The Cambrian Fossil Record and the Origin of the Phyla[1]

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Synopsis. Whilst the "Cambrian Explosion" continues to attract much attention from a wide range of earth and life scientists, the detailed patterns exhibited by the terminal Proterozoic–Early Cambrian biotas remain unclear, for reasons of systematics, biostratigraphy and biogeography. In particular, recent changes in absolute dating of the Cambrian have refined the period of time that the fossil record might be of most help in revealing the dynamics of the undoubted radiation taking place at this time. The famous exceptionally preserved faunas seem to be rather close temporally, and as yet reveal little about the earliest and critical period of evolution, deep in the Cambrian. Nevertheless, the most parsimonious interpretation of the Cambrian fossil record is that it represents a broadly accurate temporal picture of the origins of the bilaterian phyla.

Introduction

The "Cambrian explosion" is a poorly-defined term that refers to a period of time some 600–500 years ago ("Geon 5" [Hofmann, 1990]) during which the biosphere, as reflected in the eukaryotic fossil record, underwent a great expansion. Most popularly, the appearance in the fossil record of the first undoubted animals has, especially since the critical studies of Preston Cloud (*e.g.,* 1968), been regarded as truly documenting the evolutionary origins of the animals. Nevertheless, this straightforward view has rightly been regarded sceptically, for several reasons. The first of these is that the apparent very rapid appearance of taxa in the record must inevitably imply a period of cryptic evolution before this point (Dawkins, 1998; Cooper and Fortey, 1998). Secondly, high-profile "molecular clock" estimates of the timing of splits between the various phyla have suggested that animal lineages actually diverged up to 800 Ma or more before their appearance in the fossil record (*e.g.,* Runnegar, 1982; Wray *et al.*, 1996; see review in Fortey *et al.*, 2002). This sort of discrepancy clearly demands resolution. However, it is important that any resolution is of the appropriate data sets, *i.e.,* the best estimates of molecular timings of divergences (Bromhall, 2003) and the most accurate picture of what the Cambrian fossil record actually suggests about timing and nature of the relevant radiations. As the molecular clock evidence is increasingly coming under critical review (*e.g.,* Rodríguez-Trelles *et al.*, 2001), it is reasonable to subject the fossil record to similar scrutiny. To do so requires a careful look at the many current problems presented by Cambrian fossils, including those stemming from systematics, taphonomy (see Butterfield, 2003) and dating.

Cambrian Fossils and Systematics

In 1979, the Systematics Association published an important volume summarising the fossil evidence for the origins of various major invertebrate groups (House, 1979). It is notable for its juxtaposition of two papers, one Whittington's summary of the phanerozoic fossil record of arthropods (Whittington, 1979; Fig. 1 herein), and the other Jefferies' version of Hennig's views on fossils and systematics (Jefferies, 1979; Fig. 2 herein). These papers stand at opposite ends of the spectrum of the attempts to discover the true relevance of fossils to phylogenetic studies. Whittington's groundbreaking studies of the Burgess Shale led him to conclude that previous attempts to place Cambrian taxa in extant groupings did not fairly reflect their provocative morphology. This insight was quite correct but, under the influence of Sidney Manton (*e.g.,* Manton, 1977) and her strongly polyphyletic views of the origin of the arthropods, Whittington concluded from this that the various arthropods in the Cambrian represented lineages as separate as the modern groups are (chelicerates, insects etc). This view merely reflected the general Zeitgeist of the time, and the problems that systematists had had in trying to assign fossils to systematic positions. The net effect was that, although fossils were generally thought of as providing the answer to the origins of major groups, in practice they tended to shed very little light on them. The sense of unease engendered by this tension between expectation and delivered results culminated in the famous paper by Colin Patterson (1981)—himself a palaeontologist—when he launched a devastating effect on conventional wisdom about the importance of fossils. If fossils were going to contribute to discussions about phylogeny in a serious way, a considerable rethink on how they were dealt with was clearly required. It is a matter of some irony therefore, that a key for this rethink was provided in the same volume on invertebrate origins. Jefferies published here his critical paper that effectively introduced Hennig's views on the systematisation of fossils to the English-speaking world, with some important modifications of his own. In particular,
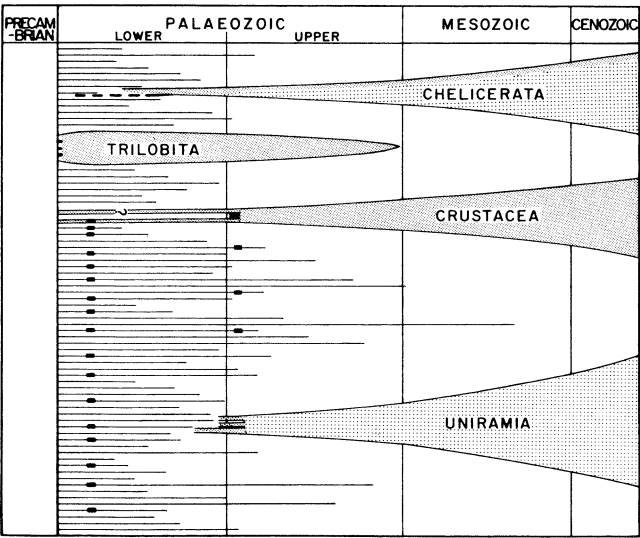
FIG. 1. Whittington's diagram of the Phanerozoic diversity of the arthropods, extending Manton's views of arthropod polyphyly to the fossil record. Bold lines represent the known record: dense stipple represents marine habitat, light stipple, terrestrial. From Whittington (1979).

