 2000). In particular, large numbers of putative lophotrochozoans (i.e. annelids, brachiopods, molluscs and their close relatives) have been described, although their phylogeny is poorly resolved. A central research theme of this thesis (*papers I, II, IV and V*) is to move towards a more complete understanding of these enigmatic Cambrian faunas and their evolutionary significance, in particular the relationship of tommotiids to the stem-group brachiopods.

*Figure 4.* Purported phylogenetic relationships of small shelly tommotiid taxa with crown brachiopods and phoronids. The ‘tommotiid origin’ hypothesis after Williams & Holmer (2002), Skovsted *et al.* (2009c, 2011), Holmer *et al.* (2008a) and Zhang *et al.* (2013, 2014) *papers IV–V*. 

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Fate of the Small Shelly Fossils

The abundance and diversity of SSFs decline during a major extinction event at the end Botoman (Porter, 2004) they then progressively disappear later in the Cambrian. Since most SSFs do not form a clade or natural grouping, we cannot say that they became extinct in any meaningful sense. Rather, it seems that they evolved into, and were eventually competitively replaced by, more recognisable forms of the classic ‘Palaeozoic evolutionary faunas’ such as brachiopods, bivalves, arthropods and gastropods. This pattern can be reconciled with the fact many small shelly fossils form stem-groups of recognisable Cambrian and later clades e.g. cap shaped fossils and helcionellids with molluscs, protoconodonts as stem-Chaetognatha (Szaniawski, 2002). An aspect of typological thinking sensu Mayr (1970) also factors in here since many stem-group animals do not fit into recognisable groups they are dubbed ‘problematica’ and treated as ‘waste-basket’ taxa and thus not informative in the context of known animal diversity, the case with many small shelly fossils e.g. *Dailyatia*. When their affinity can be established these animals become allied to a known group and thus escape the wastebasket designation as a SSF, e.g. the sclerites of lobopods and halkierids that were placed in context as stem-ecdysozoans and molluscs.
Aims of this thesis

The early Cambrian is clearly a critical time interval for understanding the origin and evolution of metazoans. Nowhere is this more apparent than in the case of the Lophotrochozoa, whose origins are long suspected (Conway Morris, 2006) of being intimately linked with the ‘Cambrian explosion’. Less clear, however, is the precise significance of many enigmatic early Cambrian fossil ‘problematica’ (e.g. many small shelly fossils) that have been described as potential stem-group members of lophotrochozoan clades, but have evaded a solid placement in terms of their phylogenetic and consequently, evolutionary significance.

The overall aim of this thesis is to clarify the nature of this purported early origination and radiation of this major animal group. This was tackled through the following objectives.

- Description of novel fossil species of suspected phylogenetic significance, from exceptional faunas and normally preserved biomineralised fossils, expanding the known diversity of Cambrian early animals (Papers I-V).
- Critical examination of the purported link between tommotiid small shelly fossils and Brachiopoda through comparative anatomy (Paper II).
- Searching for possible character homologies that link candidate lophophorate stem-group taxa (Papers I, II, IV and V).
- Establishing a cladistic framework to test the hypothesised phylogenetic significance and affinity of these lophophorate ‘problematica’ (Papers IV and V)
- Making the significance and findings made in the course of this research accessible to the wider public beyond a technical scientific audience (Palaeontology online article).

Methodological advances through the utilisation of microtomographic techniques are central to the achievement of the fossil description efforts (papers II and III) and retrieving novel character data through in depth anatomical investigation.

The ultimate synthesis of these research efforts attempts to provide an integrated framework from which to understand the early evolution of lophophorate animals.
Significance of Cambrian exceptional faunas

Taphonomy and preservation

An infamous quip from the late Adolf Seilacher “Here we have a fossil: what went wrong?” (Sperling, 2013) elegantly sums up the seeming paradox of fossilisation and even more so, exceptional preservation of soft tissues. The act of fossilisation is an escape of a biological entity from the normal cycles of death, decay, ecological recycling, and into the geological record (Briggs, 2003; Sperling, 2013). Since biomineralised anatomy is more favourably predisposed to entering the rock record it must be recognised that that these shells, bones and teeth present a fundamentally biased (though extremely useful) window into the palaeobiology of fossil organisms. The Cambrian fossil record is deeply biased in favour of shelly fossils, a pattern we can infer from exceptionally preserved Burgess Shale and Chengjiang biotas, where the vast majority of taxa and individuals present are soft bodied (Conway Morris, 1986). Exceptional faunas thus give a ‘snapshot’ of the normally missing soft-bodied component of palaeodiversity in typical fossil assemblages of biomineralised organisms.

