A new assemblage of juvenile Ediacaran fronds from the Drook Formation, Newfoundland

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Abstract: A new assemblage of frondose and filamentous Ediacaran macrofossils is reported from the upper Drook Formation of Pigeon Cove, Newfoundland. The frondose forms, all less than 3 cm in length, are considered to represent the juvenile growth stages of Ediacaran organisms including Charnia spp. and Trepassia spp. This is the first report of an assemblage wholly dominated by such small juvenile rangeomorph forms, and provides insights into the ontogeny and ecology of these earliest members of the Ediacara biota. The fronds occur alongside filamentous forms with similarities to microbial taxa, and both morphotypes are considered to postdate an assemblage of large ivesheadiomorphs on the same bedding plane. If so, the assemblage represents one of the oldest documented examples of secondary community succession. The new Pigeon Cove fossils also extend the stratigraphic ranges of several key frondose taxa (Charnia masoni, Charniodiscus spp.) back into some of the oldest known macrofossil-bearing strata. These revised ranges lend support to the suggestion that the previously observed low diversity within the Drook Formation may represent a combination of taphonomic and sampling artefacts. Furthermore, this assemblage implies that the diversification of architectural morphotypes within the Ediacara biota took place earlier than hitherto suspected.

Supplementary material: A document containing figures of additional juvenile rangeomorphs and filamentous specimens, a table of specimen dimensions, and a complete digitized map of the Pigeon Cove bedding plane, is available at www.geolsoc.org.uk/SUP18529.

The Ediacaran strata of eastern Newfoundland, dated at c. 579–550 Ma (Van Kranendonk et al. 2008), preserve abundant fossils of large, complex macro-organisms. Fossil assemblages of the Conception Group are dominated by the remains of soft-bodied frondose taxa (e.g. Charnia, Bradgatia), and various discoidal forms (e.g. Aspidella, Hiemalora; Narbonne 2005; Hofmann et al. 2008; Brasier & Antcliffe 2009). Most fronds within these assemblages show varying levels of display within their Rangea-like elements, characterized by branches that alternate along a growth axis, and we therefore follow Brasier & Antcliffe (2009) in calling such fronds ‘rangeomorphs’. Importantly, the Conception Group assemblages include the oldest Ediacaran macrofossils with associated geochronological dates, dated at 578.8 ± 0.5 Ma (Van Kranendonk et al. 2008). These specimens lie in the upper Drook Formation of Pigeon Cove, within the Mistaken Point Ecological Reserve (Narbonne & Gehling 2003; Fig. 1).

The turbiditic mudstones and tuffs of the Drook Formation are interpreted to have been deposited in a deep marine basinslope setting, associated with an active volcanic island arc (Gardiner & Hiscott 1988; Wood et al. 2003; O’Brien & King 2005; Ichaso et al. 2007). The low-diversity assemblage of Ediacaran taxa previously documented from the Drook Formation includes: (1) Trepassia wardae Narbonne et al. (2009), a rangeomorph frond capable of growing to 2 m in length (Narbonne & Gehling 2003); (2) the shorter rangeomorph Charnia antecedens Laflamme et al. (2007); (3) the enigmatic triangular form Thecadias Avalonensis Clapham et al. (2004); (4) rare forms of Aspidella terranovica, a taxon thought to record the holdfasts of frondose organisms (Gehling et al. 2000; Fig. 2a–c). However, the most commonly observed fossils are the forms previously referred to Ivesheadia (Fig. 2d), which have recently been reinterpreted as preservational variants of other Ediacaran fossils (Liu et al. 2011), a hypothesis discussed in more detail below.