FIG. 2. Jefferies' diagram introducing the "stem" and "crown" group concepts, modified after Hennig, to the English-speaking world, from the same volume as Figure 1. From Jefferies (1979).

he laid out clearly the fact that as a general feature, extinct organisms always fall outside a systematics established on extant forms (Fig. 2). Of course, this exclusion is a hierarchical one. A fossil can, for example, lie with in the grouping of extant echinoderms. However, its position within the echinoderms will at a certain level never be fully reflected by extant systematics—the only type then available. Whilst this seems surprising, the reason is clear. Extant monophyletic groupings are always morphologically distinct from their extant sister-group, and that distinctness is brought about by subsequent extinction of the lineages (plus its offshoots) that led to each of them, away from their last common ancestor. As random extinctions through time slowly remove lineages, the most basal taxon of a clade will sometimes be the victim, thus widening the path-length between the surviving most basal members of extant sister clades (Fig. 3). The bases of clades are therefore eroded by extinction, and, as only living members of the clade can rediversify, this is a permanent loss. These extinct basal taxa will not possess all of the apomorphies that define the basal node of the surviving clade. It should be noted that this process will occur whether or not basal members of clades are particularly prone to extinction or not; there does not have to be anything "special" about basal taxa. One further aspect about these now extinct basal taxa is that they would have accumulated their own autapomorphies not possessed by the extant taxa. As a result, these basal fossil taxa are bound to differ from the extant clades: they will not be diagnosable as members of those clades; and they will show a confusing mixture of some but not all features of those clades, together with a set of features absent from them. It should be noted that this characteristic mix
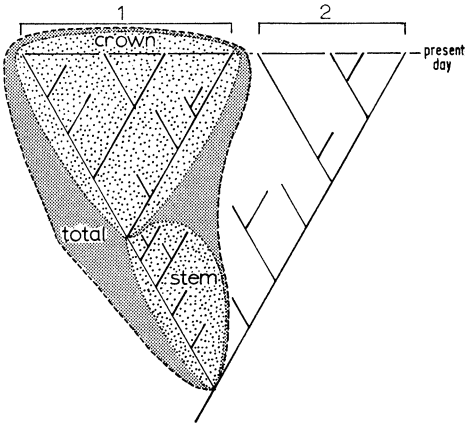
has been repeatedly noted in Cambrian fossils. For example, Hughes (1975) said of the Cambrian arthropod *Burgessia*: "what is apparent from this restudy is that Burgessia did possess a mixture of characters . . . many of which are to be found in modern arthropods of various groups" (Hughes, 1975, p. 434).

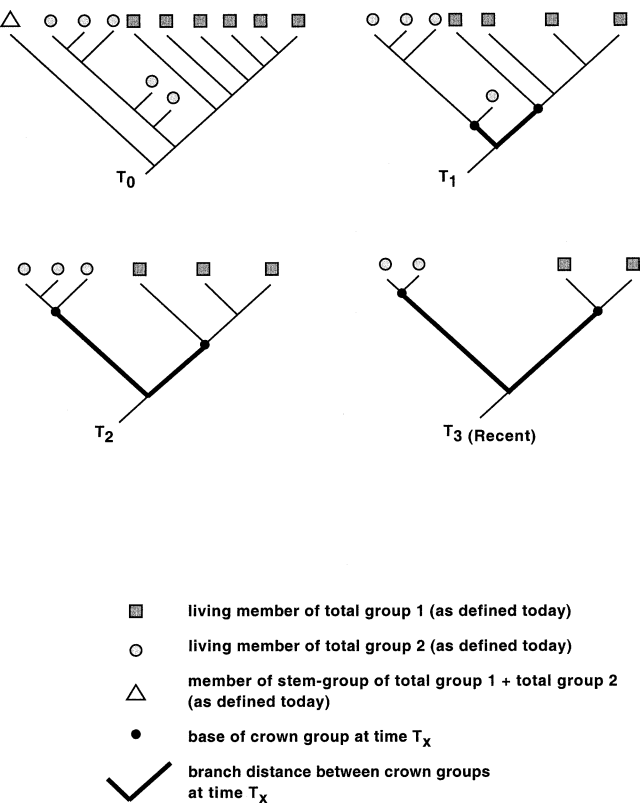Whilst the apparent oddness of Cambrian fossils is

FIG. 3. The growth of a stem group. Random extinctions within a group will sometimes remove its most basal member, thus enlarging the phylogenetic distance between it and its closest living relative. As diversification can only take place within surviving lineages, this loss is a permanent one, leading to the sometimes great distinctions between high-level extant groups such as the phyla.

no different in kind from that of any other fossils, it was brought to prominence in two different ways. First, the spectacular preservation of the various Cambrian exceptionally-preserved biotas such as the Burgess Shale (Whittington, 1985) and, more recently, Chengjiang (*e.g.,* Hou and Bergström, 1997), Sirius Passet (Conway Morris, 1998) and Orsten biotas (*e.g.,* Walossek, 1993), revealed a great array of unusual taxa, almost unparalled in the subsequent fossil record. Second, these taxa did seem to fall outside conventional taxonomic levels at a greater depth in the taxonomic hierarchy than later fossils tend to. For example, ammonites can be assigned, not just to the Mollusca, but also to the cephalopods, and indeed, are close relatives to the Coleoidea. Many of the Cambrian taxa, conversely, are not even encompassed by the phylum level. Given the hypothesis that the base of an extant phylum will be eroded through time, it is clear that the older a fossil is, the more likely it is to fall outside the phylum-level of classification (*i.e.,* classification at a very broad level). The pattern demonstrated by the Cambrian fauna (early taxa being problematic at high levels in a taxonomic hierarchy) therefore seems to be explicable by recourse to the stem-/crown-group division, rather than to any particular evolutionary mechanism. It is unfortunate, however, that this conceptual framework has been very slow in gaining acceptance, perhaps because of the vigorous espousal of what might be called the "classical view" by Gould (1989). This work did more than any others, perhaps, in promulgating the view that the patterns demonstrated by Cambrian fossils implied rapid appearance of many high-level taxa without precedents; perhaps implying unusual evolutionary mechanisms as a result. Nevertheless, in the last few years, several studies have been published that have made attempts to assign problematic Cambrian taxa to a stem-group placement of an appropriate phylum or group of phyla. These include arthropods (Budd, 1996); protostomes (Conway Morris and Peel, 1995; Conway Morris, 1998; see discussion in Runnegar, 1996); echinoderms (Mooi *et al.*, 1994); cycloneuralians (Budd, 2001*a*); deuterostomes (Shu *et al.*, 2001) and brachiopods (Williams and Holmer, 2002). The reception of many or all of these attempts has been mixed, and they stand at different stages of maturity. Nevertheless, it seems likely, as these efforts continue, that our view of the phylogenetic pattern of the Cambrian explosion will change dramatically in the next few years.