Incidences of exceptional soft tissue preservation in the Cambrian are anomalously common when compared with later geological periods, some possible explanations include: the unique ocean chemistry of the Cambrian, a possible consequence of through guts increasing the fossilisation potential of bilaterian animals (Butler et al., 2015) and a lack of bioturbators (Orr et al., 2003) that subsequently close the Cambrian Lagerstätte window. Gaines et al. (2012) however surmised that bioturbation alone could not account for the apparent loss of Burgess Shale-type preservation from the fossil record. Instead benthic anoxia, that is implied to have been widespread, and possibly other related geochemical factors enabled the spike in occurrence of exceptional preservation in the Cambrian. In the earliest Cambrian, the BST window is absent in strata predating the Attabanian (Budd, 2003) and aside some isolated examples such as Markuelia and Olivooides (Dong et al., 2013; Steiner et al., 2014), exceptional faunas in the Fortunian and Cambrian Stage 2 are all but absent.

Much of the current knowledge of stem-group animals in the critical phase of the early evolution of many phyla during the Cambrian radiation is based upon fossils described from these sites of exceptional preservation. A few of the more well-known include the Burgess Shale, Sirius Passet and...
Chengjiang sites from which a plethora of bizarre and evolutionary critical fossils have been described. These include stem members of Arthropoda, Echinodermata, and Chordata (Budd, 2008) all of which have radically shaped evolutionary thinking in these clades. Exceptionally preserved fossils have also enabled the resolution of seemingly insoluble palaeontological dilemmas including: the nature and reconstruction of the halkierid and lobe-pod animals known only from isolated sclerites until the complete animals were discovered with sclerites in-situ. Linking the comparatively rich record of biomineralised animals with exceptionally preserved examples of the same species allows us to more towards a more complete palaeobiological understanding of the anatomy, ecology and life history of these often enigmatic animals e.g. paper I.

Following in a similar vein of investigation, new exceptionally preserved lophophorate fossils are a central focus and are featured in all but one of the papers presented in this thesis (papers I, II, IV and V).
Figure 5. Relative timescale and stratigraphic position of described material from this thesis and major early Cambrian events. Generated with TimeScale Creator, based on The Cambrian, Geologic Time Scale 2012 (Peng et al., 2012). A, Tomteleija perturbata (paper III) B, Mickwitzia occidens (paper I) C, Yugaonotheca elegans and Cotyledion tylodes (papers IV-V). D, Micrina etheridgei (paper II).

Indian Springs Lagerstätte: Mickwitzia from Nevada

The fauna of the Indian Springs locality (paper I) presents a window of exceptional soft tissue preservation, in this case containing mickwitziid stem-group brachiopods that occur alongside a rich Lagerstätte fauna including arthropods, sponges and hyoliths (English & Babcock, 2010). The records of Mickwitzia with exceptional preservation from this location are significant in that they closely resemble the Chengjiang organism Heliomedusa and provide the first incidence of exceptional soft-tissue preservation that supports a close affinity of these taxa, the resemblance is strong enough that we suggest synonymising these taxa into a single genus in a future taxonomic revision. A further unique feature of the Indian Springs locality is that it
contains *Mickwitzia* from contrasting carbonate and mudstone depositional environments allowing us to directly compare the taphonomic effects on preservation of both biomineralised components of the organism and their soft part anatomy in both settings. With original shell material being well preserved in carbonate levels, whilst being dissolved or weathered away in shale settings where soft-tissue preservation occurred. Implications of these findings serve to inform further descriptions of similar organophosphatic lophotrochozoan fossils from the Cambrian (*paper I*). This part of project in particular re-examines the phylogenetic importance of soft anatomy and shell structure within the putative brachiopod upper stem group Mickwitziidae; another is to critically examine the record of other phosphatic lower stem group brachiopods and brachiopod-allied problematica, with the eventual aim of clarifying their relationships to the known record of Cambrian Lophotrochozoa.