We report herein a new assemblage of abundant small frondose and filamentous fossils from Pigeon Cove, all exhibiting fine preservation of morphological features on a scale of 1 mm or less. The bed on which they occur is well known for its large ivesheadiomorph impressions (sensu Liu et al. 2011), and records one of the oldest assemblages of the Ediacaran biota in the world (e.g. Narbonne et al. 2001, 2005; Narbonne & Gehling 2003; Peterson et al. 2003; Fig. 3). The remarkable diminutive Ediacaran fossils preserved alongside the ivesheadiomorphs are, however, a completely new discovery.

Description of the fossil assemblage

The new components of the Pigeon Cove fossil assemblage include frondose rangeomorphs and similar Ediacaran taxa, along with thin filamentous fossils. The Pigeon Cove bed has been extensively mapped by the authors to document all such impressions, revealing 129 fronds and 139 filaments to date (Fig. 3). Only those forms exhibiting undoubted frondose branching have been recorded, meaning that abundance values probably underestimate the total population size. All fronds and filaments are preserved on the siltstone bedding plane as low (<1 mm) positive epirelief casts. This preservation is consistent with the Conception-type taphonomic model, which invokes casting of the organisms beneath rapidly lithified volcanic ash (Narbonne 2005). Interestingly, taxa found elsewhere within the Avalon region as predominantly negative epirelief impressions (e.g. Charnia masoni) occur here in positive epirelief (e.g. Fig. 4b). It is possible that the unusually great thickness of tuff covering this horizon (>30 cm) is responsible for these differences. Other researchers...
have noted that thicker, coarse-grained tuffs preferentially preserve 3D morphology (Narbonne & Gehling 2003; Laflamme et al. 2007), but it may be that of these variables, tuff thickness is responsible for fossil relief, whereas grain size (which is relatively fine at Pigeon Cove) is the dominant factor influencing fossil resolution (see Gehling et al. 2005). One possible mechanism by which thicker tuffs could retain higher relief impressions may be via the additional weight of the excess tuffaceous material indurating its lower surface (preserving a mould of the top surface of the organisms), prior to decay and collapse of the organic material. Alternatively, the small surface area of the specimens may play a role; it is noted that comparable well-preserved rangeomorph specimens from Upper Island Cove, which are only a few centimetres larger than those described here, are also capable of being preserved in positive epirelief (Narbonne 2004). Numerous large ivesheadiomorph forms present on the bedding plane are considered to be preserved by 'effaced' preservation (Fig. 2d; Liu et al. 2011).

Frondose fossils

The 129 fronds identified in the field are in the range of 3–30 mm in length and 1–6 mm in width (Figs 4 and 5). Several of the small rangeomorph fronds are considered to be juvenile forms of taxa commonly seen preserved in high fidelity on younger Avalonian bedding surfaces (e.g. Charnia masoni; Fig. 4a and b). Indeed, a number of specimens appear to possess basal holdfast discs (Fig. 5b) and stems (Fig. 5b and c), and the population shows a broad northeasterly alignment on the bedding plane (Fig. 6a). This alignment is taken to suggest that the fronds were true juvenile forms, once tethered to the sea floor and influenced by currents flowing over the sediment–water interface (see Seilacher 1992). No clustering of fronds is evident (Fig. 3), though extensive weathering, and patchy preservation of the overlying tuff, precludes the production of reliable statistical data for analysis of such patterns.

Small specimens confidently referred to Charnia masoni show regular parallel series of primary branches alternating along a characteristic zigzag midline, within a parallel-sided, ovate frond (Fig. 4b; Ford 1958). Other specimens show typical furled, rotated and undisplayed branching patterns that are Charnia-like at the first, second and third order (Fig. 4a; terminology of Brasier & Antcliffe 2009). We note that these other specimens, presumably juvenile forms of Charnia, possess unusual strongly distally tapering frond morphologies, which precludes their confident species-level identification. In contrast, the closely related species Charnia antecedens tapers proximally toward the frond base (see Laflamme et al. 2007), a feature not seen in any of the specimens from this assemblage. These Pigeon Cove forms are consequently ascribed
Fig. 3. Digitized map of the Pigeon Cove bedding plane (as of the summer of 2008), showing the location of ivesheadiomorphs, and the small fronds and filaments discovered by this study. The bedding plane has been split in two, with the upper image being the northernmost portion of the surface. Scale bar represents 1 m. The fracturing of the surface by wave action and erosion should be noted. Substantial areas have been lost to winter storms since this map was compiled. Fortunately, some of the loose fossil-bearing blocks have been salvaged (e.g. specimen NFM F-794 in The Rooms Provincial Museum, St. John’s, NL).

