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Interpreting the Earliest Metazoan Fossils: What Can We Learn?[1]

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SYNOPSIS. The Ediacaran fossils of the latest Precambrian have at one time or another been grouped with almost every extant kingdom, and also lumped into separate kingdom-level taxa. This has often been based on the facile use of a few characters, or on some sort of "overall similarity." This has not been a very fruitful approach; if anything, it has held back understanding of the Ediacaran organisms and of their significance for later history. While many of the simpler forms remain problematic, careful study of the more complex forms gives good reasons to place at least some of them with the Animalia. A complementary approach is to use sources of information such as the distribution of fossils across space, time, and paleoenvironments. The results may feed back into systematic work, allowing us to construct and test more robust hypotheses of these organisms' evolutionary relationships.

INTRODUCTION

In 1947, Australian geologist Reginald C. Sprigg published a paper titled "Early Cambrian (?) jellyfishes from the Flinders Ranges, South Australia," describing some unusual impressions of unmineralized organisms that he had found in the Ediacara Hills, 600 km north of Adelaide, Australia. Sprigg interpreted the discoidal fossils he found as jellyfish; they were later determined to be late Precambrian in age. Sprigg was not the first to describe members of this "Ediacara biota" (*e.g.*, Hill and Bonney, 1877; Gürich, 1930). However, although his work was viewed with skepticism at first (Sprigg, 1991), it sparked an interest in this biota which has continued to the present. Today, over one hundred genera have been described, from over twenty localities around the world. The biota is now known to have existed from 600 to 540 million years ago—a time almost as long as the entire Cenozoic—with a few survivors persisting into the Cambrian (Conway Morris, 1993; Narbonne, 1998). Notwithstanding a few problematic reports of pre-Ediacaran body fossils and trace fossils (*e.g.*, Sun, 1994; Breyer *et al.*, 1995) the Ediacaran fossils—or at least some of them—remain the oldest fossils widely thought to represent animals.

As an increasing number of these organisms were described, from Ediacara as well as from sites in Namibia, Russia, England, Newfoundland, and elsewhere, later workers placed most of them in the Cnidaria, with a few annelids and possible arthropod relatives. This interpretation is still popular (*e.g.*, Glaessner, 1984; Jenkins, 1992). Late Precambrian trace fossils provide strong evidence that metazoans of some sort were present at the time. But a series of provocative papers by Adolf Seilacher (Seilacher, 1985, 1989, 1992) challenged this interpretation of the Ediacaran body fossils as early metazoans. Seilacher interpreted the Ediacaran organisms as hollow, fluid-filled, partitioned or "quilted" organisms, unrelated to metazoans or to anything else living. These papers opened floodgates of speculation on the affinities of the Ediacaran organisms. Various forms have been called algae (Bergström, 1991); fungi or lichens (Retallack, 1994); the outgroup to the Kingdom Animalia (Buss and Seilacher, 1994); single-celled protists (Zhuravlev, 1993); colonial protists (Duval and Margulis, 1995); or "metacellular" multicellular things (McMenamin, 1997).

This paper is not intended as a comprehensive review of the Ediacaran biota or of

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the current "state of the art" (for recent reviews see Fedonkin, 1994; Sun, 1994; Runnegar, 1995; Narbonne, 1998). The aim of this paper is not to solve the conundrum of "what are the Ediacaran organisms?" In fact, the question has no single correct answer. While several Ediacaran forms are turning out to be close to familiar metazoans, such as sponges (Gehling and Rigby, 1996) and arthropods (Jenkins, 1992; Waggoner, 1996), others are much less like any known metazoans (Gehling, 1991; Runnegar, 1995). Many are simply not well-known enough for informed judgment. Yet as strange and contentious as they are, the Ediacaran fossils must not be neglected; they give us a close look at the evolution of biological complexity, at both organismal and ecosystem levels, immediately before the pivotal evolutionary events of the Cambrian.

What I wish to do is to point to some promising ways in which these fossils may be interpreted. I believe that broad, speculative hypotheses on the affinity of the entire biota can be misleading and even counterproductive. I will argue that the most fruitful approach is a synthesis of comparative analyses of the fossils' structure with "non-comparative" methods.