### Chengjiang Lagerstätte stem-lophophorates

Continuing on the theme of stem group lophotrochozoans, two enigmatic taxa are also described from collaborative research efforts on the Chengjiang Lagerstätte. The first of these *Cotyledion tylodes* is reinterpreted here as a stem-group entoproct (*paper V*). Interestingly this organism bears sclerites on its external surface in a similar fashion to tommotiids and other enigmatic stem-group Cambrian Lophotrochozoa. Comparative homology assessments with the scleritomes of organisms such as *Eccentrotheca*, *Paterimitra*, *Sunnaginia*, *Micrina* (*paper II* and figured on cover), and *Lapworthella* make the case for an expansive grade of stem-lophotrochozoan allied taxa. Evaluating hypotheses of tommotiid relationships from the perspective of a cladistic approach has to date only been preliminary (Murdock *et al*. 2014), and this is addressed in *papers* (IV-V), in which a subsequent attempt to address this issue is presented.

The second organism described from the Chengjiang locality *Yuganotheca elegans* (*paper IV*) is a profoundly strange animal that displays a novel intermediate morphology, only parsable in a phylogenetic context when viewed through the lens of a stem-group affinity (i.e. a way of reconciling the combination of phoronid and brachiopod characters) since it fails to fit into a single extant clade of lophophorates satisfactorily, rather retaining diagnostic characters of both.

### Early Cambrian exceptional preservation

Exceptional preservation of fossils prior to the Atdabanian (Stage 3) is all but absent, excepting a limited number of small embryonic animals that in-
clude *Olivoooides* and *Markuelia* (Bengtson & Zhao, 1997). *Olivoooides* was later identified as a likely cnidarian scyphozoan stem group member (Dong *et al*., 2013), or cycloneuralian (Steiner *et al*., 2014) while *Markuelia* was interpreted as a stem-scalidophoran or a stem-priapulid (Dong *et al*., 2010).

It is interesting to note that thus far the only examples of Cambrian Stage 1-2 Lagerstätten are small Orsten-type phosphatised fossils. The observation of phosphatised soft anatomy in the form of setae and the probable secreting follicular cells in the tommotiid *Micrina etheridgei* (*paper II*) is of significant interest. The character is of intrinsic value in reconstructing the phylogeny of stem-lophophorates but also implies that similar cryptic soft tissue preservation may be present in other small shelly fossils and assemblages of a similar or older age. The potential to gain access to novel soft-part morphological data in stem-group animals from the Tommotian or earlier would be a hugely important advance in Cambrian palaeobiology with implications for early animal evolution.

The taphonomic implications of finding soft-tissue from an otherwise relatively ‘normal’ fossil deposit opens the potential to find soft tissues in other tommotiids. This is an exciting new possibility for trying to solve the position of these early Cambrian problematica.
X-ray Microtomographic techniques: a novel tool in recovering character data from early Cambrian lophophorates

Little was known about the internal structure and anatomy of most small shelly fossils, and what was understood had been gathered through random breakage of the fossil, exposing fortuitous surfaces of interest, or by destructively grinding samples into thin sections and analyses by light and electron microscopy. Recent advances in virtual palaeontological techniques (Sutton et al., 2014) have enabled researchers to move beyond these limitations and similar efforts have revolutionised the study of many fossil groups e.g. arthropods from the Silurian Herefordshire Lagerstätte (Sutton et al., 2001). The advent of 3D virtual-palaeontological techniques has been revolutionary in allowing researchers to examine fossil organisms internal structure in great detail and often non-destructively. Building on the initial success of tomographic studies on Cambrian and pre-Cambrian problematica, including a number of small shelly fossils (Murdock et al., 2012) further application of these techniques was explored in this thesis to gain new data on early lophophorates.

In brief, CT techniques involve rotation of a specimen between an X-ray source and detector and taking a sequential series of images or projections. The projections are analysed with tomographic reconstruction algorithms to produce a serial sequence of slices. These slice datasets are reconstructed into a 3D model with this thesis either volumetric rendering in the Drishti package (Limaye, 2012), the most computationally intensive approach that renders every voxel, or alternatively a polygon surface mesh based approach in the SPIERS package (Sutton et al., 2012).

