Cambrian Explosion

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Glossary

Bilateria Animals with bilateral symmetry as an embryo (i.e., having a left and a right side that are mirror images of each other), displaying a head and a tail (anterior-posterior axis) and a belly and a back (ventral-dorsal axis).

Biodiversity Number and variability of genes, species, and communities in space and time.

Cambrian evolutionary fauna Sepkoski's evolutionary fauna dominated by trilobites—being inarticulate brachiopods, hyolithids, monoplacophorans, eocrinoids and hexactinellid sponges other components—and whose main elements first appeared during the Cambrian explosion and were severely affected by the end-Ordovician mass extinction.

Ecosystem engineers Organisms that modify the physical environment, directly or indirectly modulating the availability of resources to other species and exerting a large impact on the species richness and landscape-level heterogeneity of an area.

Molecular clocks Technique that uses the mutation rate of biomolecules to infer the time when two or more life forms diverged in the geologic past.

Introduction

Historian of Science Stephen Shapin's famous opening lines of his book "The Scientific Revolution" read "There was no such thing as the Scientific Revolution, and this is a book about it." Current arguments in paleobiology regarding the very existence and nature of the Cambrian explosion prompt us to paraphrase Shapin by saying "There was no such thing as the Cambrian explosion, and this is a chapter about it". The term "Cambrian explosion" refers to an event in the history of the biosphere when the vast majority of metazoan phyla (approximately 30 body plans) that populate the Earth today first appeared in the fossil record (Valentine, 2002; Marshall, 2006; Budd, 2008; Erwin et al., 2011; Erwin and Valentine, 2013). The explosive appearance of mineralogically diverse (e.g., calcium phosphate, aragonite, high-magnesium calcite, low-magnesium calcite, silica) biomineralized skeletons is the signature of the Cambrian explosion. However, the independent acquisition of biomineralized skeletons by multiple clades was most likely an epiphenomenon of the general radiation of metazoan body plans and tissues (Bengtson, 2004; Kouchinsky et al., 2012). This marks a sharp contrast with the preceding Ediacaran radiation, which was characterized by soft-bodied organisms of unfamiliar morphologies and highly debated phylogenetic affinities, regardless of exhaustive past and ongoing efforts (e.g., Runnegar, 1982a; Glaessner, 1984; Seilacher, 1989, 2007; Budd and Jensen, 2000; Narbonne, 2005; Xiao and Laflamme, 2009; Dunn and Liu, 2019).

Deciphering the evolutionary events that led to the Cambrian explosion, as well as dissecting this radiation from phylogenetic and ecosystem perspectives, has been at the forefront of paleobiology for a long time (e.g., Knoll and Carroll, 1999; Marshall, 2006; Erwin et al., 2011; Erwin and Valentine, 2013; Erwin, 2015, 2020; Butterfield, 1997, 2011; Budd, 2008; Budd and Jensen, 2000, 2017). Historically, there have been two opposing ways of assessing the Cambrian explosion. One line of thought, while recognizing limitations, emphasizes the merits of the fossil record as a reliable source to reconstruct the origin and diversification of Metazoa. In this view, the abrupt appearance of fossils in the stratigraphic column reveals the late origin of modern lineages (shallow Ediacaran roots) and explosive Cambrian diversification, particularly of bilaterians, that led to modern phyla. The opposing view highlights the incompleteness of the fossil record, and points to other sets of data (e.g., molecular clocks, bio-markers) as fundamental to unraveling the hidden metazoan evolutionary history. This second approach outlines an origin and diversification of Metazoa long predating the Cambrian explosion. In its most extreme version, the Cambrian explosion is an artifact of an imperfect, enormously incomplete, fossil record, and the deep Precambrian history represents the so-called "slow phylogenetic fuse" (Wray et al., 1996; Fortey et al., 1996; Conway Morris, 2000; Blair and Hedges, 2005). In other words, the abrupt appearance of fossils is understood as reflecting an increase in preservability resulting from the acquisition of mineralized skeletons.

In the last two decades, however, due to the advent of new conceptual and methodological tools in the area of molecular genomics and comparative development, and an increased scrutiny of the fossil record (including both body fossils and trace fossils), a more coherent picture of animal evolutionary history is starting to emerge (Fig. 1). A Cryogenian origin for Metazoa has received increasing support from molecular clocks (e.g., Erwin et al., 2011; dos Reis et al., 2015; Lozano-Fernandez et al., 2017; Erwin, 2020), but the first uncontroversial evidence of bilaterians based on trace fossils is dated at ~560 My (Jensen, 2003; Budd and Jensen, 2000; Mángano and Buatois, 2014, 2020). In turn, the first diverse bilaterian clades occur in the early Cambrian during the so-called Cambrian explosion (Marshall, 2006). This significant gap in the fossil record between alleged origin and major diversification of bilaterians represents a large conundrum (Erwin et al., 2011). It is still a matter of controversy if this "gap" is a collection bias, resulting from the incompleteness of the fossil record, or reflects the nature of evolutionary processes (dos Reis et al., 2015; Erwin et al., 2011; Erwin, 2015). Regardless of the fast-paced advances in the last two decades of intense research, numerous fundamental questions remain on the table: When did Metazoa evolve? How deep can the origin of bilaterians be tracked? Which was the role of animals in changing oxygen conditions? Is the Cambrian explosion a new phase of an Ediacaran radiation of bilaterians? Which was the role of oxygen during the explosion? Can we identify the "cause" of the Cambrian explosion or should we search for other explanation schemata that involve interaction networks? Are internal factors (i.e., genomic and developmental) or external ones (i.e., environmental and ecological) the main drivers of this evolutionary process? These and many other questions are at present hotly contended and approached by an artillery of new tools and conceptual frameworks.
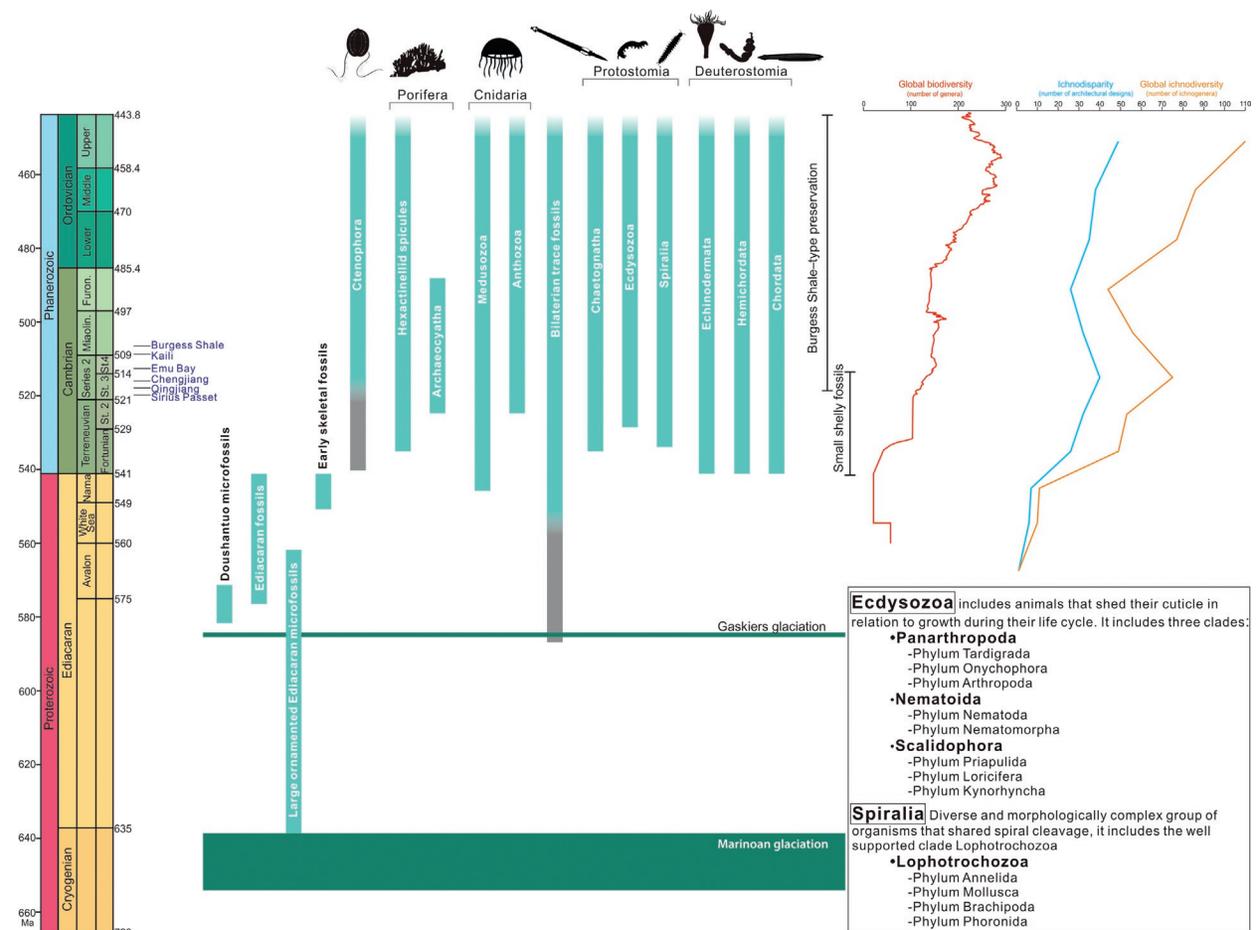
Fig. 1   Milestones in the construction of Cambrian biodiversity and the roots of the radiation. Stratigraphic locations of the most important Cambrian Lagerstätten are shown in the column. First appearance of major animal groups in: Dunn CW, Giribet G, Edgecombe GD and Hejnol A (2014) Animal phylogeny and its evolutionary implications. *Annual Review of Ecology, Evolution, and Systematics* 45: 371–395, biodiversity curve in: Fan JX, Shen SZ, Erwin DH, Sadler PM, MacLeod N, Cheng QM, Hou XD, Yang J, Wang XD, Wang Y and Zhang H (2020) A high-resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity. *Science* 367: 272–277, and ichnodiversity and ichnodisparity curves in: Buatois LA, Mángano MG, Minter NJ, Zhou K, Wisshak M, Wilson MA and Olea RA (2020) Quantifying ecospace utilization and ecosystem engineering during the early Phanerozoic—The role of bioturbation and bioerosion. *Science Advances*. All organism silhouettes from PhyloPic (www.phylopic.org). They are available for reuse under the Creative Commons Attribution-ShareAlike 3.0 Unported license. Silhouettes of Ctenophora, Porifera, Chaetognatha illustrated by Noah Schlottman; Cnidaria illustrated by Severine Martini; Ecdysozoa illustrated by Renato de Carvalho Ferreira; Spiralia illustrated by Scott Hartman; Chordata illustrated by Yan Wong; and Echinodermata and Hemichordata illustrated by Kai Zhou.

Sources of Data to Reconstruct the Cambrian Explosion

Historically, the different views on the Cambrian explosion have been strongly influenced by the type of data that are considered crucial, although there is an increasing trend towards recognizing the merits of different datasets (Donoghue and Benton, 2007; Erwin et al., 2011). The view of the Cambrian explosion as a time of emergence of new clades and relatively rapid evolutionary change relies strongly on the fossil record. In contrast, those proposing deep roots, advocate the idea of a long protracted radiation on the basis of genomic information. In recent years, however, a more nuanced scenario is in the process of construction with valuable attempts to consider all available evidence and integrate datasets, in particular molecular clocks, developmental information and fossils (Donoghue and Benton, 2007; Erwin et al., 2011; dos Reis et al., 2015).

Although the body-fossil record favors the existence of the Cambrian explosion (Conway Morris, 2000; Budd and Jensen, 2000; Budd, 2008, 2013), the reading of this record is far from being straightforward. Intense scrutiny of Ediacaran strata has revealed roots, albeit not deep, of the explosion. For example, in addition to the soft-bodied Ediacara biota, the terminal Ediacaran is host to organisms that developed hard parts, including tubular fossils, such as *Cloudina* and related structures (the wormworld fauna of Schiffbauer et al., 2016) and the reef-builder *Namacalathus,* of probable cnidarian affinity (Wood and Curtis, 2015; but see Antcliffe et al., 2014), recording a fundamental change in community structure and an increased metazoan participation setting up the stage for the Cambrian explosion. In particular, the recent discovery of possible digestive tracts in some of these tubular fossils provides strong evidence of their bilaterian affinity (Schiffbauer et al., 2020).

