

# Discoidal fossils of the Ediacaran biota: a review of current understanding

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**Abstract:** Discoidal fossils, despite being the oldest, youngest, and most common elements of the Ediacaran biota, have not received their fair share of attention. Taxonomy of discoidal fossils is currently dubious, and some forms have not been properly re-examined since the initial incorrect descriptions as medusae. Attachment discs of benthic stalked forms, which adhere to microbial mats at the sediment–water interface, are unequivocally present without stalks or other upper parts in most discoidal Ediacaran assemblages. However, many discoidal assemblages are likely to have represented a heterogeneous mixture of benthic discoidal organisms, including bacterial colonies, fungi, actinian-grade cnidarians, and perhaps poriferans. Such organisms probably account for the vast majority of fossils in the Fermeuse Formation of Newfoundland and similar assemblages from Norway, England, and Wales. Discs in the underlying complex Mistaken Point assemblages, however, likely mostly represent holdfasts. Other complex assemblages, such as those of South Australia and the White Sea of Russia, unequivocally contain more than one biological construction responsible for the discoidal structures, but holdfasts likely represent a significant proportion. The disc-dominated Fermeuse assemblages and the nearby rangeomorph-dominated Mistaken Point assemblages are unlikely to merely represent different taphonomic windows on identical communities, as previously suggested, but rather reflect environmental control on both biotic composition and taphonomy.

Discoidal fossils were the first described elements of the Ediacaran biota (Billings 1872) and are by far the most abundant component. In terms of age, they are the oldest (Hofmann *et al.* 1990) and, indeed, the youngest (Crimes & McIlroy 1999; Hagadorn *et al.* 2000) Ediacaran-type fossils known. For this reason they represent, potentially, the most important constituent of the biota; however, knowledge of both disc palaeoecology and affinities does not reflect this. In particular, current understanding of disc taxonomy is rather convoluted. Indeed, one of the legacies of initial descriptions of Ediacaran discs as medusae has been a plethora of generic and specific names in the literature. Many of these were described or are known only from single (often unrepresentative, damaged or incomplete) specimens, with genera and species often distinguished by only minor differences, which may, in fact, be taphonomic artefacts or morphologically insignificant from a taxonomic perspective. It did not help that most original descriptions did not separate interpretation from observation, leaving them rather bloated with inappropriate and wildly incorrect interpretative terminology. The situation was perhaps best summarised by Runnegar and Fedonkin (1992), who noted, with reference to the genus *Ediacaria*, that ‘Many of the fossils that have been referred to *E. flindersi* do not resemble the holotype, and specimens identified as *E. flindersi* by different authors

may be totally dissimilar. This is a common situation in the literature and the result is a jumble of useless and misapplied names’ (Runnegar & Fedonkin 1992, p. 379).

In light of this, this contribution sets out to summarize our current knowledge of the Ediacaran discs, highlighting several major issues and inconsistencies, and outlining potential directions for future research.

## History of research

Serious study of Ediacaran discoidal fossils began after Sprigg (Sprigg 1947, 1948, 1949) described the first-found elements in the type area in South Australia as ‘jellyfish’, and Glaessner and Wade (Glaessner 1959, 1984; Glaessner & Wade 1966; Wade 1969, 1972) more or less followed this interpretation, considering them stranded pelagic medusae. Seilacher disagreed, describing the discs as a ‘heterogeneous group of trace fossils and the remains of unidentified benthic organisms’ (Seilacher 1984, p. 163), but description of discs as ‘medusae’ continued (e.g. Sun 1986a, b). In the meantime, others had suggested that at least some discs actually represented the basal parts of frond-like taxa (e.g. *Charniodiscus concentricus* Ford, 1958), and this has been borne out by later work (e.g. Jenkins & Gehling 1978; Laflamme *et al.* 2004).

**Table 1.** *Principal localities of discoid Ediacaran fossils*

| Location  |                                             | Palaeo-continent | References                                                                                                                                                                                                                                                          |
|-----------|---------------------------------------------|------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Algeria   |                                             | Gondwana         | Bertrand-Sarfati <i>et al.</i> 1995                                                                                                                                                                                                                                 |
| Australia | <i>Stirling Range</i>                       | Australia        | Cruse & Harris 1994; Rasmussen <i>et al.</i> 2002                                                                                                                                                                                                                   |
|           | <i>Adelaide Geosyncline</i>                 | Australia        | Sprigg 1947, 1948, 1949; Southcott 1958; Glaessner 1959, 1984; Glaessner & Wade 1966; Wade 1972; Jenkins & Gehling 1978; Sun 1986 <i>a, b</i> ; Gehling 1987, 1988, 1991; Jenkins 1992; Gehling & Rigby 1996; Gehling <i>et al.</i> 2005; Droser <i>et al.</i> 2006 |
| Canada    | <i>C. Australia</i>                         | Australia        | Wade 1969; Mapstone & McIlroy 2005                                                                                                                                                                                                                                  |
|           | <i>Northwestern &amp; Yukon Territories</i> | Laurentia        | Hofmann 1981; Hofmann <i>et al.</i> 1983, 1990; Narbonne & Hofmann 1987; Narbonne & Aitken 1990; Narbonne 1994                                                                                                                                                      |
|           | <i>British Columbia</i>                     | Laurentia        | Hofmann <i>et al.</i> 1985; Hofmann <i>et al.</i> 1991; Ferguson & Simony 1991                                                                                                                                                                                      |
|           | <i>Newfoundland</i>                         | Avalonia         | Misra 1969; Gehling <i>et al.</i> 2000; Clapham <i>et al.</i> 2003; Laflamme <i>et al.</i> 2004, 2007; O'Brien & King 2004; Hofmann <i>et al.</i> 2005; Narbonne 2005                                                                                               |
| England   |                                             | Avalonia         | Ford 1958, 1963, 1999; Boynton & Ford 1995; McIlroy <i>et al.</i> 2005                                                                                                                                                                                              |
| India     |                                             | Gondwana         | De 2003; De 2006                                                                                                                                                                                                                                                    |
| Ireland   |                                             | Avalonia         | Crimes <i>et al.</i> 1995; MacGabhann <i>et al.</i> 2007                                                                                                                                                                                                            |
| Mexico    |                                             | Laurentia        | McMenamin 1996                                                                                                                                                                                                                                                      |
| Namibia   |                                             | Gondwana         | Germs 1972; Crimes & Germs 1982; Hahn & Pflug 1988                                                                                                                                                                                                                  |
| Norway    | <i>Finnmark</i>                             | Baltica          | Farmer <i>et al.</i> 1992; Crimes & McIlroy 1999                                                                                                                                                                                                                    |
| Russia    | <i>White Sea</i>                            | Baltica          | Fedonkin 1978, 1980, 1981, 1990; Martin <i>et al.</i> 2000; Serezhnikova 2005, 2007; Leonov 2007                                                                                                                                                                    |
|           | <i>The Urals</i>                            | Baltica          | Bekker 1977, 1990; Grazhdankin <i>et al.</i> 2005                                                                                                                                                                                                                   |
|           | <i>Siberia</i>                              | Siberia          | Sokolov 1973; Sokolov & Fedonkin 1984; Vodanjuk 1989; Serezhnikova 2007                                                                                                                                                                                             |
| Ukraine   |                                             | Baltica          | Zaika-Novatskiy <i>et al.</i> 1968; Palij 1976; Palij <i>et al.</i> 1979; Fedonkin 1983                                                                                                                                                                             |
| USA       | <i>California &amp; Nevada</i>              | Laurentia        | Hagadorn <i>et al.</i> 2000; Hagadorn & Waggoner 2000                                                                                                                                                                                                               |

