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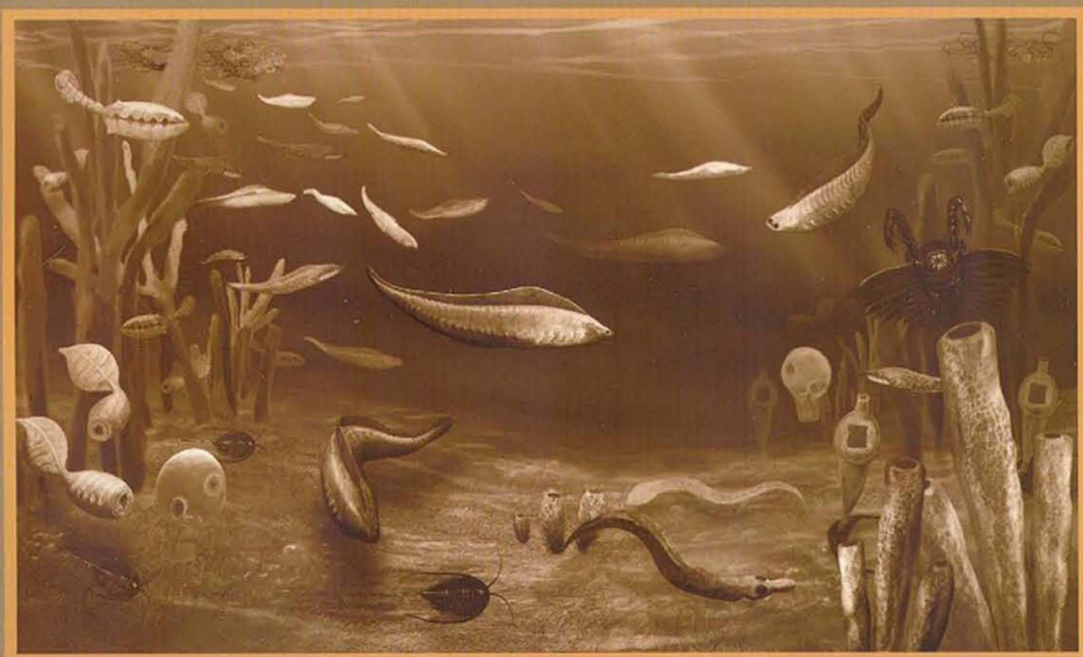
Ancestors from Cambrian Explosion

Degan SHU & the Team



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Preface

Ancestors from Cambrian Explosion

Degan Shu & Simon Conway Morris

Who am I? It is the question that many people would ask themselves. I look in the mirror. I see myself, but also something deeper. First I am human, a representative of *Homo sapiens*. We are an unusual species, one that likes to ask questions. What are humans, where did they arise and whence did they come? Most of us can trace a family history, but what about our real ancestors, far back in geological time? The central insight offered by Charles Darwin was that not only are we descended from animals, but our roots go far deeper, ultimately of course to the origin of life itself. A few million years ago Man was an ape transforming himself from his immediate ancestors by first becoming upright and then seeing a steady enlargement of the brain. Further back we can trace a story that over about 350 million years takes us back via ever more primitive mammals to reptiles and ultimately those fish that walked onto land. Nor is this the end of the story because, as Philippe Janvier aptly called "the first fish", our origins amongst the grand assemblage of vertebrates takes us to the momentous Cambrian explosion, some 520 million years ago.

More than a hundred years of extensive and intensive investigations into dozens of fossil treasure-troves spanning the Cambrian-Precambrian boundary across the world have resulted in a series of major achievements. In particular, study of the early Cambrian Chengjiang fauna now allows us to see not only the framework of animal evolution, including the three major bilaterian groups (respectively the deuterostomes, ecdysozoans and lophotrochozoans), but also in particular the earliest fish as well as their more remote ancestors amongst the invertebrates.

