



GR Focus Review

The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat?

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ABSTRACT

The Ediacaran–Cambrian transition signals a drastic change in both diversity and ecosystem construction. The Ediacara biota (consisting of various metazoan stem lineages in addition to extinct eukaryotic clades) disappears, and is replaced by more familiar Cambrian and Paleozoic metazoan groups. Although metazoans are present in the Ediacaran, their ecological contribution is dwarfed by Ediacaran-type clades of uncertain phylogenetic affinities, while Ediacaran-type morphologies are virtually non-existent in younger assemblages. Three alternative hypotheses have been advanced to explain this dramatic change at, or near, the Ediacaran–Cambrian boundary: 1) *mass extinction* of most Ediacaran forms; 2) *biotic replacement*, with early Cambrian organisms eliminating Ediacaran forms; and 3) a *Cheshire Cat* model, with Ediacaran forms gradually disappearing from the fossil record (but not necessarily going extinct) as a result of the elimination of unique preservational settings, primarily microbial matgrounds, that dominated the Ediacaran. To evaluate these proposed explanations for the biotic changes observed at the Ediacaran–Cambrian transition, environmental drivers leading to global mass extinction are compared to biological factors such as predation and ecosystem engineering. We explore temporal and biogeographic distributions of Ediacaran taxa combined with evaluations of functional guild ranges throughout the Ediacaran. The paucity of temporally-resolved localities with diverse Ediacaran assemblages, combined with difficulties associated with differences in taphonomic regimes before, during, and after the transition hinders this evaluation. Nonetheless, the demonstration of geographic and niche range changes offers a novel means of assessing the downfall of Ediacara-type taxa at the hands of emerging metazoans, which we hypothesize to be most likely due to the indirect ecological impact metazoans had upon the Ediacarans. Ultimately, the combination of studies on ecosystem construction, biostratigraphy, and biogeography showcases the magnitude of the transition at the Ediacaran–Cambrian boundary.

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1. Introduction

The Cambrian explosion of metazoans represents the greatest and most rapid expansion in higher-order animal disparity, with crown members of nearly every animal phylum originating within 10–20 million years (Knoll and Carroll, 1999; Erwin et al., 2011). This biological diversification has been extensively studied (see reviews by Marshall, 2006; Erwin et al., 2011; Erwin and Valentine, 2012). However, the burst of crown group metazoans near the base of the Cambrian was preceded by a less widely appreciated suite of large complex multicellular organisms of considerable diversity and morphological disparity: the Ediacara biota (Fig. 1; Narbonne, 2005; Fedonkin et al., 2007a; Xiao and Laflamme, 2009).

The Ediacara biota are globally-distributed and temporally restricted (579–542 Ma; Narbonne et al., 2012) macroscopic organisms traditionally regarded as closely related to metazoans, either as stem/crown group animals (e.g. Gehling, 1991), or more controversially, as belonging to the extinct clade Vendobionta (previously Vendozoa; Buss and Seilacher, 1994). The variability in overall shape, growth polarity, body symmetry, and branching modularity found across the Ediacara biota is such that these organisms most likely represent an assortment of clades, including extinct lineages as well as potentially stem- and even crown-group animals, with distinct evolutionary histories, all sharing a common mode of preservation (Narbonne, 2005; Xiao and Laflamme, 2009; Erwin et al., 2011). In this review, we restrict the term Ediacara biota to refer to lineages of large, soft-bodied organisms preserved as casts and molds in sediments of Ediacaran (and perhaps Cambrian) age. This excludes metazoan trace fossils (e.g. Jensen et al., 2005) and the earliest skeletal fossils of late Ediacaran age.