Discoidal fossils have now been described from most Ediacaran assemblages. A list of some of the more important sites, including all material referred to in the text is given in Table 1. It should be noted that this list is in no way exhaustive and, indeed, some of the material is of doubtful biogenicity.

**Taphonomy of discoidal fossils**

Since basic taxonomic methods and comparative morphology have proved unreliable in trying to gain a better understanding of the true nature and affinities of discoidal Ediacarans, other parameters need to be considered. An important factor in this respect is taphonomy, which must be the primary consideration in investigation of such fossils, and the context in which discoidal assemblages are viewed. Discoidal Ediacaran fossils are preserved in three main styles: these are now discussed.

*Conception-style preservation*

This form of preservation is currently known only from the Avalon Zone of Newfoundland, and the laterally equivalent Charnwood Forest inlier in central England. Fossils are preserved at these localities by obrution by volcanic ash. This ash moulded the upper surface of the organisms, and rapidly lithified, allowing the mould to be cast by sediment from the bed below, upon which the organisms had originally lived. Weathering of the ash reveals vast surfaces covered in fossils, including discoidal holdfasts and solitary discs, which are thus found as low positive epirelief casts (Narbonne 2005).

*Death mask-style preservation*

Many Ediacaran genera, principally bilaterally symmetrical forms like *Dickinsonia* and *Yorgia*, are found as positive epirelief casts, or negative relief moulds on bed soles (Gehling 1999;

Gehling *et al.* 2005). This particular style of preservation was, until recently, very difficult to account for. It has now been explained as being due to the influence of the microbial mats, a ubiquitous feature of Ediacaran seafloors. On burial of the organisms by event beds, anaerobic decay of the microbial mat caused the precipitation of diagenetic iron sulphide minerals in the sole of the event bed, rapidly lithifying it. This caused external moulds to form around the upper surface of the organisms, which decayed allowing sediment to cast the mould from below. This mode of preservation only occurs in organisms which were more resistant, and not instantly compacted by the rapid sedimentation (Gehling 1999; Gehling *et al.* 2005; Droser *et al.* 2006). Although in general this preservation is limited to complex fossils, some discs are preserved in this style, e.g. *Sekwia* (Hofmann 1981).

### Gravity cast preservation

Most discoidal Ediacaran genera, as well as a few rare, complex forms such as *Palaeopascichnus* and *Phyllozoon*, are preserved as positive hyporelief casts on bed soles. Consensus is yet to be reached on the precise details of the taphonomy in the case of the more complex forms. Seilacher *et al.* (2003), for example, regard *Phyllozoon* as living under the mat, although Gehling (1999) regarded it as simply a less resistant form, which was easily compacted. In contrast, this particular mode of preservation is much better understood for discoidal fossils. The organisms were living partially or quasi infaunally within the upper layers of the microbial mat, and on burial, they decayed before a death mask could form. However, the microbially bound sediment was cohesive and firm enough to retain a mould of the lower surface of the organism. This was then cast from above by sediment moving under the influence of gravity. A slightly modified but essentially identical path was followed in the cases of organisms which were removed, perhaps by current action, before burial, in which case sediment cast the vacated mould at the time of sedimentation.

'Gravity cast and death mask' styles of preservation are often found to occur on the same surfaces. However, it may also be the case that no death masks are present, with all the fossils on a particular surface being gravity casts. Narbonne (2005) has labelled surfaces where both occur as 'Flinders-style' assemblages, and surfaces where only gravity casts occur as 'Fermeuse-style' assemblages. These two terms ('Flinders-style' and 'Fermeuse-style') are useful when considering entire assemblages, but the terms 'gravity cast' and 'death mask' are more appropriate when dealing with individual fossils.

### Morphology of discoidal fossils

As noted above, taxonomy of discoidal fossils is currently in a state of considerable confusion, and it would, therefore, be of very limited value to simply review all the currently named genera from the literature. In fact, a far more comprehensive resurvey is required (see discussion below). An additional problem is that many descriptions, including most early work, ignored the taphonomy and did not describe the sense of relief (positive hyporelief or positive epirelief) of the fossils. However some mention of the various morphologies is necessary and the general morphological traits of some examples are summarized below and also in Figure 1.

Most discs are preserved as gravity casts, and are comparatively simple, exhibiting various combinations of radial and concentric elements, with or without a central tubercle. This ranges from the flat *Nimbia* (Fedonkin 1980, 1990), with a single ring and occasionally a central tubercle, to the slightly more convex *Tirasiana* (Palij 1976; Palij *et al.* 1979; Fedonkin 1990), with several concentric annuli surrounding a prominent tubercle, to *Springia* (Southcott 1958; Sun 1986a), which is flat with dense concentric ridges and grooves, to *Cyclo-medusa* (Sun 1986a), with a combination of several concentric and numerous unbranched radial grooves. Several discs, including the small and simple *Medusinites* and the largest disc *Ediacaria*, show a bipartite organization, often described as 'superimposed discs' or an 'inner disc and outer ring' (Glaessner & Wade 1966; Narbonne & Hofmann 1987). In the case of *Medusinites* the inner disc is smooth, but the outer ring may have some radial elements. *Ediacaria* commonly has concentric features on the inner disc and radial grooves on the outer ring. Although most of these exhibit only low to moderate relief, others such as *Nemiana* (Leonov 2007), which is ornamented only by simple concentric rings, are considerably more three-dimensional.