Nearly all articles in this selection, except for the last one, result from investigations of Chengjiang fauna, which is particularly important because of its rich diversity of early deuterostomes. In the selection presented here are details of the first fish (the Myllokunmingiida) and close contemporary relatives in the deuterostomes, as well as variety of other groups, such as trilobites, brachiopods, worms and the strange vendobionts. The book has four sections. Part One deals with the nature of Cambrian Explosion. Unlike the popular idea of a "sudden" explosion here we delineate the Cambrian explosion as essentially composed of three distinct episodes, spanning an interval of approximately 40 million years. This evolutionary Big Bang gave birth to the Tree of Animals (or metazoans). First we see the burst of various basal animals in the Ediacaran (the latest Precambrian). This is followed in the first Cambrian interval (Meishucunian Age) by the explosive radiations of both the Protostomia (so-called because of the embryological origin of the mouth, literally "first-mouth") as well as more basal animals. Finally we see a remarkable proliferation of phyla across the three major subgroups of animals. This event includes the radiation of the Deuterostomia (literally "second-mouth") and occurs in the second interval (that is the Chengjiang fauna) .

Part Two comprises the core of the book. Here are reported, chiefly from papers in *Nature* and *Science*, examples of the earliest representatives of the five major living groups as well as an extinct phylum belonging to the Deuterostomia. The most advanced chordates from Chengjiang represent the earliest vertebrates, leading to the identification of a new Order, the Myllokunmingiida, which is represented of three species, i. e. *Myllokunmingia fengjiaoa*, *Haikouichthys ercaicunensis* and *Zhongjianichthys rostratus*. These first fish have both a real head (hence are craniates), including a brain, paired eyes and other sensory organs, as well as a primitive backbone (hence qualify as vertebrates). The lower chordates, which have neither a true head (acraniates), nor a backbone (hence technically invertebrates) are the *Pikaia*-like *Cathaymyrus* and *Cheungkongella*. They can be compared respectively to modern cephalochordates (amphioxus) and tunicates. Possible ancestral soft-bodied echinoderms, the vetulocystids, are also known from the Chengjiang. Another group, the yunnanozoans, have long been controversial, but are believed to represent a side-branch amongst the lower deuterostomes, and perhaps are close to hemichordates. One of the most significant groups of Chengjiang deuterostomes are the extinct Phylum Vetulicolia. These animals lacked a head, notochord and myomeres, but had already evolved five pairs of primitive gill slits. Vetulicolians have attracted wide attention—and controversy, but a compelling case can be made that these strange-looking animals lie at the very roots of the deuterostomes.

Part Three documents some of the major groups amongst the ecdysozoans and lophotrochozoans. Together they define the protostomes, the largest supergroup amongst animals. In terms of ecdysozoans, new material of *Eoredlichia* and *Yunnanocephalus*—the best known trilobites of South China—have for the first time been found with beautifully preserved soft parts. These include the digestive tract and contiguous caeca, as well as the antennae and biramous appendages. A small larva—like arthropod had been considered to be a protaspid stage of the naraoiids. However, restudy of many well-preserved specimens reveals that they represent adults of a new arthropod, *Primicaris larvaformis*. Its larva-like form is believed to have arisen by the heterochronic process of progenesis. It displays primitive aspects of bodyplan and limb morphology, suggesting a basal position within arthropods. Bivalved arthropods such as *Kunmingella* and *Isoxys* are amongst the most abundant fossils in the Chengjiang fauna. These are found preserved with not only typically soft parts such as appendages and eyes, but more remarkably also the eggs in the former and poison glands in the latter.

Priapulids are also ecdysozoans and so relatives of the arthropods. Today they are relatively uncommon and not particularly diverse, but in the Cambrian the exact opposite was the case, displaying a remarkable range of morphologies and represented by numerous taxa. Various lobopods, which are effectively worms with legs, are central to understanding the earliest evolution of the arthropods as well as possibly providing a link to the priapulids. Lobopods are also frequent in the Chengjiang fossil *Lagerstätte*. The most interesting forms amongst the lobopods are surely *Diania cactiformis* and *Onychodictyon ferox*. The former is remarkable because it possesses robust sclerotized appendages composed of a series of articulated units (as in a fly leg). This arrangement is closer to the arthropod condition than any other known lobopodian. In contrast *Onychodictyon* lacks specialised mouthparts and opens the debate as to whether amongst the panarthropods the definitive mouth opening had a single origin.

In the Lophotrochozoa, the most abundant forms are represented by the brachiopods, including linguloids and rhynchonelliforms. There are, however, some other fossils whose interpretations are tantalizingly difficult. Particularly interesting is *Cotyledion tylodes*. This has recently been reinterpreted as a sclerite-bearing stem-group entoproct. If correct then this might have important implications for the earliest evolution of this group and perhaps its wider relationships.