DESCRIPTIVE AND COMPARATIVE METHODS

A great deal of descriptive work still needs to be done. Many Ediacaran forms have still not been described at all. I estimate that at least ten distinctive new morphospecies could be described from unfigured or sparsely figured material from the White Sea coast of Russia alone. There are entire biotas that have not received adequate attention, in particular the unusual biota from Mistaken Point, Newfoundland. The Mistaken Point biota was first brought to the attention of scientists in 1969 (Misra, 1969). Nearly thirty years later, these unusual organisms have been figured many times (*e.g.*, Anderson and Conway Morris, 1982) and been the basis for important paleoecological and evolutionary studies (e.g., Seilacher, 1992; Jenkins, 1992; Bendick, 1994)—but still have not been formally described.

Other Ediacaran fossil forms are known only from one or a few specimens. New specimens of these forms may force radical alteration of taxon reconstructions. The fossil *Kimberella quadrata* was described from four specimens from Australia, first as a jellyfish, later more specifically as a cubozoan (box jelly). But in 1994, abundant fossils of *Kimberella* were found at a new locality on the White Sea in Russia, covering a wide range of sizes and preservational variants. Mikhail A. Fedonkin and I are redescribing *Kimberella* based on these new fossils, and have revised the reconstruction accordingly (Fedonkin and Waggoner, 1997). *Kimberella* had no tentacles, no tetraradiate symmetry, and no bell. It was bilaterally symmetrical with seriated body architecture, and bore a highly compaction-resistant structure that we interpret as a stiff but unmineralized shell. *Kimberella* is therefore a bilaterian, more complex than a platyhelminth, and more like a mollusk than anything else living. Not only does our reinterpretation have implications for metazoan evolution, it also alters our concepts of late Proterozoic ecology. *Kimberella* was formerly considered one of the few definite predators in the ecosystem, as living cubozoans are (Jenkins, 1992). Now, *Kimberella* may be a benthic deposit feeder or a microbial mat feeder (Seilacher, 1997). Multiply the impact of the new interpretation of *Kimberella* by the number of poorly known or *incertae sedis* Ediacaran forms—more than half of the total number described (Runnegar, 1992)—and the potential for major re-

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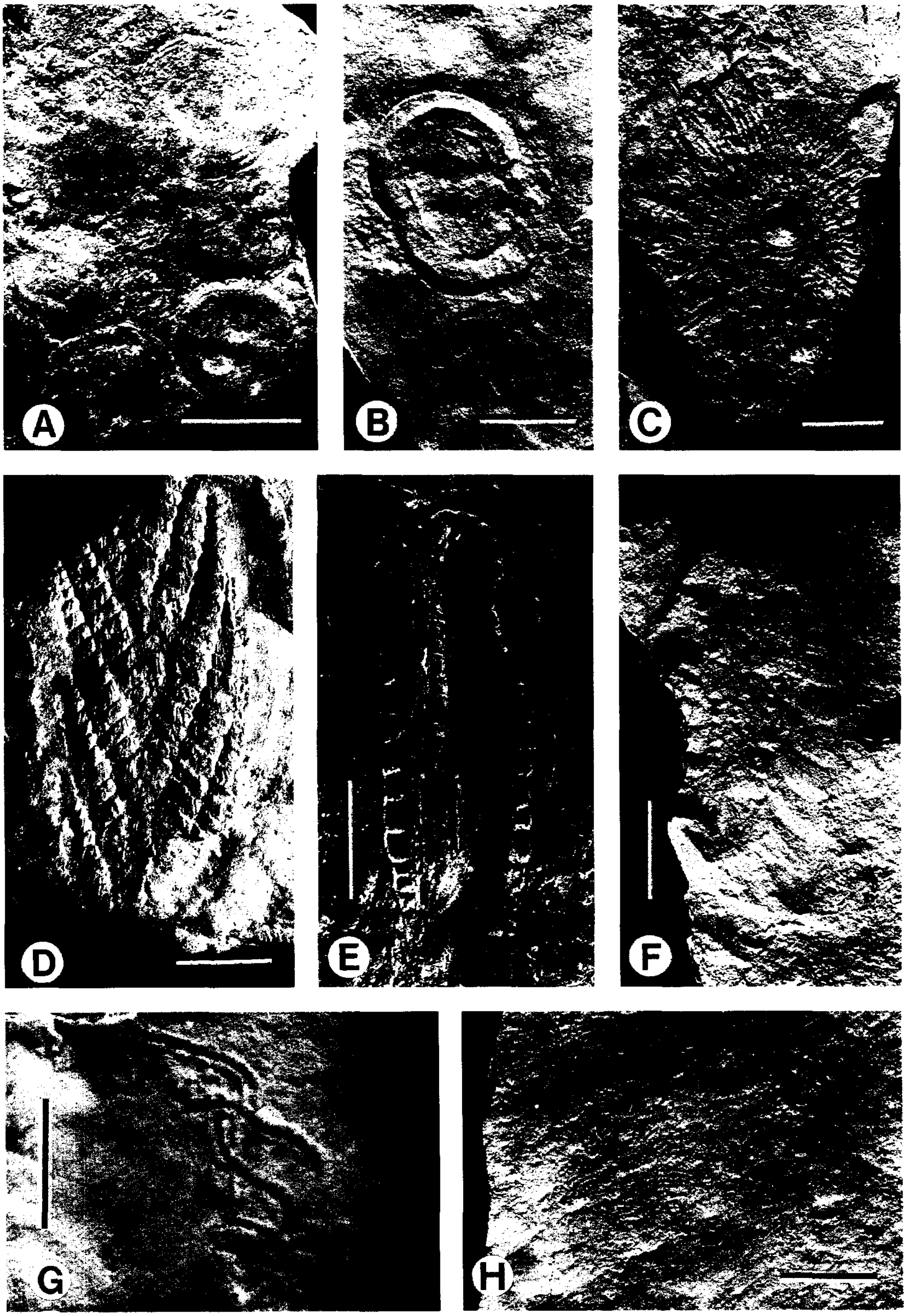
FIG. 1. Representative members of the Ediacara biota; all from the Winter Coast region of the White Sea, Russia. Scale bars all equal 2 cm. (A) *Nemiana*, morphologically one of the simplest "medusoid" forms. (B) Cast of *Nimbia*, another simple "medusoid" preserved in the act of dividing. (C) *Eoporpita*, a putative tentaculate form (counterpart). (D) Partial specimen of *Charnia*, a frond-like form. (E) *Kimberella*, a mollusc-like bilaterian. (F) Cast of *Bomakellia*, an arthropod-like or anomalocarid-like form. (G) *Aulichnites*, a typical trace fossil in positive epirelief (coated with NH_4Cl). (H) *Yelovichnus*, a tightly meandering trace fossil.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vision of Ediacaran paleobiology becomes obvious.