One example of the sorts of possibilities that stem-group reconstruction offers is provided by the arthropods (*e.g.,* Budd, 1998, 2001*b*). Optimization of the terminal character states of the various stem-group demonstrates the most parsimonious reconstruction of the evolutionary stages passed through by ancestral arthropods. A remarkably complete series is now available, demonstrating how the most basal, worm-like taxa of the entire Arthropoda sequentially acquired the important features characteristic of their clade, including the sclerites and lever-style musculature (Budd,

2001*b*), components of the biramous limb (Budd, 1996), and even how the complexities of the arthropod head were assembled (Budd, 2002), a construction that can be corroborated by the recent fauna (Eriksson *et al.*, 2003). Within the euarthropods themselves, considerable progress has also been made in sorting out the stem group of the crustaceans (*e.g.,* Walossek, 1999) and some of the putative stem-group chelicerates (Edgecombe and Ramsköld, 1999), although this is the area where most work is still required. Clearly, for the arthropods at least, current opinion now stands rather far away from the view expressed only a decade ago that the Cambrian record did not reveal anything of the origin of the phyla. The sequential unraveling of how the phyla were assembled also allows an approach to be made both to the developmental background to these changes (*e.g.,* Budd, 2001*b*), and to the construction of sensible ecological and selective pressures and changes that were associated with them. It is possible to plot acquisition of characters together with their implications for functional innovations and thus for the general ecology of the organism onto the same cladogram, showing the cross-relationship between them. I have attempted this for the stem-group of the arthropods in Figure 4.

PRESERVATION PROBLEMS

Whilst the difficulties inherent in interpretation of Cambrian fossils are dealt with elsewhere (Butterfield, 2003), the temporal aspects of exceptional preservation are also worth remarking on. Almost all of our detailed knowledge of the macro-fossil record of the Cambrian explosion comes from the exceptionally preserved biotas, of which the Burgess Shale is merely one representative among many (Butterfield, 1995). Indeed, the Lower Cambrian Chengjiang fauna is already rivalling it for fame and importance; and vital material has also come from the other of the "big three" Lower-Middle Cambrian lagerstätten, the Sirius Passet biota from Greenland. Whilst highly significant, these are not the only important data sources in the Cambrian. Many of the small skeletal fossils are also, in their way, exceptionally preserved, typically by phosphatization of their interior (so-called "steinkern" preservation), that can often preserve cellular details (see *e.g.,* Bengtson *et al.*, 1990). Another source of information is provided by "orsten" preservation, typically tiny organisms or fragments of organisms that were phosphatised very early; probably within hours of death. Some of the most remarkable fossils in the record have been preserved in this manner, such as the original "orsten fauna" from the Upper Cambrian of Sweden, largely consisting of stem- and crown-group crustaceans (*e.g.,* Walossek, 1993, 1999). Another sort of fossil preserved in a similar way is represented by examples of phosphatised embryos (*e.g.,* Bengtson and Zhao, 1997), dating not just from the Lower Cambrian, but also, apparently from the terminal Proterozoic (Xiao *et al.*, 1998), although the status of the latter (whether or not they represent a poriferan or higher
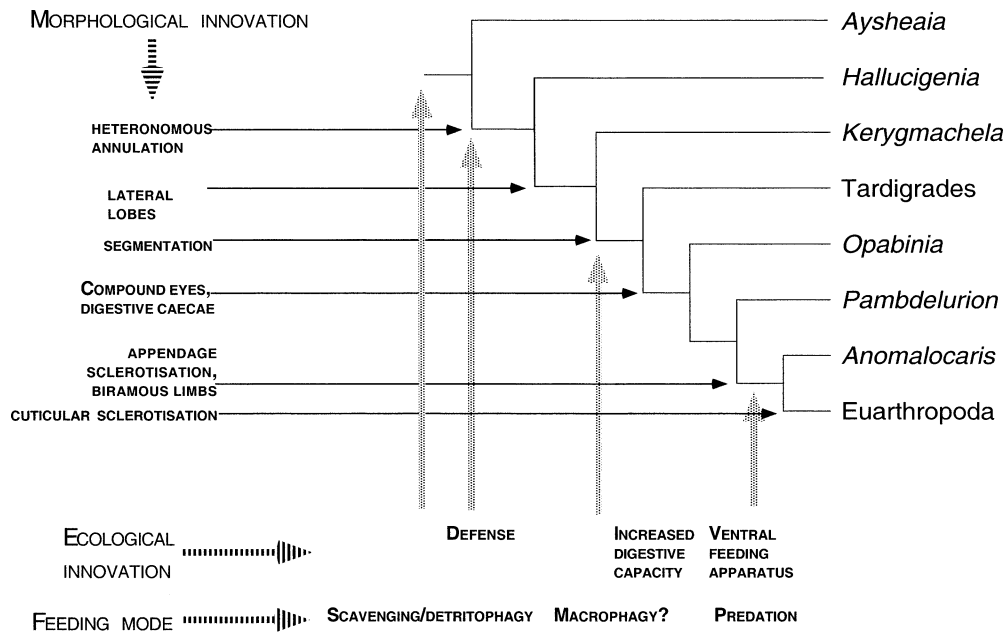
FIG. 4. A phylogeny of the arthropod stem-group (modified from Budd, 1996, 1999), showing successive morphological innovations, and correlated functional and ecological shifts, with particular reference to feeding mode.

grade of organisation, for example) is less clear (Xiao *et al.*, 2000). Finally, the still-enigmatic preservation (Gehling, 1999) associated with the problematic ediacaran fossils from the terminal Proterozoic also provides an important window on evolution at this time, although as is well-known, the significance of the fossils from this period is still widely debated (see *e.g.,* Grazdhankin and Seilacher, 2002 for an important recent contribution to the topic). It is important to note that these preservational modes are not always randomly distributed. Hence, ediacaran-style preservation seems to be restricted to a period of time from about 570 Ma onwards, probably just reaching into the Cambrian (Jensen *et al.*, 1998), whereas so-called "Burgess Shale" style preservation is more restricted to the Atdabanian (see below) through to the end of the Middle Cambrian (Butterfield, 1995). The temporal importance of this restriction, and its effect on our view of the Cambrian explosion, can only be assessed if we have some understanding of the absolute timing of these periods, and their relationship to each other.