Fig. 4. Juvenile frondose organisms from Pigeon Cove, Avalon Peninsula, Newfoundland. (a) *Charnia* aff. *masoni*, frond C8 on the map. A replica cast of this specimen is housed in the Oxford University Museum of Natural History, OUM AT.426/p. (b) *Charnia masoni*, C1, OUM AT.425/p. (c) Aff. *Trepassia wardae*, C84, OUM AT.428/p. It should be noted that in aff. *Trepassia* specimens, primary branching angles vary substantially within the population. (d) A specimen likely to be a partially folded aff. *Trepassia*, showing just one row of primary branches, C42, OUM AT.427/p. All figured specimens remain in situ on the bedding plane. Scale bars represent 5 mm.

Fig. 5. Further examples of small fronds from the Drook Formation, Pigeon Cove, Newfoundland. (a) *Charnia* aff. *masoni*, specimen C63. (b) Specimen showing similarities to *Charniodiscus* sp., C16, with an apparent basal disc (arrowed), and an enclosing margin around the basal portion of the frond. (c) A possible new form, C136, with a long curved stem (arrowed), and fine primary branching (the finest scale of preservation seen on this surface). Alternatively, it is a taphomorph aff. *Trepassia*, with fossil morphology subdued by modern erosion of the surface. Hints of branching halfway down the stem (arrowed) support the latter suggestion. Replica casts of these specimens are housed in the Oxford University Museum of Natural History, OUM AT.429/p–OUM AT.431/p respectively. All figured specimens remain in situ on the bedding plane. Scale bars represent 5 mm.
here to C. aff. masoni. Specimens attributed to Charnia comprise 14 of the 60 identifiable frondose individuals documented from this locality.

The most common frondose taxon on the Pigeon Cove surface is similar to Trepassia wardae (31 of 60 identifiable frondose specimens). Trepassia is characterized by its long, narrow gross morphology, the common presence of a central stalk-like ridge, and finely divided rows of primary branches (Fig. 4c; Narbonne et al. 2009). The small Trepassia specimens documented herein show a variety of primary branching angles within the population, explained either by primary branches that were free to ‘pivot’ relative to one another (see Laflamme et al. 2007; Narbonne et al. 2009; Fig. 4c) and/or by branch axes that developed a tendency to radiate (Brasier & Antcliffe 2009). Some specimens are partially folded, such that only one row of primary branches is visible (Fig. 4d).

Three of the small fronds are compared with Charniodiscus spp. on the basis of their having a clear raised margin to the frond ‘petalodidium’ (sensu Laflamme & Narbonne 2008), and evidence for poorly preserved circular holdfast discs (e.g. Fig. 5b, arrowed). Further specimens do not closely resemble any frondose Ediacaran organisms yet described, and may belong within a new taxon (Fig. 5c). These individuals possess a long stem (c. 70% of total organism length), and a remarkably finely branched elongate and parallel-sided frond, with no clear continuation of the stem along the frond axis. Caution must be exercised, however, as the lack of observed branches along the majority of the main stem could result from modern erosion of the surface. Hints of lateral branching along the inside curve of the proposed stem (Fig. 5c) support this hypothesis, and may suggest a close affinity with Trepassia wardae. The marked curvature of the specimen in Figure 5c, if correctly identified as a single stem, implies that the original material from which the organism was constructed was relatively flexible.