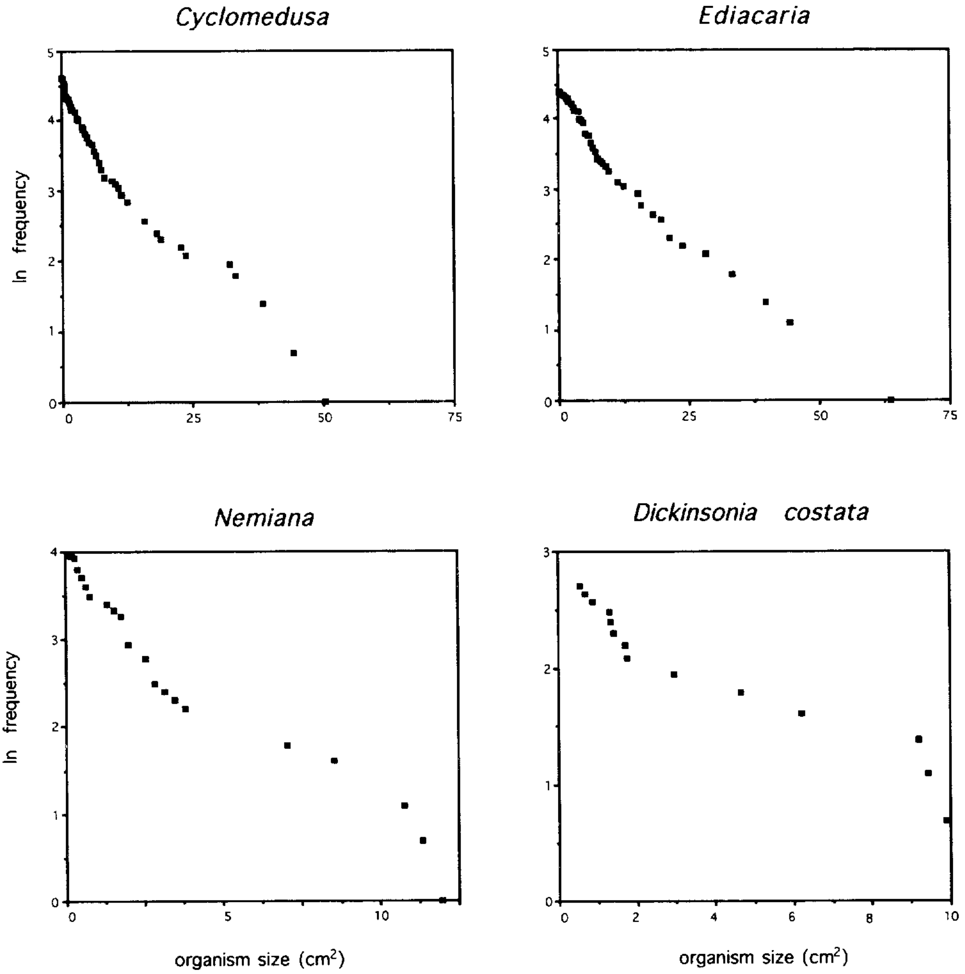
A major limitation on descriptive studies, however, is taphonomy. Most Ediacaran fossils are found in event beds—sedimentary rock layers laid down rapidly (Narbonne, 1998). However, the type of sediments and circumstances of burial vary among and even within localities. These varying modes of burial and diagenesis can affect the morphology of the fossils, obscure key morphological features, and create artifacts that may be mistaken for morphological features. Part of the resolution of this problem turns back to careful descriptive and comparative work: recognizing the range of preservational variation in a taxon, looking for unusually preserved specimens that show features not seen elsewhere, and examining specimens from as many localities and styles of preservation as possible. This can turn an apparent weakness into a strength: uniquely preserved specimens, and specimens from a range of taphonomic environments, may show important features not usually seen. But comparative studies should be complemented by the construction and testing of taphonomic models: what were the important environmental conditions at the time and place of fossilization, as inferred from the geological setting? What effects would they have on organisms in order to produce the observed fossils? Recent models are now focusing on the effects of sedimentary microbial mats on Ediacaran fossil preservation; these mats stabilized the sediment and created "death masks" of the fossils, a process not normally seen in modern environments (*e.g.*, Gehling, 1991, 1996; Narbonne, 1998). Such models can be tested by taphonomic experiments on extant organisms. Relatively few such experiments have been carried out that specifically relate to the Ediacara fossils (Norris, 1989; Bruton, 1991) but much work is being done on general problems of soft-bodied fossil preservation and on microbial mat sedimentology and geochemistry. This is an exciting area for future research.