To collect the tomographic data a suite of different scanning hardware was employed, depending on the size, composition and resolution required for each sample. Large fossils and those still embedded in matrix were scanned in a Nikon Metris 225/320 kV X-ray CT system in a customised bay, smaller samples for high resolution tomography were scanned on an Xradia MicroXCT-200 system. Scans of selected fossils were also performed within the TOMCAT synchrotron beamline at the Swiss Light Source.
The investigation of fossils through the use of X-ray computed tomography enabled visualization of the detailed anatomy of a number of early Cambrian lophotrochozoan organisms namely *Micrina* (**Paper II**, Fig. 6), *Heliomedusa* and the new taxon *Tomteluva* (**Paper III**). Since the primary research goals of this thesis were focused on the search for putative morphological homologies and characters of phylogenetic utility in members of the stem-brachiopods and allied lophophorates, the comparative datasets derived from these scans were of great utility in furthering this objective. After acid processing to facilitate removal from the host carbonate rock, phosphatic small shelly fossils are well suited to investigation with tomographic techniques as a result of the high density contrast between the phosphatic skeleton and air spaces vacated by the dissolution of carbonate matrix.

*Figure 6. Examples of tomography derived virtual ‘slices’ from the tommotiid *Micrina* in transverse and planar orientations, lamellar phosphatic fabric of high density is bright. Features visible include setal canals and perpendicular columns D-E (**paper II**).*

Experimental scanning of exceptionally preserved pyritised fossils of *Heliomedusa orienta* from Chengjiang also proved extremely successful, unexpectedly, with recovery of 3-dimensional soft tissue anatomy from within samples otherwise not exposed by standard mechanical preparation techniques (Fig. 7B). This is a significant advance in non-destructive imaging of these evolutionary important fossils revealing detailed anatomy including the lophophore, gut, mouth, and mantle and associated internal organs. The stem brachiopod *Heliomedusa orienta* (Fig. 7A, B) was also scanned at the TOMCAT beamline at SLS revealing for the first time the interaction of tangential to shell surface pyritised setae, and also conical structures perpendicular to the shell surface that resemble the inward pointing cone diagnostic character of the genus *Mickwitzia* (**Paper I**). This provides strong evidence
*Heliomedusa* is a mickwitiid and thus its exceptionally preserved soft anatomy can be used to infer the palaeobiology of other closely related species.

*Figure 7.* Examples of CT scans and reconstructions. B, *Heliomedusa* a probable mickwitiid showing marginal setae, mantle tissue, visceral area and lophophore. Tubular structure to left is likely an attached scyphozoan similar to *Byronia*. Scale bar = 1mm. (A: light photograph of same specimen). C, Silicified *Tomteluva pertubata* ([paper III](#)) with internal anatomy visible. Scale bar = 500µm (1, 4) and 100µm (2-3). D, *Micrina etheridgei* with setal canals visible by reducing opacity of the shell surface during volume rendering. Scale bar = 500µm ([paper II](#)).

In [paper III](#) the description of *Tomteluva pertubata* is greatly aided with the use of tomography to reveal the delicately preserved internal anatomy of silicified fossils from the Stephen Formation and enable the direct comparison with similarly aged enigmatic brachiopod fossils, the naukatids.
Phylogeny of early lophophorates

Influence of fossil organisms and stem-groups for phylogenetic reconstruction

“Fossils matter first and foremost as samples of morphology that would not otherwise be known.” Edgecombe, (2010).

Much progress has been achieved in understanding the origin of major clades of metazoan life in and around the Cambrian explosion. Of particular utility has been the recognition of the unique position occupied by species present at this time interval, most evidently when the principles of the stem- and crown-group concept are applied to the seemingly bizarre collection of problematic taxa of uncertain biological affinity (Budd & Jensen, 2000; Budd, 2008).