Several of the features required by the current formal diagnoses of Ediacaran rangeomorphs, and therefore necessary for objective species-level classification, are too small to have been preserved in specimens of this size. Consequently, 53% of the individuals on the surface were not identifiable at the generic level. Some specimens may also represent taphonomically degraded individuals in which only the internal ‘supportive struts’ remain (see Narbonne 2004; Liu et al. 2011). Our conservative taxonomic approach to study of the Drook Formation biota may therefore underestimate the total palaeoecological diversity within this assemblage.

Valuable information regarding the ontogeny and development of Ediacaran fronds can be obtained from the Pigeon Cove fossil assemblage, but care should be taken to ensure that specimens are correctly classified before proceeding with further detailed analyses. The two best examples of Charnia masoni from the Pigeon Cove bed (C1 and C63; Figs 4b and 5a) are 13 mm and 10 mm long respectively. Their fronds possess seven and five primary branches per row, with the largest and presumably oldest branches (containing the most secondary branches) located proximally, at the base of the frond (see Brasier & Antcliffe 2009 for rangeomorph terminology). This can be compared with the holotype of Charnia masoni from Charnwood Forest (length 188 mm, 18 primary branches; Antcliffe & Brasier 2008), which also shows its largest (and developmentally earliest) primary branches at the proximal end of the frond (Antcliffe & Brasier 2007). These simple observations alone tell us that C. masoni did not possess its full complement of primary branches during its early life stages. Instead, it can be inferred to have added new primary branches at its distal end throughout its frondose life cycle (confirming the findings of Antcliffe & Brasier 2007, 2008), with inflation of single branches accompanied by distal addition during ontogeny. Juvenile specimens of aff. Trepassia appear to show a similar trend (compare Fig. 4c with Fig. 2a). The number of confidently identified taxa within this assemblage is not yet sufficient to take this study further, but such information is vital if we are to fully understand and document the life cycles and ontogenetic growth patterns of the Ediacaran rangeomorph taxa.

Filaments

Filamentous fossils on the Pigeon Cove surface range from 6 to 130 mm in length, and are typically 0.5–1 mm in width (Fig. 7). Filaments are often smoothly curved, with some looping back on themselves (but never coiling), implying that the organic material from which they were constructed was flexible. No primary organic material is found in association with these impressions. Some filaments appear to bifurcate (Fig. 7, white arrows), whereas other examples are clearly superimposed (Fig. 7a, black arrows). Importantly, the filaments are preserved in positive epirelief, and show no evidence of sediment displacement, making it highly unlikely that they represent trace fossils (see Jensen et al. 2005). The filamentous fossils are unevenly dispersed across the bedding plane (Fig. 3), and rarely come into contact with one another. They also exhibit a strong NE–SW general alignment of long axes (Fig. 6b), broadly parallel to neighbouring fronds. This alignment does not necessarily suggest that the filaments were tethered to the sea floor in the same way as the rangeomorphs, but it does imply that they were influenced by bottom-water currents.
Discussion

The Pigeon Cove bedding plane reveals the potential for preservation of significant assemblages of small fossils on Ediacaran bedding planes (see also Gehling 1999; Narbonne 2004). Fossils of juvenile Ediacaran organisms are rare in the Avalon region, potentially owing to taphonomic biases determined by the coarse grain size of the casting medium (Gehling et al. 2005). The possibility that the occurrence of juvenile forms is controlled by a temporal factor, such as a limited reproductive period, cannot yet be rejected. However, the relative scarcity of juvenile forms increases the importance of the Pigeon Cove specimens for studying early ontogenetic development within the rangeomorph group.