Even when fossils are well-preserved—that is, when the morphology of the living organism can be reconstructed in detail with some certainty—their morphology may be so simple that there is little to be learned from their morphology. Many of the "medusoid" forms fall into this category (*e.g.*, Fig. 1a, b). However, when a fossil is both well-preserved and sufficiently complex, then its evolutionary relationships can be worked out—not based on its "overall similarity" with something, which has proven to be a rather slippery concept, but based on identifiable discrete characters. In a few cases, cladistic methods can then be profitably used (Waggoner, 1996). Cladistics are not a panacea; they cannot make poor material better or bad interpretations good. However, when the fossils are sufficiently well known, plausible hypotheses of homology become possible, and the characters supporting each node may be evaluated.

Even when explicit cladistic methods are not used, character-based hypotheses of evolutionary relationships have a great deal of predictive value. For example, did *Kimberella* have jaws and/or a radula-like structure? Its hypothesized close relatives did and do—but none has yet been found in association with the fossils. However, small, sclerotized toothed fossils (*Redkinia*) have been found in Vendian rocks; while they have usually been compared to annelid jaws (Sokolov, 1985), some of them resemble rachiglossate radular teeth, or possibly the jaws of the Cambrian fossil *Wiwaxia* (*e.g.*, Schopf, 1992, pl. 52 figs. B–D). Furthermore, Ediacaran trace fossils have been found in southern Australia that are attributed to a radula-like toothed structure scraping over a microbial mat (Gehling, 1996). Seilacher (1997) has explicitly associated these traces with *Kimberella*. Although at this time I am less confident of the association, I predict that *Redkinia* or similar fossils, or these fossil scratches, will be found in close association with *Kimberella*.

