

Nipping the Cambrian “explosion” in the bud?

Simon Conway Morris

Summary

In recent years, two schools of thought have emerged with regard to the Cambrian “explosion”. One argues that it was very quick, with phyla tumbling into existence in a virtual geological instant. The other view has a more relaxed temporal perspective. It looks to slow aeons of cryptic metazoan history, which led to a final breakthrough in the Cambrian, not in evolution but of fossilization potential. Yet both views have serious difficulties. Now, in a recent issue of *Biological Reviews*, Graham Budd and Søren Jensen⁽¹⁾ argue for a third way. In an intriguing blend of functional morphology, the fossil record and cladistic thinking, they suggest that the assembly of metazoan bodyplans took place in a surprisingly straightforward manner. *BioEssays* 22:1053–1056, 2000. © 2000 John Wiley & Sons, Inc.

Introduction

The other day I was walking past an immense building from which emanated uproar. The noise was terrific. A door swung open and, looking in, I saw to my surprise that nearly everyone was dressed in white. But, strange to say there was not one pulpit but two. The crowd surged back and forth, spotless laboratory coats streaming in the rush. From one pulpit the proclamation rang out: “The Cambrian ‘explosion’ is real!!! Hundreds of phyla evolved, almost instantaneously. Listen, neo-darwinism is in terminal crisis, we must summon forth new mechanisms of macroevolution”. From the other pulpit, however, I heard the following: “No, the Cambrian ‘explosion’ is a mirage, a mere artefact! For aeons tiny animalcules slithered through the slime, avoiding fossilization, hoarding their *Hox* genes, swaying to the sonorous tick of molecular horology.”

This pastiche has a serious scientific point. Is the Cambrian “explosion” a real event, and if so did the welter of metazoan bodyplans pour forth in a geologically brief episode of relative genomic chaos and ecological mayhem? Alternatively, is this evolutionary event no more than an artefact? In this second scenario, it is still an “explosion” but one of fossils. In this view, the Cambrian explosion was the result of a breakthrough in fossilization potential, linked to skeletonization and increasing body size, which in reality concealed an immensely long

history of cryptic diversity extending deep into the Precambrian. Opinions are, indeed, deeply polarized. Now, in an exciting paper Graham Budd and Søren Jensen⁽¹⁾ provide a series of provocative and timely insights that neatly seem to defuse the Cambrian “explosion”, but in a way that is quite different to the many strident claims issuing from either of those two metaphorical pulpits.

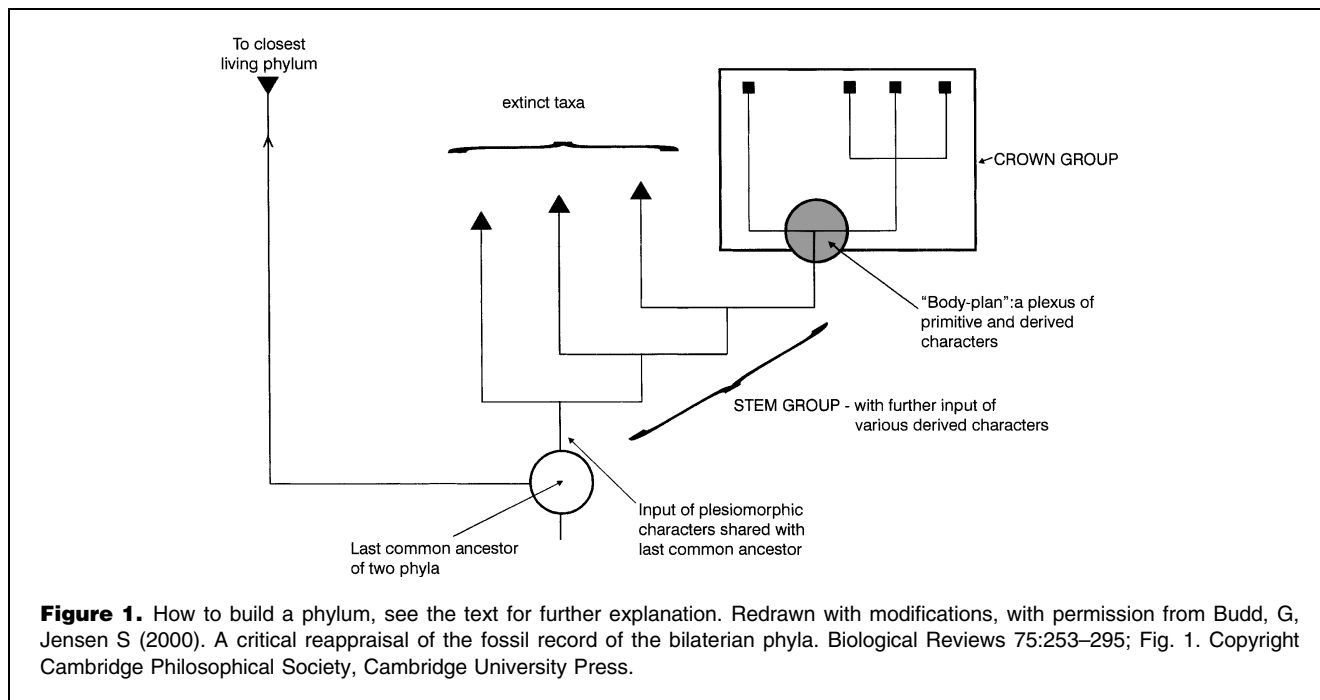
What is a phylum?