DATING THE CAMBRIAN

The age of the Cambrian has been difficult to constrain on both biostratigraphic (Palmer, 1998; Geyer, 2001) and absolute radiometric grounds (Bowring *et al.*, 1993; Tucker and McKerrow, 1995). These problems in fact reach back to the middle years of the 19th century, when Adam Sedgwick and Rodney Murchison clashed over its upper boundary (see *e.g.,* Cowie *et al.*, 1972). However, the most problematic boundary has been its lower one; although Upper Cambrian biostratigraphy is now relatively precise, Lower Cambrian biostratigraphy remains in need of a great deal of attention. A complex mass of problems lies behind this unsatisfactory situation (see discussion in Brasier, 1989), consisting (non-exhaustively) of nationalistic clashes in evaluating the importance of potential type sections; the existence of extensive unconformities (*i.e.,* missing periods of time) in the rock record; widespread endemism of taxa (leading to difficulties in inter-continental correlation); the problems of correlating between different facies (*e.g.,* the siliclastic rocks of Newfoundland and the carbonates of Siberia) and the enormous difficulties of establishing a satisfactory taxonomy, especially for small skeletal fossils that are often only components of multi-element skeletons. Furthermore, until recently, the lack of good volcanic rocks that could be used for reliable radiometric dating, meant that the absolute age of the Cambrian has also been in considerable doubt. Indeed, over the last decade or so, there has been a considerable shift in our appreciation of the timing and duration of the Cambrian, both of which are vital to understanding the processes that gave rise to the biological events recorded in the rocks during this time (Bowring *et al.*, 1993; Grotzinger *et al.*, 1995; Tucker and McKerrow, 1995; Davidek *et al.*, 1998; Landing *et al.*, 1998; Fig. 5). The international community recently agreed to fix the base of the Cambrian on the first appearance of the trace fossil *Treptichnus pedum* in a section in Newfoundland (Landing, 1994), although this decision has not been received with universal acclamation (Rozanov *et al.*, 1997). One consequence of the boundary being fixed here is that strata in Siberia conventionally considered to be terminal Proterozoic turn out to be Cambrian, thus repositioning the old Siberian base of the Cambrian (at the base of the Tommotian [Rozanov *et al.*, 1969] to be middle Lower Cambrian in age [Landing, 1994]). Complex body and especially trace
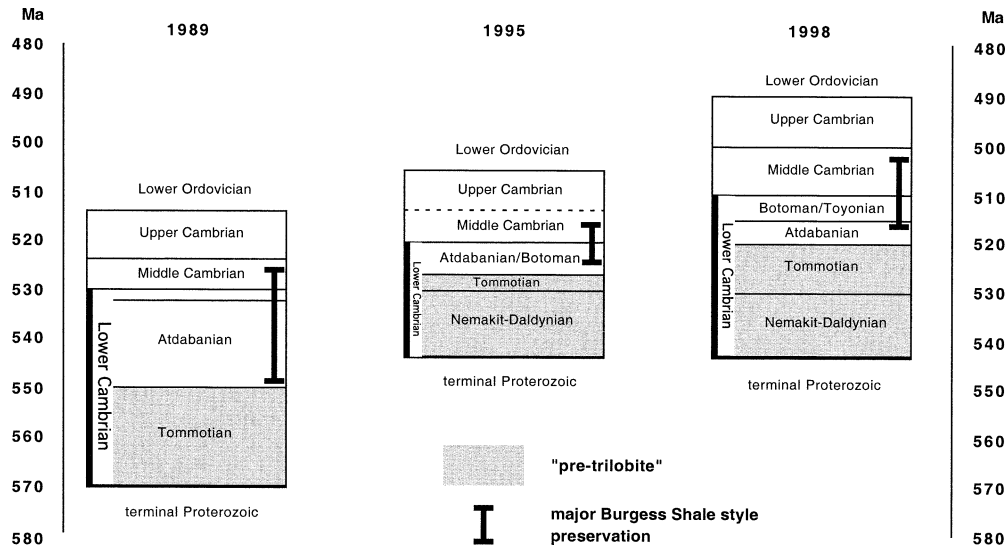
FIG. 5. Changing Cambrian time. The evolution of consensus views on the length and timing of the Cambrian over the last few years. Data for 1989 from the IUGS timechart (Cowie and Bassett, 1989); for 1995 from Grotzinger *et al.* (1995) and for 1998 from Davidek *et al.* (1998) and Landing *et al.* (1998). For comparison, the oldest trace fossils are approximately 550 Ma, giving a period of at least 30 Ma before the appearance of trilobites at the base of the Atdabanian. Note also the relatively short period of time encompassed by the major Burgess Shale-type faunas (Butterfield, 2003) and the long period of time after the base of the Cambrian before their appearance.

fossils thus lie below the old conventional base of the Cambrian. Although strata assigned to, or generally correlated with, the Nemakit-Daldynian or Manikayan (although these are not strictly identical) in most regions are characterized by trace fossils (Narbonne *et al.*, 1987), some small skeletal fossils such as possible stem-group molluscs (*e.g., Anabarella*), the tube-like *Anabarites* and the teeth-like (of chaetognath affinity?) protoconodonts and probably arthropod trace fossils (*e.g., Rusophycus*) are known from at least the upper portion (Narbonne *et al.*, 1987; Khomentovsky and Karlova, 1993; Shields, 1999). However, the Newfoundland type section largely lacks skeletal fossils in its lower portions, and it is as yet not clear exactly how the Nemakit-Daldynian corresponds to this section; perhaps the lower portion of the Nemakit-Daldynian is of terminal Proterozoic age as currently defined (Zhuravlev, 1995).

However, before this intercontinental correlation can be refined and agreed on, several important biostratigraphic problems must be resolved. Lower Cambrian biostratigraphy has been based on several organisms, including archaeocyathans (probable calcareous sponges), trilobites, and acritarchs, organic-walled microfossils of uncertain affinities. The biostratigraphic schemes erected from each of these do not fully agree with the others (*e.g.,* as discussed by Palmer, 1998). Another important problem is presented by the widespread unconformities near the base of the Cambrian (Kouchinsky *et al.*, 2001). In the classic basal Cambrian sections in the south of Siberia, for example, the base of the Tommotian is now widely recognised as being marked by a definite gap in time (although the extent of the missing interval is debated). More complete sections of this period of time though, in North-

ern Siberia and Mongolia, suggest that the abruptness of appearance of many taxa above the break does not reflect the true tempo of appearance (Brasier *et al.*, 1996). The Mongolian sections, for example, imply a still rapid, but sequential increase in the number of taxa present.