The bold conjecture of Patterson (1981) that fossil data could have no influence on reconstructions of phylogeny of extant organisms, more specifically as a consequence of their incompleteness (Ax, 1987) has since been overturned in a number of real world datasets of diverse clades including amniotes (Gauthier et al. 1988) and crustaceans (Huelsenbeck, 1991). Furthermore, fossils have been demonstrated as being able to break long-branches and resolve character conflicts (Forey & Fortey, 2001; Smith, 1998) especially in clades where living diversity is highly pruned. Brachiopoda is a prime example of this pattern, thus fossil data are of particularly high importance when attempting to reconstruct brachiopod phylogeny. Fossils also have the power to remedy a hugely significant misleading systematic artefact, namely long branch attraction (Felsenstein, 1978) when constructing phylogenetic hypothesis, by breaking long branches with intermediate fossil derived morphological transformations.

Fossils are a direct source of temporal data for evolutionary events, and in a phylogenetic sense, that data is accessible only through the morphology of an organism. Fossils also sample less-derived character states (plesiomorphies) as well as morphological variation otherwise pruned from the record of extant diversity by extinction (Edgecombe, 2010).

One such group that has proved particularly elusive in terms of its biological affinity is the purported stem-group brachiopods. For example those affiliated with the family Mickwitziiidae and their purported close relatives
within the tommotiid small shelly fossils (Williams & Holmer 2002; Skovsted et al., 2008, 2009a, 2009b, 2009c). It has been suggested that SSFs are a vital link in the series of character acquisitions involved in assembling the brachiopod plan (Skovsted et al., 2008), although this interpretation has been questioned in recent times (Murdock et al., 2014).

Since a significant portion of the biological diversity of the early Cambrian fossil record is likely comprised of lophotrochozoans (Kouchinsky et al., 2012) and the record of their radiation as disclosed by biomineralised tissues significantly predates that of ecdysozoans and deuterostomes, proper placement of these problematica on the tree of Spiralia/Lophotrochozoa is fundamental to assess their phylogenetic significance and thus evolutionary implications for the nature of animal diversification associated with the Cambrian explosion.

Despite the enormous advances in animal phylogeny enabled by modern molecular phylogenetic and phylogenomic methods, the interrelationships of constituent groups within Lophotrochozoa remains unresolved and represents a major gap in our understanding of deep animal phylogeny (Dunn et al., 2014). Morphological and systematic investigations remain critical despite the seemingly overshadowing role molecular systematics (Giribet, 2015), since ultimately the evolution of morphology is what most evolutionary biologists are ultimately drawn to investigate in some capacity. Nowhere is this more evident than with fossils, which can provide a unique temporal signal to bear when investigating evolutionary questions.

Phylogenetic significance of newly described fossil material

The description of the taxa Yuganotheca elegans and Cotyledion tylodes (Papers IV and V) as stem-lophotrochozoans has significant implications for the relationships among members of Lophophorata. Whilst as we approach crown brachiopods (Fig. 4), re-examination of Micrina etheridgei (paper II) and Mickwitzia occidens (paper I) provide novel insight into the stem of the linguliform brachiopods. The problematic form Tomteluva perturbata on the other hand is recognized as a probable crown-group rhychonelliform brachiopod and thus not informative for determining the deep splits between major brachiopod clades. This remains to be tested in a cladistic framework, however.

The tree topology of brachiopod relationships is fundamentally the same even in seemingly conflicting molecular and morphological datasets, the main issue identified by Sperling et al. (2011) was that the root position of the tree was an underlying cause of conflicting phylogenetic signals. If phoronids can be independently verified as emerging at a coeval or earlier
time to brachiopods this strongly weighs against the case for brachiopod paraphyly, that implies this branching event should occur later in the evolutionary history of brachiopods with the absence of a shell as secondary loss rather than a primitive feature of phoronids. The characters polarized by the anatomy of *Yuganotheca elegans* (paper IV), namely the combination of supposed brachiopod and phoronid apomorphies in a single organism i.e. the presence of mantle canals, pedicle, a bivalved shell and u-shaped gut, indicates that the case for monophyly is supported by the presence of transitional morphologies in the fossil record.

The cladistic treatment of morphological data expands the tentative phylogenetic framework previously established (Skovsted et al. 2011; Holmer et al., 2011; Skovsted et al., 2009c) in a testable, reproducible way. The key critique of interpretations as to the stem-brachiopod tommotiid relationship hypothesis (Murdock et al., 2012, 2014) justifiably focused on the scarcity of characters to support the affinities of tommotiids such as *Micrina* (paper II) with linguliform brachiopods. In addition a number of the purported homologies, such as the presence of a closed filtration chamber, were products of circular reasoning.