The principal aim of Budd and Jensen⁽¹⁾ is to undermine the venerable notion that all the phyla appeared suddenly at the base of the Cambrian. This literalist view of the Cambrian “explosion” is fast becoming embedded in the textbooks, and it is surely of more than passing interest⁽²⁾ that this argument has also started to attract the attention of the creationists.⁽³⁾ The assault on this position by Budd and Jensen starts with a careful look at the twin concepts of bodyplan and phyla. As is widely appreciated, the popularity of these terms is only matched by a notorious imprecision in their meanings. Yet, a proper understanding of what we want to mean by phylum and bodyplan has important implications for the way we view Cambrian evolution. First, we need to know the plans, if not rules, of assembly,⁽⁴⁾ yet all too often the origin of phyla has attracted a sort of macroevolutionary mysticism.

Properly understood, the construction of a bodyplan offers evolutionary insights into the roles of preadaptation and co-option of gene function, not to mention the identification of functional constraints. Moreover, at the early stages of divergence, phyla per se are not going to be recognizable. Far from being a problem, this actually offers rich opportunities to palaeontologists both to contribute to the historical documentation of bodyplan assembly, and also to constrain, if not resolve, conflicting models of metazoan phylogeny.⁽⁵⁾ Yet, as others have pointed out this remains a substantial challenge because the closely related taxa that will eventually diverge into different phyla may well look very similar initially.^(4,6) For this discussion, Budd and Jensen⁽¹⁾ develop concepts, which have long been familiar to adherents of cladistic methodology, of the stem and crown groups (Fig. 1). In doing so they aim to define operationally useful concepts of the bodyplan and a tractable definition of the phylum.

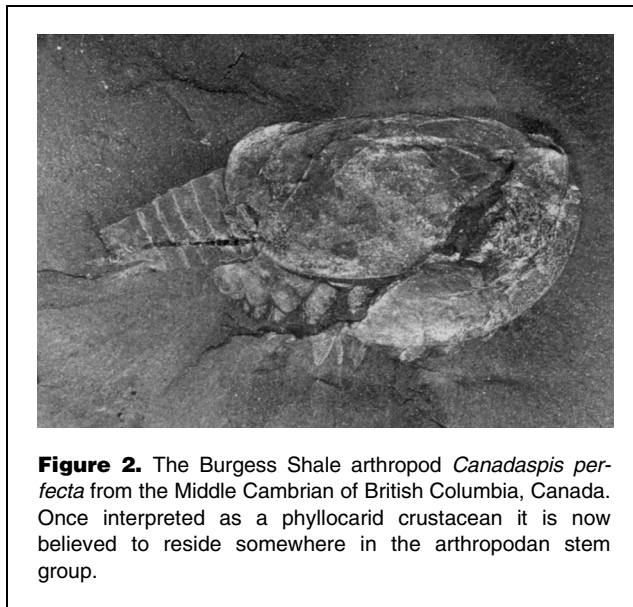
Central to this definition is the assumption of an orderly acquisition of derived characters, which in their totality will define the phylum. This procedure is then applied to the Cambrian fossil record, our understanding of which continues