Other discs are more complex, or with more eccentric structures. *Hiemalora*, known from both positive hyporelief and positive epirelief specimens, consists of a large, smooth central disc surrounded by radial structures, variously interpreted as tentacles or rhizoids (see review in Serezhnikova 2007). *Eoporpita* consists of a small, concentric, ornamented central disc preserved in positive hyporelief, surrounded by rings of prominent tubercles, which have been suggested to represent tentacles (Wade 1972; Narbonne & Aitken 1990). *Sekwia* (found as death masks) is a simple smooth disc with a single crescentic groove (Hofmann 1981). *Mawsonites*, one of the most recognizable Ediacaran taxa and also preserved as

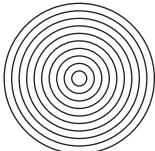
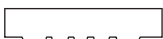
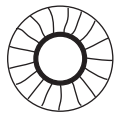
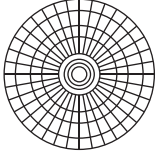
|                                                                                     |                                                                                     |                                                                                                                                                |                                                                                                        |
|-------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------|
|    |    | <i>Aspidea</i><br>Invaginated disc with radial ribs extending from centre to margin. 2–30 mm.                                                  | Billings 1872; Gehling <i>et al.</i> 2000                                                              |
|    |    | <i>Spriggia</i><br>Flat disc with dense concentric ridges and grooves. May also be fine radial lines extending from specimen margin. 10–80 mm. | Sprigg 1949; Southcott 1958; Sun 1986a; Gehling <i>et al.</i> 2000                                     |
|    |    | <i>Nimbia</i><br>Flat disc with or without central tubercle, enclosed by a single circular ridge. 4–15 mm.                                     | Fedonkin 1980, 1990; Hofmann <i>et al.</i> 1990; Crimes & McIlroy 1999                                 |
|    |    | <i>Tirasiana</i><br>2–5 concentric annuli separated by grooves, surrounding a prominent central tubercle. 10–60 mm.                            | Bekker 1977, 1990; Crimes & McIlroy 1999; Hagadorn <i>et al.</i> 2000                                  |
|    |    | <i>Hiemalora</i><br>Flat or convex central disc surrounded by irregular radial structures. 3–40 mm.                                            | Fedonkin 1980, 1990; Vodanjuk 1989; Serezhnikova 2007                                                  |
|   |   | <i>Ediacaria</i><br>Concentrically-ornamented central disc surrounded by outer annulus, which may have thin, unbranched radial lines. ≤1m.     | Sprigg 1947; Glaessner & Wade 1966; Wade 1968; Fedonkin 1990; Jenkins 1992; Gehling <i>et al.</i> 2000 |
|  |  | <i>Medusinites</i><br>Smooth central disc separated from radially-ornamented outer annulus by a deep groove. 1–50 mm.                          | Sprigg 1947; Glaessner & Wade 1966; Fedonkin 1990; McIlroy <i>et al.</i> 2005                          |
|  |  | <i>Cyclomedusa</i><br>Concentrically-structured inner discs surrounded by outer area with both radial and concentric structures. 5–100 mm.     | Sprigg 1947, 1949; Glaessner & Wade 1966; Wade 1972; Sun 1986a; Gehling <i>et al.</i> 2000             |
|  |  | <i>Nemiana</i><br>Highly convex disc with weak concentric ornament. 2–60 mm.                                                                   | Palij 1976, 1979; Narbonne & Hofmann 1987; Leonov 2007                                                 |
|  |  | <i>Sekwia</i><br>Convex disc with prominent crescentic groove(s). 9–33 mm.                                                                     | Hofmann 1981; Narbonne & Aitken 1990                                                                   |

**Fig. 1.** Outline morphology of some common Ediacaran discs, with indication of structure, relief and key references. Sketches are approximate, and not to scale.

a gravity cast, has a central disc surrounded by rings of lobes, which increase in size outwards (Glaessner & Wade 1966). Finally, *Palaeophragmodictya* (Gehling & Rigby 1996), found in death mask preservation, has a central disc surrounded (in well preserved specimens) by an outer reticulate area, and *Inaria* (Gehling 1988) is a lobate disc (found as both death mask and gravity cast), which often shows evidence for a stalk.

Whilst the more complex discs seem to be fairly well defined, it should be stressed that the overwhelming majority of discs, including the oldest and youngest examples, belong to the morphologically simple group. The oldest discs, reported by Cruse and Harris (1994) from the Stirling Range in Australia, are concentrically arranged discs comparable to *Tirasiana* and *Cyclomedusa* on first glance, but importantly, some are preserved as positive epireliefs and thus cannot be assigned to these genera. Assemblages from strata underlying glaciogenic diamictites attributable to the Elatina glaciation, reported by Hofmann *et al.* (1990) and Bertrand-Sarfati *et al.* (1995) (note that these authors wrongly attributed this diamictite to an Early Cambrian glaciation) are also simple concentrically structured annuli and discs, similar to *Nimbia*. Younger, Cambrian-aged discs, described by Crimes & McIlroy (1999) from northern Norway, and by Hagadorn *et al.* (2000) from the southwestern United States, are again concentrically structured, and are comparable to *Nimbia* and *Tirasiana* (supposedly younger discs described by Crimes *et al.* 1995 are in fact likely to be unrelated to Ediacaran fossils; see MacGabhann *et al.* 2007).

## Discoidal pseudofossils

The problem of understanding the Ediacaran discs is exacerbated by the existence of discoidal pseudofossils. The nature of Ediacaran fossils—being preserved as imprints on bed surfaces—has led to Ediacaran bed surfaces in general being examined in much more detail than typical Phanerozoic surfaces, and this has led to a plethora of published descriptions of suspect structures, not all of which seem to represent fossils (e.g. McMenamin 1996; De 2003, 2006). Often copious and highly significant phylogenetic interpretations have been based on discs, which later turn out to be something else entirely. A good example in this regard is the structure *Kullingia*. Originally described as representing a fossil chondrophorine (Føyn & Glaessner 1979; Narbonne *et al.* 1991; Jensen *et al.* 1998) (a medusoid hydrozoan of the subclass Athecatae), *Kullingia* is now known to be a swing mark, an organically generated tool mark consisting of arcuate sets of grooves cut in the sediment by current-forced

oscillation of elongate tethered benthic organisms, such as the sabelliditids (Jensen *et al.* 2002).

Other discs have been regarded as dubiofossils or inorganic structures (e.g. Hofmann 1971), such as sand volcanoes (often modified by tectonic deformation or interaction with microbial mats; Seilacher *et al.* 2005), fluid or gas escape structures, concretions or loading (Cloud 1960; Sun 1986a). While in some cases this is well justified (e.g. Cloud 1973; Sun 1986a), others have previously been interpreted as pseudofossils simply on the basis that they occurred in rocks thought to be too old to contain evidence of life. Indeed, one such case was the first named Ediacaran body fossil *Aspidella terranova* from the Avalon Peninsula of Newfoundland, described in the late nineteenth century by Billings (1872). It was only after the discovery of much more complex undoubted fossils at Mistaken Point (Misra 1969), in strata stratigraphically beneath *Aspidella*-bearing beds, that *Aspidella* was finally confirmed as a fossil (Gehling *et al.* 2000).

