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The discs of Avalon: Relating discoid fossils to frondose organisms in the Ediacaran of Newfoundland, Canada

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ABSTRACT

The oldest members of the Ediacara biota include discoid and frondose forms. The fronds have been well described, but little has been done to quantify the relationship between the discoid fossils and the discoid holdfasts of fronds. Fossil surfaces from the middle Ediacaran of southeastern Newfoundland preserve fronds directly attached to their discoid holdfasts, along with numerous specimens of the isolated discoid fossils *Aspidella* and *Hiemalora* of less certain affinities. However, most specimens of *Aspidella* in Newfoundland are known from Fermeuse-style preservation of the base of discs, whereas most Mistaken Point fronds are known from Conception-style preservation of the tops of discs, hindering direct comparison of these fossils. The Discovery Surface on Bonavista Peninsula preserves both basal and top views of *Aspidella*-type discs on the same fossil surface, and thus serves as a morphological link between these preservational modes and permits reconstruction of these circular holdfasts in three-dimensions. We find a significant positive correlation between disc size and frond size within each frondose species, which is consistent with the purported function as holdfasts, tethering the frondose organisms to the seafloor. This supports the notion that discoid fossils relatable to *Aspidella* and its junior synonyms, and to *Hiemalora*, are the holdfasts of frondose forms whose petalodia escaped preservation, and not whole organisms or microbial colonies as has been suggested by some authors.

1. Introduction

Much work accomplished over the past several decades has helped to decipher many traits of the previously enigmatic organisms and communities of the Ediacaran Period. The Ediacara biota arose in the mid-Ediacaran Period, starting around 580 Ma, and disappeared at the Ediacaran–Cambrian boundary at 541 Ma (Narbonne et al., 2012a). With a few prominent exceptions (e.g. Retallack, 1994, 2013), most workers regard the Ediacara biota as representing a mix of stem-group metazoans and/or stem-groups of modern metazoan phyla (Narbonne, 2005; Xiao and Laflamme, 2009; Knoll, 2011; Laflamme et al., 2013). The earliest assemblage of what is traditionally regarded as the Ediacara biota, the Avalon assemblage (580–560 Ma), is known from exclusively deep-water deposits in southeastern Newfoundland, Charnwood Forest in England, and the Mackenzie Mountains of NW Canada (Ford, 1958; Myrow, 1995; Narbonne and Gehling, 2003; Wood et al., 2003; Waggoner, 2003; Narbonne, 2005; Ichaso et al., 2007; Antcliffe and Brasier, 2008; Hofmann et al., 2008; Narbonne et al., 2009, 2014; Xiao and Laflamme, 2009; Wilby et al., 2011; Mason et al., 2013). It is dominated by rangeomorphs (macroscopic forms possessing several orders of repeating, self-similar, "fractal" modules; Jenkins, 1985; Seilacher, 1992; Narbonne, 2004; Brasier and Antcliffe, 2009; Brasier et al., 2012; Narbonne et al., 2009, 2014) along with other frondose and discoid forms, displaying early examples of ecological complexity (Clapham and Narbonne, 2002; Clapham et al., 2003; Wilby et al., 2011; Laflamme et al., 2012; Liu et al., 2012; Darroch et al., 2013; Ghisalberti et al., 2014); bilaterian body fossils and trace fossils are absent or rare (Waggoner, 2003; Narbonne, 2005; Xiao and Laflamme, 2009; see Liu et al., 2010, 2014 for an example of possible cnidarian trails from the Avalon assemblage). A few members of the Avalon assemblage also occur in the younger White Sea assemblage (560–550 Ma) and Nama assemblage (550–541 Ma), which are recorded in both deep and shallow-water settings (Grazhdankin, 2004; Narbonne, 2005; Xiao and Laflamme, 2009; Gehling and Droser, 2013; Chen et al., 2014), but are not ecologically dominant.