The evolutionary relationships of the Ediacara biota have been historically controversial. Traditionally regarded as representing crown groups of living phyla of marine animals (Glaessner, 1984), alternative views emerged early in the history of this field of research, placing them in their own new animal phyla (Pflug, 1972) to be later considered a degree of organization intermediate between animals and plants (Pflug, 1973). However, the most radical hypothesis was proposed by Adolf Seilacher in one of his successive papers tacking the affinities of the Ediacara biota (Seilacher, 1989, 1992, 1994, 2007). His innovative idea was to cluster Ediacara macrobiota displaying either serial or fractal symmetry into a high-rank clade. In terms of construction, these organisms were more similar to each other than they were to any other organism, and similarities between this biota and modern animals were considered either accidental or convergent. The so-called "Vendobionta" was proposed as a new kingdom of life (Seilacher, 1989, 1992), although Seilacher himself subsequently included this biota as a new phylum, sister group of Metazoa (Seilacher, 1994), to finally interpret the members of this biota as gigantic protozoans (Seilacher, 2007; see Dunn and Liu, 2019 for review).

In more recent years, however, there has been a growing consensus that metazoans are represented at least by some members of the Ediacara biota (in addition to associated trace fossils), re-affirming an evolutionary link between Ediacaran and Cambrian biotas. Some authors favor placing many of the representatives of the Ediacara biota as very basal stem groups of modern animal Phyla (Droser and Gehling, 2015; Budd, 2008, 2013). The tendency has been to consider the Ediacara biota a paraphyletic or polyphyletic group (Xiao and Laflamme, 2009; Dunn and Liu, 2019). Some emblematic forms of the Ediacara biota, such as *Kimberella* (a putative stem mollusk, Fedonkin and Waggoner, 1997), has been tentatively related to *Odontogriphus,* a stem mollusk from the Burgess Shale, stressing the idea of links between biotas on the two sides of the Ediacaran-Cambrian divide (Caron et al., 2006). Still, relationships between Ediacaran and Cambrian biotas are unclear and strongly debated not only in terms of phylogenetic relationships, but also at the large scale of the ecological changes across this boundary.

Trace fossils provide an independent source of data (Budd and Jensen, 2000, 2017; Jensen, 2003; Seilacher et al., 2005; Jensen et al., 2006; Mángano and Buatois, 2014, 2016, 2017, 2020). The trace-fossil record is continuous through the critical time represented by the Ediacaran-Cambrian transition and, because it represents the activity not only of animals with hard parts but mostly of soft-bodied organisms, it helps to fill gaps in the body-fossil record (Mángano and Buatois, 2014). Leaving apart some controversial records, there is an overall agreement that trace fossils, particularly shallow burrows and trails, provide the oldest, strong evidence of animal motility and bilaterian activities in the Ediacaran by ~560 My ago (Jensen, 2003; Budd and Jensen, 2000; Mángano and Buatois, 2014, 2020). An increase in complexity and density of trace fossils is revealed towards the latest Ediacaran, but a drastic increase in new architectures reflecting new behaviors and new producers took place during the earliest Cambrian (Fortunian).

The introduction of molecular clocks to track the origin of animals has offered an additional line of evidence to reconstruct the tree of life and to test the Cambrian explosion (Runnegar, 1982b, 1986; Erwin et al., 2011; dos Reis et al., 2015; Cunningham et al., 2017). However, molecular clocks have been quite controversial, and the history of this approach explains at least part of the problem (see Pisani and Liu, 2015). Early attempts at molecular sequencing indicated very deep Proterozoic divergence estimates, with the origin of Metazoa approximately 1 billion years ago, completely at odds with the fossil record (e.g., Wray et al., 1996; Blair and Hedges, 2005). In turn, these deep Proterozoic diversification estimates were taken as strong support of the entrenched idea of the Cambrian explosion as an artifact of the fossil record rather than a real evolutionary event (e.g., Runnegar, 1982b; Fortey et al., 1996). A plethora of seemingly precise molecular clock divergence times seemed to support the idea of an unreliable fossil record, flawed by incompleteness and preservational problems. Subsequent work, however, pointed to serious conceptual and methodological issues with the molecular clocks (Graur and Martin, 2004; Peterson et al., 2008), revealing poor support for pre-Cryogenian divergence (Erwin et al., 2011; Erwin, 2015; dos Reis et al., 2015; Cunningham et al., 2017).

A new era in molecular research has adopted Bayesian methods and new algorithms that allow calibration of molecular clocks using probability distributions to account for multiple fossil calibrations and the associated levels of uncertainty (Pisani and Liu, 2015). These new methodologies and comprehensive data (including genomes for multiple species representing diverse clades and

numerous fossil calibrations) have resulted in a significant decrease of the gap between molecular estimates and the fossil record. The dominant trend in molecular studies is to place the origin of the Metazoa by the Cryogenian, around 750 My (Erwin et al., 2011; Erwin and Valentine, 2013; Erwin, 2015; dos Reis et al., 2015). As a result, there is still at least a 150–200 My gap between these estimates and the fossil record (Erwin, 2015). Noteworthy, some recent molecular clocks exhibit excellent congruence with paleontologic evidence, such as the split of euarthropods in the late Ediacaran with major clade diversification during the Cambrian (Daley et al., 2018). Regardless of the substantial advances, any attempt to reconstruct an evolutionary narrative using molecular data must be considered preliminary awaiting integration of fundamental fossil data (i.e., new fossils, improved understanding of phylogenetic affinities of Ediacaran fossils) and improved methods (dos Reis et al., 2015).

Biomarkers (also called molecular fossils) represent another source of data to unravel the roots of the Cambrian explosion. For example, the presence of cholesteroids in *Dickinsonia* has been regarded as evidence of this iconic member of the Ediacara biota being a basal animal (Bobrovskiy et al., 2018). However, caution should be taken as recent research revealed that discerning between genuine signals resulting from biosynthesis and artifacts (e.g., background, dietary signals) is still not clearly resolved. Contamination has been a problem in many instances as demonstrated by recent studies (e.g., French et al., 2015). In addition, complications in assessing the reliability of biomarker data are well illustrated by the present controversies regarding the existence of sponges in the Precambrian (Love et al., 2009; Antcliffe, 2013; Antcliffe et al., 2014; Gold et al., 2016). Recent studies have challenged 24ipc, a proposed molecular fossil for sponges, by the finding of 24ipc and 26 me in recent foraminiferans (Nettersheim et al., 2019; Hallmann et al., 2020; but see Love et al., 2020).

In short, we have a wealth of resources to tackle the reconstruction of the Cambrian explosion but, paraphrasing Marshall and Valentine (2010), different databases can sometimes behave like the diverse testimonies offered by the witnesses of a crime recording different perspectives. In the midst of these sometimes discouraging disagreements, integrative, multidisciplinary research efforts supported by new methods and conceptual frameworks bring the promise of articulating the incomplete, slanted sources, and produce an increasingly more coherent and fascinating story.

The Construction of Cambrian Biodiversity

Regardless of its roots into the Ediacaran, understanding the construction of Cambrian biodiversity requires establishing a chronology of the so-called lower Cambrian (541–509 My), which is now formally divided into the Terreneuvian (541–521 My) and Series 2 (521–509 My). The former is divided into the Fortunian (541–529 My) and Stage 2 (529–521 My) and the latter into Stages 3 (521–514 My) and 4 (514–509 My) (Fig. 1). Notably, new geochronologic information indicates that the base of the Cambrian may be at ∼539 My (Linnemann et al., 2019). The Terreneuvian corresponds to the time interval informally known as "pre-trilobitic." The Ediacaran-Cambrian transition is officially placed at the FAD (first appearance datum) of the trace fossil *Treptichnus pedum* (see Buatois, 2018 for discussion).

The Fortunian is remarkably poor in body fossils and dominated by small shelly fossils (SSF), typically preserved in limestone and absent or rare in siliciclastic deposits. The so-called "small shellies" is a heterogeneous group comprising both entire skeletons of minute animals or fragments of larger ones (Figs. 2A–Q and 3A–T) (Kouchinsky et al., 2015, 2017). Some metazoan affinities of Fortunian SSF include poriferans, cnidarians, scalidophorans, and mollusks (Erwin and Valentine, 2013; Kouchinsky et al., 2017; Liu et al., 2017). In particular, the presence of stem-group Hexacorallia has been proposed on the basis of very well-preserved polyps in Fortunian rocks (Han et al., 2010). The Fortunian is also host to the oldest uncontroversial body-fossil evidence of sponges (Antcliffe et al., 2014), whereas putative lobopodian sclerites and plates have been recorded as well (Liu et al., 2008). The phylogenetic breadth recorded by these fossils clearly indicates that the radiation event was well in progress. Small carbonaceous fossils (SCF) are a promising new paleontological source to track the radiation of non-mineralized clades (Butterfield and Harvey, 2012; Slater et al., 2017) (Fig. 4A–J). Earliest Cambrian assemblages of SCF seem to be of relatively low diversity compared with younger lower Cambrian ones, being essentially dominated by protoconodonts (sclerites of chaetognathans), cuticular fragments and spines of scalidophorans, and a variety of protist-grade elements (Slater et al., 2018a).

Because of the paucity of body fossils, the trace-fossil record (Fig. 5A–F) is particularly useful to provide insights into a potentially hidden diversity of bilaterians during the Fortunian. Notably, Fortunian strata show an impressive increase in trace-fossil diversity and disparity with respect to the Ediacaran, in fact, the largest increase in these metrics in geologic history (Mángano and Buatois, 2014; Buatois and Mángano, 2018). Although establishing the producers of these trace fossils is not straightforward, ichnologic data provide evidence of the unquestionable existence of arthropods, and the most likely presence of platyhelminths, priapulids, nematodes, enteropneusts, and polychaetes (Narbonne et al., 1987; Jensen, 2003; Mángano and Buatois, 2014, 2020; Laing et al., 2019). This increase in trace-fossil diversity predates the drastic increase displayed by body fossils by ∼20 My (Mángano and Buatois, 2014, 2020; Buatois et al., 2016).