## The *Aspidella* controversy

Detailed examination of the *Aspidella*-bearing beds in the Fermeuse Formation of Newfoundland has revealed that the discs, previously assumed to be inorganic pseudofossils, are indeed true fossils. Rare examples of the tentaculate disc *Hiemalora*, the tri-radially symmetrical *Triforillonia*, and the enigmatic serial fossil *Palaeopaschichnus* are found to occur in the section, but the vast majority of the fossils are simple discs, examples of which resemble not only the type material of *Aspidella*, but also most other Ediacaran discoidal genera (Gehling *et al.* 2000). Many of the discs were also seen to strongly resemble those known to be the basal attachment discs of known stalked frondose taxa. Furthermore, there was seen to be no clear distinction between different genera. Instead, it was proposed that the discs could be described in terms of three end-member preservational morphs of *Aspidella*, between which there exists an ‘insensible gradation’ (*sic*) in morphological form (Gehling *et al.* 2000). These were labelled the convex-morph (strong hyporelief, similar to *Ediacaria*), the flat-morph (low hyporelief with common concentric rings, similar to *Spriggia*), and the type morph (invaginated disc with radial ribs, similar to the type *Aspidella*). These were not distinguished as separate genera, as there was no satisfactory way to differentiate between the different forms. Observing that many Ediacaran discoidal fossils were represented within this gradation, Gehling *et al.* (2000) listed no less than twenty-four discoidal species in sixteen genera as junior synonyms of *Aspidella terranova*. This list is reproduced in Table 2.

**Table 2.** Probable junior synonyms of *Aspidella*, according to Gehling *et al.* (2000)

| Taxon                              | Author                                  | Location        | Morph       |
|------------------------------------|-----------------------------------------|-----------------|-------------|
| <i>Paramedusium africanum</i>      | Gürich 1933                             | Namibia         | Flat        |
| <i>Ediacaria flindersi</i>         | Sprigg 1947                             | South Australia | Convex      |
| <i>Beltanella gilesi</i>           | Sprigg 1947                             | South Australia | Convex      |
| <i>Cyclomedusa davidi</i>          | Sprigg 1947                             | South Australia | Convex      |
| <i>Protodipleurosoma wardi</i>     | Sprigg 1947                             | South Australia | Flat-type   |
| <i>Tateana inflata</i>             | Sprigg 1947                             | South Australia | Convex      |
| <i>Cyclomedusa radiata</i>         | Sprigg 1949                             | South Australia | Flat-convex |
| <i>Cyclomedusa gigantea</i>        | Sprigg 1949                             | South Australia | Convex      |
| <i>Madigania annulata</i>          | Sprigg 1949                             | South Australia | Flat        |
| <i>Cyclomedusa plana</i>           | Glaessner & Wade 1966                   | South Australia | Flat        |
| <i>Planomedusites patellaris</i>   | Sokolov 1972                            | Ukraine         | Flat        |
| <i>Medusinites patellaris</i>      | Sokolov 1972                            | Ukraine         | Flat        |
| <i>Tirasiana disciformis</i>       | Palić 1976                              | Ukraine         | Convex      |
| <i>Tirasiana coniformis</i>        | Palić 1976                              | Ukraine         | Convex      |
| <i>Tirasiana concentralis</i>      | Bekker 1977                             | Urals           | Convex      |
| <i>Paliella patelliformis</i>      | Fedonkin 1980                           | White Sea       | Flat        |
| <i>Protodipleurosoma rugulosum</i> | Fedonkin 1980                           | White Sea       | Flat        |
| <i>Cyclomedusa minima</i>          | Fedonkin 1981                           | White Sea       | Type-convex |
| <i>Cyclomedusa delicata</i>        | Fedonkin 1981                           | White Sea       | Flat-convex |
| <i>Irridinitus multiradiatus</i>   | Fedonkin 1983                           | Ukraine         | Type        |
| <i>Spriggia wadea</i>              | Sun 1986a                               | South Australia | Flat        |
| <i>Vendella larini</i>             | Gureev 1987                             | Ukraine         | Type        |
| <i>Glaessneria imperfecta</i>      | Gureev 1987                             | Ukraine         | Flat        |
| <i>Jampolium wyrzhykoowskii</i>    | Gureev (in Ryabenko <i>et al.</i> 1988) | Ukraine         | Flat        |

This was not the first time that such intergradation had been noted, or caused problems. For example, the genus *Tateana* has variously been considered a separate genus (Sprigg 1949), a junior synonym of *Ediacaria* (Harrington & Moore 1956), or a junior synonym of *Cyclomedusa* (Glaessner & Daily 1959; Sun 1986a). Jenkins (1984) however, suggested that one species of *Cyclomedusa*, *C. radiata*, did not belong to this genus, and assigned it as a junior synonym of *Tateana inflata*.

Glaessner and Wade (1966) suggested that the separation of *Spriggia* from *Cyclomedusa* was impractical due to intergrading, and Sun (1986a) similarly referred to the gradation in *Cyclomedusa* and *Spriggia* as the '*Cyclomedusa plexus*' although he considered the two genera as separate entities. Jenkins (1992) later recorded a gradation between *Cyclomedusa*, *Ediacaria* and *Spriggia* in South Australia, while Fedonkin (1990) observed that many forms assigned to *Ediacaria* intergraded with forms assigned to *Tirasiana*. Hagadorn *et al.* (2000) restated this, noting that a thorough revision of 'medusoid' taxonomy was necessary.

### A. terranovica—a single species of organism?

One thing which Gehling *et al.* certainly did not intend by this synonymization was to imply that all Ediacaran discs belong to a single species of

organism, stating explicitly that the name carried 'no implied interpretation of the biological origins or affiliations of discs, unlike such genera as *Cyclomedusa* and *Charniodiscus*'. (Gehling *et al.* 2000, p. 446). The intention was simply to stress the fact that no consistent distinction can be made between the various discoidal structures preserved in Ediacaran assemblages and, indeed, this is, to some extent, justified. In particular, the discs of the Fermeuse Formation do exhibit the indefinable variation in form noted (personal observations). However, evidence that more than one type of organism is now included in *Aspidella* from the Fermeuse Formation of Newfoundland is plentiful.