Although Lower Cambrian stratigraphy remains in a state of some uncertainty, therefore, it is possible at present to present a provisional view of the sequence of events in at least some areas of the world. This ability is being increasingly enhanced by the accelerating use of radiometric dating in Lower Cambrian strata (Bowring and Erwin, 1998). Although sedimentary rocks can be dated radiometrically (using, for example, included zircon crystals), such dates are often unreliable. Conversely, there is during this time interval a general scarcity of erupted igneous rocks that can be reliably tied into relative stratigraphy. Nevertheless, the results that emerged from the initial efforts at obtaining more rigorous absolute dates from the Lower Cambrian were striking. The base of the Cambrian, which has been considered to be as old as 600 Ma in the past, resolved at an age close to 543 (Bowring *et al.*, 1993). This had the effect of apparently compressing the Cambrian into a far shorter time than previously thought: indeed, the Cambrian went almost overnight from being the longest to the shortest period. Recent modifications to this absolute timescale have tended to decrease the age of the upper boundary of the Cambrian, so that the net effect has been to shift the entire Cambrian later in absolute time (Landing *et al.*, 1998; Davidek *et al.*, 1998). What is particularly significant about Cambrian time now is the rather long period of time available at the base of the Cambrian (as presently defined) before a good fossil record of

macro-invertebrates commences—the so-called sub-trilobite period. Another noteworthy feature of the revisions is the short period of time covered by the exceptional preservations of the so-called "Burgess Shale" types faunas—perhaps not much more than ten million years, a reasonable explanation for the striking similarity between, for example, the Burgess Shale and Chengjiang faunas. All of these biotas—one of the principal sources of information about the Cambrian explosion—are considerably removed from the base of the Cambrian, when both trace fossils and some small skeletal fossils begin to diversify. In terms of understanding the early stages of the Cambrian diversification then, they may not be of too much help, nor can comparisons between the faunas be hoped directly to reveal important temporal trends in evolution.

The reorganisation and compression of Cambrian time implies an important preservational gap between the exceptional preservations of the terminal Proterozoic (the "Ediacaran" assemblages) and upper Lower–Middle Cambrian ("Burgess Shale" assemblages). This gap is important, because finding exceptional preservations within it would provide an important test of the various hypotheses of what the Cambrian explosion really represents. At least some hope is provided by the so-called "orsten fauna" style of preservation, *i.e.,* very early phosphatization of soft tissues (see Butterfield, 2003), which does not seem to be so temporally restricted as Burgess Shale-style preservation. Its disadvantage is that it only preserves very small fossils—typically less or much less than 2 mm in length. As a result, the fossils preserved by it are sometimes or often fragmentary (*e.g.,* Butterfield and Nicholas, 1996), and are also difficult to tie in with the parallel trace fossil record.

At present therefore, most information about this critical early period comes from the trace fossil record (Jensen, 2003), and the "conventional" skeletal record. Both of these also present problems. The small skeletal fauna (*e.g.,* Bengtson *et al.,* 1990) consists of a variety of tubes, cap-shaped shells (presumed to be the only sclerite covering an animal), and a variety of other skeletal elements that are thought to be components of multi-element ("scleritome" or "cataphract") skeletons, either external (for example, the tommotiids) or internal (*e.g.,* echinoderms, although these appear relatively late in the fossil record). Scleritome reconstruction is a difficult task, rendered more so by the extremely poor taxonomy of many of the fossils. Many skeletal elements that may be components of the same skeleton may have been assigned to different species or even genera. Secondly, particular scleritomes may contain sclerites of very different shape, making assignment of all of the components to the same animal very difficult to predict. Whilst some progress has been possible with disarticulated sclerites (Bengtson and Conway Morris, 1984), it has been the exceptional faunas such as the Burgess Shale (*Wiwaxia*; Conway Morris, 1985; Butterfield, 1990), Chengjiang (*Microdictyon* [Ramsköld and Hou, 1991]) and

Sirius Passet faunas (*Halkieria* [Conway Morris and Peel, 1995]) that have been most useful here: they have all provided articulated specimens of various scleritomes. Whilst in some cases (especially *Microdicyton* [Ramsköld and Hou, 1991]) these specimens have provided decisive evidence about the affinities of the organism in question, in other cases, they have engendered a great deal of debate. Whilst many of the simpler forms (such as tubes, including *Anabarites* and *Cloudina* [Kouchinsky *et al.,* 1999]) could belong to a variety of groups, a relatively fruitful approach is to take a phylogenetically conservative view: in other words, not to assume any more complexity than is necessary. This includes not assuming crown-group affinities when the organism could lie in the stem-group; and not assuming triploblasty when a diploblastic affinity is also possible. Some of the assignments under this set of assumptions are bound to be incorrect, but they are in principle testable by better understanding of the fossils in question. It is in any case the parsimonious approach: if it is not known whether a particular fossil demonstrates a certain derived character state, then—all things being equal—the parsimonious assumption must be that it does not. The usefulness of this approach becomes apparent through the temporal pattern that emerges when this procedure of assignment is carried out: the earliest skeletal fossils do not demand any greater complexity than diploblasty; and they are followed by taxa that are reasonably considered to lie in the stem-groups of triploblastic phyla or groups of phyla (Fig. 6). It is not until the Mid-Tommotian–Atdabanian, some 20–25 Ma after the beginning of the Cambrian, that definitive crown-group members of the various phyla in general start to emerge (Budd and Jensen, 2000, 2003). There is thus an important asymmetry in the fossil record of the earliest Cambrian compared to that of the Atdabanian and later. Whilst certain early fossils could indeed belong to crown-groups of the phyla, they normally require special pleading in their defence; whereas later fossils are much more readily accepted. A similar argument applies to the many structures claimed to be trace fossils from the Proterozoic before about 550 Ma. Whilst some of these structures might plausibly be true trace fossils of animals, their structural ambiguity means that none of them compel us to believe that. I believe that this asymmetry is a telling one, and that the reason behind it is a simple one: terminal Proterozoic and early Cambrian fossils in general are phylogenetically basal.