Ediacaran discs and fronds were discovered and described separately during the first 80 years of description of what is now called the Ediacara biota, and this greatly shaped interpretations of their affinities. The first recognized body fossils named from conclusively Precambrian strata in the fossil record were discoid forms from St. John's, Newfoundland (Billings, 1872; see update and review in Gehling et al., 2000). This fossil, *Aspidella terranovica* Billings, 1872, was originally regarded as an animal, but was quickly reinterpreted by other workers as an inorganic sedimentary structure (see review in Hofmann, 1971), as it was the paradigm of the time that macroscopic body fossils did not exist below the Cambrian (Gehling et al., 2000). Sprigg (1947, 1949), Glaessner and Wade (1966), Wade (1972), and other workers in the

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Ediacara Hills of Australia, along with Fedonkin (1978, 1980) and other workers in the East European Platform, subsequently described abundant discoid forms such as *Ediacaria* Sprigg, 1947, *Cyclomedusa* Sprigg, 1947, *Hiemalora* Fedonkin 1982, and *Eoporpita* Wade, 1972. Most of these discoid fossils were originally interpreted as the remains of pelagic medusoid cnidarians. Seilacher (1984) refuted this, pointing out morphologic and taphonomic features of these discs that were inconsistent with a pelagic organism and strongly implied that most or all of these discs were attached to the sea bottom during life, a view that has found widespread support. Three interpretations have been published that attempt to relate Ediacaran discs to benthic organisms: Jenkins (1992) regarded these isolated discoid impressions as the bases or tops of fossil polyps; Gehling et al. (2000) regarded isolated Ediacaran discs such as *Aspidella* as holdfasts for which the overlying frond was not preserved; and Grazhdankin and Gerdes (2007) regarded many of them as microbial colonies. Some workers have suggested different origins for different discoid structures; for example, Grazhdankin (2014) regarded unornamented discoid taxa as (such as *Cyclomedusa*) as microbial in origin but ornamented discoid taxa with radiating extensions (such as *Hiemalora* and *Eoporpita*) as the bases of frondose taxa. Interpretation of isolated Ediacaran discs as frond holdfasts has received the greatest support (Mapstone and McIlroy, 2006; MacGabhann, 2007; Serezhnikova, 2007, 2013; Hofmann et al., 2008; Hofmann and Mountjoy, 2010; Tarhan et al., 2010, 2015; Laflamme et al., 2011; Narbonne et al., 2014) However, with the exception of Tarhan et al. (2015) from the Ediacaran of Australia, few comparisons between isolated Ediacaran discs and those preserved at the bases of fronds have been carried out to test this relationship or to determine whether any specific discoid form-taxa can be consistently related to specific frondose form-taxa.

The present study compares the morphology and biometrics of isolated discs with those of attachment discs of fronds in the same succession. The Ediacaran of eastern Newfoundland represents a nearly ideal location for this study. Ediacara-type fossils occur abundantly on hundreds of bedding surfaces on the Avalon and Bonavista peninsulas (Fig. 1). Fossils occur through more than 2 km of stratigraphy encompassing portions of the Conception and St. John's groups (Fig. 2). Conception-style preservation throughout the Conception Group has preserved both complete fronds and isolated discs beneath beds of volcanic ash. In contrast, Fermeuse-style preservation in the St. John's Group preserved mainly isolated discs beneath sandy event beds (Narbonne, 2005), providing two contrasting preservational styles for comparison. The systematic paleontology of the 11 species of fronds (Narbonne and Gehling, 2003; Laflamme et al., 2004, 2007, 2012; Antcliffe and Brasier, 2008; Bamforth and Narbonne, 2009; Brasier and Antcliffe, 2009; Narbonne et al., 2009; Brasier et al., 2012) and the five form-genera of discs (Gehling et al., 2000; Hofmann et al., 2008; Liu et al., 2011) reported from Avalonian Newfoundland is well established. This paper will investigate the relationship between these discoid and frondose taxa.