Department of Earth Sciences, University of Cambridge, Cambridge
CB2 3EQ, U.K. E-mail: sc113@esc.cam.ac.uk



to be enriched with the remarkable insights from the soft-bodied Burgess Shale-type assemblages^(7,8) as well as the phosphatized microfaunas from the Orsten⁽⁹⁾ deposits. Despite their-by-now relative familiarity, the surprising result is that these faunas are not repositories of phyla, completely formed and all set to embark on the great Phanerozoic adventure. Rather what we see are assemblages largely represented by the stem groups (Fig. 1). These, by definition, represent the series of extinct organisms that possess some, but not (crucial to note) all, of the defining characters that delineate a phylum. In contrast, the crown group, again by definition, consists of the last common ancestor of all the extant taxa and all of its descendants. These concepts are perhaps the most fruitful results of cladistic thinking. In such a formulation, phyla may still be described as the debris of the Cambrian “explosion” but rather than being the result of a single macroevolutionary blast, they emerged sporadically throughout the Cambrian, and probably later.

This is a sweeping revision; how do we know it is correct? Take, for example, the Burgess Shale taxon *Canadaspis* (Fig. 2), a taxon that has played a key role in the reformulation of the importance of early arthropod evolution. As the knowledge of Cambrian arthropods has grown, so it now transpires that *Canadaspis*, long thought to be a phyllocarid crustacean,⁽¹⁰⁾ must be embedded somewhere in the stem group. As a phylum, the arthropods only appeared about 500 Ma ago, that is at least 50 Ma later than the time of divergence from other ecdysozoans. The arthropods are only one such example, and in a comprehensive survey of Cambrian faunas, Budd and



Jensen scrutinize the fossil record of the other main players, notably the annelids, brachiopods, chordates, echinoderms, and priapulids. They conclude that much of what we see in the Cambrian is telling us that the given bodyplans were assembled by familiar processes in a believable biological fashion and on a credible geological time-scale.

Budd and Jensen,⁽¹⁾ therefore, defuse the Cambrian “explosion” in a way quite contrary to the usual fashion, in

which there has been a widespread appeal^(11,12) to a deep and, it must be noted, conveniently cryptic, history of metazoans. The agreed corollary of this latter view is that the Cambrian “explosion” must be effectively an artefact whereby the animals, hitherto minute and unfossilizable, underwent a quantum jump in size, perhaps in response to changing levels of atmospheric oxygen. In the last few years, several groups have been busy weaving a series of hypotheses that attempt to portray the possible nature of these hypothetical metazoans. Yet, building upon earlier comments^(13,14) Budd and Jensen seriously doubt the feasibility of this enterprise. Accordingly, the second part of their paper is an enjoyable excursion with a skilled sabotage team dynamiting evolutionary shibboleths.

Meiofauna and plankton

One area that Budd and Jensen⁽¹⁾ scrutinize is the notion, promulgated by Fortey and colleagues,⁽¹⁵⁾ that a pre-Ediacaran metazoan record is best sought amongst equivalents of the living meiofauna, namely the marine denizens inhabiting the interstices between sand grains. As Budd and Jensen⁽¹⁾ point out, the process of miniaturization, which is almost universally accepted as the evolutionary route to the meiofauna, simply is not the mirror image of an enlargement in body size. The latter is a very different process. As they write: “Large animals . . . in general possess a structural apparatus that is closely linked with their particular environmental challenges. Body cavities, blood vascular systems, complex muscular and support systems, and nephridia (or—critically—some sort of functional equivalents) are all features that are required in large animals, but not in tiny ones, where ciliated soles may suffice for movement, and diffusion for excretion and respiration”. Thus, when we think about Precambrian ancestors, Budd and Jensen⁽¹⁾ conclude that “the appearance of [this] integrated complex or syndrome of features is highly implausible” (Ref. 1, p. 275). This is not necessarily to deny that the ancestral metazoans may have been very small and, indeed, the functional sophistication of such single-celled eukaryotes as the ciliates is a constant reminder against taking a too metazoan-centric view of organismal complexity. Yet, as Budd and Jensen⁽¹⁾ stress, whatever might be lurking in the Neoproterozoic pond it is unlikely to be some sort of Lilliputian worm, all organs duly in place, poised for a monstrous bout of inflation to a size large enough to make a burrow, bear a skeleton and thus usher in the Cambrian “explosion”.