The more primitive animals, exemplified by the cnidarians, are also central to our understanding of early animal evolution. Representatives of these basal animals are known from sediments of both Meishucunian Age and Chengjiang Age and could be as rich as (or richer than) the record from the latest Precambrian. Here two significant groups are reported in Part Four. Until now very few early cubozoan fossils were known, principally from the Middle Cambrian of Utah and the Carboniferous Mazon Creek of Illinois. Fortunately, undisputed cubozoan fossils are now known from Shaanxi Province and are of Meishucunian Age. The well-preserved anatomical features such as gastric lamellae and vascular pouches in these embryonic fossils display a perfect pentaradial symmetry and imply that ancestral cubozoans display unexpected complexity at the dawn of the Cambrian.

Vendobionts were thought to be characteristic of life in the Vendian (or Ediacaran). However, a frond-like fossil (*Stromatoveris*) is now known from the Chengjiang fauna. This animal is strikingly similar to Ediacaran vendobionts. The exquisite preservation reveals closely spaced branches, probably ciliated, that appear to represent precursors of the diagnostic comb rows of ctenophores. This discovery, therefore, has significant implications for understanding the early evolution of this phylum (and related diploblasts), some of which independently evolved a frondose habit.

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Part One Nature of Cambrian Explosion

Cambrian Explosion: Birth of Tree of Animals

Degan Shu[1,2,*]

1. Early Life Institute and State Key Laboratory of Continental Dynamics, Northwest University, Xi'an 710069, China

2. China University of Geosciences, Beijing 100083, China

* *Corresponding author: E-mail: elidgshu@nwu.edu.cn*

Abstract: Excluding the sponges the Kingdom Animalia is usually divided into three subkingdoms: Diploblasta, Protostomia and Deuterostomia. The Cambrian Explosion consists of three major episodes, two of which were in the early Early Cambrian (one represented by the small skeletal fossils "SSFs" at the base of the Cambrian and the other represented by the succeeding Chengjiang faunas "CFs"), and the other episode as their prelude took place in the "Eocambrian" (i.e. the latest Precambrian), represented by the Ediacaran faunas. This unique Big Bang of life has been recognized as giving birth to the entire morphological Tree Of Animals (or metazoans), in short the TOA. Its "seed" in the deep Precambrian, represented by some sort of protist from which the complete TOA must have grown, remains unknown paleontologically. However, the fossil evidence suggests that the three major episodes of the Cambrian Explosion are responsible for the earliest radiations of the three subkingdoms of animals respectively. While the observed Ediacaran fauna might constitute only a small part of the whole Ediacaran biota, our evidence supports that it was dominated by diploblasts (the "trunk" of the TOA) with only a few possible stem-group triploblasts. The Early Cambrian in turn in two phases explosively yielded almost all the major triploblastic crown-branches (Bilateria: the huge "crown" of the TOA), which include the other two subkingdoms: first the extremely diverse protostomes in the Meishucunian Age and then followed by a nearly entire lineage of early deuterostomes from the Chengjiang, including even its most derived member—the earliest true vertebrates. Among the four most significant milestones of morphological origins and radiations in animal history, the first one (i.e. appearance of metazoans) took place in the Ediacaran Period or earlier times, and the other three can be seen in the windows available from the Chengjiang and the Meishucunian fossil assemblages. The newly discovered extinct Phylum Vetulicolia, which has primitively segmented body with simple gill slits in its anterior division, most probably represents one of the roots of the deuterostome subkingdom. Showing a mosaic of basic features possessed in both the bilateral vetulicolians and some primitive echinoderms, the soft-bodied vetulocystids are best regarded as one of the roots of the extant pentamerous echinoderms. Standing on the "top" of the deuterostome super-branch in the early

Cambrian TOA are the "the first fish" *Myllokunmingia* and *Haikouichthys*, which bear paired eyes and salient protovertebrae. These animals represent the real root of the remainder of the vertebrates or craniates. On the contrary, yunnanozoans, including *Yunnanozoon* and *Haikouella*, possess neither eyes nor unequivocal vertebrae, and may have nothing to do with the craniates, let alone the vertebrates. Those enigmatic creatures share a similar body-plan with vetulicolians and should be treated as a side-branch within the lower deuterostomes.