*Figure 8.* Tentative placement of *Yuganotheca* and *Cotyledon* (from Zhang et al., 2014, fig. 4; paper IV).
A smaller focused dataset was established in papers IV-V as a tool to determine the placement of the enigmatic animals *Yuganotheca elegans* and *Cotyledion tyloses*.

It should be noted that one obvious limitation with the dataset collected thus far is a focus on phosphatic linguliform brachiopods and small shelly fossils with relatively few taxa sampled from purported stem-rhynchonelliform calcitic representatives. This is partially a sampling issue due to the commonly used acetic acid recovery methods that dissolves calcitic matrix and fossils equally well, resulting in a relative paucity of described material.

In paper III a new family of calcitic brachiopods is erected with the description of the new species *Tomteluva perturbata* and *Nasakia thulensis*. They are recognised as crown-group members of rhynchonelliform brachiopods. Their affinity with a small group of early and middle Cambrian brachiopods, the naukatids, currently appears to be most parsimonious. These taxa are of interest since they display an unusual morphology, which might represent an early phase of specialisation and adaption of brachiopods. However, their likely highly derived morphology and phylogenetic position gives no additional resolution to the deep nodes of brachiopod phylogeny.
Future Directions

This thesis has shed new light on the morphology, phylogenetic significance and evolutionary context of some of the most problematic lophophorate animals, namely the stem-group brachiopod taxa *Mickwitzia* (paper I), the tommotiid *Micrina* (paper II), the enigmatic Chengjiang forms *Yuganotheca elegans* (paper IV) and *Cotyledion tylodes* (paper V) and the now recognised crown rynchonelliform *Tomteluva* (paper III). Since the material described in this thesis is primarily derived from our own field collections, it serves to display the continuing importance of researchers to continue field exploration and as a result enhance museum collections in addition to the research outcomes.

Future work to conduct systematic revision of the genus *Mickwitzia* is now a priority, with a complete global picture of diversity and diagnostic characters in place. This includes a systematic revision of the Chengjiang animal *Heliomedusa orienta* (Fig.7) of which the preliminary data provides a character based supporting link that this taxon is a constituent of the genus *Mickwitzia* i.e. the presence of inward pointing cones on the interior shell surface, an up until present recognised autapomorphy of *Mickwitzia* (paper I). If the designation of *Heliomedusa* stands up under further scrutiny, it provides a unique opportunity to integrate the data from exceptionally preserved soft part anatomy of the Chengjiang fossils that answers many questions about the ground plan and early evolution of linguliform brachiopods. The columnar structures in *Micrina*/Mickwitzia (paper I-II) have a close morphological similarity and likely homology with acrotretid columns, these appear to have a wider taxonomic distribution than has been first suspected and are a prime target for recovery of phylogenetically useful data from further tommotiids and stem-brachiopods (Holmer et al., 2008b). A census of shell structure utilising microtomographic techniques would be an ideal way of assessing this.

3D virtual palaeontological techniques also allowed significant advances in deciphering the anatomy and thus systematic position of the enigmatic fossils *Heliomedusa* and *Tomteluva*. A solid framework is now established to further investigate character homologies in additional samples of SSF animals and those from Chengjiang similarly preserved in pyrite. Of particular interest to solving the lophophorate origin question would be additional scans of the tommotiids *Tannuolina, Patermitra, Kulparina and Sunnaginia.*
Especially if there is the potential to recover exceptionally preserved soft tissues structure similar to the setae we described in paper II.

Reconstructing the scleritome of Micrina presents a continuing palaeobiological dilemma as to whether this organism possesses a bivalved scleritome sensu Holmer et al. (2008a), is a slug like animal with an imbricating row of sclerites (Li & Xiao, 2004) or possibly retains a more tubular scleritome similar to its sister taxon Tannuolina reconstructed in Skovsted et al. (2014). Two possible approaches to shed light on this problem are suggested. Firstly, make attempts to find additional material with articulated sclerites similar to efforts with Eccentrotheca (Skovsted et al., 2011). Secondly, to reconstruct the animal from 3D models of tomographically scanned sclerite specimens in silico with the Blender package (Garwood & Dunlop, 2014), or alternatively with 3D printed models. Applying this technique is possible for other tommotiids with poorly understood scleritome reconstructions including Sunnaginia, Kulparina and Paterimitra.