Cambrian Stage 2 strata are still quite poor in terms of macrofossils. However, SSF are diverse, including a wide variety of the so-called "tommotids" and strong representation of early mollusks, brachiopods, and uncontroversial lobopodians and paleoscolicids (Erwin and Valentine, 2013; Kouchinsky et al., 2015, 2017). Biomineralized SSF in the Fortunian and Stage 2 had a dominant aragonitic mineralogy, and this is considered the early phase of the Cambrian radiation by Kouchinsky et al. (2012). Interestingly, trace-fossil diversity had similar levels to those in the Fortunian (Mángano and Buatois, 2014). In addition, a group of heavily calcified sponges, referred to as archaeocyathans, formed the first animal-dominated Phanerozoic reefs (Rowland, 2001).
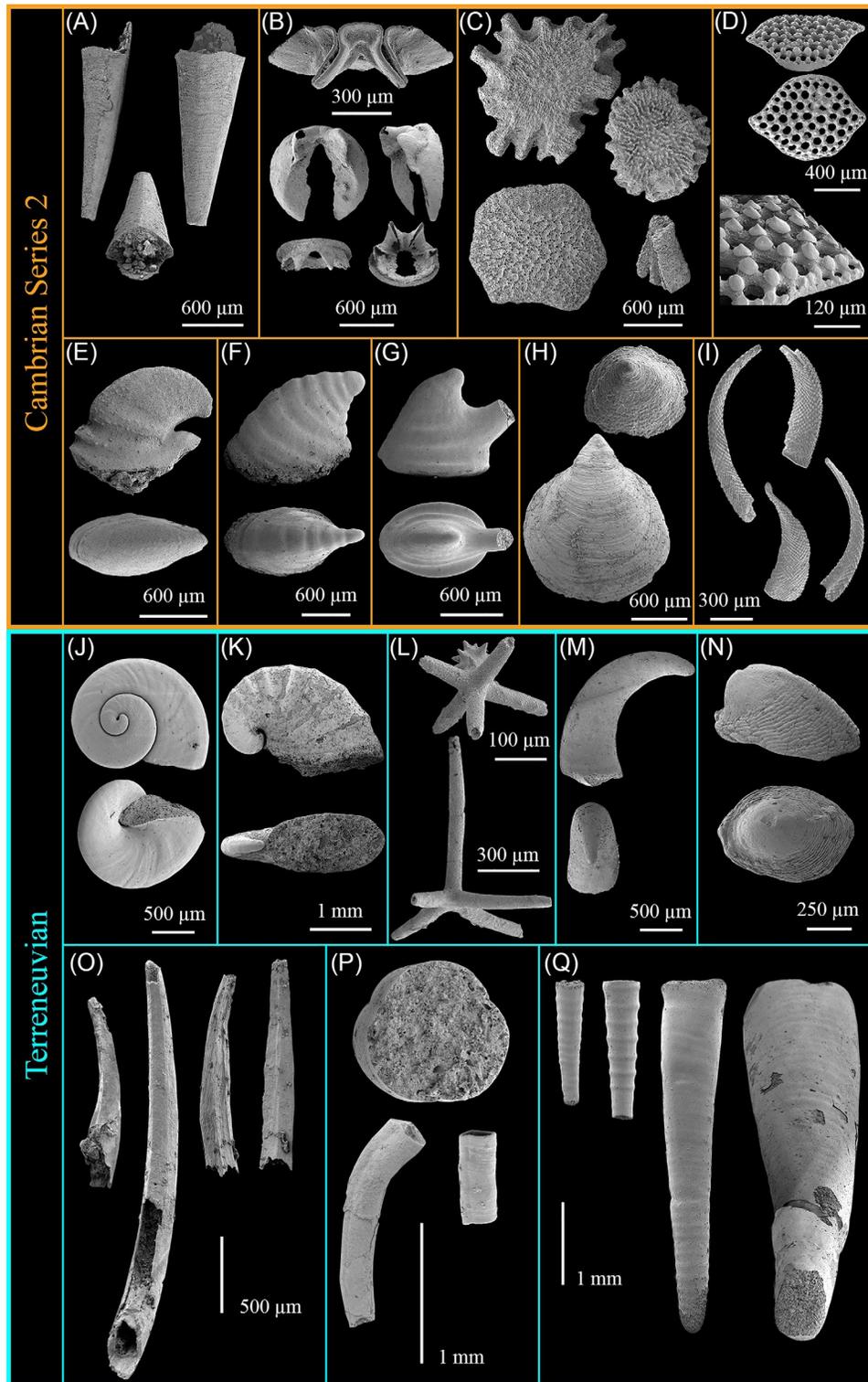
Fig. 2 Representative examples of lower Cambrian small shelly fossils (SSF) from the Anabar Uplift, Siberia, Russia. (A–I) are from the Cambrian Series 2. (J–Q) are from the Terreneuvian (A) Hyolith conchs, Emyaksin Formation; (B) Hyolith opercula, Emyaksin Formation; (C) Eocrinoid thecal plates and eocrinoid brachiolar plate (lower right, twisted elongated plate), Emyaksin Formation; (D) *Microdictyon* cf. *M. rhomboidale*, a lobopodian plates, Emyaksin Formation; (E) *Mackinnonia anabarica,* a helcionellid mollusk, internal mold, Emyaksin Formation; (F) *Parailsanella* sp., a helcionellid mollusk, internal mold, Emyaksin Formation; (G) *Yochelcionella* cf. *Y. greenlandica,* a helcionellid mollusk, internal mold, Emyaksin Formation; (H) *Oymurania?gravestocki,* a stem group-brachiopod, orthoconic valve (presumably dorsal), (upper), and *Oymurania gravestocki,* cyrtoconic valve (presumably ventral), (lower), both from Pestrotsvet Formation; (I) Problematicum *Rhombocorniculum cancellatum,* Emyaksin Formation; (J) *Aldanella attleborensis,* a mollusk, internal mold, Medvezhya Formation; (K) *Oelandiella korobkovi,* a helcionellid mollusk, internal mold, Medvezhya Formation; (L) Hexactinellid spicules, Emyaksin Formation; (M). *Ceratoconus striatus,* internal molds, Emyaksin Formation; (N) *Purella antiqua,* a mollusk, calcium phosphate shell coatings, Emyaksin Formation; (O) *Protohertzina anabarica* and *P. unguliformis*-type sclerites, protoconodonts, Nemakit-Daldyn Formation; (P) *Anabarites trisulcatus,* unknown affinity, Nemakit-Daldyn Formation; (Q) Orthothecid hyolith conchs, Medvezhya Formation. For Terreneuvian further information in: Kouchinsky A, Bengtson S, Landing E, Steiner M, Vendrasco M and Ziegler K (2017) Terreneuvian stratigraphy and faunas from the Anabar Uplift, Siberia. *Acta Palaeontologica Polonica* 62: 311–440 and for Series 2 in: Kouchinsky A, Bengtson S, Clausen S and Vendrasco MJ (2015) An early Cambrian fauna of skeletal fossils from the Emyaksin Formation, northern Siberia. *Acta Palaeontologica Polonica* 60: 421–512. All images courtesy of Artem Kouchinsky.
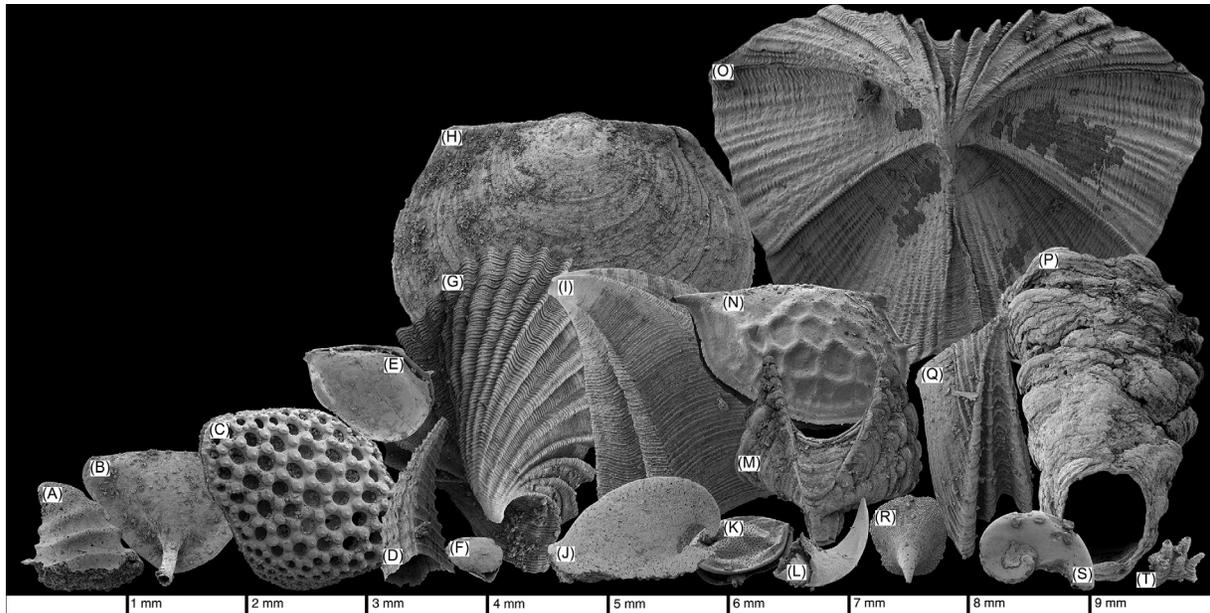
Fig. 3 Representative examples of lower Cambrian small shelly fossils (SSF) from Australia. All specimens are from Stages 2 to 4 in the Flinders Ranges of southern Australia (A) *Davidonia rostrata* (internal mold); (B) *Mongolitubulus descensus;* (C) *Microdictyon* sp.; (D) *Lapworthella fasciculata*; (E) *Jiucunella phaseloa*; (F) *Minlatonia tuckeri*; (G) *Dailyatia ajax;* (H) *Askepasma toddense*; (I) *Dailyatia odyssei*; (J) *Anabarella australis* (internal mold); (K) *Eozhexiella adnyamathanha*; (L) Protoconodont element; (M) *Paterimitra pyramidalis*; (N) *Jixinlingella daimonikoa*; (O) *Dailyatia bacata*; (P) *Eccentrotheca helenia*; (Q) *Camenella reticulosa*; (R) *Stoibostrombus crenulatus*; (S) *Pelagiella subangulata* (internal mold); (T) *Lapworthella fasciculata* (articulated sclerites). Further information in: Betts MJ, Paterson JR, Jago JB, Jacquet SM, Skovsted CB, Topper TP and Brock GA (2016) A new lower Cambrian shelly fossil biostratigraphy for South Australia. *Gondwana Research* 36: 176–208; Betts MJ, Paterson JR, Jago JB, Jacquet SM, Skovsted CB, Topper TP and Brock GA (2017) Global correlation of the early Cambrian of South Australia: Shelly fauna of the Dailyatia odyssei Zone. *Gondwana Research* 46: 240–279; Betts MJ, Paterson JR, Jacquet SM, Andrew AS, Hall PA, Jago JB, Jagodzinski EA, Preiss WV, Crowley JL, Brougham T and Mathewson CP (2018) Early Cambrian chronostratigraphy and geochronology of South Australia. *Earth-Science Reviews* 185: 498–543. Figure courtesy of Marissa Betts.

Strictly speaking, the Cambrian explosion understood as an outburst of macrofossil skeletal remains (Fig. 6A–I) clearly related to modern phyla, is recorded in Cambrian Series 2 rocks. A major shift in skeletal mineralogy is evidenced at the base of Stage 3, largely coincident with the explosive evolution of groups having calcitic exoskeletons (e.g., echinoderms, trilobites, calcareous brachiopods, sponges). The oldest trilobites appeared approximately at 521 My, and this first occurrence worldwide defines the base of this series. The breadth of this radiation is fully revealed by the body-fossil record of Konservat Lagersttäten preserving soft-bodied animals as carbonaceous films, known as Burgess Shale-type preservation. Examples of the latter are the well-known early middle Cambrian Burgess Shale in Canada (Series 3, Stage 5) (Fig. 7A–O), subsequent discoveries of similar age in the same region, such as Marble Canyon (Caron et al., 2014) and Tokumm (Moysiuk and Caron, 2019), and several outstanding early Cambrian localities worldwide, including Chengjiang (Fig. 8A–L) (Hou et al., 2004) and Qingjiang in China (Fu et al., 2019), and Sirius Passet in Greenland (Fig. 9A–N) (Harper et al., 2019), all of Cambrian Age 3.

Exceptionally preserved faunas represent unique windows to assess Cambrian diversity and disparity, and to reconstruct the ecology of early Phanerozoic communities. Euarthropods dominate Cambrian Burgess Shale-type Lagerstätten, and many taxa differ significantly from extant arthropods (Daley et al., 2018). Of particular interest are the stem arthropod radiodonts (Figs. 7A and D, 8K and 9K) (stem arthropods), including the emblematic *Anomalocaris*, and characterized by the absence of lobopods, the presence of lateral flaps (used for swimming), two sclerotized head appendages, stalked compound eyes, and circular mouth parts (Daley et al., 2018). Based on radiodont frontal appendage morphology and mouth elements, a range of feeding strategies, such as active predation, scavenging, suspension feeding and sediment sifting, have been inferred (Van Roy et al., 2015; Moysiuk and Caron, 2019), expanding significantly our understanding of the role of arthropods in Cambrian ecosystems. Exquisite preservation of anatomical features in Burgess Shale-type fossils is also critical to unraveling the phylogenetic affinities of these early animals and to help reconstruct bilaterian phylogeny. In fact, with the exception of Bryozoa, all living phyla having hard parts are known from these deposits, showing that by the end of the early Cambrian, the explosion was essentially over (Marshall, 2006; Erwin and Valentine, 2013).