### Distribution of various morphs

The variation in form of *Aspidella* has been attributed as being due to two factors; namely the size of the discs and the clay/sand ratio of the host sediment. Gehling *et al.* (2000, text-fig. 7) presented a graph of distribution of the three end-member morphs against these two factors. The three morphs clearly fall within specific, and sometimes discrete, fields and it was proposed that this demonstrated disc preservation to be a two-variable system. It is, however, significant that, while the *Spriggia* field does not overlap the other two, the *Ediacaria* field overlaps most of the *Aspidella* field. This clearly demonstrates that a two variable system is not sufficient to

differentiate the morphs: a third factor needs to be considered in order to segregate the forms in discrete morphospace. The precise nature of this extra factor, be it intrinsic or extrinsic, is of course difficult to clearly identify; however if it was intrinsic, the most likely candidate would be biological affinity.

## Ecology

*Aspidella* was interpreted as a holdfast based on two specimens with putative stems (Gehling *et al.* 2000), although it was stressed that this could not necessarily be extrapolated to all specimens. These specimens have since been examined by the author and also other rare stem-bearing discs observed in the Fermeuse Formation, and there is no doubt that some specimens are indeed holdfasts. Discoidal specimens from Australia and Russia have also been interpreted as holdfasts (Jenkins 1992; Serezhnikova 2005). However, the density of discs on some surfaces in the Fermeuse Formation is extremely high (Fig. 2), with up to 3000–4000 individuals per m<sup>2</sup> on some surfaces (Gehling *et al.* 2000). Such densities stand in stark contrast to those reported by Clapham *et al.* (2003) of all taxa from the stratigraphically underlying assemblages at Mistaken Point. These assemblages are preserved in Conception-style (i.e. buried by volcanic ash). Weathering of this ash reveals vast surfaces covered in complex fossils (Fig. 3), dominated by taxa belonging to the rangeomorph group (Misra 1969; Narbonne 2004, 2005). Of seven surfaces measured by Clapham and colleagues, six had densities between 7 and 40 individuals per m<sup>2</sup>. The seventh, and densest surface, at Bristy Cove, was still an order of magnitude lower than the Fermeuse assemblages at 149.3 individuals per m<sup>2</sup>. It should be noted, however, that this density is based on a total exposed surface area of only 0.71 m<sup>2</sup>, contrasting strongly with the E surface at Mistaken Point, which has a density of 39.7 individuals per m<sup>2</sup>, measured from a surface area of 103.7 m<sup>2</sup> (Clapham *et al.* 2003). The Bristy Cove density is, thus, unlikely to be statistically representative.

Clapham and colleagues also analysed the ecological structure of the Mistaken Point surfaces in detail (Clapham & Narbonne 2002; Clapham *et al.* 2003), and showed this to be strikingly similar to modern marine communities. Included in this was evidence of spatial distribution patterns for certain taxa, including frondose forms. Given the spatial distribution and relatively low population densities of frondose taxa at Mistaken Point, it would seem unlikely that a double order of magnitude increase in population to the levels seen in the Fermeuse Formation could be ecologically sustainable (see below for further discussion). Overprinting of larger specimens onto underlying laminae, which was suggested to occur by

Gehling *et al.* (2000), cannot account for more than a fraction of this difference; only a small number of specimens from each surface will overprint through, onto a small number of underlying laminae. Even if it is assumed that the extraordinarily high fossil density at Bristy Cove was representative of Mistaken Point communities, every fossil on each of 20 laminae would need to be imprinted onto a single surface to reach a density of 3000 individuals per m<sup>2</sup>. A much more likely interpretation is that although some discs represent frond holdfasts, the vast majority represent other discoidal morphologies.

## Mode of growth

Some of the discoidal fossils of the Fermeuse assemblages resemble stacked discs, growing larger upwards (Gehling *et al.* 2000, text-fig. 8a). Other fossils have a similar morphology, but are not quite as three-dimensional in aspect (Fig. 4). A possible interpretation of these differences is that the organisms were growing upwards to keep pace with sedimentation; where sedimentation rates were lower, fossils are less three-dimensional. Such a growth pattern has not been observed for confirmed holdfasts, indicating that these fossils may represent a different mode of growth.

## Size

Discs in the Fermeuse Formation can grow quite large (Fig. 5), with some reaching c. 15 cm in diameter. Holdfasts of this size have not been positively identified to date; most holdfasts in the Mistaken Point assemblages would be below half this size (a similar point was made by Peterson *et al.* 2003). Limitation of such large holdfasts to the Fermeuse assemblages seems unlikely: a better interpretation may be that the larger discs represent a different construction.

Individually, perhaps none of these factors is entirely compelling but, taken in combination, they provide good evidence for the existence of several different biological constructions in the Fermeuse assemblages. This makes the synonymization of sixteen described Ediacaran genera with *Aspidella* a wholly unsatisfactory solution to the discoidal fossils issue.

## Controls on composition of Avalonian assemblages

Fermeuse discs should not, however, be solely considered in isolation, but also in the context of other Avalonian biotas. Considerable differences are demonstrable between the disc dominated Fermeuse and the nearby rangeomorph dominated



**Fig. 2.** High density of discs in the Fermeuse Formation, Silos Cove, Ferryland. Coin (Canadian \$1) is 26 mm in diameter.

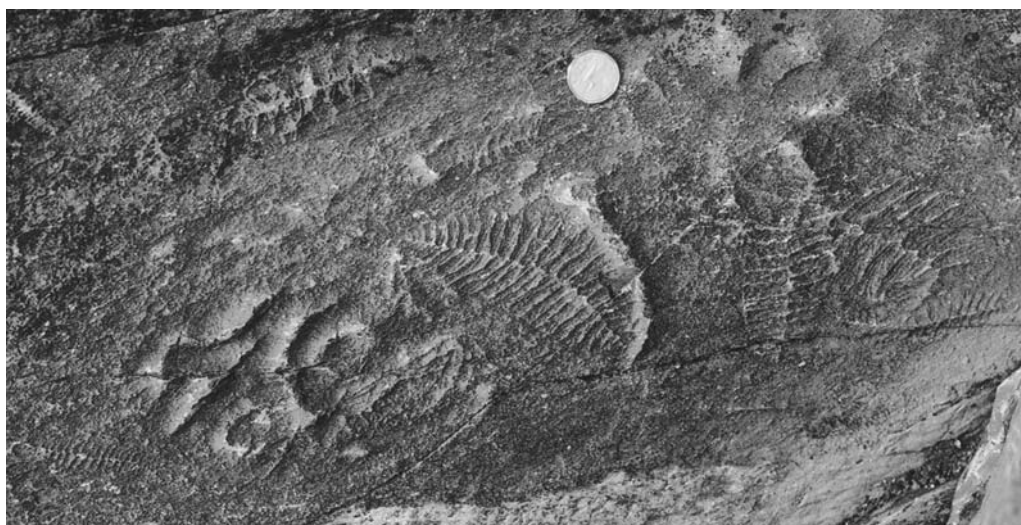


**Fig. 3.** Mistaken Point Biota: different taphonomic window or different organisms? Mistaken Point Formation, Mistaken Point. Coin (Canadian \$1) is 26 mm in diameter.