Key words: Ediacaran biota; Chengjiang faunas; Phylogeny of deuterostomes; Phylum Vetulicolia; Origin of vertebrates

Introduction

Our Earth is the unique planet in the solar system because it is full of life, particularly various active animals, which are biologically called metazoans (in contrast to the single-celled protozoans). When and how metazoans first appeared on the Earth and what was the manner of their early evolution has long been a challenging topic in biology and geology. Did they appear gradually or suddenly? Did they evolve gradually or episodically, was their diversification governed by trends or did it occur randomly?

The sudden appearance of early animals was recognized at least as early as the time of William Buckland, Oxford's first principal incumbent of paleontology in 1830s (see "Geology and mineralogy considered with reference to natural theology" by Buckland, 1836, from Conway Morris, 1998). By 1859 this problem had been even more clearly articulated by Ch. Darwin in his famous "On the Origin of species". This extraordinary event subsequently was widely realized as amongst the most striking of episodes in the history of life, and has been aptly nicknamed the "Cambrian Explosion" (Cloud, 1948). This explosive evolutionary event was recognized as being so significant that it served as the first-rank landmark dividing Earth history into two major divisions, the time of visible life, that is the Phanerozoic and the preceding Pre-Cambrian.

In the past 60 years, and particularly the recent three decades, both the biological and physical events around the Proterozoic-Phanerozoic boundary have been extensively and intensively investigated, and a variety of hypotheses have been proposed (Glaessner, 1958, 1984; Seilacher, 1989; McMenamin, 2005; McMenamin and McMenamin, 1990; Bengtson *et al.*, 1990; Bergström, 1990; Fedonkin, 1992; Runnegar, 1992; Seilacher, 1992; Conway Morris, 1993b; Fedonkin, 1994; Runnegar, 1994; Grotzinger *et al.*, 1995; Conway Morris, 1998; Collins, 1998; Runnegar, 1998; Knoll, 1999; Erwin, 1999; Conway Morris, 2000b, 2003; Erwin and Davidson, 2002; Valentine, 2002, 2004; Waggoner, 2003; Benton and Ayala, 2003). However, little consensus was emerged. Most of the disagreements (Runnegar, 1982a, b; Signor and Lipps, 1992; Valentine, 2004) center on:

1) Is the Cambrian Explosion a genuine biological event or an artifact of taphonomy or incomplete preservation of strata?
2) Was there a very long hidden history of metazoans before their appearance in the fossil record?
3) What was the major trigger to initiate this explosion?
4) What is the relationship between the Cambrian explosion and the formation of the Tree of Animals (TOA)?

Following a brief review on the first three questions above, I will focus on the discussion of the fourth question in this review, and particularly on recent advances in the investigations into the Chengjiang fauna.

Cambrian Explosion

Nature of Cambrian Explosion

More than a half century of extensive and intensive investigations to both the late Precambrian and the early Cambrian unmetamorphosed sedimentary strata in the whole world have shown that Cambrian Explosion or Bioradiation was indeed a real biological event rather than an artifact of taphonomy or incomplete preservation of strata. This rapid diversification of metazoans in the Early Cambrian is largely witnessed by at least three aspects of the fossil record (Conway Morris, 1993b): the sudden appearance of skeletal faunas (Bengtson, 1992a; Qian and Bengtson, 1989), a striking increase in the diversity and complexity of trace fossils (Crimes, 1992; Fortey and Seilacher, 1997), and the remarkably well-preserved faunas in Konservat Lagerstätten (Conway Morris, 1989; Briggs *et al.*, 1994; Shu *et al.*, 1996c; Chen and Zhou, 1997; Hou *et al.*, 1999; Shu, 2005a, 2006).