Although Burgess Shale-type fossils have captured most of the attention, SSF continued being a source of information, displaying diverse lophotrochozoan elements (e.g., mollusks, hyolithids, brachiopods), and the first occurrences of trilobite sclerites, bradoriids and echinoderms by Cambrian Age 3 (Kouchinsky et al., 2012, 2015). This calcite-dominated burst of skeletons is considered the second phase of the Cambrian explosion by Kouchinsky et al. (2012). A similar diversity trend has also been observed in SCF of Cambrian Ages 3 and 4, best recording the diversification and abundance of ecdysozoan groups. Assemblages feature increasing
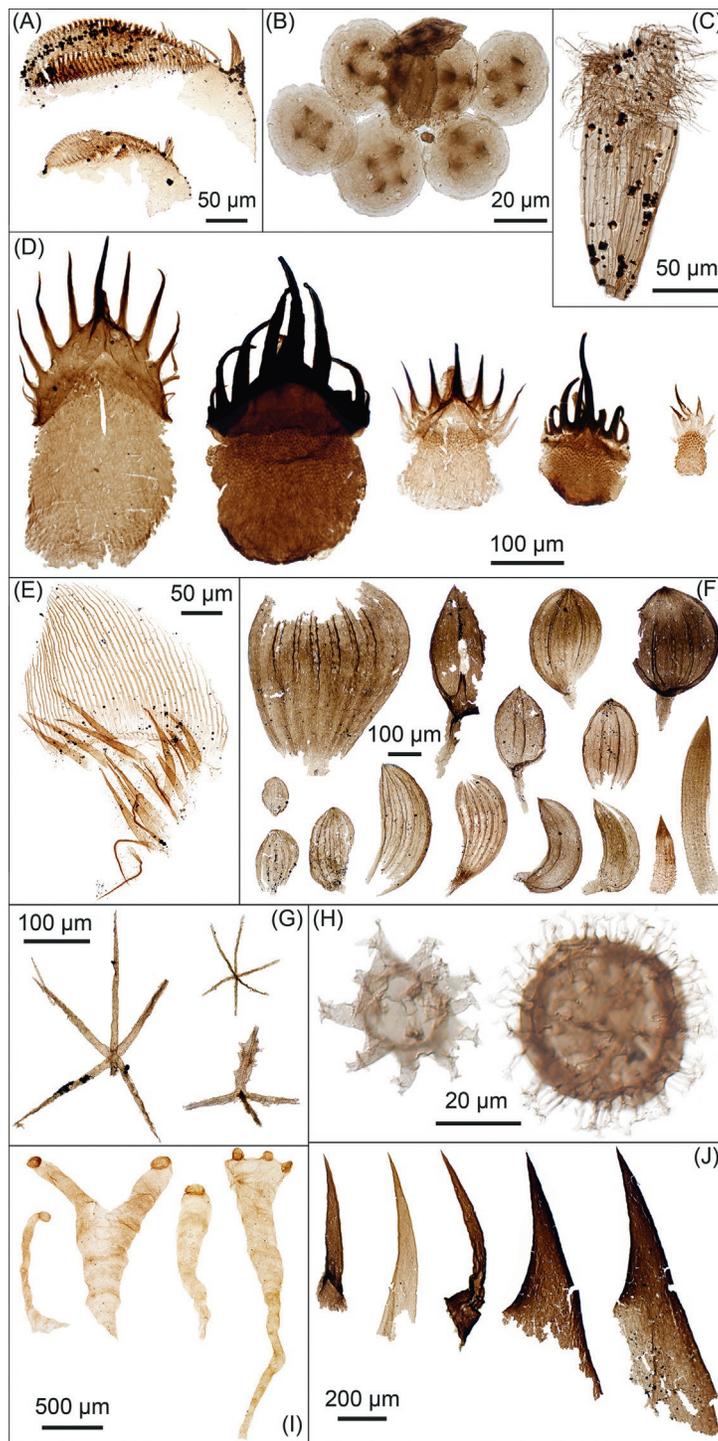
Fig. 4 Representative examples of Cambrian small carbonaceous fossils (SCF) (A) Crustacean mandibles, Deadwood Formation (Furongian), Saskatchewan, western Canada. (B) Palaeoscolecid sclerites, Deadwood Formation (Furongian), Saskatchewan, western Canada. (C) *Eolorica deadwoodensis,* a loriciferan, Deadwood Formation (Furongian), Saskatchewan, western Canada. (D) Priapulid pharyngeal teeth, Deadwood Formation (Furongian), Saskatchewan, western Canada. (E) Arthropod filter setae, Earlie/Deadwood formations (Miaolingian), Saskatchewan, western Canada. (F) *Wiwaxia* sclerites, Kaili Formation (Miaolingian), Guizhou, China. (G) Sponge spicules, Forteau Formation (Stage 4), Newfoundland, Canada. (H) Acritarchs, Forteau Formation (Stage 4), Newfoundland, Canada; (I) *Retiranus balticus,* a possible algae, Voosi Formation (Fortunian or Stage 2), Estonia. (J) Organically preserved protoconodont spines, Kestla Member, Lontova Formation (Fortunian or Stage 2), Estonia. (A) Further information in: Harvey TH, Vélez MI and Butterfield NJ (2012) Exceptionally preserved crustaceans from western Canada reveal a cryptic Cambrian radiation. *Proceedings of the National Academy of Sciences* 109: 1589–1594; (B) Further information in: Butterfield NJ and Harvey THP (2012) Small carbonaceous fossils (SCFs): A new measure of early Paleozoic paleobiology. *Geology* 40: 71–74; (C) Further information in: Harvey THP and Butterfield NJ (2017) Exceptionally preserved Cambrian loriciferans and the early animal invasion of the meiobenthos. *Nature Ecology & Evolution* 1: 1–5; (D) Further information in: Smith MR, Harvey THP and Butterfield NJ (2015) The macro- and microfossil record of the Cambrian priapulid *Ottoia. Paleontology* 58: 705–721; (E) Further information in: Harvey TH, Vélez MI and Butterfield NJ (2012) Exceptionally preserved crustaceans from western Canada reveal a cryptic Cambrian radiation. *Proceedings of the National Academy of Sciences* 109: 1589–1594; (F) Further information in: Butterfield NJ and Harvey THP (2012) Small carbonaceous fossils (SCFs): A new measure of early Paleozoic paleobiology. *Geology* 40: 71–74; (G) Further information in: Butterfield NJ and Harvey THP (2012) Small carbonaceous fossils (SCFs): A new measure of early Paleozoic paleobiology. *Geology* 40: 71–74; (H) Further information in: Slater BJ, Harvey TH and Butterfield NJ (2018) Small carbonaceous fossils (SCFs) from the Terreneuvian (lower Cambrian) of Baltica. *Paleontology* 61: 417–439; (J) Further information in: Slater BJ, Harvey TH and Butterfield NJ (2018) Small carbonaceous fossils (SCFs) from the Terreneuvian (lower Cambrian) of Baltica. *Paleontology* 61: 417–439. All images courtesy of Thomas Harvey, with the exception of J, which is courtesy of Thomas Harvey and Nicholas Butterfield.
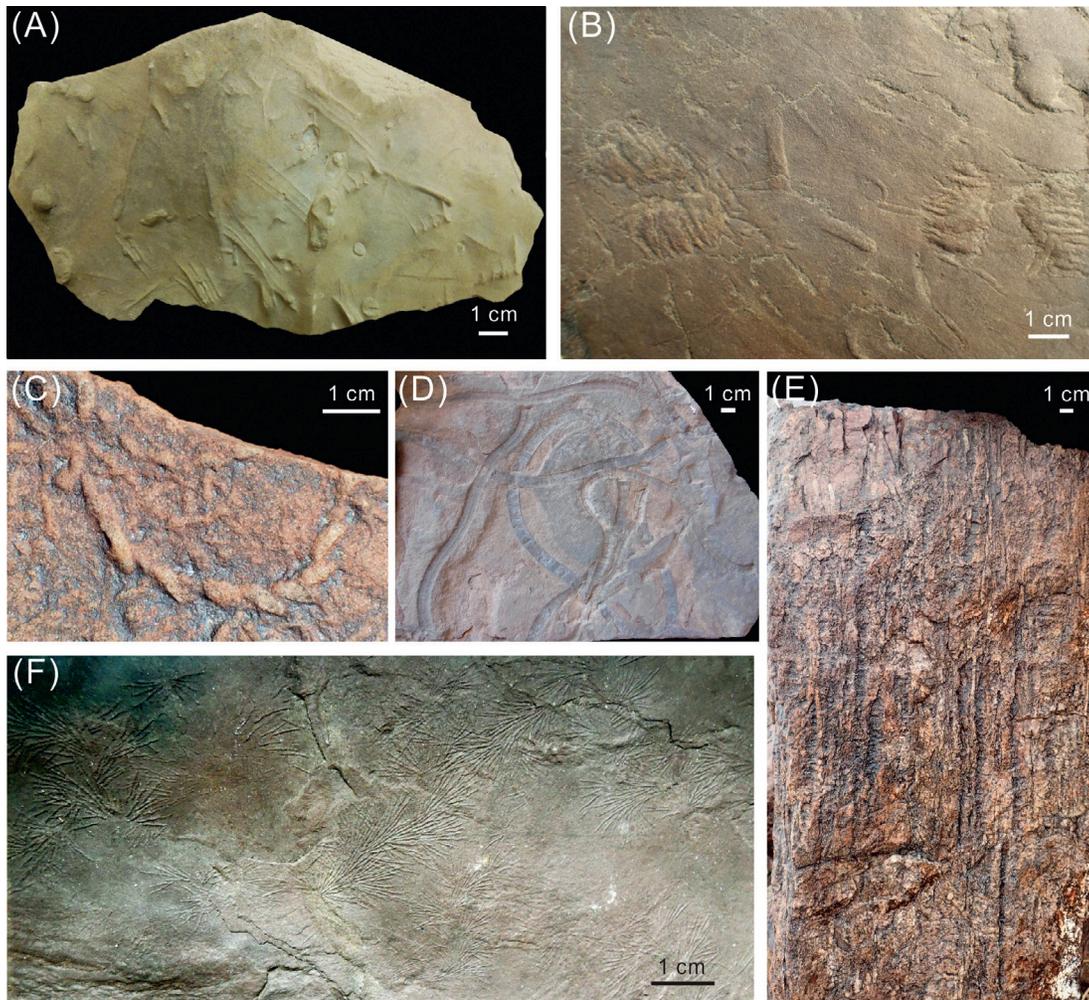
Fig. 5   Representative trace fossils of the Cambrian explosion (A) Arthropod scratch imprints, Lukati Formation (Cambrian Stage 3), Estonia. Preserved as positive hyporelief. Specimen housed in the collections of the Department of Geology, Tallinn University of Technology; (B) *Rusophycus avalonenesis*, Member 2, Chapel Island Formation (Fortunian), Burin Peninsula, Canada. Specimen housed in the collections of the Geological Survey of Canada in Ottawa; (C) *Treptichnus pedum*, preserved as positive hyporelief. Lower Member, Wood Canyon Formation (Fortunian), Death Valley, western United States. Preserved as positive hyporelief. Field specimen; (D) *Psammichnites gigas*, Shiyantou Formation (Cambrian Age 2), Meishucun, Yunnan Province, China. Preserved as positive hyporelief. Specimen housed in the collections of the Meishucun Geological Preserve. (E) *Skolithos linearis*, Zabriskie Quartzite (Cambrian Ages 3–4), Death Valley, western United States. Preserved as full relief. (F) *Oldhamia antiqua*, Bray Group (Cambrian Ages 3–4), Bray Head, Ireland. Preserved as positive hyporelief. Specimen housed at the National Museum of Ireland, Dublin. Scale bars are 1 cm.

diversity and abundance, including scalidophorans (e.g., priapulid teeth and scalids, paleoscolicids), arthropod remains (e.g., fragments of trilobites, *Isoxys* spines, bradoriid cuticle), lophotrochozoan elements (e.g., annelid chaeta, wiwaxiid sclerites), pterobranch hemichordate cuticle, and diverse fecal strings, with protoconodonts and protozoan-grade elements also present (Slater et al., 2017, 2018b). Integration of SSF and SCF provides a picture of the rapid diversification of ecdysozoans and deuterostomates during Cambrian Epoch 2, accompanying the ongoing further diversification of lophotrocozoans that started earlier during the Terreneuvian (Kouchinsky et al., 2015, 2017; Slater et al., 2017, 2018b).