NON-COMPARATIVE METHODS

For all the value of descriptive and comparative studies, they only provide a part of the story. The simpler Ediacaran forms lack distinctive and informative characters; something like *Nemiana* (Fig. 1a), which is



Cyclomedusa

Ediacaria

Nemiana

Dickinsonia costata

FIG. 2. Four survivorship curves for samples of Ediacaran fossils from the White Sea, north Russia. The first three, for "medusoid" taxa, are near-linear; the fourth, for the possible bilaterian *Dickinsonia*, may imply a more complex life history. The y-axis represents the natural logarithm of the number of organisms in the population larger than the size given on the x-axis (in cm^2).

basically a featureless round sac, resembles extant organisms in several kingdoms. Attempts to compare such fossils with known organisms will run afoul of convergent evolution. Yet at many sites, the simplest forms are the most common and typical. In a sample from the lowermost member of the Winter Coast section on the White Sea, for instance, half of all species and 85% of all specimens are simple "medusoids" (Waggoner, personal observations). Furthermore, even when we know something of the affinities of complex forms, it is desirable to know something of the paleoenvironment in which they lived. A second, complementary approach is to analyze information that is not based on comparisons of the fossils with each other or with any extant organisms. Sources of information such as size distribution, species diversity, and biogeographic distribution are largely independent of taxonomic judgments. All that is required is the ability to identify different taxa consistently and reproducibly—although the confounding variables of taphonomy make this a non-trivial problem, as has been mentioned.

Stanley (1973) has emphasized the sudden origin of predation during the Cambrian (see also McMenamin 1986). It has been well established that predation—at least on and by macroorganisms—was rare, though not completely absent, in Ediacaran ecosystems. Few Ediacaran body fossils anywhere show scars or traces of predation, few bore appendages that could have been used in predatory attack, and no trace fossils can be attributed to predatory activity. The only direct evidence of predation in the Vendian is the boreholes found in the calcareous fossil *Cloudina* (Bengtson and Zhao, 1992). Further support for the general scarcity of predation in Ediacaran biotas comes from survivorship curves for Ediacaran fossil populations from Newfoundland and from Russia, most of which—though not all—are linear (Fig. 2; Bendick, 1994). This implies age-independent mortality over the age range represented in the fossil record, and is consistent with a general lack of predation (Bendick, 1994). In contrast, predation is well-documented in the Cambrian on mineralized organisms (*e.g.*, Conway Morris and Jenkins, 1985; Babcock, 1993; Conway Morris and Bengtson, 1994). Predation by and on non-mineralized organisms is also recognized in the Cambrian, both from body and trace fossils (Conway Morris and Robinson, 1988; Jensen, 1990; Briggs *et al.*, 1994).

I would add that predation is not the only interaction that increased in the Cambrian. Less commonly noted, but potentially quite significant, is the fact that epibiosis is equally rare. Aside from transiently attached individuals during budding or fission, Ediacaran organisms did not live on top of each other. The only exception, again, is the mineralized fossil *Cloudina*, specimens of which have been found growing on each other (Germs, 1972). Again, the contrast with Phanerozoic faunas is striking; in the Cambrian, both mineralized organisms (Debrenne and Zhuravlev, 1992) and non-mineralized organisms (Briggs *et al.*, 1994) grew on top of each other. Furthermore, an analysis of co-association between different Ediacaran taxa on the same slabs, based on material from the White Sea coast of Russia, has failed to show evidence for positive or negative interactions among the taxa represented. The presence of one taxon apparently neither encouraged nor discouraged the presence of any other (Waggoner, personal observations). This may not be true for all Ediacara-type biotas; spatial analysis of the Newfoundland biota shows some positive and negative interactions between different forms. However, these interactions are still less frequent than in extant ecosystems (Bendick, 1994). Finally, the metazoan trace fossil record shows marked increases in overall complexity, diversity of ichnogenera, and depth of sediment penetration by putative metazoans around the Proterozoic-Cambrian boundary (Crimes, 1992).

In summary, the "Cambrian explosion" was not only a major evolutionary radiation of taxa; it encompassed the widespread adoption of ecological strategies and modes of interaction that were rare—though not entirely absent—in Ediacaran biotas. Furthermore, the "Cambrian explosion" may not have encompassed the origin of the animal phyla (Wray *et al.*, 1996; but see Conway Morris, 1997), but it must have encompassed the appearance of evolutionary innovations that made these new strategies possible. Widespread biomineralization was one of these innovations, but there were others.

CONCLUSIONS

What can we learn from the Ediacaran organisms? Probably not as much as we would like, yet more than we might expect. If careful attention is paid to taphonomic effects, comparative morphological study can help us create character-based hypotheses of the relationships of at least some of the Ediacaran organisms. Even when a conclusive affinity cannot be demonstrated, competing hypotheses can often be narrowed down considerably. Analyses like these, however, need to be combined with taxonomy-independent studies in order to devise the most complete, most predictive models possible of metazoan evolution.

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