If this view is correct, then it is of considerable importance for interpreting the Cambrian explosion. It implies that the early fossil (both body and trace) record may be read as recording a reasonably accurate temporal approximation to the true times of divergence of the phyla. If this were not the case, one would not expect to see a broad correspondence between stratigraphic and phylogenetic position (as argued in Budd and Jensen, 2003). This is therefore a telling correspondence that is difficult to explain away on an *ad*
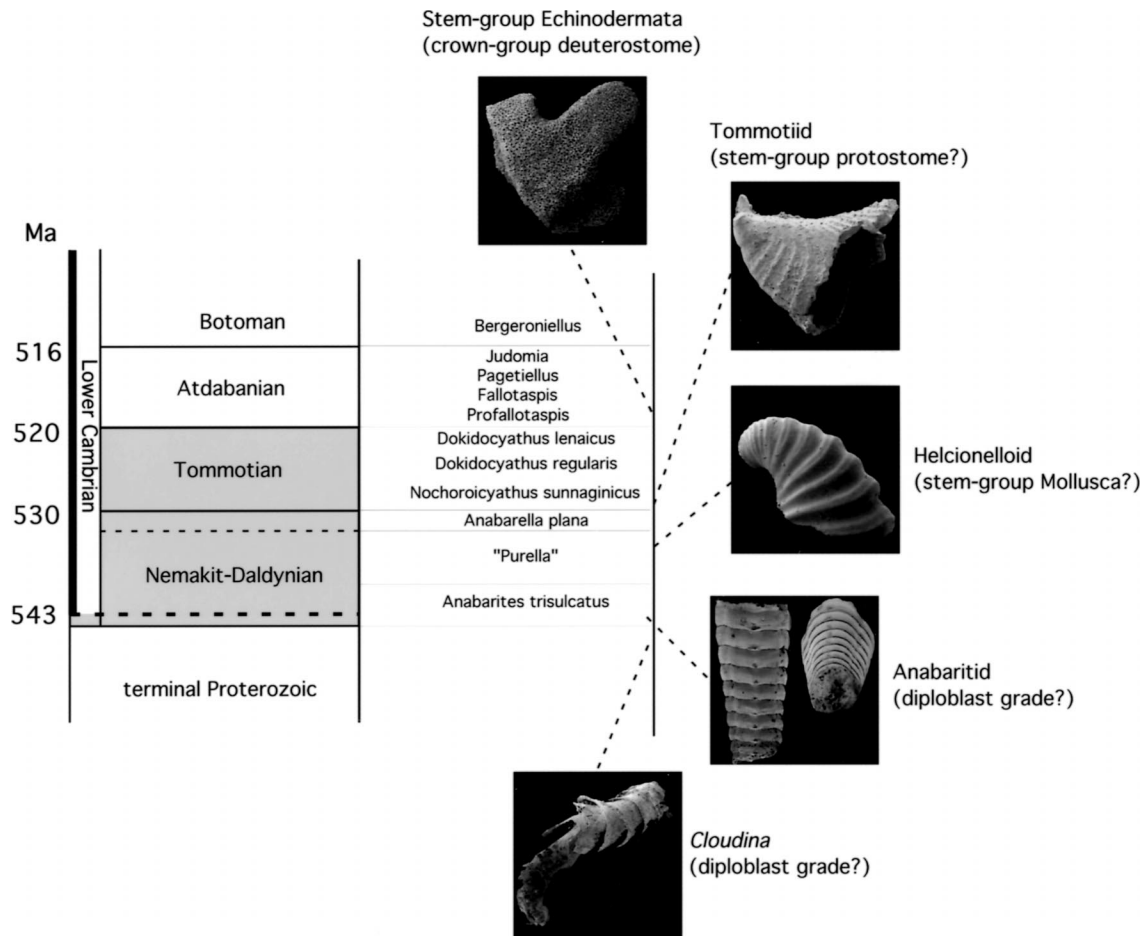
FIG. 6. A detailed consensus biostratigraphy for base of the Cambrian, based on strata in Siberia (see Kouchinsky *et al.*, 2001). Several aspects are controversial. The base of the Nemakit-Daldynian may extend below the base of the Cambrian as currently defined in Newfoundland. Some workers refer to the Nemakit-Daldynian and a period of time (represented here by the *Anabarella plana* Biozone) as the ''Manykaian''; although others consider the *A. plana* biozone to be contemporaneous with the base of the Tommotian. Representative small skeletal fossils are illustrated together with an indication of their affinities and their first appearance in the record world-wide (oldest examples not always shown). Note that the fossil record can be read as broadly demonstrating the appearance of first cnidarian-grade diploblasts (*Cloudina*, anabaritid), followed by representatives of the stem-groups of phyla or groups of phyla (helcionelloid, tommotiid) with crown-group representatives of the phyla not in general appearing until after the period in question. Overall, the pattern of increasing diversification and phylognetic consonance with stratigraphy suggests a genuine origination of the phyla during this critical time, not merely a manifestation in the fossil record of already-established groups. *Cloudina*: phosphatised tube from the terminal Proterozoic Dengying Formation, China (image courtesy of S. Bengtson). Image width ca. 2 mm. Anabaritid: *Aculeochrea*; Two views of an internal mould of a tube from the Manykay Formation of Northern Sibera (image courtesy of S. Bengtson). Image width ca. 3 mm. Tommotiid: *Lapworthella*; this specimen from the Botoman of North-East Greenland (image courtesy of C. B. Skovsted). MGUH 26760, Geological Museum, Copenhagen. Image width ca. 0.6 mm. Helcionelloid: *Bemella*; this specimen from the basal Tommotian of the Pestrotsvet Formation, South-East Siberia (image courtesy of A. Gubanov). Image width ca. 1 mm. Echinoderm plate from Botoman of North-East Greenland (Image courtesy of C. B. Skovsted). MGUH 26761, Geological Museum, Copenhagen. Image width ca. 1 mm.

hoc basis if the deep metazoan splits suggested by some molecular analyses are to be sustained (Fortey *et al.*, 2003).

CONCLUSIONS

The combination of important refinements in the treatment of the systematics of Cambrian fossils, and in our understanding of Cambrian stratigraphy is leading to a more precise view of the Cambrian explosion. Phyla do not appear in a sudden jumble, implying an appearance in the fossil record induced by some external influence (*e.g.*, a rise in atmospheric oxygen lev-

els) that allowed a standing diversity already present to be manifested in the record. Rather, the impression rather is of a rapid, but nevertheless resolvable and orderly appearance, starting with the earliest skeletal forms such as *Cloudina* that are reasonably assignable to a diploblast grade (*i.e.,* stem- or crown-group cnidarians or basal stem-group bilaterians). These are followed by taxa that lie in basal positions within bilaterian clades, and (in general) considerably later by representatives of the crown-groups of phyla. Revisions to the Cambrian time-scale allow a moderately long period of time, some tens of millions of years,

between the first likely bilaterian trace fossils, and the general appearance of crown-group members of the phyla.

This hypothesis has the direct implications that many more very basal bilaterians remain to be discovered in basal Cambrian strata, *i.e.,* in the Nemakit-Daldynian and Tommotian stages. The search for ancestral bilaterians should therefore not be directed to the early Neoproterozoic, some 700–800 Ma, but within the Cambrian. Consistent failure to find basal bilaterians in this period, or the discovery or recognition of many phyletic crown-group representatives, will falsify this hypothesis, and give more credence to those theories of animal origins that require or are consistent with a much earlier appearance of bilaterians. For palaeontologists, this conclusion is of considerable importance insofar as the Cambrian record should in theory record the actual stages of assembly of body plans (*sensu* Budd and Jensen, 2000), rather than being forever silent on the topic. If so, then fossils may have a much greater role in the future than presently in constraining the routes that assembly of the phyla took place through, and thus act as a restraint on the ways in which development has also evolved throughout these critical periods of animal evolution.