The Emergence of Phanerozoic-Style Ecosystems

The evolutionary innovations that produced the build-up of Cambrian diversity were accompanied by profound re-structuring at the ecosystem scale (Fig. 10). In order to assess the magnitude of this ecologic change, a comparison with Ediacaran ecosystems, best represented by the White Sea assemblage, should be made. Ediacaran sediments were dominantly stabilized by extensive microbial binding (Seilacher, 1999; Buatois and Mángano, 2012). These widespread matgrounds sealed the infaunal ecospace with a diffusive boundary layer generating a sharp geochemical gradient into the sediment and precluding efficient exchange of organics and nutrients with the water column. Ediacaran ecosystems were dominated by benthic lifestyles reflecting interactions between
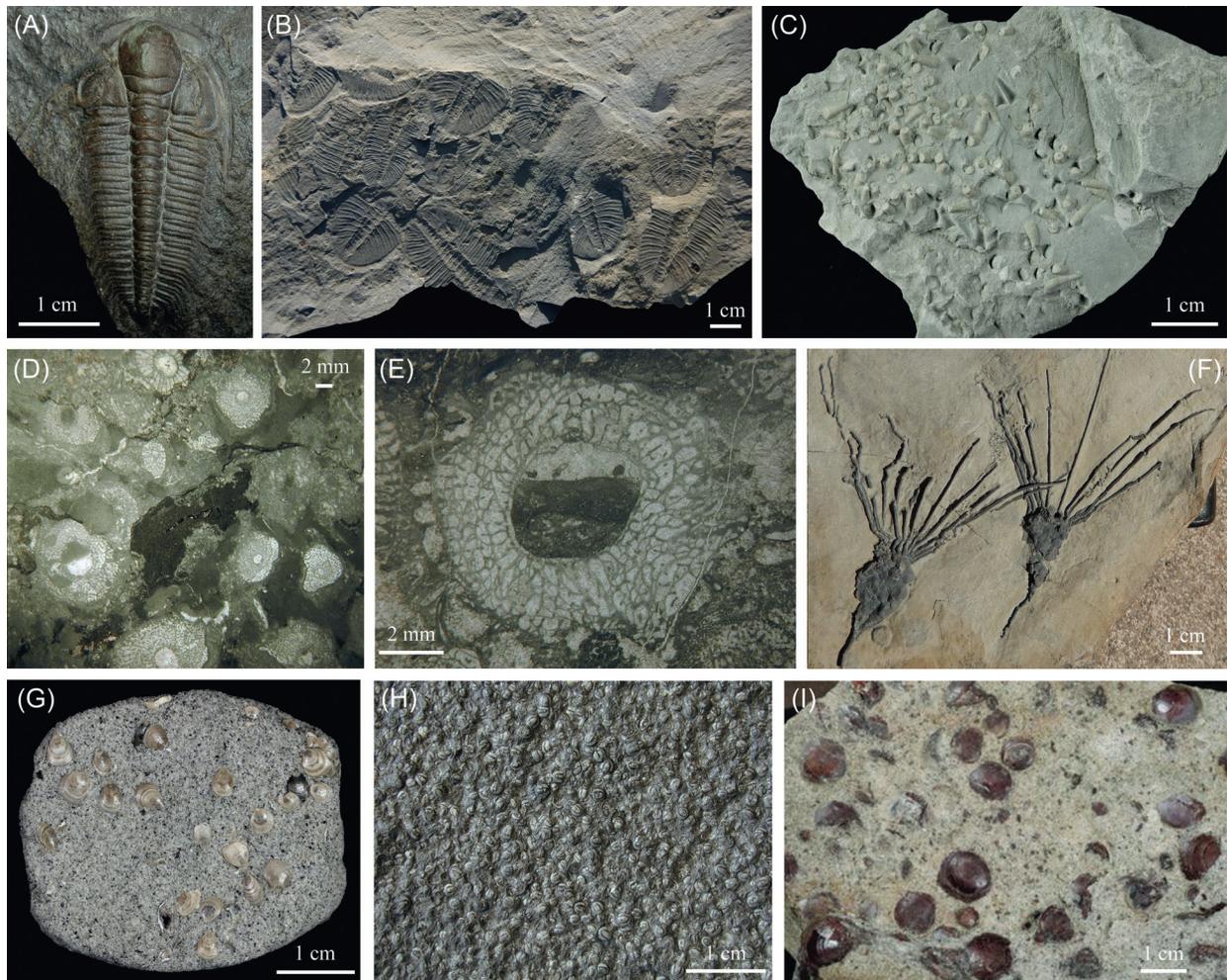
Fig. 6 Representative skeletal fossils from the Cambrian explosion (A) *Paradoxides gracilis*, a trilobite, Jince Formation (Miaoliangian), Bohemia, Czech Republic; (B) Molts of trilobite *Ogygopsis klotzi*, Trilobite Beds, Stephen Formation (Miaoliangian), Canadian Rockies; (C) *Volborthella tenuis*, a problematic fossil, Lükati Formation (Terreneuvian-Series 2), subsurface Estonia. GIT 398–963; (D) General view of archaeocyaths, Zwethau Formation (Series 2), subsurface Torgau-Doberlug Syncline, eastern Germany; (E) Close-up of archaeocyaths surrounded by calcimicrobes, Zwethau Formation (Series 2), subsurface Torgau-Doberlug Syncline, eastern Germany; (F) Pelmatozoan echinoderm *Gogia* sp., Spence Shale (Series 3), Utah, United States; (G) Linguliform brachiopod concentration, Ulgase Formation (Furongian), subsurface Estonia. GIT414"; (H) Mass layer of trilobite *Agnostus pisiformis*, Alunm Shale (Furongian), Vastergotland, Sweden; (I) *Ungula convexa*, a linguliform brachiopod, Laadoga Formation (Furongian), Lava River, Russia. GIT 275. (A) Further information in: Elicki O and Breitkreuz C (2016). Die Entwicklung des Systems Erde. *Springer Spektrum*: 296 S. (F) Further information in: Zamora S, Darroch S, and Rahman IA (2013) Taphonomy and ontogeny of early pelmatozoan echinoderms: A case study of a mass-mortality assemblage of *Gogia* from the Cambrian of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 377: 62–72. (H) Further information in: Elicki O (2003) Das Kambrium. *Biologie in unserer Zeit* 33: 380–389. Wiley. (A), (B), (D–E), and (H) courtesy of Olaf Elicki. (C), (G) and (I) courtesy of Ursula Toom. (F) courtesy of Samuel Zamora. GIT is Geosciences Collections of Estonia.

organisms and microbial mats. These include mat encrusters (suspension-feeding organisms attached to the microbial mats), mat stickers (presumed suspension-feeding organisms growing upward with the surrounding mats), mat scratchers (organisms rasping on the microbial mats), mat digesters (organisms feeding from direct external digestion of the mat), mat grazers (organisms browsing through the microbial mat), and undermat miners (organisms that constructed tunnels below the mat). Although the phylogenetic affinities of many Ediacaran organisms are controversial, mat grazers and undermat miners record the activities of bilaterians. Towards the end of the Ediacaran, other feeding strategies typical of Phanerozoic ecosystems are first recorded. These include efficient deposit feeding (i.e., sediment bulldozing; Buatois et al., 2018) and most notably predation, albeit limited, as revealed by holes in the tubular fossil *Cloudina* (Bengtson and Zhao, 1992). Active predation (i.e., capturing and defeating a prey) is an energetically costly, high oxygen demand, feeding strategy that has been repeatedly highlighted as an important ecologic innovation, generating a catalyzing effect via escalation in the construction of biodiversity and complex Cambrian ecological networks (Vermeij, 1989; Vannier et al., 2007).

Fortunian ecosystems were in a way reminiscent of Ediacaran ones in that microbial binding remained widespread (Buatois et al., 2014; Mángano and Buatois, 2014). As a result, some of the Ediacaran-style interactions (e.g., mat grazers, undermat miners) persisted. However, Fortunian rocks attest to a wide variety of trace-fossil morphologies (so-called architectural designs; Buatois

Fig. 7 Body fossils from the middle Cambrian Burgess Shale Lagerstätte of Canada (A) *Anomalocaris canadensis*, a radiodont. ROMIP 51211; (B) *Wiwaxia corrugata*, a mollusk or an annelid. ROMIP 56950. (C) *Choia ridleyi*, a demosponge. ROMIP 61036; (D) *Cambroraster falcatus*, a radiodont. ROMIP 65079. (E) *Tuzoia* sp., a bivalve arthropod. ROMIP 57394. Bioturbated specimen displaying a high density, widespread distribution of trails and shallow burrows. (F). *Yawunik kootenayi,* a leanchoiliid arthropod. ROMIP 64017. (G). *Hallucigenia sparsa*, a lobopodian. ROMIP 57776. (H). *Canadia spinosa*, an annelid. ROMIP 56972. (I) *Odontogriphus omalus*, a mollusk. ROMIP 57723. (J) *Oesia disjunta*, a hemichordate. ROMIP 63709. (K) *Ottoia prolifica*, a stem-group archaeopriapulid worm. ROMIP 60747. (L) *Orthrozanclus reburrus*, a lophotrocozoan of uncertain affinities. ROMIP 57197. (M) *Pikaia gracilens*, a chordate. ROMIP 61172. (N) *Opabinia regalis,* a stem group arthropod. ROMIP 59873. (O) *Olenoides serratus*, a trilobite. ROMIP 56629. ROMIP is Royal Ontario Museum Invertebrate Paleontology. From (B) Further information in: Caron JB, Scheltema A, Schander C and Rudkin D (2006) A soft-bodied mollusk with radula from the Middle Cambrian Burgess Shale. *Nature* 442: 159–163; Smith MR (2012) Mouthparts of the Burgess Shale fossils *Odontogriphus* and *Wiwaxia*: Implications for the ancestral molluscan radula. *Proceedings of the Royal Society B: Biological Sciences* 279: 4287–4295; Zhang Z, Smith MR and Shu D (2015) New reconstruction of the *Wiwaxia* scleritome, with data from Chengjiang juveniles. *Scientific Reports* 5: 1–9; (D) Further information in: Moysiuk J and Caron JB (2019) A new hurdiid radiodont from the Burgess Shale evinces the exploitation of Cambrian infaunal food sources. *Proceedings of the Royal Society B* 286: 20191079; (E) Further information in: Mángano MG, Hawkes CD and Caron JB (2019) Trace fossils associated with Burgess Shale non-biomineralized carapaces: Bringing taphonomic and ecological controls into focus. *Royal Society open science* 6: 172074; (F) Further information in: Caron JB, Gaines RR, Aria C, Mángano MG and Streng M (2014) A new phyllopod bed-like assemblage from the Burgess Shale of the Canadian Rockies. *Nature Communications* 5: 1–6.; Aria C, Caron JB and Gaines R (2015) A large new leanchoiliid from the Burgess Shale and the influence of inapplicable states on stem arthropod phylogeny. *Paleontology* 58: 629–660; (G) Further information in: Smith MR and Ortega-Hernández J (2014) *Hallucigenia*'s onychophoran-like claws and the case for Tactopoda. *Nature* 514: 363–366; (H) Further information in: Parry L and Caron JB (2019) *Canadia spinosa* and the early evolution of the annelid nervous system. *Science advances* 5: eaax5858; (I) Further information in: Caron JB, Scheltema A, Schander C and Rudkin D (2006) A soft-bodied mollusk with radula from the Middle Cambrian Burgess Shale. *Nature* 442: 159–163; Smith MR (2012) Mouthparts of the Burgess Shale fossils *Odontogriphus* and *Wiwaxia*: implications for the ancestral molluscan radula. *Proceedings of the Royal Society B: Biological Sciences* 279: 4287–4295; (J) Further information in: Nanglu K, Caron JB, Conway Morris S and Cameron CB (2016) Cambrian suspension-feeding tubicolous hemichordates. *BMC Biology* 14: 1–9; (K) Further information in: Smith MR, Harvey TH and Butterfield NJ (2015) The macro-and microfossil record of the Cambrian priapulid *Ottoia*. *Paleontology* 58: 705–721; (L) Further information in: Conway Morris S and Caron JB (2007) Halwaxiids and the early evolution of the lophotrochozoans. *Science* 315: 1255–1258; (M) Further information in: Conway Morris S and Caron JB (2012) *Pikaia gracilens* Walcott, a stem-group chordate from the Middle Cambrian of British Columbia. *Biological Reviews* 87: 480–512; (N) Further information in: Briggs DE (2015) Extraordinary fossils reveal the nature of Cambrian life: A commentary on Whittington (1975) The enigmatic animal *Opabinia regalis*, Middle Cambrian, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370: 20140313. All images courtesy of Jean Bernard Caron.