Proposed juvenile rangeomorphs such as Avalofractus, Beothukis and Bradgatia sp. have been described from Upper Island Cove, Newfoundland (Flude & Narbonne 2008; Narbonne et al. 2009), but those examples are, for the most part, considerably larger (length 15.6–82.5 mm, width 7.0–23.0 mm; Narbonne et al. 2009, table 1) and more ontogenetically developed than the specimens described herein. Specimens considered to be juvenile Charnia and Trepassia from the Mistaken Point Formation (Laflamme et al. 2007; down to 60 mm length), are again significantly larger than those described from Pigeon Cove. The only other reported Avalonian occurrences of comparably small Ediacaran body fossils are: (1) a handful of juvenile rangeomorphs from Charnwood Forest in the UK (e.g. Boynton & Ford 1995, fig. 2); (2) several Charniodiscus specimens from the Mistaken Point Formation of the SE Avalon Peninsula (Laflamme et al. 2004, fig. 4, 5; Laflamme & Narbonne 2008); and (3) ‘locality 14’ of Hofmann et al. (2008) from the Bonavista Peninsula (with Fractofusus andersoni specimens less than 10 mm in length). Other than the Upper Island Cove locality, these cited juvenile occurrences differ from Pigeon Cove specimens in forming only minor components of the preserved assemblages.

Morphological diversification of Ediacaran organisms, and their stratigraphic ranges in the Conception Group

The diminutive Ediacaran frondose taxa at Pigeon Cove demonstrate a range of morphological diversity. Prior to this study, the only reported Ediacaran macro-organisms from the Drook Formation of the Conception Group were Trepassia wardae, Thectardis avalonensis, Charnia antecedens, Aspidella terranovica, and the ivesheadiomorphs (Narbonne et al. 2005). The new small fronds reported herein represent two taxa identified to species level (Charnia masoni and Trepassia wardae), with aff. Charniodiscus spp. and Charnia aff. antecedens also being tentatively recognized. Neither Charnia masoni nor Charniodiscus spp. (Fig. 5a and b) have previously been reported from rocks of this antiquity (Fig. 8).

The newly expanded diversity of Ediacaran macro-organisms at Pigeon Cove demonstrates that a range of rangeomorph structural architectures, including the majority of those exhibiting ‘undisplayed’ branching architecture (sensu Brasier & Antcliffe 2009), had evolved only 3 Ma after the deposition of the Gaskiers tillite (Fig. 8). Interestingly, no ‘bipolar’ or ‘non-deterministic’ fronds (e.g. Fractofusus or Bradgatia; terms sensu Brasier & Antcliffe 2009) are currently known from below the upper Briscal Formation (Fig. 8). Determining whether rangeomorph structural architecture really does show a distinct and real evolutionary pattern through the late Ediacaran represents a significant avenue for future research.

The morphological diversity recorded in the Pigeon Cove assemblage raises questions concerning the timing of the evolutionary events leading to the diversification of macroscopic multicellular life. These questions resonate with those relating to the timing and nature of the Cambrian Explosion of metazoan morphological diversity, which has been a subject of debate since the proposal of evolution through natural selection by Charles Darwin (see historical discussion by Brasier 2009). The Ediacaran diversification of body plans can similarly be considered to result from either (1) taphonomic biases hiding an earlier phase of evolutionary diversification, with evolution of the Ediacaran biota being contemporaneous with or perhaps even prior to the Gaskiers glacial event (see Love et al. 2009; Maloof et al. 2010; Meert et al. 2011; Yuan et al. 2011), or (2) genuine explosive rates of evolution, which given our discoveries would require evolution of this morphological diversity within 3 Ma of the end of the Gaskiers glacial (see Shen et al. 2008). Determining which of these possibilities is correct, and their ultimate causes (e.g. a rise in atmospheric oxygen, the end of the glacial conditions, or other factors; e.g. Halverson et al. 2005; Butterfield 2009b), represents a major continuing focus of Precambrian research. Efforts should now be made to explore this problem by reducing the current gap in our knowledge of the macrofossil record prior to the Gaskiers glaciations.