The claim that the disappearance of the Ediacara biota represents a global mass extinction event provides a series of testable hypotheses. Sepkoski (1986) argued that a mass extinction required a “substantial increase in the amount of extinction (i.e., lineage termination) suffered by more than one geographically widespread higher taxon during a relatively short interval of geologic time, resulting in an at least temporary decline in their standing diversity”. As such, this review will evaluate the higher-order diversity (i.e. disparity) during the Ediacaran by investigating the biostratigraphic and biogeographic distributions of the newly defined Ediacaran clades. As Ediacaran fossil localities are exceptional in preserving soft-bodied organisms, understanding the nuances in Ediacaran preservation is necessary to disentangle taphonomic biases associated with proposed temporal and spatial trends in Ediacaran fossil distributions, and in evaluating the hypothesis suggesting that the disappearance of the Ediacara biota is largely a taphonomic artifact. Furthermore, as mass extinctions drastically affect the ecological structure of communities, Ediacaran paleoecology and niche subdivision will be investigated. With this conceptual framework in place, this review will evaluate evidence for three different primary causes of the Ediacaran–Cambrian transition: a *mass extinction model*, which posits a rapid, environmentally-driven event, analogous to Phanerozoic mass extinctions; a *biotic replacement model*, in which the expansion of new clades in the Cambrian ecologically displaced Ediacaran clades; and a *Cheshire Cat model* focusing on taphonomy, in which the Ediacara biota effectively vanish from the fossil record due to the disappearance of the unique circumstances allowing for their preservation (closing of a taphonomic window). Each of these models allows for basic predictions that can be tested against existing data.

Furthermore, this predictive approach will highlight areas where data are deficient and therefore provide fruitful avenues of future research.

2. Ediacaran classification: stems, crowns, and extinct clades

Although pioneering studies by Billings (1872), Gürich (1929, 1930, 1933), and most famously Sprigg (1947, 1949) were the first to describe what have come to be known as Ediacara biota, these efforts were mostly overlooked until Ford (1958) and Glaessner and Daily (1959) demonstrated a pre-Cambrian age for these fossils (as reviewed in Fedonkin et al., 2007a). Previous attempts at classification (see review in Fedonkin et al., 2007a) focused on their gross morphology, assigning forms to crown animal clades (Glaessner, 1979; Gehling, 1991) including (but by no means limited to) cnidarians (Glaessner and Wade, 1966), sponges (Gehling and Rigby, 1996; Sperling et al., 2011), annelids (Wade, 1972), arthropods (Lin et al., 2006), and echinoderms (Gehling, 1987). Others have allied at least some of these fossils with algae (Ford, 1958), fungi (Peterson et al., 2003) and even lichen (Retallack, 1994, 2007).

A major paradigm shift occurred when Seilacher (1984, 1985, 1989, 1992) proposed, based primarily on similarities in morphological construction and mode of preservation, that the Ediacara biota were independent of Metazoa and constituted an extinct, higher-order clade of giant single-celled organisms he termed Vendozoa (Seilacher, 1989; amended to Vendobionta Seilacher, 1992; Buss and Seilacher, 1994). According to Seilacher (1984, 1992), the Vendobionta was a diverse and highly successful group of macroscopic organisms who actively competed with metazoans, and he hypothesized that they were eventually driven to extinction by macroscopic predation (Seilacher et al., 2003). The Vendobionta hypothesis highlights the “fractal quilting” (Fig. 1.1–3) and “serial quilting” (Fig. 1.6–7) common to many Ediacaran fossils but seemingly absent from known metazoan body plans. Seilacher (1992) also underscored the preservational style in which coarse sands were able to cast the external morphology of non-skeletonized Ediacarans. Later refinements (Seilacher et al., 2003; Seilacher, 2007) of the Vendobionta focused on the fractally- and serially-quilted forms, citing their modular construction (and specifically the ensuing compartmentalization) to argue for a unicellular mode of life similar to xenophyophores, a group of giant single-celled protists that inhabit the deepest regions of the ocean. Several difficulties arise with a unicellular interpretation though, most notably the ability of Ediacaran fronds to construct meter-long complex morphologies complete with varying integument strength and rigidity (Laflamme et al., 2004; Laflamme and Narbonne, 2008a; Laflamme et al., 2012).

Despite their fundamental differences, the Metazoa vs. Vendobionta hypotheses both interpret the majority of the Ediacara biota as representing a single clade. Recently, Xiao and Laflamme (2009) and Erwin et al. (2011) have instead proposed that members of the Ediacara fauna represent several independent clades, including extinct lineages as well as stem/crown group animals. This marks an important shift from considering all Ediacara biota as a unified group, as these studies subdivide fossils into subsets that can be studied independently. Erwin et al. (2011) emphasized branching and segmented architecture, body symmetry, associated trace fossils, and growth parameters, while limiting direct comparisons with modern taxa unless they share unquestionable synapomorphies. Whenever possible, unique synapomorphies were used to recognize clades within the Ediacara biota; however the phylogenetic relationships amongst these clades is difficult to pinpoint, especially as most do not share characters with any extant eukaryotes.

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