The Cambrian Explosion as a whole is composed of three major phases or episodes. Immediately after a relatively long prelude episode in the "Eocambrian" (i.e. the latest Precambrian and represented by the Ediacaran faunas), the two major explosive episodes took place in the early Early Cambrian: the first one is represented by the "small shelly fossils" (SSFs) or more precisely the small skeletal faunas near or even cross the base of the early Cambrian, while the following main episode represented by the Chengjiang faunas. The last two faunas cover the majority of the living metazoan phyla. However, the remaining extant phyla that are not seen in these two faunas are largely represented by tiny creatures and/or parasites, which with very few exception have not left any fossil record in the rest of the Phanerozoic. Therefore, it may be safe to say that "nearly all the modern phyla of animals appeared in the early Cambrian", not to mention some additional extinct phyla, such as Vetulicolia (Li *et al.* 2006). On the other hand, except for a few skeletalized fossils, such as *Cloudina* (Glaessner, 1984; Grant, 1990; Hua *et al.*, 2003), *Namacalathus* (Grotzinger *et al.*, 2000) and *Conotubus* (Hua *et al.*,

2006) as well as some trace fossils from the latest Precambrian, nearly all the skeletal creatures from the early Cambrian have never been reported in the Ediacaran, not to mention the Chengjiang-type or Burgess-type soft-bodied metazoans. It should be clear that if there had been any early Cambrian SSFs-like animals existing in the Precambrian, they should have easily preserved in the fossil record. Such an obvious and big gap between life in the Cambrian and Precambrian has forced us to draw the conclusion that the Cambrian Explosion is a genuine evolutionary event, and not any sort of artifact. Valentine (1994) is correct when he wrote: "The radiation remains spectacular… the metaphor of explosion is most apt, for most of the body plans that characterize living phyla, and numbers of extinct ones, probably arose during the Precambrian-Cambrian transition". In other words, the morphological TOA, rather than the genetic TOA, which could have existed earlier, was largely born from this unique Big Bang in the history of life.

Phylogenic fuse

Concerning the Cambrian Explosion the first question we are faced with is: Was it a slow-fuse or megatonnage? (Conway Morris, 2000a,b; Fortey, 2001; Fortey *et al.*, 2004) This is not to say that every evolutionary event is known, on the contrary much remain hidden. The available fossil record now shows there is no doubt some sorts of metazoans existed in the Ediacaran Period (Sprigg, 1988; Fedonkin, 1992, 1994; Fedonkin and Waggoner, 1997; Xiao *et al.*, 1998; Chen, 2004). Although Seilacher (1989, 1992) has even created the term vendobionts to unite most of the Ediacaran fossils as non-metazoans, he accepted that trace fossils were made at this time by worm-like bilateral metazoans. Without doubt, the Cambrian faunas stemmed from some members of Ediacaran life. But what do they look like? Currently, the majority of paleontologists prefer to stress the difference between Ediacaran creatures and the Cambrian faunas. Indeed, they are very distinct from each other, and any interpretation of Ediacaran organisms as possible forerunners to the Phanerozoic metazoans is controversial. Nevertheless, to try to detect the first ripple of the Cambrian Explosion in the Ediacaran times must be central if we wish to understand better the earliest evolutionary history of the TOA. For example, recognition of survivors of some kinds of vendobionts in the Cambrian is a promising avenue of research (Conway Morris, 1993a,b; Shu *et al.*, 2006, Shu and Conway Morris, 2006). And, it should be self-evident that much more evidence is needed to relate these two distinct animal assemblages.

Certain metazoans, principally of diploblasts or other type of the lower animals, most of which look very strange to us, were present in the Ediacaran or maybe existed even earlier. However, it has been uncertain how long the hidden history existed prior to this remarkable bioradiation. In other words, how long might be the "phylogenetic fuse" leading to this Big Bang? People have tried to employ the method of molecular clock to answer this question (Runnegar, 1982a; Erwin, 1989; Ayala and Rzhetsky, 1998), and the method's strengths and weaknesses are well covered by Donoghue and Smith (2004). The analyzed results, however, remain very controversial. The majority of age estimates (750—1000 Ma) are much older than the fossil record, while contrary to some researchers Ayala and Rzhetsky (1998) declared that "molecular clocks confirm paleontological estimates". Most authors now hold that there exist real problems with the molecular clock method as applied to the evolution of early life, based as it is on genetic molecular chemistry. Graur and Martin (2004) go further, presenting what can be described as a demolition job. Anyway, although this molecular tool is at present controversial, we still can be fairly optimistic that in the future improved and more critical approaches will yield much better results.