The meiofaunal hypothesis of Fortey and others⁽¹⁵⁾ appears, therefore, to lack a certain biological credibility. The demolition team faces a seemingly more significant challenge from the proposals of Davidson and colleagues who have been vigorously promulgating an alternative hypothesis^(16,17) for the origins of the Cambrian “explosion”. This hypothesis also looks to minute animals but this time in the form of something similar to a planktotrophic larvae, perhaps most familiar in the form of the trochophoran larva of polychaetes. Today these

larvae are associated with maximal indirect development where the life-cycle is biphasic. The latter term refers to the alternation between the tiny ciliated larva, the initial product of the fertilized egg, and a much larger adult that emerges from the larva by an abrupt metamorphosis. The potential for the adult is, however, already present in the larva, as the so-called “set-aside cells”. These provide the rudiment that during catastrophic metamorphosis rapidly develops into the adult. The hypothesis of Davidson and colleagues that the Cambrian “explosion” effectively originated with the invention of the “set-aside cells” that permitted the emergence of large, predominantly benthic, adults has received considerable attention, and also some criticism.^(14,18)

A central question, of course, is what functional significance these “set-aside cells” might have had in a Neoproterozoic larva before it “knew” they were to form an adult. An earlier suggestion⁽¹⁶⁾ involving the possible role of oncogenes appears not to have been pursued. Alternatively, it is suggested by the Davidson group that possibly “set-aside cells” first evolved “to produce additional useful structures, which contained more cells than their ancestors could mobilize. Perhaps they used these to generate simple lobes as an aid for feeding, locomotion, or gas exchange”. Somewhat lamely, they continue: “they must have conferred some practical advantage”. (Ref. 17, p. 13). Just so, but a more precise set of predictions would be welcome.

Echoing some of these points, Budd and Jensen⁽¹⁾ present a comprehensive critique of this larval hypothesis.^(16,17) Somewhat cheekily, they enquire how these animals managed to reproduce given that the gonads necessary for the process could not have evolved given the germ-cells themselves arise from the “set-aside cells”. There are also problems of whether this type of life cycle can be described as universal. Seemingly not, and as also pointed out by Valentine and Collins,⁽¹⁹⁾ at least the Ecdysozoa seem never to have had such a biphasic pattern. What matters, say Budd and Jensen, and here their argument has a number of parallels with their critique of the meiofaunal hypothesis, is to enquire into the functional context in which the various complex anatomical features necessary for adult but, emphatically, not larval, existence were able to evolve in a believable evolutionary framework. This problem, which remains central, is hardly addressed by Davidson and colleagues.^(16,17) It seems more likely that such anatomical features as musculature or excretory nephridia arose in larger animals and that the genetic instruction necessary for their ultimate expression was only subsequently incorporated into the larva in the rudiment or “set-aside cells”. The potential importance of this process was identified many years ago by Jägersten⁽²⁰⁾ who coined the term “adultation” to describe it.

Notwithstanding these difficulties, this larval hypothesis seems to be developing a life of its own, especially in the context of dramatic new evidence from the Neoproterozoic.

For example, the conclusion that the so-called “Snowball Earth” may have escaped total refrigeration, with an equatorial zone of oceanic blue-water remaining free of ice⁽²¹⁾ might seem to offer an intriguing opportunity for pelagic evolution, perhaps including larval-like forms. Some of the implications for this idea have been explored by Runnegar.⁽²²⁾ He points out that recruitment of the putative “set-aside cells” for adult morphogenesis remains an interesting hypothesis, yet if it is to retain its credibility, an explanation needs to be found as to why the impact of this evolutionary novelty was then somehow delayed, given that the hypothesized “Snowball Earth” is estimated to have melted tens of millions of years before the onset of the Cambrian “explosion”.

Conclusion

The paper by Budd and Jensen⁽¹⁾ will ruffle plenty of feathers but their reformulation of the fossil record makes sense in depicting the phyla as having evolved in an orderly and coherent fashion. Such an emphasis on functional constraints throws yet more doubt on the appealing, but probably mistaken, views of cryptic and microscopic antecedent metazoan forms swarming undetected in the Precambrian seas. As such, their paper remains a landmark in attempting to restore some degree of biological credibility to this fast-moving, complex and fascinating field.

Acknowledgments

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