Mistaken Point assemblages. Three main potential explanations for these differences follow.

#### *Age (biostratigraphic)*

Since the main Fermeuse assemblages in Newfoundland are stratigraphically much younger than the Mistaken Point assemblages, differences between the two in terms of fossil content and morphology may simply be a reflection of this temporal disparity. However, the occurrence of both Fermeuse- and Mistaken Point-style assemblages

in the Trepassey Formation (which occurs stratigraphically between the two) may rule this out. This seems to be consistent with evidence from other locations with Fermeuse-style assemblages. In particular, a discoidal biota reported from the Innerelv Member of the Stappogiedde Formation in northern Norway (Farmer *et al.* 1992) occurs only 160 m stratigraphically above Mortensnes Formation (the upper of the two Varanger glacial diamictites). This is thought to be equivalent in age to the Gaskiers Formation of Newfoundland (e.g. Halverson *et al.* 2005), but in Newfoundland the stratigraphic

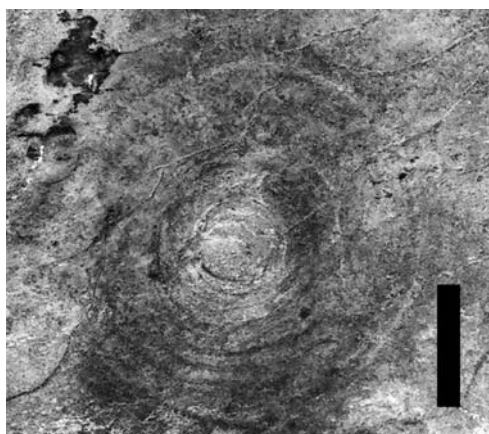


**Fig. 4.** Flat 'stacked discs' form of *Aspidella* with low relief, Fermeuse Formation, Silos Cove, Ferryland. Scale bar 20 mm.



**Fig. 5.** Large specimen of flat morph of *Aspidella*, Fermeuse Formation, Silos Cove, Ferryland. Scale bar 20 mm.

distance between the glacial diamictites and overlying Ediacaran fossils is 1.5 km to the oldest Mistaken Point-style assemblage in the Drook Formation (Narbonne & Gehling 2003). Fermeuse assemblages are separated from the Gaskiers by the entire thicknesses of the Drook, Briscal, and Mistaken Point formations. Even considering the potential effects of differential subsidence and sedimentation rates between the two basins, it is possible that the Norwegian discs may be much older than the lowest Fermeuse-style assemblages in Newfoundland. This is perhaps supported by the occurrence of the triradially symmetrical fossil *Triforillonia* in the Fermeuse Formation; similar fossils are elsewhere confined to the Ediacara/White Sea type assemblages, thought to be c. 555 Ma in age (Gehling *et al.* 2000; Martin *et al.* 2000; Narbonne 2005). Recent discoveries in the north of Newfoundland (O'Brien & King 2004) may also support this, with Mistaken Point style assemblages occurring much higher in the stratigraphic column than previously recorded on the Avalon Peninsula (Hofmann *et al.* 2005).

### *Preservation (taphonomic)*

An alternative consideration may be that the preservation of the fossils is the key factor. The importance of taphonomic style with regard to the fossils from the Avalon Zone of Newfoundland was noted by Narbonne (2005). He observed that while the Mistaken Point assemblages were preserved in Conception-style, fossils of the stratigraphically overlying St. John's Group were preserved in Fermeuse-style (in fact, both represent the type areas for these particular styles of preservation). Noting that both styles occurred in the intervening Trepassey Formation, along with one example of three-dimensional preservation within a bed (a less significant form of preservation with regard to discoidal fossils), and that each style of preservation was associated with a very different biotic composition, Narbonne (2005) concluded that the different assemblages reflected merely different preservational windows into identical communities.

### *Environmental (ecological)*

However, when palaeoecology is taken into consideration along with taphonomy, a different story emerges. Fossil population densities in the Fermeuse Formation are, as noted above, an order of magnitude higher than the Mistaken Point assemblages. Accepting that the different assemblages are merely different preservational windows on the identical communities means that potentially ninety five percent of the organisms originally present at Mistaken Point are not preserved. Even

assuming lower values of around 1000 individuals per m<sup>2</sup> in the Fermeuse Formation, and taking the Bristy Cove population density for the Mistaken Point assemblages, this would mean that at Bristy Cove, the preserved fossils represent only a mere fifteen percent of the organisms originally present. It is extremely difficult to envisage how this is compatible with the finely balanced ecological structure demonstrated for these surfaces by Clapham and colleagues (Clapham & Narbonne 2002; Clapham *et al.* 2003), especially if many of the discs represent holdfasts. A better interpretation may be that both the biotic composition of the assemblages and the preservation style were environmentally controlled. Fermeuse organisms may have lived only on sediment bound by a different type of microbial mat, or where sedimentation was too rapid for microbial mats to form. This may not have encouraged rapid lithification of volcanic ash if buried, preventing Fermeuse assemblages from being preserved in Mistaken Point style. Conversely, if Mistaken Point assemblage organisms could not live on Fermeuse substrates, they would not have been preserved in Fermeuse-style. This hypothesis is always going to be extremely difficult to validate, however palaeoecological segregation does appear to be consistent with the available sedimentological evidence. Fermeuse assemblages occur in the thinly bedded siltstone and mudstone dominated (and commonly slumped) slope facies of the Fermeuse Formation, whilst the Mistaken Point assemblages are restricted to the deeper basinal and lower slope facies, characterized by thickly bedded turbidites and contourites. Occurrence of both assemblages in the intervening transitional Trepassey Formation, which is dominated by mudstones and thinly bedded turbidites with some slumped beds, is not inconsistent with an environmental control interpretation (Wood *et al.* 2003). This should be testable by detailed integrated sedimentological and taphonomic analysis of the Mistaken Point, Trepassey, and Fermeuse formations: if this hypothesis is correct, Fermeuse assemblages should be limited to the shallower facies, and Mistaken Point assemblages limited to ash horizons in deeper facies. Ash horizons in the shallower facies should not preserve fossils in Mistaken Point style. The new occurrences of Ediacaran fossils on the Bonavista Peninsula of Newfoundland (O'Brien & King 2004; Hofmann *et al.* 2005), in which the typical Mistaken Point assemblages occur much higher in the stratigraphy than on the Avalon Peninsula, may be of fundamental significance in answering this particular question.

