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# Diverse perspectives on the Protozoan – Metazoan transition

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# Introduction

In order to represent adequately the increasingly interdisciplinary nature of evolutionary research, five scientists with strikingly different backgrounds were invited to record their individual perspectives on the Protozoan-Metazoan transition. This was no easy request considering the broadness of the subject and it is pertinent to note how freely the authors cross disciplines in their narratives, frequently covering common ground, but from quite different viewpoints. Comparative anatomy, molecular biology, geochemistry, paleontology and geology can all be found within these contributions. Here we outline four major issues that have emerged recently as "challenges and stimulants" to our understanding of the Protozoan-Metazoan transition.

### 1. The brush phenomenon problem

Recent exponential increases in information, whether taxonomic, morphological, molecular or paleontological, might be expected to shed light on the pathway(s) from protozoa to metazoa. However, each new package of information or research direction, while leading to greater knowledge overall, tends to blur rather than clarify the evolutionary pathways of protozoan and metazoan taxa. Increasingly, the data do not produce an evolutionary "tree" but more of a "bush" or "brush". Impressive examples of this problem can be found in papers by Cavalier-Smith (1998) on protists and by Abouheif *et al.* (1998) on multicellular organisms. The brush phenomenon is scale-independent, that is, it can be observed between kingdoms and phyla as well as families and genera. Accordingly, common mechanisms may be at work, possibly involving parallel and convergent evolution. As more taxa are analyzed, more hidden convergences can accumulate that disturb the tree, especially in molecular systematics, where plesiomorphies and apomorphies cannot yet be distinguished. In addition, molecular-based tree construction has encountered other obstacles, such as long-branch attraction (Morin, 2000) and the unsuitability of most molecules for kingdom-scale phylogenetic

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analyses (Abouheif *et al.* 1998), which necessitate the successful marriage of morphological (ultrastructural) and molecular techniques in any modern study. Despite the recent advances outlined below, it is not clear at present how this brush phenomenon can be circumvented.

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## 2. Hunting the ancestral metazoan

The hunt for the ancestral metazoan has been the focus of much speculation in the published literature. Rieger (this volume) takes the reader through a comprehensive survey of hypotheses that explain the sequence of changes, which led from unicellular to multicellular organization. In agreement with the emerging consensus from molecular phylogeny (Hackstein, this volume), Rieger concludes on the basis of ultrastructure that unicellular organisms similar to choanoflagellates are the most likely candidates for the ancestral metazoan. Recently, this hypothesis has been invigorated following the publication of morphological and molecular evidence that a flagellate, *Ancryonnous*, could be the closest extant relative of the common ancestor to the metazoans, fungi and choanoflagellates (Atkins *et al.* 2000).

Other major events in metazoan diversification are also discussed below. For example, the introduction of a biphasic lifestyle, common in primitive animals such as porifera and bryozoa, with a microscopic, ciliated, dispersive larval stage and a macroscopic, colonial adult stage, is proposed to have been one such significant event (Rieger, this volume). This idea is further embellished by Dewel *et al.* (this volume) who maintain that the "morphology of living metazoans indicates that the adult bilaterian ancestor was both macroscopic and complex" (see also Budd & Jensen 2000). Indeed, it is argued that the fossil record, in the form of the large, latest Neoproterozoic Ediacaran fauna (580 – 540 Ma), may lend support to this idea. However, it is still far from clear whether these enigmatic frond- and disc-like fossils were in any way ancestral to later lines of extant phyla (Knoll & Carroll 1999). The recent discovery of new taphonomic windows for the preservation of microscopic metazoans, such as phosphatized embryos (Bengtson, this volume), will certainly help in establishing the relevance or irrelevance of Ediacaran fossils to later metazoan diversification during the Cambrian explosion.

#### 3. Molecular phylogeny vs. Fossil records: how real is the Cambrian explosion?

Paleontologists worldwide have recently been able to reach agreement on a number of important issues regarding the fossil record (Bengtson, this volume). Most importantly, all reports of pre-580 Ma metazoan fossils are now widely considered to be of dubious nature. This is especially important as it comes in the light of rapidly improving knowledge of our global fossil archive and serves to firmly close the door on the possibility of a long, but hidden history of macroscopic metazoan evolution. This consensus has led many to consider the "Cambrian explosion" of greatly increasing metazoan diversity between 545 Ma and 510 Ma to represent a real evolutionary event, and one that needs to be incorporated into future hypotheses of metazoan origins. However, molecular studies generally do not support such a late branching of metazoan phyla (Bengtson and Hackstein, both this volume), while studies that have, on the basis of irresolvable nodes, lent weight to the notion of a period of very rapid evolutionary expansion, are themselves open to ambiguous interpretation (Abouheif *et al.* 1998).

The joint ancestor of the protostomes and deuterostomes is consistently estimated by "molecular clocks" to have existed more than 670 million years ago. This highlights a possible gap in the current fossil record, especially if one considers Rieger's arguments (this volume) that the ancestral bilaterian possessed a macroscopic adult phase, which ought certainly to have left a recognizable fossil record during the long period between 580 and >670 Ma. This apparent contradiction can be partially resolved by assuming a long, hidden history of microscopic metazoan evolution (Fortey et al. 1997, Peterson & Davidson 2000) but a hypothesis based on a lack of evidence is unsatisfactory. Bengtson (this volume) makes the important point that distinguishing features are acquired successively throughout the evolution of a lineage, causing the first members of that lineage to go unrecognized, if indeed any representatives of crown-group phyla were present during the earliest phases of metazoan diversity expansion (Budd & Jensen 2000). However, at the present time there are no fossil candidates for an ancestral metazoan within this crucial pre-Ediacaran period. Although the lack of macroscopic metazoans in the Precambrian awaits definitive interpretation, more recent research has significantly narrowed the gaps between fossil and molecular-based estimates of metazoan branching (Ayala et al. 2000, Smith & Peterson, 2002), leaving us optimistic that this will continue.

#### 4. Unraveling the geological context behind early metazoan evolution

By analogy to Phanerozoic evolutionary events, such as the Permian-Triassic boundary, the geological context is likely to have been an exceedingly important factor in early metazoan evolution (Knoll & Carroll 1999). Bengtson, Brasier, Dewel *et al.*, and Hackstein (all this volume) all emphasize the role of massive climate upheaval in causing potential population bottlenecks. Global glaciations, such as occurred during the late Neoproterozoic, are likely to have led to small, isolated gene pools, thus helping to maximize mutation rates. Intense glaciations repeatedly disrupted Earth's surface environment between 720 and 580 Ma, causing ocean anoxia, and massive sea-level change (Brasier, this volume). Although increases in atmospheric oxygen concentrations may have acted as a trigger for higher metazoan evolution (Runnegar 1991), repeated environmental stress over millions of years caused by fluctuating oxygen and nutrient levels (Brasier, this volume) may have had a greater effect on the pace and nature of early metazoan evolution. Bearing such environmental instability in mind, it is certainly worth considering that the early adoption of a biphasic lifestyle (Rieger, this volume) would have proved advantageous to the first true metazoans.

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