The Cambrian Fossil Record and the Origin of the Phyla

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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 undisputed 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 phanerzoic 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 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).

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.

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...
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 unparalleled 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, 2001a); deuto- stomes (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, 2001b). 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, 2001b), 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, 2001b), 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
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 Atabanian (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 Mc Kerrow, 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 siliciclastic 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 Mc Kerrow, 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...
 Cambrian fossils and origins of phyla

**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 northern 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 re-
visions is the short period of time covered by the ex-
ceptional 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
evolution—are considerably removed from the base of
the Cambrian, when both trace fossils and some small
skeletal fossils begin to diversify. In terms of under-
standing the early stages of the Cambrian diversifica-
tion 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 Proter-
ozoic (the “Ediacaran” assemblages) and upper Lower-
Middle Cambrian (“Burgess Shale” assemblages). This
gap is important, because finding exceptional preserva-
tions within it would provide an important test of
the various hypotheses of what the Cambrian ex-
losion really represents. At least some hope is pro-
vided by the so-called “orsten fauna” style of pres-
ervation, i.e., very early phosphatization of soft tissues
(see Butterfield, 2003), which does not seem to be so
temporally restricted as Burgess Shale-style preserva-
tion. 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 re-
cord. 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 compo-
nents of multi-element (“scleritome” or “cataphract”) skeletons, either external (for example, the tomom-
toids) or internal (e.g., echinoderms, although these ap-
pear relatively late in the fossil record). Scleritome re-
construction 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 scleri-
tomes may contain sclerites of very different shape,
making assignment of all of the components to the
same animal very difficult to predict. Whilst some pro-
gress has been possible with disarticulated sclerites
(Bengtson and Conway Morris, 1984), it has been the
exceptional faunas such as the Burgess Shale (Wiwax-
ia; Conway Morris, 1985; Butterfield, 1990), Cheng-
jiang (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 Micro-
dictyon [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 nec-
essary. This includes not assuming crown-group affin-
ities when the organism could lie in the stem-group;
and not assuming triploblasty when a diploblastic af-
finity 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 parsi-
ominous approach: if it is not known whether a par-
ticular 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 assign-
ment is carried out: the earliest skeletal fossils do not
demand any greater complexity than diploblasty; and
they are followed by taxa that are reasonably consid-
ered to lie in the stem-groups of triploblastic phyla or
groups of phyla (Fig. 6). It is not until the Mid-Tom-
motian–Atdabanian, some 20–25 Ma after the begin-
ning 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 ear-
liest 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 fos-
sils 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 im-
portance for interpreting the Cambrian explosion. It
implies that the early fossil (both body and trace) re-
cord 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 strati-
graphic and phylogenetic position (as argued in Budd
and Jensen, 2003). This is therefore a telling corre-

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 phylogenetic 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 Siberia (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.

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 levels) 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.

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