Affinities of the Drook Formation filamentous fossils

The role of filamentous fossils in Ediacaran ecosystems remains to be fully resolved. Similar structures preserved as casts within siliciclastic successions have been reported from nearby beds within the Drook Formation, by Callow & Brasier (2009a), and also from the shallow marine to fluvial Ediacaran successions of the Long Mynd Hills in Shropshire, UK, by Peat (1984) and Callow & Brasier...
The forms described by those workers are of similar size to the material documented herein, and have been interpreted as microbial filaments (Callow & Brasier 2009a, b). The filamentous fossils documented herein from Pigeon Cove occur in substantially lower fossil densities, and lack both the distinctive hook shape and strongly parallel orientations of the only other filaments previously reported from the Conception Group (Callow & Brasier 2009a). A lack of preserved cell walls, of distinguishable sheaths or membranes, or indeed of any fine external or internal detail, precludes attempts to objectively test the proposed biological affinity of these Avalonian filamentous macrofossils. They seem unlikely to be cyanobacterial, as they occur in sediments postulated to have been deposited below the photic zone (e.g. Wood et al. 2003; Liu et al. 2010). Filamentous fossils such as Grypania (e.g. Butterfield 2009a), may provide useful analogues, being of similar dimensions to the Avalonian filament assemblages. Other Ediacaran fossils of similar dimensions include the purported alga Vendotaenia (Gnilovskaya 1983; Cohen et al. 2009), sabelliditids (Urbanek & Mierzejewska 1983; Jensen et al. 2007), or the test linings of agglutinated foraminifera such as Platysolenites (McIlroy et al. 2001; Winchester-See To & McIlroy 2006), but those forms differ in possessing features such as longitudinal striae or transverse ornamentation. However, the absence of these features in the Pigeon Cove assemblage may be a taphonomic artefact resulting from preservation as siliciclastic casts, as opposed to reflecting an original unornamented morphology.

Of more comparative value are the dimensions of the Pigeon Cove filaments, and the presence of simple ‘Y’-branching in some specimens (Fig. 7). Such branching is seen in extant marine organisms including fungi, actinobacteria and siphonalean green algae, and in several pre-Ediacaran multicellular fossils (e.g. Butterfield 2009a; Brasier et al. 2010). If correctly interpreted, this ‘Y’-shaped branching would argue against the filaments representing the sheaths of giant sulfur bacteria like those of extant Thioploca or Beggiatoa (Schulz et al. 1996; Teske & Nelson 2006; Cohen et al. 2009; Høgslund et al. 2009). The ‘H’- and ‘T’-shaped branching typical of fungal hyphal fusion (e.g. Butterfield 2005) has not been seen, but this observation alone cannot rule out a fungal affinity for the filaments.

Some tubular and filamentous fossils of the Miaohe biota of China show similar simple gross morphologies (e.g. Xiao et al. 2002; Yuan et al. 2005), but are smaller and do not exhibit branching. Unclassified tubular fossils from the Nama assemblage are strikingly similar in general appearance to the Pigeon Cove material, but again do not branch (Cohen et al. 2009, fig. 4.3). Meanwhile, the Ediacaran tubular body fossil Somatohelix sinuosus from Australia is of similar simple morphology, but is commonly of larger dimensions (3–7 mm width), and has not been observed to branch (Sappenfield et al. 2011).
The possibility that the filaments could be part of a larger Ediacaran macro-organism is worthy of discussion. Some of the ‘rays’ of the discoidal fossil *Hemialora stellaris*, found to bear a strong resemblance to the holdfast of the frondose taxon *Primocandelabrum hemialorum* (Hofmann *et al.* 2008, are of similar dimensions to the Pigeon Cove filaments, and can be observed to extend for tens of centimetres away from their discs (Hofmann *et al.* 2008). *Hemialora* is, however, not associated with the filamentous fossils at Pigeon Cove, and is not currently known from rocks of the Drook Formation. Alternatively the filaments could be part of a larger filament-bearing organism, comparable with the probable algae *Doushantouphycnon cometa* or *Huangzhophycnon fluticulosum* from the Lantian Formation of China (Yuan *et al.* 2011, Fig. 2a and b), but the significantly different modes of preservation between these two assemblages make direct comparison difficult. One ivesheadiomorph specimen on the Pigeon Cove surface is seemingly attached to a large filamentous strand that stretches for a distance of several metres (Narbonne *et al.* 2001; Liu *et al.* 2011, plate 1.5). However, the uniqueness of this specimen, combined with the lack of any preserved features at the end of the small filaments described herein, suggests that the two morphotypes are not easily related.