Fig. 8 Body fossils from the lower Cambrian Chengjiang Lagerstätte of China (A) *Fuxianhuia protensa,* a stem-group euarthropod. YKLP 11321. (B) Specimen of *Fuxianhuia protensa* with preserved cardiovascular system. YKLP 11335. (C) Specimen of *Fuxianhuia protensa* showing head region with preserved brain. YKLP 15006.; (D) *Yunnanozoon lividum,* a bilaterian of uncertain affinity. RCCBYU 10310. (E) *Cricocosmia jinningensis*, a palaeoscolicid worm. RCCBYU 10218. (F) *Eldonia eumorpha,* a possible deuterostome. RCCBYU 10304. (G) *Eoredlichia intermedia,* a redlichiid trilobite with exceptionally well-preserved antennae. YKLP 10973. (H) *Luolishania longicruris*, a lobopodian. RCCBYU 10242. (I) *Microdictyon sinicum,* a lobopodian. RCCBYU 10249. (J) Cluster of *Inquicus fellatus* attached to *Cricocosmia jinningensis*, the earliest evidence of metazoan symbiosis. YKLP 13226. (K) *Lyrarapax unguispinus*, a radiodont with brain preservation. YKLP 13305. (L) *Cindarella eucalla,* a stem-group euarthropod. YKLP 11427. YKLP is Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China. RCCBYU is Research Center for the Chengjiang Biota, Yunnan University. From (A) Further information in: Ma X, Hou X, Edgecombe GD and Strausfeld NJ (2012) Complex brain and optic lobes in an early Cambrian arthropod. *Nature* 490: 258–261; (B) Further information in: Ma X, Cong P, Hou X, Edgecombe GD and Strausfeld NJ (2014) An exceptionally preserved arthropod cardiovascular system from the early Cambrian. *Nature Communications* 5: 1–7; (C) Further information in: Ma X, Hou X, Edgecombe GD and Strausfeld NJ (2012) Complex brain and optic lobes in an early Cambrian arthropod. *Nature* 490: 258–261; (D, E, F, I, and L) Further information in: Xian-Guang H, Siveter DJ, Siveter DJ, Aldridge RJ, Pei-Yun C, Gabbott SE, Xiao-Ya M, Purnell MA and Williams M (2004) *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life*. John Wiley & Sons (G) Further information in: Hou X, Clarkson EN, Yang J, Zhang X, Wu G and Yuan Z (2008) Appendages of early Cambrian Eoredlichia (Trilobita) from the Chengjiang biota, Yunnan, China. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 99: 213–223; (H) Further information in: Ma X, Hou X and Bergström J (2009) Morphology of *Luolishania longicruris* (Lower Cambrian, Chengjiang Lagerstätte, SW China) and the phylogenetic relationships within lobopodians. *Arthropod Structure & Development* 38: 271–291; (J) Further information in: Cong P, Ma X, Williams M, Siveter DJ, Siveter DJ, Gabbott SE, Zhai D, Goral T, Edgecombe GD and Hou X (2017) Host-specific infestation in early Cambrian worms. *Nature Ecology & Evolution* 1: 1465–1469; (K) Further information in: Cong P, Ma X, Hou X, Edgecombe GD and Strausfeld NJ (2014) Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature* 513: 538–542; (A–C) and (G–K) courtesy of Xiaoya Ma. (D–F) and (I) courtesy of Derek Siveter.
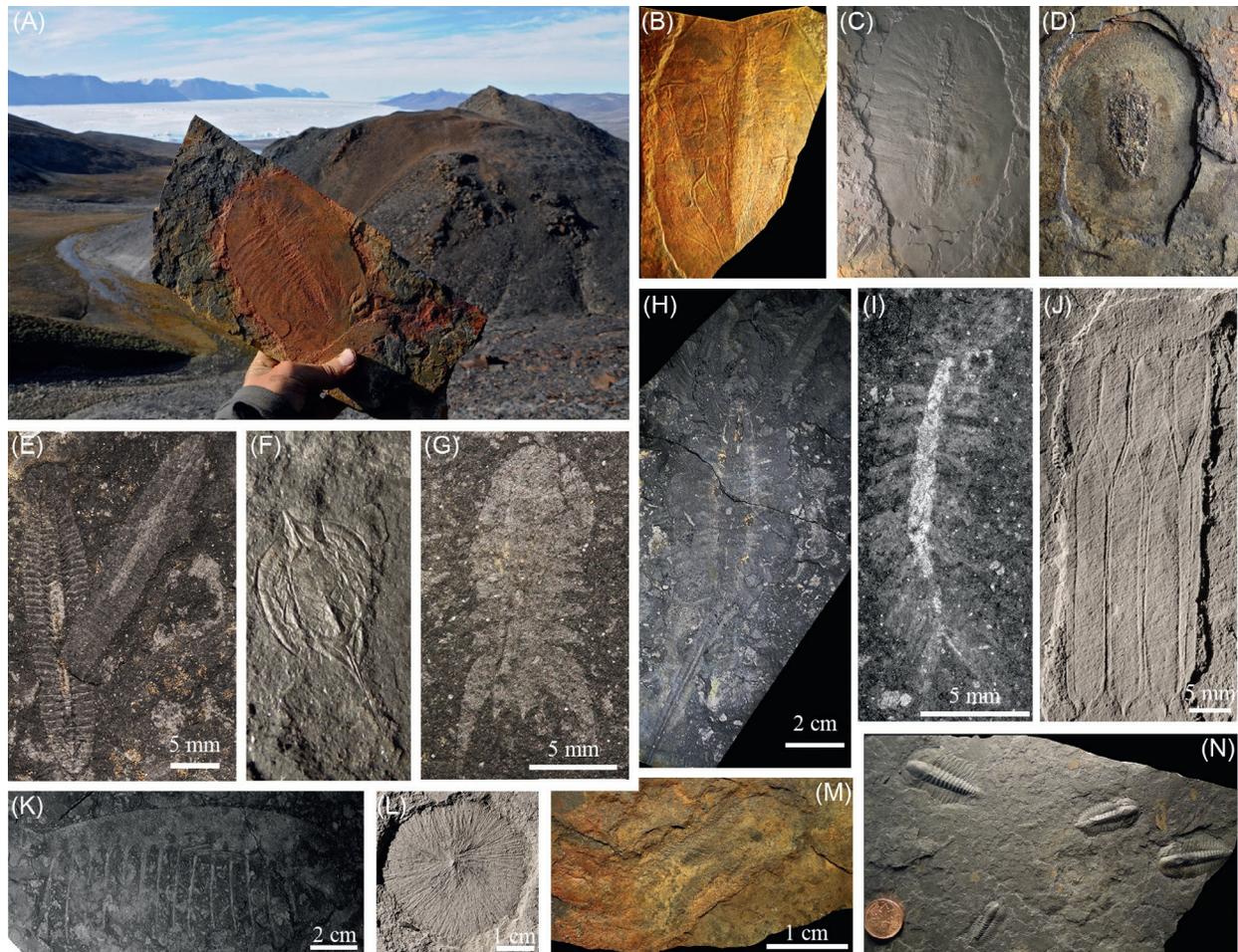
Fig. 9 Body fossils from the early Cambrian Sirius Passet Lagerstätte of Greenland (A–C). *Arthroaspis bergstroemi*, an euarthropod. Note associated trace fossil on carapace in B. (D) *Campanamuta mantonae*, an euarthropod. (E) *Kleptothule rasmusseni*, an euarthropod. MGUH 33379; (F) *Isoxys volucris*, an euarthropod; (G) *Aaveqaspis inesoni*, an euarthropod. MGUH 33386; (H) *Kergymachela kierkegaardi*, a lobopodian. MGUH 32048; (I) *Pygocirrus butyricampum*, an annelid. MGUH 29288; (J) *Sirilorica carlsbergi*, a loriciferan. MGUH 33383; (K) *Tamisiocaris borealis*, a radiodont. MGUH 30500; (L) *Lenica hindei*, a poriferan. MGUH 33385; (M) *Halkieria evangelista*, a mollusk; (N) *Buenellus higginsi*, a trilobite. From (A–C) Further information in: Stein M, Budd GE, Peel JS and Harper DAT (2013) *Arthroaspis* n. gen., a common element of the Sirius Passet Lagerstätte (Cambrian, North Greenland), sheds light on trilobite ancestry. *BMC Evolutionary Biology* 13: 99; Mángano MG, Bromley RG, Harper DAT, Nielsen AT, Smith MP and Vinther J (2012) Nonbiomineralized carapaces in Cambrian seafloor landscapes (Sirius Passet, Greenland): Opening a new window into early Phanerozoic benthic ecology. *Geology* 40: 519–522; (D) Further information in: Budd GE (2011) *Campanamuta mantonae* gen. et. sp. nov., an exceptionally preserved arthropod from the Sirius Passet Fauna (Buen Formation, lower Cambrian, North Greenland). *Journal of Systematic Paleontology* 9: 217–260; (N); *(E–N) Further information in: Harper DA, Hammarlund EU, Topper TP, Nielsen AT, Rasmussen JA, Park TYS, and Smith MP (2019) The Sirius Passet Lagerstätte of North Greenland: a remote window on the Cambrian explosion. Journal of the Geological Society* **176**, *1023–1037.* (A) courtesy of Jakob Vinther. (E) and (G–L) courtesy of David Harper.

et al., 2017) unknown in the Ediacaran that provide evidence of a new cast of characters, arthropods being among the most significant. In addition, a wider range of behaviors records the activities of vermiform producers of diverse phylogenetic affinities, most likely including priapulids, nematodes, and deuterostomates (Mángano and Buatois, 2014, 2020; Buatois et al., 2014; Laing et al., 2019). Notably, Fortunian SSF also depict a sort of hinge between Ediacaran and younger Cambrian assemblages, displaying siliceous tubes (e.g., *Platysolemites*, *Cambrotubulus*-like) that are similar to those present in late Ediacaran assemblages, and mineralized forms (e.g., maikhanellids, helcionellid mollusks) recording the novel radiation of lophotrochozoans (Kouchinsky et al., 2017). SCF include abundant protoconodonts (Chaetognatha) and priapulid spines (scalidophorans) in association with protist-grade components (Fig. 4I–J). Collectively, the SSF and the SCF provide additional support of the ongoing radiation of lophotrochoans and ecdysozoans taking place mostly in benthic and hyperbenthic (1–10 m above the substrate) habitats, and featuring some voracious predators (chaetognathans) (Vannier et al., 2007; Kouchinsky et al., 2017; Slater et al., 2018a).

However, even more dramatic changes at ecosystem scale took place later in the early Cambrian. These have been referred to as the "Agronomic revolution" by Seilacher (1999). In essence, this concept refers to the advent of penetrative bioturbation and the replacement of matgrounds by mixgrounds that took place by Cambrian Age 2 (Mángano and Buatois, 2017), and reached widespread development in shallow-water settings later in the early Cambrian. This breakthrough involved intense substrate
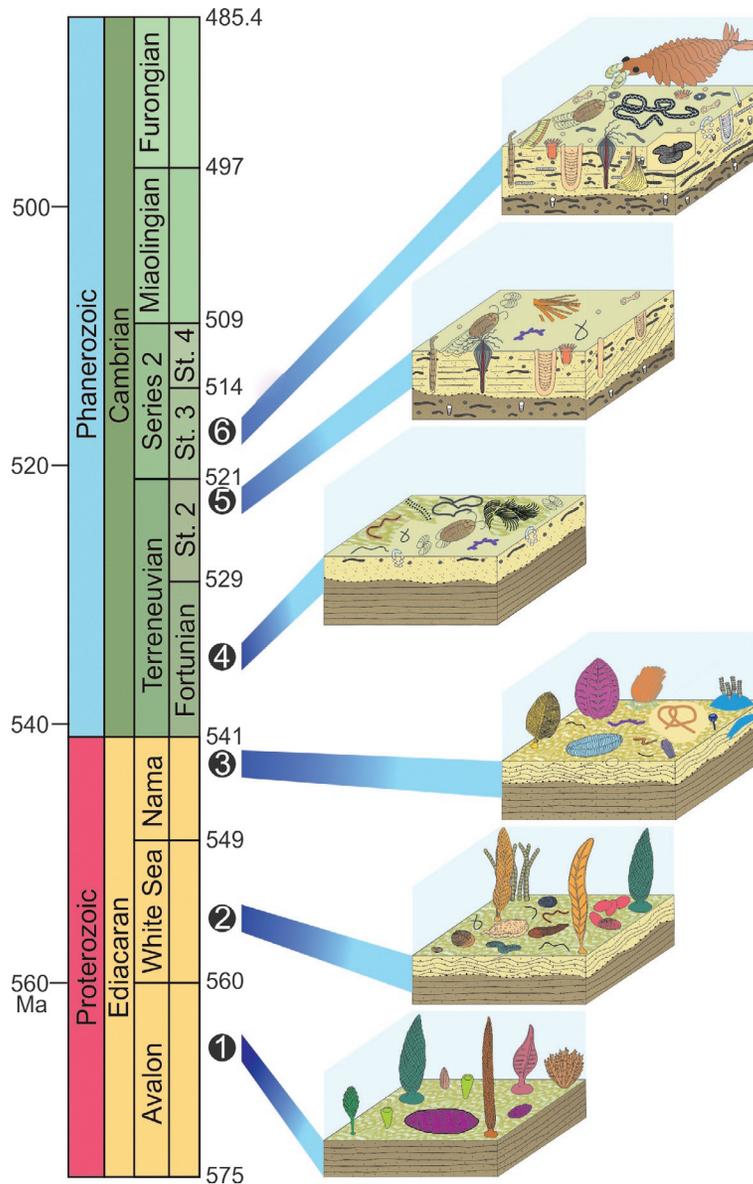
Fig. 10 Milestones in paleoecologic changes during the Ediacaran-Cambrian transition. (1), Earliest evidence of megascopic complex life (deep sea Avalon assemblage). The Avalon assemblage is dominated by sessile organisms, most notably rangeomorphs and arboreomorphs; (2), Diversification of the Ediacara biota (shallow marine White Sea assemblage) and appearance of bilaterian trace fossils in matground-dominated ecosystems. The White Sea assemblage is typified by diverse segmented fossils, discoid fossils, and fronds, as well as uncontroversial evidence of mobile bilaterians (e.g., simple trace fossils) and putative stem-group mollusks; (3), Decline of the Ediacara biota (shallow marine Nama assemblage), appearance of skeletal organisms (including reef builders), and initial increase in infaunalization and trace fossil complexity. The Nama assemblage is dominated by multifoliate fronds and early calcified metazoans, as well as bilaterian trace fossils. (4), Persistence of microbially stabilized surfaces, increase in trace fossil diversity, complexity and disparity, and increase in diversity of small shelly fossils. Animal-matground interactions still extensive. The Fortunian is poor in macrofossils, but is host to abundant trace fossils, as well as SSF and SCF. The presence of euarthropods (possible trilobites) in these strata is based on trace-fossil evidence; the oldest trilobite body fossils occurred in rocks near the Terreneuvian-Series 2 boundary; (5), Establishment of extensive and deep bioturbation, replacement of matgrounds by mixgrounds (Agronomic revolution), coupling of the pelagic and benthic realms, onset of the sediment mixed layer, and establishment of modern-style food webs. Diversification of SSF, and SCF. First animal-dominated Phanerozoic reefs; (6), Oldest occurrences of Burgess Shale-type preservation and renewed diversification of trace fossils, SSF, and SCF. Series 2 is host to the animal explosion in macrofossils (i.e., Cambrian explosion as expressed by skeletal body fossils). By the end of the so-called early Cambrian, the explosion is essentially over. From (3) Ediacaran diagrams and further information in: Narbonne GM (2005) The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences* 33: 421–442; Droser ML, Tarhan LG and Gehling JG (2017) The rise of animals in a changing environment: Global ecological innovation in the late Ediacaran. *Annual Review of Earth and Planetary Sciences* 45: 593–617; (6) Cambrian diagrams and further information in: Mángano MG and Buatois LA (2020) The rise and early evolution of animals: Where do we stand from a trace-fossil perspective? *Interface Focus* 10: 20190103.