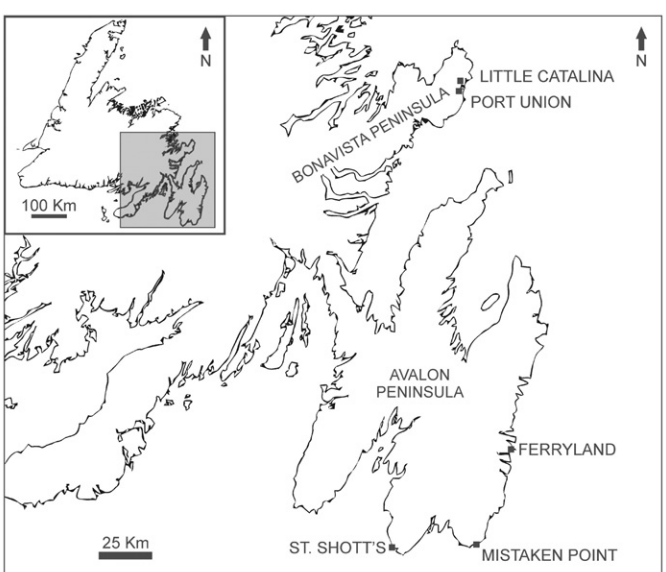

Fig. 1. Localities in southeastern Newfoundland observed in this study.

2. Geological setting

Fossiliferous outcrops of this study occur in the Avalon and Bonavista peninsulas of southeastern Newfoundland (Fig. 1). Fossils of southeastern Newfoundland are known from the Drook, Briscal, and Mistaken Point formations of the Conception Group, and the Trepassey and Fermeuse formations of the St. John's Group (Fig. 2), with the Drook through Mistaken Point formations typically showing discs directly attached to fronds. Discoid fossils include all morphotypes of *Aspidella* (Gehling et al., 2000) and *Hiemalora* (Hofmann et al., 2008). Several frondose taxa are known, including *Beothukis* Brasier and Antcliffe, 2009, *Charnia* Ford 1958, *Charniodiscus* Ford 1958, *Culmofrons* Laflamme et al., 2012, *Primocandelabrum* Hofmann et al., 2008, and *Trepassia* Narbonne et al., 2009 (Anderson and Misra, 1968; Misra, 1971; Seilacher, 1992, 1999; Narbonne and Gehling, 2003; Laflamme et al., 2004, 2007, 2011, 2012; Hofmann et al., 2008; Laflamme and Narbonne, 2008; Brasier and Antcliffe, 2009; Narbonne et al., 2009) which form the basis of this study. *Beothukis*, *Charnia*, *Culmofrons*, and *Trepassia* are included in the “charnid” clade of the Rangeomorpha (Laflamme and Narbonne, 2008a,b; Narbonne et al., 2009), *Charniodiscus* is a member of the Arboreomorpha (Xiao and Laflamme, 2009; Erwin et al., 2011; Laflamme et al., 2013), and *Primocandelabrum* cannot yet be related to any major Ediacaran clade (Hofmann et al., 2008; Narbonne et al., 2014).

The major stratigraphic units of the upper Neoproterozoic of southeastern Newfoundland are shown in Fig. 2. Above the igneous rocks of the Harbour Main Group, the overall trend is shallowing, from a deep basin-floor setting in the lower Conception Group to a shallow-marine to alluvial fan setting of the Signal Hill Group. In contrast to the paleosol interpretation put forth for these strata by Retallack (2014), the abundance of turbiditic features and the complete absence of wave-generated structures or evidence of emergence through thousands of meters of stratigraphy imply that the Conception and lower St. John's groups were deposited significantly below both storm wave base and the photic zone. The abundance of volcanic and volcaniclastic layers in the Conception Group of the Avalon Peninsula, and in the Conception and lower St. John's groups of the Bonavista Peninsula, is responsible for exceptional preservation of the fossils, and permit precise radiometric dating (Benus, 1988; Narbonne et al., 2012a). The Conception Group was deposited in a deep-water, active margin setting below the photic zone, progressing from a basin floor setting in the Mall Bay, Gaskiers, Drook, and Briscal formations to a deep-water slope setting in the Mistaken Point Formation. The overlying St. John's Group displays an overall shallowing-upward sequence, from a progradational slope setting in the Trepassey and Fermeuse formations to a prograding delta/terrestrial setting in the Renews Head Formation. The Signal Hill Group continues this shallowing trend, passing upward from fluviodeltaic to terrestrial deposits (Gardiner and Hiscott, 1988; Conway Morris, 1989; Myrow, 1995; Wood et al., 2003; Ichaso et al., 2007; Hofmann et al., 2008; Mason et al., 2013).

3. Terminology

No consistent terminology exists to describe the anatomical/morphological features common to discoid fossils and holdfasts. In a manner analogous to the work of Laflamme and Narbonne (2008) on frondose fossils, we present terminology to be used to describe the