As can be seen, there exists a wide range of potential affinities for the Pigeon Cove filamentous fossils. At this point in time we are not in a position to confidently identify them, but the relationship between filamentous fossils and Ediacaran body fossils in Avalonia certainly warrants further investigation.

**Ecological succession**

To find numerous frondose fossils possessing finely preserved small features, on a bed where much larger fossil impressions are present but comparatively poorly preserved, is intriguing. A recently proposed model for ivesheadiomorph preservation suggests that many effaced forms, such as the ‘pizza discs’ from this bedding plane, are preservational relicts created by microbial growth on and around decaying Ediacaran macro-organisms (Liu *et al.* 2011). Ivesheadiomorphs at Pigeon Cove can be preserved in high positive epirelief, can be up to 0.5 m in diameter, and are highly variable in morphology. Their low fidelity has been explained by a combination of microbially mediated and autolytic decay processes (Liu *et al.* 2011), a hypothesis that has generated considerable debate (Wilby *et al.* 2011; Laflamme *et al.* 2012). An important implication of this hypothesis is that the preserved fossil communities are time-averaged assemblages, preserving organisms that were both living and dead at the time of burial.

Two contrasting models have since been proposed to explain ivesheadiomorph morphologies, both of which argue against significant time-averaging of the fossilized biological assemblages. First, Wilby *et al.* (2011) suggested that ivesheadiomorphs represent the sedimentary infill of hydraulic voids created by contemporaneous specimens caught within the ash fall or flow that smothered the organisms, and held clear of the substrate. We argue that this suggestion has less explanatory power than the ‘effaced preservation’ hypothesis of Liu *et al.* (2011). It cannot explain why ivesheadiomorphs on Avalonian bedding planes can often be seen to lie beneath benthic reclining organisms (such as *Fractofusus*; see Gehling & Narbonne 2007; Liu *et al.* 2011). It also predicts the presence of a well-preserved tethering holdfast adjacent to the ivesheadiomorph, a feature not consistently observed during our extensive field investigations. Finally, this hydraulic model is challenged by the numerous intermediate stages of preservation preserved on Avalonian bedding planes, ranging from high to low fidelity, that we have documented from multiple taxa and localities (Liu *et al.* 2011).

The second alternative, that of Laflamme *et al.* (2012), interprets the ivesheadiomorphs as discrete microbial colonies living on or within the microbial mats that covered the sea floor. Those workers viewed the irregular lobate morphology as the combined result of sediment capture from the water column, and trapping of bacterially produced gases beneath the colony (Laflamme *et al.* 2012). Many of the points put forward in support of this microbial colony argument, such as the juxtaposition of ivesheadiomorph specimens, and the superimposition of fronds above ivesheadiomorphs, are also consistent with ivesheadiomorphs being the products of microbial decay (see Liu *et al.* 2011). Other arguments, such as the absence of *Charniodiscus* or other rangeomorphs in the Drook Formation, are overcome by the findings presented herein. The microbial colony model also struggles to explain the observed spectrum of good to effaced preservation on single bedding planes.

