

New Perspectives on the Origin of Metazoan Complexity: An Introduction to the Symposium¹

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Impressive gains have been made in our understanding of metazoan complexity at the molecular level, especially those in the field of developmental evolution, but our understanding at other levels has lagged behind. This symposium attempts to bring diverse perspectives to bear on the causes and mechanisms of the explosive growth in metazoan complexity in the late Precambrian and Lower Cambrian. A primary goal is to broaden the framework for study of animal origins by introducing topics that are often overlooked by comparative biologists. An additional goal is to bring together workers that hold very different views on the early evolution of metazoans. For example, paleontologists and neontologists vary widely in their interpretations of a remarkable assemblage of fossils, the so-called Ediacara biota that existed in the latest Neoproterozoic (600–543 Ma). This assemblage is widely regarded as belonging to a metazoan or premetazoan radiation by paleontologists and yet the construction of these organisms is rarely taken into consideration by neontologists. Very often metazoan ancestors are assumed to have been a simple larva or flatworm-like organism, such as the microscopic acoelomate considered to have been the bilaterian ancestor (see Rieger *et al.*, 1991) in spite of the fact that many Ediacarans are large frond- or slug-like organisms, and highly modular.

The theory that early metazoans were simple and that complexity has been assembled incrementally is flawed for other reasons. Such a trajectory is not required by logic, because the first metazoans could have been complex, with complexity decreasing in some or most clades. In addition, a “complexity late” scenario provides no clues about the structure of the intermediate forms connecting the simple common ancestor with later more complex forms; indeed, little work of even a speculative nature has been done to address this issue (Conway Morris, 2000). The assumption is also challenged by the discovery that protostomes and deuterostomes share complex developmental programs, such as the Hox cluster regulating spatial patterning (Balavoine and Adoutte, 1998; de Rosa *et al.*, 1999; Holland, 1998), and that even cnidarians possess a complex set of Hox genes (Finnerty and Martindale, 1999; Gauchat *et al.*, 2000; Kourakis and Martindale, 2000). Although genetic complexity usually is thought to have preceded increases in body plan complexity,

the possibility that morphological complexity grew concomitantly with or even before (Budd, 1999) diversification of the genome cannot be dismissed. The Cambrian fossil record suggests that many metazoans were macroscopic and adapted for life in the macrobenthos (Gehling, 1991; Dzik, 1993; Fedonkin and Waggoner, 1997; Valentine *et al.*, 1999; Martin *et al.*, 2000). Metazoan characters are more typical of large organisms, and large organisms are likely to be more complex (Bonner, 1988), and the functions, at least of bilaterian characters, indicate that they arose in large organisms (Budd and Jensen, 2000; Dewel, 2000).

The relationship of the Ediacarans to other organisms has been a contentious issue. Hypotheses on what they are range from the interpretation that they fit into metazoan classes and phyla to the assertion that they are not metazoans but are protists or even lichens. Such discrepancy in their interpretation underscores the need to understand, for example, the factors affecting their preservation (Gehling *et al.*, 2000), before testable hypotheses can be formulated. Many questions are begging for an answer. What grades of cellular or tissue organization do they exhibit? Can we demonstrate higher metazoan taxa in the assemblage? What is the relationship between the trace and body fossil record? Are many Ediacarans truly modular? Do they exhibit serial and fractal patterns of growth and the same trends toward higher levels of integration found in colonial organisms? Difficulties in answering these questions have discouraged many biologists from incorporating data from the assemblage into their work. Conversely, while paleontologists have produced significant advances in our understanding of these organisms, this knowledge has not been fully evaluated in the context of recent progress in developmental and molecular biology. If basal metazoans were modular, then their history may have included integration of those modules into a new entity with a higher level of nested hierarchical complexity. Such an event should have left a record in the geno- or phenotypes of living metazoans. The goal of this symposium, therefore, is to expose biologists and paleontologists to both fields of study and by doing so identify promising areas for future research on the origin of metazoan complexity.

TRIBUTE TO REINHARD M. RIEGER

Reinhard M. Rieger has served as an inspiration for the theme of this symposium. As a neontologist he was one of first to recognize the significance of the fossil record and has taken a leadership role in challenging the idea that early metazoan history was hidden in a microscopic realm populated with tiny ancestors. As

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