disruption by animals, modifying substantially the original fabric and geochemical properties within the sediment, opening ecological space to other animals and microbial communities (Seilacher, 1999; Erwin and Tweedt, 2012). Evolutionary innovations in the water column and in the sediment played important roles in the coupling of the pelagic and benthic realms and the advent of modern infaunal ecology. In the water column, the evolution of mesozooplankton and filter feeding nekton, able to pack small phytoplankton into larger particles as pellets efficiently reaching the seafloor, provided a rich food resource to an emerging epifaunal and infaunal animal community (Butterfield, 1997, 2011; Lerosey-Aubril and Pates, 2018). In the benthos, infaunal suspension feeders colonized sand-dominated nearshore deposits, producing deep and dense, vertical burrow fabrics, and deposit and detritus feeders contributed to intense biogenic reworking of the sediment in mud-dominated offshore deposits (Mángano and Buatois, 2014; Gougeon et al., 2018). These physical and chemical ecologic engineers favored increased ventilation within the sediment, and generated new available ecospace, facilitating efficient exchange of nutrients and carbon between the water column and the substrate (Erwin et al., 2011; Erwin and Tweedt, 2012; Mángano and Buatois, 2014; Gougeon et al., 2018). A related, but distinct concept is the Cambrian Substrate Revolution (Bottjer et al., 2000; see Mángano and Buatois, 2017 for a review). This protracted process involves the effects of bioturbation on the evolution and ecology of early Cambrian metazoans, particularly underscoring the response of non-burrowing, epibenthic animals. Substrate changes may have caused extinction (e.g., helicoplacoids), adaptation (e.g., edriasteroids and eocrinoids adapted to upper Cambrian hardgrounds), or environmental restriction (e.g., monoplacophoran migration to the deep sea).

These changes at ecosystem scale are also manifested by exceptionally preserved faunas, which have provided a wealth of evidence to reconstruct the complexity of Cambrian food webs. Our understanding of Cambrian ecosystems emerges from a combination of a wide range of fossil evidence and analogies with modern communities (Butterfield, 2001). Paleontologic evidence to reconstruct feeding ecologies includes: (1) functional morphology of skeletal (e.g., appendage morphology) or anatomical parts (e.g., presence of vesicles in the gut), (2) analysis of gut contents, (3) analysis of coprolites (including so called "fossil aggregates"), and (4) bioturbation and bioerosion structures (e.g., bites, holes), including trace-fossil functional analysis (e.g., mode of burrow construction) (Vannier and Chen, 2005). All lines of evidence indicate that the basic ecologic principles that regulate modern ecosystem functioning were in place by Cambrian Epoch 2 (Vannier and Chen, 2005; Vannier, 2007; Dunne et al., 2008). All levels of the food web were represented, including primary production by phytoplankton (e.g., acritarchs), primary mesozooplanktonic consumers (e.g., crustaceans), secondary planktonic and nektonic consumers (e.g., chaetognaths, radiodonts), suspension feeders (e.g., sponges, brachiopods), detritivores and scavengers (e.g., hyolithids, lobopodians, priapulids, arthropods), and benthic-nektobenthic primary consumers (e.g., priapulids, radiodonts, other arthropods) (Vannier, 2007; Vannier et al., 2007). Although there is no direct evidence of secondary consumers, SCF provide information on the existence of interstitial ecosystems during the early Phanerozoic. Of particular importance is the recovery of the smallest animal (Ecdysozoa, Phylum Loricifera, Fig. 4C) living permanently among grains in Cambrian sediments (Harvey and Butterfield, 2017). Animal invasion of interstitial habitats may reflect the exploration of available, underutilized ecospace created by metazoan bioturbation, but may also have been a response to strong predation pressures on the benthic prey, leading to small size refuge (Harvey and Butterfield, 2017). In this regard, the reconstructed feeding ecologies of some large nektobenthic arthropods based on anatomical data (radiodont appendage morphology) supports sediment-sifting habits and a diet most likely based on small macrofauna and meiofauna (Moysiuk and Caron, 2019). Large benthic Tegopelte-like arthropods skimming surficial sediments (Minter et al., 2012) may also reflect the use of meiofaunal food resources in Cambrian ecosystems.

High-density trace-fossil assemblages associated with non-biomineralized carapaces characteristic of Burgess Shale-type Lagerstätten open a unique window to benthic ecology and the increasing heterogeneity of the Cambrian sea floor (Mángano et al., 2012, 2019; Mikuláš et al., 2012). Molds and carcasses delivered from the water column and lying on the sea bed engineered the Cambrian seascape, providing food and shelter for small macrofauna, larvae and juveniles, and promoting the development of a rich meiobenthic fauna. Abundant trails (Fig. 7E), interconnected burrows (Fig. 9B), thin caliper structures with tree-like terminations, and pellet-infilled and annulated burrows record the activities of grazers, shallow deposit feeders and bacterial farmers that used the sharp geochemical gradient at the sediment-water interface (enhanced by the presence of the organic carapace), exploiting organic resources and gaining protection from benthic and nektobenthic predators.

Similarities between Cambrian and recent food webs outline the surprisingly strong and long-lasting constraints on the organization of complex feeding interactions in metazoan communities (Dunne et al., 2008). A few differences between Cambrian and modern trophic webs, such as longer path lengths between species (mean length path systematically decreases with increased connectivity), frequent feeding loops (A eats B eats C eats A), and high variability in the distributions of links across species, may reflect the still-in-flux construction of the Phanerozoic ecosystem yet not fully constrained, integrated, hierarchical and stable (Dunne et al., 2008).

Important evolutionary innovations took place in carbonate reef environments as well, as shown by the replacement of Ediacaran reefs dominated by microbial communities by Cambrian reefs dominated by sessile animals (Pratt et al., 2001). From a paleoecological point of view, this replacement was accompanied by a marked increase in the complexity of trophic webs, diversity, and niche partitioning. However, microbial communities were still dominant during the Fortunian, although characterized by a new type of builders, such as *Epiphyton* and *Renalcis* (Rowland and Gangloff, 1988; Pratt et al., 2001). By Cambrian Age 2, archaeocyathids were added as major reef builders (Rowland and Gangloff, 1988; Pratt et al., 2001; Lee and Riding, 2018). As a result, archaeocyath calcimicrobe reefs became the dominant carbonate buildups during the rest of the early Cambrian (Zhuravlev et al., 2015) (Fig. 11A–I). Archaeocyaths (Fig. 6D–E) reached peak diversity by Cambrian Ages 3–4 and became widespread in low-latitude settings (Rowland and Gangloff, 1988; Zhuravlev et al., 2015). Although archaeocyath reefs were small compared to
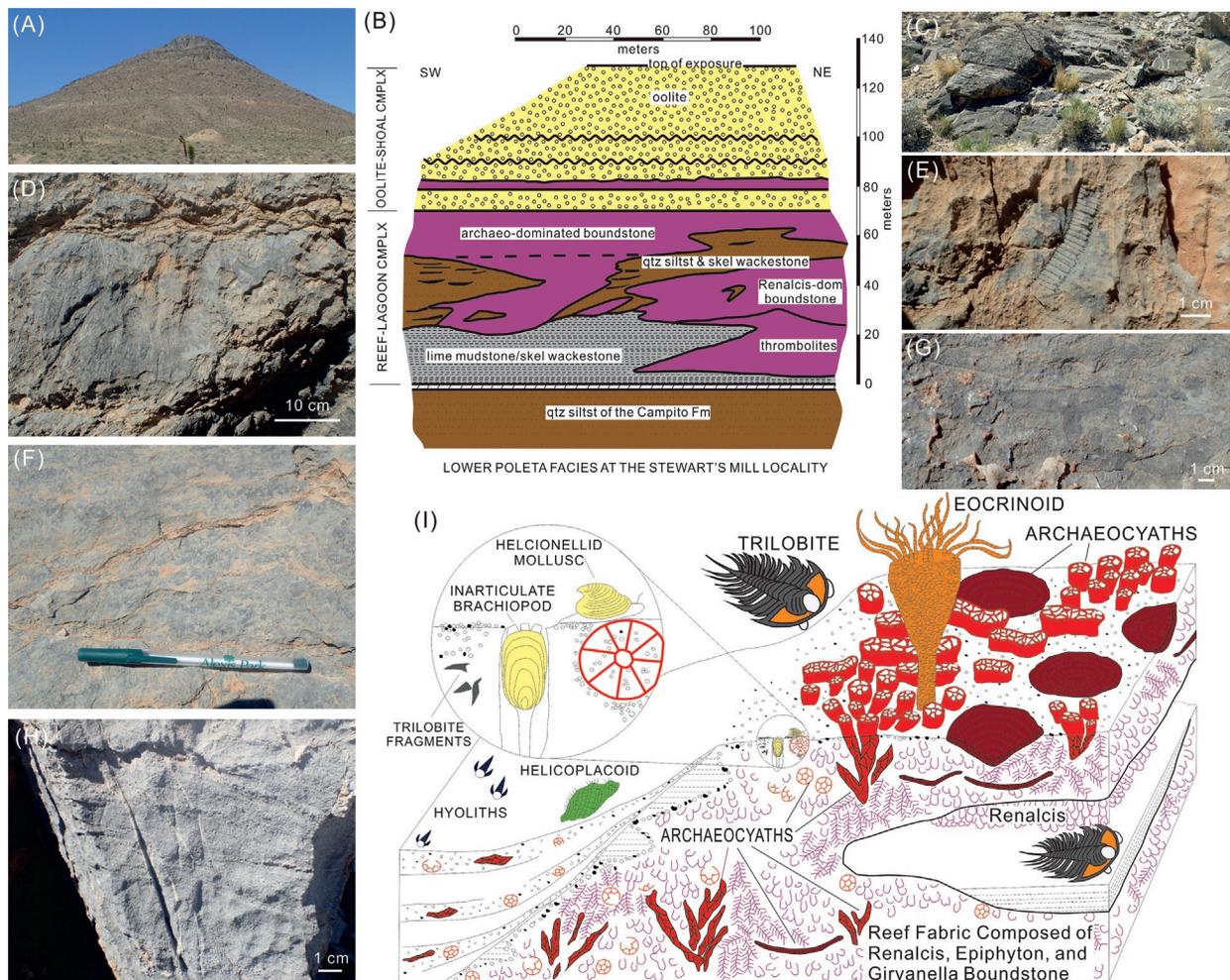
Fig. 11 Lower Cambrian reefs, Lower Member of the Poleta Formation (Cambrian Stage 3) at Stewart's Mill, Nevada (A) General view. Recessive lower interval represents offshore deposits of the Montenegro Member of the Campito Formation, middle interval consists of thrombolytic and archaeocyathid-*Renalcis* boundstone (reef-lagoonal complex) of the Lower Member of the Poleta Formation, and upper resistant interval is dominated by oolite, biostromes and packstone (oolite shoal complex) of the Lower Member of the Poleta Formation; (B) Reconstruction of reef architecture. (C) General view of lime mudstone (middle interval), representing low-energy lagoonal deposits; (D) Low-energy lagoonal deposits dominated by thrombolites with sparse archaeocyaths (middle interval); (E) The skeletal cyanobacteria *Epiphyton*, a primary boundstone builder in lower Cambrian reefs (middle interval); (F) *Renalcis*-dominated boundstone (middle interval); (G) Branching archaeocyaths characteristic of high-energy reef crest deposits (archaeocyathid-dominated boundstone in middle interval); (H) Close-up of upper interval showing cross-bedded oolite grainstone (oolite shoal complex); (I) Schematic reconstruction of the reef. From (B) Diagram and further information in: Rowland SM (1981) Archaeocyathid bioherms in the lower Poleta Formation, Esmeralda County, Nevada. In: Taylor ME and Palmer AR (eds.), *Cambrian Stratigraphy and Paleontology of the Great Basin and Vicinity, Western United States: International Symposium on the Cambrian System*, 2nd edn., Guidebook for Field Trip 1: Denver, pp. 44–49, U.S. Geological Survey and International Union of Geological Sciences; (I) Diagram and further information in: Rowland SM and Gangloff RA (1988) Structure and paleoecology of Lower Cambrian reefs. *Palaios* 3: 111–135.