ACKNOWLEDGMENTS

REFERENCES

Bengtson, S. and S. Conway Morris. 1984. A comparative study of Lower Cambrian *Halkieria* and Middle Cambrian *Wiwaxia*. Lethaia 17:307–329.

Bengtson, S., S. Conway Morris, B. J. Cooper, P. A. Jell, and B. N. Runnegar. 1990. Early Cambrian fossils from South Australia. Mem. Ass. Aust. Pal. 9:1–364.

Bengtson, S. and Y. Zhao. 1992. Predatorial borings in late Precambrian mineralized exoskeletons. Science 257:367–369.

Bengtson, S. and Y. Zhao. 1997. Fossilized metazoan embryos from the earliest Cambrian. Science 277:1645–1648.

Bowring, S. A. and D. H. Erwin. 1998. A new look at evolutionary rates in deep time: Uniting paleontology and high-precision geochronology. GSA Today 8(9):1–8.

Bowring, S. A., J. P. Grotzinger, C. E. Isachsen, A. H. Knoll, S. M. Pelechaty, and P. Kolosov. 1993. Calibrating rates of early Cambrian evolution. Science 261:1293–1298.

Brasier, M. D. 1989. Towards a biostratigraphy of the earliest skeletal biotas. *In* J. W. Cowie and M. D. Brasier (eds.), *The Precambrian–Cambrian boundary,* pp. 117–165. Oxford University Press, Oxford.

Brasier, M. D., G. Shields, V. N. Kuleshov, and E. A. Zhegallo. 1996. Integrated chemo- and biostratigraphic calibration of early animal evolution: Neoproterozoic early Cambrian of southwest Mongolia. Geol. Mag. 133:445–485.

Bromham, L. 2003. What can DNA tell us about the Cambrian explosion. Integr. Comp. Biol. 43:000–000.

Budd, G. E. 1996. The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. Lethaia 29:1–14.

Budd, G. E. 1998. Arthropod body-plan evolution in the Cambrian with an example from anomalocaridid muscle. Lethaia 31:197–210.

Budd, G. E. 1999. The morphology and phylogenetic significance of Kerygmachela kierkegaardi Budd (Buen Formation, Lower Cambrian, N. Greenland). Trans. R. Soc. Edinb.: Earth Sci. 89:249–290.

Budd, G. E. 2001*a*. Tardigrades as 'stem-group' arthropods: The evidence from the Cambrian fauna. Zoolog. Anz. 240:265–279.

Budd, G. E. 2001*b*. Why are arthropods segmented? Evol. Dev. 3:132–142.

Budd, G. E. 2002. A palaeontological solution to the arthropod head problem. Nature 417:271–275.

Budd, G. E. and S. Jensen. 2000. A critical reappraisal of the fossil record of the bilaterian phyla. Biol. Rev. 75:253–295.

Budd, G. E. and S. Jensen. 2003. The limitations of the fossil record and the dating of the origin of the Bilateria. Syst. Assoc. Spec. Vol. (In press)

Butterfield, N. J. 1990. A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa*. Paleobiology 16:287–303.

Butterfield, N. J. 1995. Secular distribution of Burgess-shale-type preservation. Lethaia 28:1–13.

Butterfield, N. J. 2003. Exceptional fossil preservation and the Cambrian explosion. Integr. Comp. Biol. 43:000–000.

Butterfield, N. J. and C. J. Nicholas. 1996. Burgess Shale-type preservation of both non-mineralizing and 'shelly' Cambrian organisms from the Mackenzie Mountains, northwestern Canada. J. Paleont. 70:893–899.

Cloud, P. 1968. Pre-metazoan evolution and the origins of the Metazoa. *In* E. T. Drake (ed.), *Evolution and environment,* pp. 1–72. Yale University Press, New Haven.

Conway Morris, S. 1985. The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia. Phil. Trans. R. Soc. London B 307:507–586.

Conway Morris, S. 1998. *The crucible of creation.* Oxford University Press, Oxford.

Conway Morris, S. and J. S. Peel. 1995. Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. Phil. Trans. R. Soc. London B 347:305–358.

Cooper, A. and R. Fortey. 1998. Evolutionary explosions and the phylogenetic fuse. TREE 13:151–156.

Cowie, J. W. and M. G. Bassett. (eds.) 1989. Global Stratigraphic Chart with geochronometric and magnetostratigraphic calibration. Episodes 12(2, suppl.).

Cowie, J. W., A. W. A. Rushton, and C. J. Stubblefield. 1972. A correlation of Cambrian rocks in the British Isles. Geological Society of Britain Special Report 2.

Davidek, K., E. Landing, S. A. Bowring, S. R. Westrop, A. W. A. Rushton, R. A. Fortey, and J. M. Adrain. 1998. New uppermost Cambrian U-Pb date from Avalonian Wales and age of the Cambrian-Ordovician boundary. Geol. Mag. 135:303–309.

Dawkins, R. 1998. *Unweaving the rainbow.* Penguin Books Ltd, Harmondsworth, Middlesex, UK.

Edgecombe, G. D. and L. Ramsköld. 1999. Relationships of Cambrian Arachnata and the systematic position of Trilobita. J. Paleont. 73:263–287.

Eriksson, B. J., N. N. Tait, and G. E. Budd. 2003. Head development in the onychophoran *Euperipatoides kanangrensis* with particular reference to the central nervous system. J. Morph. 255:1–23.

Fortey, R., J. Jackson, and J. Strugnell. 2003. Phylogenetic fuses and evolutionary "explosions": Conflicting evidence and critical tests. Systematics Association Special volume. (In press)

Gehling, J. G. 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. Palaios 14:40–57.

Geyer, G. 2001. Correlation in the Cambrian: Puzzling facts or wrong concepts? Palaeoworld 13:87–98.

Gould, S. J. 1989. *Wonderful life.* W. W. Norton, New York.

Grazdhankin, D. and A. Seilacher. 2002. Underground Vendobionta From Namibia. Palaeontology 45:57–78.

Grotzinger, J. P., S. A. Bowring, B. Z. Saylor, and A. J. Kaufman. 1995. Biostratigraphic and geochronological constraints on early animal evolution. Science 270:598–604.

Hofmann, H. J. 1990. Precambrian time units and nomenclature—the geon concept. Geology 18:340–341.

Hou, X. and J. Bergström. 1997. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. Fossils and Strata 45:1–116.