At present, we therefore find that the effaced preservation hypothesis (Liu *et al.* 2011) provides the most parsimonious explanation for ivesheadiomorph morphology, with the power to explain a highly diverse collection of ivesheadiomorph traits. The effaced preservation hypothesis also holds substantial predictive power. It predicts the presence of a gradation in preservational fidelity of rangeomorph specimens, and the superimposition of ‘living’ rangeomorphs on top of ivesheadiomorphs (both of which are observed). Consequently, ivesheadiomorphs remain best regarded as the microbially effaced remains and overgrowths of dead and decaying organisms that lay upon the sea floor.

One final prediction is that if we are seeing time-averaged assemblages on single bedding planes, there should be evidence of cycles of growth and decay, followed by evidence for colonization of substrates by pioneer communities. The fossil assemblage at Pigeon Cove appears to show evidence for this, since it records the co-occurrence of large degraded Ediacaran macro-organisms (ivesheadiomorphs) alongside well-preserved, ‘living’ juvenile fronds at the time of the smothering ashfall event. This suggests that a population of mature, possibly senescent organisms was succeeded by a juvenile generation prior to burial. If our interpretation is indeed correct, then a smothering ash was able to record a remarkable snapshot of secondary community succession (whereby colonization took place on a previously developed substrate; e.g. Horn 1974) on a single surface (Fig. 9). Evidence of several fronds being preserved on top of ivesheadiomorph impressions (e.g. C63, Fig. 5a) supports the assertion that the small fronds postdate ivesheadiomorphs on this bedding plane. This seemingly represents the earliest documented example of such community succession in the Ediacaran macrofossil record. Although Clapham *et al.* (2003) have previously discussed ecological succession from the Mistaken Point biotic assemblages, that study documented multiple bedding-plane communities at different stages of succession in an attempt to determine whether different successional stages could be recognized. The approach of Clapham *et al.* thus differs from the occurrence described herein, in which community succession may be observed ‘in action’ on a single horizon.

**Conclusions**

The new assemblage of small fronds and filaments reported herein extends the stratigraphic ranges of several macroscopic taxa to c. 579 Ma, increasing the diversity of the earliest assemblages of the classic Ediacaran biota. Taken at face value, this suggests an ‘Ediacaran Explosion’ of macro-morphological diversity, though the possibility of a pre- or syn-Gaskiers evolutionary period remains viable. The combination of a community of juvenile rangeomorph fossils, buried alongside a collection of large ivesheadiomorphs that are presumed to represent the dead and rotting members of an earlier
community (see Liu et al. 2011), may reflect a remarkable preservation of ecological community succession upon the Avalonian sea floor. It also suggests that conditions on the sea floor were not constant through time, but heterogeneous. These variations could be related to seasonal inputs of organic matter from the ocean surface, as found on the deep sea floor beneath upwelling water masses (e.g. Ducklow 1993), or to episodic changes in bottom water conditions, as found around deep water cold seeps and vent communities (Levin 2005). Investigation of the nature of these controls warrants further research.

Macroscopic filaments, of uncertain biological affinity, appear to be a distinct component of Avalonian and indeed Ediacaran successions, and future work should be undertaken to determine whether they represent an integral component of Ediacaran ecosystem dynamics. Documentation of the full importance of this bedding plane can also be incorporated into the management of this unique palaeontological site. Our map (Fig. 3) permits quantitative monitoring of erosion and weathering rates on this surface, providing useful information for policy makers and researchers on how best to conserve and protect fossil-bearing sites within the Mistaken Point Ecological Reserve.

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Fig. 9. A simplified interpretation of the hypothesized ecosystem succession preserved on the Pigeon Cove bedding surface. An incumbent population of large rangeomorphs dies, and as they decay, a new population of juveniles enters and begins to grow. The bed is smothered by volcanic ash before the juveniles can grow to maturity, preserving all organisms. It should be noted that although rangeomorphs are illustrated here standing upright in the water column, they may in fact have been inclined or even reclining on the sea floor (see Grazhdankin 2004).
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