The suggestion that Fermeuse sediments were not microbially bound, despite preserving high densities of Ediacaran fossils, may cause some surprise given the degree to which the microbial mat death

mask model has been accepted. Indeed the idea that the Ediacaran was a time of 'special taphonomic conditions' has become completely entrenched in the literature. However, this over-reliance on microbial mats has disguised the fact that gravity cast preservation requires only a stiff substrate capable of holding the mould of a semi-infaunal organism until it is cast from above. Any stiff Proterozoic substrate, whether microbially bound or not, would have been sufficient to preserve organisms in this style. Droser *et al.* (2002) have shown that non-microbially bound substrates in the Early Cambrian were stiff and cohesive, and similar stiff substrates have existed, though more rarely, throughout the Phanerozoic. If the above suggestion is correct, then these stiff Phanerozoic substrates should have been able to hold moulds of bases of partially infaunal non-mineralized organisms as required, allowing their fossilization as gravity casts.

### Nature of the Fermeuse discs

Accepting that the fossils of the Fermeuse assemblages are not preservational variations of the rangeomorphs and other complex organisms preserved at Mistaken Point, as demonstrated above, alternative interpretations must be sought. Peterson *et al.* (2003) have clearly outlined a compelling case for interpretation of some discs as fungi or analogous forms (note that although the tiering demonstrated by Clapham *et al.* (2003) shows the erect forms from Mistaken Point to have been partitioning a food source in the water column, a notable departure from a fungal model (Sperling & Peterson 2007) there are no such complications for the discs). Grazhdankin (2001) has also suggested that some forms may represent microbial colonies. Since growth of microbial colonies is often dependant on chemical cycles, and since both fungi and microbial colonies may have no constraints on maximum colony size, concentrically ringed and very large forms are particularly amenable to these interpretations. Further, some of the Fermeuse discs are extremely similar to discs from other localities, which have previously been interpreted as fungal or microbial: for example, Figure 4 is a disc from Silos Cove, near Ferryland, Newfoundland, which strongly resembles specimens illustrated and interpreted as 'algal colonies' by Glaessner (1969, fig. 2) from the >1 Ga Bass Formation of the Grand Canyon, Arizona, USA. Similar discs are common in the Fermeuse Formation.

The possibility that some of the discs represent poriferan-grade taxa should also not be discarded. Some of the oldest discoidal Ediacaran-type fossils known are found in the Twitya Formation of the Mackenzie Mountains, below the

Elatina-equivalent Stelfox glaciogenic diamictite (Hofmann *et al.* 1990), and are thus older than the Elatina glaciation, the end of which marks the beginning of the Ediacaran Period (Knoll *et al.* 2004). In China, the Datangpo Formation, which underlies the Elatina-equivalent Nantuo diamictite, is dated at  $663 \pm 4$  Ma (Zhou *et al.* 2004), and the Twitya discs are likely of similar age—i.e. at least sixty million years older than any other Ediacaran fossils. Recent molecular clock dates have suggested that poriferan-grade organisms evolved around this time (Peterson & Butterfield 2005), and it might be useful to consider that this is perhaps not a coincidence. If poriferan-grade organisms were capable of being preserved in this style in the Cryogenian, there is no reason to believe they could not have been similarly preserved in the Ediacaran. The undoubted presence of crown-group sponges in *Palaeophragmodictya* (Gehling & Rigby 1996) supports this suggestion.

Another idea, which should be considered, is that some of the discs represent benthic cnidarians, in particular actinian dwelling traces, similar to the trace fossil *Bergaueria* (Alpert 1973). Thus, the discs as preserved would represent the bases of anemone-like organisms. Some specimens show possible evidence of upwards growth or movement through the sediment, which may support the idea that such organisms were present.

One potential interpretation which should however be unequivocally rejected is that any of the fossils represent any form of 'medusa'. Seilacher (1984) has outlined objections to pelagic forms being preserved on bed soles, and our work on Cambrian fossils (MacGabhann *et al.* 2007) has supported the view that low-density pelagic organisms cannot be preserved in this style. None of the fossils in the Fermeuse assemblages show any evidence of transport, and discs, which appear to be growing up through the sediment, must in any case be benthic. The idea that any of the Fermeuse specimens represent 'swing marks' should also be dismissed. *Bona fide* swing marks, such as *Kullingia*, are generally identifiable by the close spacing of ridges (in positive hyporelief) and presence of a central feature representing the attachment point of the tool. Finally, Gehling *et al.* (2000) have comprehensively dismissed the possibility of most other inorganic interpretations for the Fermeuse discs.

### Nature of discs in other Ediacaran assemblages

This then leaves the issue of the discoidal fossils in other Ediacaran assemblages. Most other disc dominated assemblages—in particular those from England (McIlroy *et al.* 2005), Wales (Cope 1977),

and Finnmark (Farmer *et al.* 1992)—are likely similar in biotic composition and nature to the Fermeuse assemblages. However, most of the discs in the Mistaken Point assemblages, which are of course, preserved in Conception-style rather than as gravity casts like the Fermeuse fossils, may convincingly be interpreted as holdfasts. The same has been suggested for many Australian discs preserved as gravity casts including *Ediacaria*, but Jenkins (1992) noted that specimens comparable to *Ediacaria* reach up to one metre in diameter. Such enormous size is completely inconsistent with a holdfast interpretation, clearly indicating the presence of at least two discoidal morphologies. Russian assemblages are broadly similar to those in Australia. Interestingly, fossils preserved as gravity casts from the White Sea area have recently been assigned to *Ediacaria* and interpreted as holdfasts by Serezhnikova (2005). One unusual aspect to this interpretation is the view that the holdfasts were attached not at the sediment surface, but at a particular layer underneath the sediment–water interface; this surface is hypothesized to be a bacterial film at a boundary between liquid and microbially bound sediment. It is further speculated that organisms were preserved when their top parts were removed by storms, with the gaps then being infilled by storm-carried sediment. However this interpretation may not be consistent with the proposed nature of Ediacaran substrates, which are characterized by a sharp interface between stiff, microbially bound sediment and the overlying water column (Gehling 1999; Hagadorn & Bottjer 1999). This is clearly demonstrated for the White Sea sediments by *Dickinsonia* and *Yorgia* surface trace fossils (Ivantsov & Malakhovskaya 2002; Fedonkin 2003; Gehling *et al.* 2005), which indicate the presence of a stiff upper surface to substrates capable of holding the imprints of organisms after they had moved on. As described above, preservation of discoidal fossils as gravity casts is generally believed to be due to moulding of the lower surface of the organism on this stiff substrate.