House, M. R. (ed.) 1979. *The origin of major invertebrate groups.* Systematics Association special volume 12. Academic Press, London.

Hughes, C. P. 1975. Redescription of *Burgessia bella* from the middle Cambrian, Burgess Shale, British Columbia. Fossils and Strata 4:415–435.

Jefferies, R. P. S. 1979. The origin of chordates—a methodological essay. *In* M. R. House (ed.), *The origin of major invertebrate groups,* pp. 443–477. Academic Press, London.

Jensen, S., J. G. Gehling, and M. L. Droser. 1998. Ediacara-type fossils in Cambrian sediments. Nature 393:567–569.

Jensen, S. 2003. The Proterozoic and earliest Cambrian trace fossil record; patterns, problems and perspectives. Integr. Comp. Biol. 43:000–000.

Khomentovsky, V. V. and G. A. Karlova. 1993. Biostratigraphy of the Vendian-Cambrian beds and the lower Cambrian boundary in Siberia. Geological Magazine 130:29–45.

Kouchinsky, A., S. Bengtson, and L. A. Gershwin. 1999. Cnidarian-like embryos associated with the first shelly fossils in Siberia. Geology 27:609–612.

Kouchinsky, A., S. Bengtson, V. V. Missarzhevsky, S. Pelechatys, P. Torssander, and A. Val'kov. 2001. Carbon isotope stratigraphy and the problem of a pre-Tommotian Stage in Siberia. Geol. Mag. 138:387–396.

Landing, E. 1994. Precambrian-Cambrian boundary global stratotype ratified and a new perspective of Cambrian time. Geology 22:179–182.

Landing, E., S. A. Bowring, K. L. Davidek, S. R. Westrop, G. Geyer, and W. Heldmaier. 1998. Duration of the Early Cambrian: U-Pb ages of volcanic ashes from Avalon and Gondwana. Can. J. Earth Sci. 35:329–338.

Manton, S. M. 1977. *The Arthropoda.* Clarendon Press, Oxford.

Mooi, R., B. David, and D. Marchand. 1994. Echinoderm skeletal morphologies: Classical morphology meets modern phylogenetics. *In* B. David, A. Guille, J. P. Féral, and M. Roux (eds.), *Echinoderms through time,* pp. 87–95. Balkema, Rotterdam.

Narbonne, G. M., P. Myrow, E. Landing, and M. A. Anderson. 1987. A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. Canad: J. Earth Sci. 24:1277–1293.

Palmer, A. R. 1998. Why is international correlation within the Lower Cambrian so difficult? Revista Española de Paleontología. No. extr. Homenajae al Prof. Gonzalo Vida 1:17–21.

Patterson, C. 1981. Significance of fossils in determining evolutionary relationships. Ann. Rev. Ecol. Syst. 12:195–223.

Ramsköld, L. and X.-G. Hou. 1991. New early Cambrian animal and onychophoran affinities of enigmatic metazoans. Nature 351:225–228.

Rodríguez-Trelles, F., R. Tarrió, and F. J. Ayala. 2001. Erratic overdispersion of three molecular clocks: GPDH, SOD, and XDH. PNAS 98:11405–11410.

Rozanov, A. Y., V. V. Missarzhevsky, N. A. Volkova, L. G. Voronova, I. N. Krylov, B. M. Keller, I. K. Korolyuk, K. Lendzion, R. Michnaik, N. G. Pykhova, and A. D. Sidorov. 1969. Tommotskij yarus i problema nizhney granitsy kembriya. [the Tommotian Stage and the problem of the lower boundary of the Cambrian]. Trudy Geologicheskogo Instituta AN SSSR 206:1–380.

Rozanov, A. Y., M. A. Semikhatov, B. S. Sokolov, M. A. Fedonkin, and V. V. Khomentovskii. 1997. The decision on the Precambrian-Cambrian boundary stratotype: A breakthrough or misleading action? Stratigraphy and Geological Correlation 5:19–28.

Runnegar, B. 1982. A molecular clock model for the origin of animal phyla. Lethaia 15:199–205.

Runnegar, B. 1996. Early evolution of the Mollusca: The fossil record. *In* J. Taylor (ed.), *Origin and evolutionary radiation of the Mollusca,* pp. 77–87. Oxford University Press, Oxford.

Shields, G. 1999. Working towards a new stratigraphic calibration scheme for the Neoproterozoic-Cambrian. Eclogae Geologicae Helvetiae 92:221–233.

Shu, D.-G., S. Conway Morris, J. Han, L. Chen, X.-L. Zhang, Z.-F. Zhang, H.-Q. Liu, Y. Li, and J.-N. Liu. 2001. Primitive deuterostomes from the Chengjiang Lagerstätte (Lower Cambrian, China). Nature 414:419–424.

Tucker, R. D. and W. S. McKerrow. 1995. Early paleozoic chronology—a review in light of new U-Pb zircon ages from Newfoundland and Britain. Can. J. Earth Sci. 32:368–379.

Walossek, D. 1993. The Upper Cambrian *Rehbachiella* and the phylogeny of Branchiopoda and Crustacea. Fossils and Strata 32:1–202.

Walossek, D. 1999. On the Cambrian diversity of Crustacea. *In* F. R. Schram and J. C. von Vaupel Klein (eds.), *Crustaceans and the biodiversity crisis, Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998,* Vol. 1, pp. 3–27. Brill Academic Publishers, Leiden.

Whittington, H. B. 1979. Early arthropods, their appendages and relationships. *In* M. R. House (ed.), *The origin of major invertebrate groups,* pp. 253–268. Academic Press, London.

Whittington, H. B. 1985. *The Burgess Shale.* Yale University Press.

Williams, A. and L. E. Holmer. 2002. Shell structure and inferred growth, functions and affinities of the sclerites of the problematic *Micrina*. Palaeontology 45:845–873.

Wray, G. A., J. S. Levinton, and L. M. Shapiro. 1996. Molecular evidence for deep pre-Cambrian divergences among metazoan phyla. Science 214:568–573.

Xiao, S. H., Z. Zhang, and A. H. Knoll. 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. Nature 391:553–598, 391(6667):553–558.

Xiao, S. H., Z. Zhang, and A. H. Knoll. 2000. Eumetazoan fossils in terminal Proterozoic phosphorites? PNAS 97:13684–13689.

Zhuravlev, A. Yu. 1995. Preliminary suggestions on the global Early Cambrian zonation. *In* G. Geyer and E. Landing (eds.), *Morocco '95. The Lower-Middle Cambrian standard of western Gondwana;* Beringeria Special Issue 2:147–160.