Until now, no reliable body-fossil record of metazoans is known in pre-Ediacaran times. According to the meiofauna hypothesis, however, the pre-Ediacaran animals were so tiny, only a few millimeters long and quite similar to modern larvae, that they could not be preserved as fossils at all. In this respect, trace fossils of metazoans should be of importance. Note, however, that the evidence available has shown that the diversification of trace fossils basically parallels but does not precede the diversification of shelly fossils (Crimes, 1989, 1992). However, whilst controversial there appears now some evidence of such early trace fossils from the Stirling Range, Western Australia (Rasmussen *et al.*, 2002). If confirmed in terms of their nature and age, the history of the stem group metazoans (but not, of course, the crown-group metazoans) could be extended back to as early as the Mesoproterozoic.

Major triggers to Cambrian Explosion

The question concerning major triggers to the Cambrian Big Bang of life is certainly more interesting than the "fuse puzzle", and much more difficult to answer. The explosion of animals embraces two different sorts of bio-events: the origins of various groups of metazoans and their subsequent radiations. The first appearance of a group could be related to or close to its morphological origin. However, origins and radiations are separate issues. To investigate possible triggers to the Cambrian Explosion as a whole, Signor and Lipps (1992) posed 14 questions, which were later paraphrased in 6 points by McCall (2006). To answer those questions, the former authors tabulated respectively the extrinsic factors and intrinsic factors, which had been suggested by various authorities. It is most probable that several of those factors were interrelated. Among them, it seems to me that the partial pressure of atmospheric oxygen and changes in ocean chemistry (related to the break-up of the supercontinent Rodinia and the global glaciation) are among the most important extrinsic factors, while genetic causes in terms of intrinsic factors may together have been largely responsible for the appearance of animals. On the other hand, the quick bio-radiation may be reasonably explained by the cropping principle (Stanley, 1973) and the appearance of various predators, which would place an enormous selective premium on the acquisition of skeletons (McMenamin, 1986; Conway Morris, 1998).

Without access to oxygen animals cannot exist. The early Earth's atmosphere lacked free oxygen. Available evidence shows that free oxygen began to enter the Earth's atmosphere in the early Palaeoprotozoic (Schopf, 1992). Accordingly, the origin and radiation of Metazoa must have awaited for the accumulation of sufficient free oxygen in the atmosphere to support animal life (Cloud, 1968). This scenario has gained considerable support from interpretations of the Proterozoic sedimentary record, and particularly some recent data, which demonstrates that stem group metazoans were components of earliest Ediacaran ecosystems, later expanding markedly, perhaps in association with rising oxygen level (Knoll and Carroll, 1999; Canfield *et al.*, 2006; Fike *et al.*, 2006; Yin *et al.*, 2007).

Recent studies have suggested several ways that tectonic events might have influenced the evolution of animals. Valentine and Moores (1972) related the appearance and radiation of animals to the breakup of the Neoproterozoic Rodinia and later the birth of a new supercontinent Gondwana, as well as the related glaciation (Marinoan). These include the evolution of continents and tectonic blocks, changes in the configuration of the continents, sea level and ocean chemistry, especially the concentrations of carbonates and phosphates (Knoll, 1992; Knoll and Walter, 1992; Knoll, 1994; Maruyama *et al.*, 2007). The causative link between the rifting events and the evolution of animals, however, is yet to be made explicit. In addition, the Acraman impact event (c. 580 Ma) has been suggested as being significant in the evolution of the early metazoans (Grey *et al.*, 2003).

Without doubt, a key innovation in the evolution of Metazoa was the evolution of regulatory genes or the evolution of complex genetic mechanisms to regulate development (Conway Morris, 1998; Valentine, 2004). It would be a good idea to keep in mind that the internal evolutionary processes may well have been more important in initiating the Cambrian Explosion than environmental causes. Valentine (1994) has reached the conclusion that: the explosion is rapid partly because many of the metazoan stocks reached a grade of complexity (at about the 40-50-cell-type level and had soft-part anatomies) for which durable skeletons then promoted further fitness, during a relatively narrow interval of geological time. Although the hypothesis on hybridization in the evolution of animals (Williamson, 2006) sounds interesting, it needs to be further tested by developmental, molecular and fossil data.

Although we remain as blind men interpreting elephants when we search for the origin of metazoans, more and more