younger reefs, they generated increased habitat complexity during the early Cambrian, and their local abundance may have resulted in important regional engineering effects (Erwin and Tweedt, 2012). However, archaeocyaths disappeared by the end of the early Cambrian (Rowland and Gangloff, 1988; Pratt et al., 2001). During the middle (Epoch 3) and late (Furongian) Cambrian, microbial-lithistid sponge reefs became dominant (Lee and Riding, 2018). In particular, Epoch 3 reefs were dominated by thrombolites and dendrolites, mostly constructed by *Epiphyton* and *Renalcis*, showing the persistence of calcimicrobes as builders (Lee et al., 2015). By the Furongian, maze-like maceriate reefs (including siliceous sponges and calcified microbes, such as *Girvanella* and *Tarthinia*), and columnar stromatolites (Lee et al., 2015) dominated. Notably, a level of complexity similar to that of Cambrian Epoch 2 was not achieved again until the Middle Ordovician, during the Global Ordovician Biodiversification Event (Pratt et al., 2001).

Explaining the Cambrian Explosion

We have deliberately avoided the use of the term "cause" in the title of this section. Searching for cause-effect links in connection with the Cambrian explosion would be misleading because the evolutionary processes involved may be better understood as a series of self-propagating feedback systems between the biosphere and other Earth systems, rather than strict causality (Erwin and Valentine, 2013). Multidisciplinary efforts have immensely expanded our understanding of internal and external factors that played a role in the Cambrian explosion, In other words, explanations focusing on individual triggers or mechanisms fail to recreate the intricate network of connections within a precise temporal framework that led to the Cambrian explosion. Historically, invoked explanations have been classified into environmental, genetic- developmental, and ecological (Marshall, 2006; Erwin et al., 2011).

In relation to the former (i.e., environmental), early oxygen-related explanations were fundamentally centered on oxygen increase as the necessary component and fundamental trigger for the evolution of animals (Nursall, 1959; see Mills and Canfield, 2014 for historical background). The explanation was simple, animals did not evolve until there was enough oxygen, and this did not happen until the Cambrian (Nursall, 1959). The rationale behind this explanation involves the assumption that early metazoans were obligate aerobics; accordingly, there was a minimum threshold of oxygen needed for the existence of animals. This basic idea is also referred to as the oxygen-control hypothesis (Knoll, 1992), and it has been challenged on theoretical and experimental backgrounds (e.g., Sperling et al., 2013; Mills et al., 2014).

There is, however, general agreement that the evolution of large (i.e., macroscopic) bilaterians engaged in active behavior, particularly predation, required aerobic metabolism (Budd and Jensen, 2000; Budd, 2008; Sperling et al., 2013). Also, there is evidence that Ediacaran oceans were characterized by an overall marked increase in oxygen levels (Canfield et al., 2007; Kendall et al., 2015). It has been suggested that this increase may have been rather modest, but sufficient to remove environmental barriers to the appearance of animals (Sperling et al., 2015). However, the main challenge of the oxygen hypothesis is that there is no real evidence that an increase in oxygen can create new body plans (i.e., generate disparity) (Budd, 2008; Erwin et al., 2011). In addition, in recent years the causal relationship between oxygenation and the emergence of animals has experienced an interesting twist. Several authors have argued that the appearance of complex eukaryotes and sponges may have contributed to create oxygen levels permissible for animal evolution (e.g., Sperling et al., 2007; Butterfield, 2009, 2011, 2018; Lenton et al., 2014). In this scenario, the emergence of sponges may have contributed to shelf ventilation by pumping small picoplankton and DOC, decreasing turbidity and promoting high, light-demanding eukaryotic algae. In addition, rapid sinking of large eukaryotic particles through the water column may have led to a reduction of oxygen consumption in the surface waters, allowing primary producers to photosynthesize more efficiently. Another variant of this model involves the migration of sponges from shallow to deep water, prompting ventilation of the oceans (Sperling et al., 2007, 2011). Interestingly, the view of unidirectional rise in oxygen has been challenged by the recognition of several alternating oxygenation and anoxic events during the Ediacaran (Sahoo et al., 2016). However, it has been argued that fluctuations in redox conditions may have actually promoted evolutionary innovations (Wood and Erwin, 2018). All in all, oxygen remains an important component in environmental explanations.

In addition to oxygen, other environmental triggers that have been outlined for the Cambrian explosion are the aftermath of the Snowball Earth (Hoffman et al., 1998), the large negative carbon isotopic anomaly at the Ediacaran-Cambrian boundary (Amthor et al., 2003), a major sea-level rise (Brasier, 1982), and true polar wander (Kirschvink and Raub, 2003). There is growing agreement that all these proposed potential triggers lack an evidence-supported mechanism to explain evolutionary novelty, in particularly the explosive increase in disparity.

Genetic-developmental explanations have received significant attention during the last decades due to recent discoveries in the field of evolutionary developmental biology (i.e., evo devo). Although developmental explanations have been invoked for a long time (e.g., Valentine, 1995, 2000; Valentine et al., 1999), it is not until during recent years that more sophisticated hypotheses have been put forward (e.g., Marshall and Valentine, 2010; Erwin et al., 2011; Paps and Holland, 2018). Developmental genes (i.e., those that regulate development from egg to adult), in contrast to housekeeping genes (i.e., those that control basic cellular functions) are the ones that bear key information with respect to the Cambrian explosion (Marshall and Valentine, 2010; Erwin and Valentine, 2013). The study of developmental genes in living species is crucial in order to trace back in geologic time their last common ancestors or LCA. However, there are still marked discrepancies in this regard. One line of thought places the LCA of bilaterians during the Cryogenian (700–670 My), generating a significant macroevolutionary lag between the initial construction of the bilaterian developmental toolkit and their first appearance in the fossil record (Erwin et al., 2011). From this perspective, the Cambrian explosion is understood as the final product of a long history of evolution of developmental networks and increasing ecologic interactions. Conversely, on the basis of morphologic and phylogenetic considerations, other authors have rejected the idea of placing the LCA of bilaterians that deep in time (Budd, 2003, 2013; Daley et al., 2018). Considerable discussion has centered on the split of Ecdysozoans, and in particular, the origin of arthropods (Daley et al., 2018). Integration of different paleontologic datasets, including soft-bodied macrofossils (Burgess Shale-type preservation), biomineralized skeletons, microfossils (phosphatic, siliceous and carbonaceous), and trace fossils indicates a Cambrian age for the origin of the Phylum Arthropoda and absence of support for a deep Precambrian history. Interestingly, new molecular clock analysis using multiple integrated molecular datasets and numerous fossil calibrations also points to a late Ediacaran origin of body plans followed by a rapid Cambrian radiation (Rota-Stabelli et al., 2013; Lozano-Fernandez et al., 2017).

Ecological explanations, although less popular for several years, have experienced a recent comeback (e.g., Dzik, 2007; Budd, 2008; Sperling et al., 2013; Budd and Jensen, 2017), albeit in combination with developmental and environmental ones (Erwin

et al., 2011; Erwin and Valentine, 2013; Sperling et al., 2013; Sperling and Stockey, 2018). The underlying classic rationale of ecological explanations resides in the argument that changes in trophic structures were at the root of the Cambrian explosion. In fact, increased predation pressures have figured prominently in this regard, based on the notion of coevolution linked to arms races (Vermeij, 1994; Fernandez-Valverde et al., 2018). Bioturbation has also been proposed as a major driving force in the macroevolutionary changes leading to the Cambrian explosion (e.g., Seilacher, 1999). On one hand, it has been argued that bioturbation may have negatively affected the more sessile life styles of most of the Ediacara biota, contributing to their disappearance (Darroch et al., 2015, 2018). On the other hand, by breaking the microbial seal at the sediment-water interface, bioturbation opened the infaunal ecospace, which at that point became available for colonization, triggering dramatic diversification both taxonomically and functionally (Seilacher, 1999; Mángano and Buatois, 2014, 2017). This view is supported by ecospace analysis, which shows that the number of modes of life substantially increased during the Cambrian in comparison with the Ediacaran (Bush et al., 2011). In particular, the Verdun Syndrome hypothesis put forward by Dzik (2007) attempts to establish a link among many of these factors by arguing that both burrowing and development of hard parts are a response to increased predation. However, hypotheses trying to pinpoint a succession of cause-effect explanations, although illuminating particular aspects, fail to build up a precise time frame of events. In fact, the trace-fossil record clearly shows that diversification and drastic increase in trace-fossil architectures (i.e., ichnodisparity) preceded a significant increase in bioturbation and benthic re-structuring (Mángano and Buatois, 2014).

Although treating these three sets of explanations separately may be useful on pedagogical grounds, links among them are apparent and complex. For example, environmental and ecological explanations have been linked from the perspective of physiology (Sperling et al., 2013). These authors noted that high oxygen levels support more complex food webs, including an abundance of carnivores, therefore underscoring a connection between environmental triggers and ecological drivers. Similarly, ecologic innovations are best seen through the lens of ecologic networks, resulting in positive spillover effects (Erwin and Valentine, 2013). The links between the different categories of explanations and the different factors within one set of explanations are at the core of the view that self-propagating feedback systems may be key to understanding the evolutionary dynamics of the Cambrian explosion.

Concluding Remarks

The evolutionary changes that took place between the terminal Ediacaran and the early Cambrian rank as one of the most dramatic evolutionary events in the history of life. These events not only signaled the appearance in the fossil record of all major Phyla (except Bryozoa), but also testify to the establishment of modern-style ecosystems. Notably, considerable debate still surrounds the timing, context, nature, and dynamics of these changes, collectively included in the Cambrian explosion. Although this evolutionary event has been characterized as "explosive", its length involves 40–50 My.

It is clear now that the Cambrian explosion was not a simple evolutionary radiation related to the occupation of underutilized or empty ecospace. Indeed, the emergence of multiple body plans and the profound ecological changes that took place cannot be explained by simple causal models (triggered, for example, by an increase in oxygen). The Cambrian explosion involved internal (i.e., genetic-developmental) and external (i.e., environmental and ecologic) factors, but any of these individual factors remains insufficient to explain early Phanerozoic biodiversification and ecosystem construction. We are just starting to decipher an intricate network of processes involving abiotic and biotic players that via positive feedback and spillover effects have resulted in the intricate explanatory narrative of the Cambrian explosion.

There is a growing consensus that there is a Precambrian history of metazoan evolution, and it is expected that existing disagreements on its extent will be resolved in the near future helped by better dating, new finds, and improved molecular techniques. In this regard, the trace-fossil record offers a promising venue, being more complete and continuous than the body-fossil record, and preserving small structures (i.e., micrometer scale). In addition, SCFs recording any meiobenthic metazoan component are remarkably absent in Ediacaran assemblages, also mitigating the idea of a preservational bias in the Ediacaran. All paleontological lines of evidence (i.e., SSF, SCF, macrofossils, and trace fossils) consistently point against pre-Fortunian ecdysozoan divergences.

Despite the controversies, recent advances are substantial and the future is promising. We await new exciting fossil finds, refined molecular phylogenies, reliable biomarkers, and an expanded understanding of geochemical changes and biological feedbacks. Integrated studies, including multiple datasets in an increasingly more articulated fashion, will be fundamental to generate a more robust understanding of the origin and early history of Metazoa and the Cambrian explosion.

Acknowledgments

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