### Holdfasts? Holdfasts of what?

Finally, interpretation of discs as 'holdfasts' raises the interesting question of what is on the stem. In some cases attached fronds are still visible, and in the case of the Mistaken Point assemblages assignment of many solitary discs to *Charniodiscus* may not be far off the mark. Attachment discs are also associated with *Charnia* and perhaps other rangeomorphs, however these appear to have a much narrower range—both in terms of environment and age—than the discs (Narbonne 2004, 2005), and it is unlikely that rangeomorph holdfasts form a

significant component of most other discoidal assemblages. It is also entirely possible that completely unknown taxa are represented by holdfasts alone. One suggestion, which is perhaps unlikely, is the presence of true sea pens—similarities between Ediacaran forms and Phanerozoic organisms in this regard is likely due to evolutionary convergence. In defence of this statement, frondose morphology is known to have independently evolved in several unrelated Ediacaran lineages, represented for example by the taxa *Charniodiscus* (Laflamme *et al.* 2004), *Charnia* (Laflamme *et al.* 2007), *Swartpuntia* (Narbonne *et al.* 1997), and taxa (which have not been formally described) from the Mistaken Point assemblages such as the 'Xmas tree' (e.g. Clapham *et al.* 2003).

### Taxonomy of discoidal fossils

The above discussion clearly highlights the main problem faced when trying to interpret these fossils: basic discoidal forms are geometrically and constructionally so simple that they are much more likely than other, more complex shapes, to evolve in multiple lineages. If frondose morphology can evolve independently in several unrelated groups, convergent evolution on discoidal morphology may also have been attained many times, perhaps including several extinct lineages. Further, many inorganic structures mimic biogenic forms, introducing additional complications. Thus, trying to interpret their origin is always likely to be an extremely complex problem. Integration of taphonomic and palaeoecological studies, such as the discussion above on the nature of the Fermeuse assemblage discs, is necessary to advance our knowledge of the organisms represented by the discoidal fossils.

However, the problem of disc taxonomy should not be ignored. As noted, the assignment of most discs to *Aspidella* is a rather unsatisfactory solution to the problem. Indeed, an unwelcome side effect of this has been the potential for subsequent descriptions of Ediacaran assemblages to treat the form taxon *Aspidella* as if it were a proper taxon, making no distinction between the various preservational morphs described by Gehling *et al.* (2000). This approach has the capacity to severely limit the information potential of such material. Describing all discs as *Aspidella* merely tells us there are discs present, and nothing further. Gehling *et al.* (2000, p. 446) attempted to assuage this problem by suggesting that future descriptions make reference to which preservational morph of *Aspidella* the material most closely approaches: 'in future systematic descriptions of discoidal fossils of the *Aspidella* plexus... the commonly

used names of junior synonyms should be retained as form-genera to represent certain styles of preservation...the three end members of the *Aspidella* plexus: 'Aspidella' for invaginate morphs, 'Spriggia' for flat, annulate morphs, and 'Ediacaria' for convex morphs, represent the most parsimonious form-genera under which Ediacaran discoidal fossils can be accommodated.' Unfortunately, this has not been applied in practice (e.g. Hofmann & Mountjoy 2001; Pyle *et al.* 2004; Droser *et al.* 2006).

## Conclusions and suggestions for future research

Discoidal fossils, despite their abundance in the Ediacaran biosphere, have not received their fair share of attention. Several different benthic discoidal morphologies are present in Ediacaran assemblages; no convincing cases exist for assignment of discs to pelagic 'medusae'. Attachment discs (or holdfasts) representing the basal parts of stalked forms are unequivocally present in many discoidal assemblages, but suggestions that most discs represent holdfasts are likely overstated. It is also unlikely that many holdfasts outside the Mistaken Point assemblages are attachment discs of rangeomorph taxa. The range of potential groups represented by discoidal forms is still considerable at present and may include cnidarian as well as poriferan grade organisms, whilst larger discs and concentrically ringed forms could potentially represent non-metazoan grades such as fungal or bacterial colonies. This applies to discoidal fossils from all reported Ediacaran fossil sites, but in particular the Fermeuse assemblages of Newfoundland, and similar assemblages dominated by discoidal forms. The difference between the disc-dominated Fermeuse assemblages and rangeomorph-dominated Mistaken Point assemblages in Newfoundland does not appear to be due to taphonomic style alone, but is more likely due to environmental control on the biotas. This may also have exerted an influence on taphonomy. Discoidal fossils in Australian assemblages likely represent holdfasts for the most part, although other forms are unequivocally present; the same applies to Russian assemblages.

Future research directions, which may be productive in advancing our knowledge of the Ediacaran discs, include more thorough integrated studies of the taphonomy, morphology and palaeoecology of discoidal assemblages, and a comparison of Ediacaran discs with Phanerozoic equivalents. A complete taxonomic overhaul of discoidal fossils is required: not a review from the literature, but rather a complete critical reassessment of the discs from all Ediacaran localities. It is very probably the case that due to the naming of taxa from single,

often damaged or unrepresentative specimens, the overzealous splitting of taxa in some cases, and the misuse and misapplication of names as noted by Runnegar & Fedonkin (1992), discussed above, the entire discoidal fossil taxonomy may simply have to be abandoned. Pending this revision however, future descriptions should assign fossils to whichever of the distinctive existing Ediacaran genera the material most closely approaches (see for example some of the taxa illustrated in Fig. 1), thus retaining the maximum amount of information conveyed by the names. *These disc taxa must not be used in diversity analyses, as their biological significance is not certain.* I unequivocally recommend against the establishment of new discoidal genera at present. Finally, experimental taphonomy, along the lines of Norris (1989) may also be crucial in determining the biological affinities of the various fossils.

Thanks to J. Murray for enormous support, assistance, encouragement, and constructive criticism of this research and the text. Thanks also to G. M. Narbonne for the invitation to discuss the *Aspidella* controversy over the outcrops in Newfoundland on a field trip in June 2005: the eventual argument over the outcrop with G. M. Narbonne, J. G. Gehling, D. Erwin and M. Laflamme amongst others proved extremely useful in formulating ideas expressed here. Field assistance was provided by L. Flude, E. Bamforth, and R. Martindale. Very constructive reviews of the manuscript by Marc Laflamme and Enrico Savazzi helped greatly improve the paper. BAM is supported by an NUI Galway Postgraduate Fellowship. Partial funding for the Newfoundland trip was provided by an NUI Galway Millennium Research Fund Grant to John Murray. This is a contribution to IGCP Project 493: The Rise and Fall of the Vendian (Ediacaran) Biota.

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