Building a comprehensive phylogeny of the SSF and lophophorate stem-group in a cladistic context is a further priority for unravelling the evolutionary context of these fossil organisms. This is already in motion through the establishment of an online MorphoBank effort (project number 2025), allowing a team of researchers to build a collaborative matrix that is updated on an ongoing basis.
Figure 9. Preliminary results from MorphoBank project 2025 dataset derived from Zhang et al. (2014; paper IV) SplitsTree network diagram showing rhynchonelliform brachiopods in blue, linguliform brachiopods in red and linguliform brachiopods plus stem-linguliforms and tommotiids indicated by dashed red box. Current matrix: 25 taxa, 31 characters. Dendrogram based off 18 most parsimonious trees recovered after a TBR tree search, Length 64 steps, CI=0.65 RI=0.81.

Phylogenetic network diagrams are one potentially useful technique in determining patterns of evolution of lophotrochozoans, especially in poorly sampled areas of the tree and where character support is weak or where reticulate events in evolution are suspected, e.g. hybridization during speciation (Legendre & Makarenkov, 2002). Preliminary results support the affinity of tommotiids as at least a stem-linguliform sister group (Fig. 9).

Other outstanding problems with the early fossil record of lophotrochozoans centre on the camenellans, an informal group of organisms that have been placed at the base of the tommotiid stem-group (Skovsted et al., 2009c, 2011) remain enigmatic. Until it is possible to recognise possible homologous features and establish a character based deductive framework for determining their affinities, it is uncertain they belong to the Lophophorata or are indeed even lophotrochozoan stem-group members. A further issue is that sampling of calcitic stem-group lophophorates in cladistic analyses has been sparse and remains a gap in our understanding of the early evolutionary history of Lophotrochozoa.
On the other hand, a more complete synthesis of early Cambrian lophophorate morphological phylogeny in combination with molecular systematics in a total evidence framework is now becoming feasible with the assembly of cladistic matrices for increasing numbers of fossil taxa. The end goal of a more clear reconstruction of the Lophotrochozoan stem-lineage during the critical event of the Cambrian radiation has never been closer.
Svensk sammanfattning


SSF representerar några av de tidigaste bevisen på biomineralisering och bildandet av skallett hos metazoer (djur och deras nära släktingar), och de dyker först upp en tid innan det plötsliga uppträdandet av välbevarade kropps fossil vilka ofta förknippas med den kambriska explosionen.

I inledningen av kambrium markerar närvaron av SSF en betydelsefull övergång från en värld av mikrobiella mattor, encelliga organismer och enkla former bestående av enbart mjukdelar till en värld dominerad av djurgrupper med skallett, grävande organismer och andra metazoer. Denna övergång skedde under den terreneuviska epoken; den äldsta delen av kambrium, mellan början av kambrium och uppträdandet av trilobiter (runt 20 miljoner år, inkluderar de geologiska indelningarna fortun och tommot, Fig 1.)

I takt med att vi förflyttar oss till yngre lager i kambrium (fortun) uppträder små skalförande fossil som Halwaxia, uppbyggda av ett mineral som kallas aragonit; konformade molluskliknande former och hyloliter.

Förekomsten av SSF når sin kulmen i och med kambriums andra etage (tommot) (Fig 1). Namnet har sitt ursprung från lager i närheten av Tommot i Sibirien, och dessa innehåller stora ansamlingar av tommotider, en form av SSF. Uppträdandet av dessa fossil har föreslagits som en indikator för basen av denna geologiska tidsperiod. De hittas vid sidan av tidiga och omfattande revlika avsättningar av konliknande archaeocyater, organismer som antas
vara svampar. Dessa avsättningar hittas direkt innan uppkomsten av både trilobiter och huvudparten av de berömda exceptionellt välbevarade fossil från Burgess Shale och Chengjiang.

Majoriteten av SSF hade skelett uppbyggda av mineralet apatit (en typ av kalkiumfosfat, samma material som ben och tänder består utav); de andra formerna, särskilt de tidiga varianterna, bestod utav kalkiumkarbonat, som moderna musslor och sniglar.


**Forskningsmetoder**


För modeller med en högre upplösning använder sig forskare av röntgenstrålar från en partikelaccelerator, en synkroton. Källan för röntgenstrålarna från synkrotronen är avsevärt mer intensiva än en standardkälla, och produ-
cerar strålning med endast en väglängd, likt en laser. Slutresultatet är en betydligt snabbare scan än med mindre maskiner och har dessutom en högre detaljnivå. Men att erhålla arbetstid på sådan utrustning är få förunnat då det är kostsamt och eftertraktat. Denna teknik användes i vår forskning för att skapa detaljerade modeller av våra SSF Micrina (artikel II) och Tomteluva (artikel III), deras interna strukturer och deras relation till andra djurgrupper.

Varför har hårdar delar utvecklats?
Levande djur har många olika typer av hårdvävnader och dessa har i sin tur ett spektrum av funktioner. De fungerar som interna stöd, tänder för föda, externa stöd eller exoskelett (t.ex. skal från sniglar), hudskleriter, eller fjäll, som skydd och även som assistens vid simning. Ursprunget till hårdar delar tros vara ett exempel på en evolutionär kapprustning mellan rovdjur och bytesdjur, i konstant försök att vinna fördelar och konkurrera ut varandra. Bytesdjuren försökte bygga kraftigare försvar (skal och taggar) och rovdjure berättar dem kan laga och andra strategier (som exempelvis egenskapen att kunna bryta sönder skal) för att övervinna dessa försvar. Iom biologin kallas detta koncept för ”the Red Queen hypothesis” (Hjärter Dam, efter karaktären från boken ”Alice i Underlandet”). Andra idéer som har föreslagits är att skelettbyggandet var ett sätt för djur att göra sig av med sitt överskott av metaboliskt avfall eller att lagra mineral som kalcium; användandet för försvar, support, utfodring och så vidare, var endast en bieffekt.

Vad är ”Small Shelly Fossils” (SSF)?

Det har föreslagits att vi kan, genom att studera SSFer, börja att rekonstruera det evolutionära ursprunget till brakiopodens kroppssplan - om än i flera etapper. Det förefaller existera flertalet intermediära former mellan tommotiider och brakiopoder, ett exempel är den märkliga och tidiga brakiopoden Mickwitzia (artikel I) som delar ett antal likheter i skalstrukturen med Micrina (artikel II). Även om denna uppfattnings är långt ifrån accepte-
rad, så erbjuder den en spännande möjlighet att undersöka ursprunget av ett fylum i anknytning till utvecklingen av SSFer.

Ytterligare en alternativ modell har tagit upp möjligheten att brakiopoder kan ha utvecklats genom "uppvikning" av ett snigelliknande djur, liknande *Halkieria*. Djuret skulle ha två motsatta skal med en överlappning för att bilda en sluten filtreringskammare, med andra ord tvåskalig (se Cohen et al. 2003).


Några av de SSF, som vi har sett, kan identifieras som djurens stamgrupp, som de primitiva molluskernas skal, brakiopodernas skal och tube från annelider (ringmaskar) eller taggar. Flera former förblir gåtfulla, och för tillfälle anses de tillhöra "problematica", eller fossil med en osäker relation till andra organismer.


Subtila antydningar från SSF, spårfossil och SCF ("Small Carbonaceous Fossils") ger oss en föreställning om att ett komplext djurliv hade fått fotfäste i kambrions början och kan i vissa mer kontroversiella fall eventuellt utvidgades till slutet av Ediacaran (Fig. 1).

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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 Lipalian 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 ‘Laggerstätte 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 pre-dates 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. *Yochelecionella*, 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 mollusces 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).
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.

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.

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.

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).

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

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.
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.
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).

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.

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 tommotiid 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 tommotiid *Eccentrotheca*, but the sclerites differ in structure enough that it is thought not to be a tommotiid. 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).](image)

Some additional SSFs, such as the rather beautiful but problematic *Dailyatia* (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).
Figure 12 — *Yuganotheca elegans* from Chengjiang, China, showing fossil (A–C), and reconstruction. The paired shell valves are made of agglutinated sand grains. Mouth (M), central lumen (Pc) and the terminal bulb (Dg) of the pedicle. Reconstruction of animal in life position filter feeding with its lophophore organ, on right.

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


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