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Two new Ediacaran small fronds from Mistaken Point, Newfoundland

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Abstract.—Small, stemmed frond fossils are common in Ediacaran-aged strata (ca. 565 Ma) at Mistaken Point, Newfoundland, and many of them have previously been informally referred to as 'dusters,' but due to their small size and consequent relatively poor preservation, they have not yet been described taxonomically. Two new genera are herein defined on the basis of their unique constructions: the mop-like rangeomorph *Plumeropriscum hofmanni* new genus new species, and a flabellate, lobate frond *Broccoliforma alta* new genus new species. *Plumeropriscum hofmanni* n. gen., n. sp. has a three-dimensional petalodium structure with numerous primary branches attached at the base of the petalodium rather than at a central axis. *Broccoliforma alta* n. gen., n. sp. lacks visible branching, and instead has a lobate morphology with a petalodium that is at least superficially similar to the ivesheadiomorph *Blackbrookia*. Several other previously described taxa had also been included under the umbrella of 'dusters.' Collectively, these taxa show that the low epibenthic tier that small fronds occupied was more diverse than previously realized, with multiple taxa converging on the stemmed, small-frond body plan.

Introduction

Macroscopic Ediacaran fossils range from 579 to 541 Ma and are the oldest known large, architecturally complex biota in the fossil record (Narbonne, 2011). Ediacara-type taxa consist of soft-bodied organisms preserved as casts or molds, typically at the bases of event beds induced by storms, turbidity currents, or volcanic eruptions. Preservational conditions characteristic of the Ediacaran sea floor, e.g., the prevalence of microbial mats and a lack of pervasive bioturbation (Gehling, 1999; Seilacher, 1999), allowed for their preservation in numerous fossil localities around the world (Narbonne, 2005; Fedonkin et al., 2007; Xiao and Laflamme, 2009; Erwin et al., 2011). There has been a great deal of controversy surrounding the affinities of the Ediacara biota with a wide variety of interpretations. In general, however, focus has shifted from classifying the Ediacara biota as a whole to evaluating each Ediacaran taxon separately, and at present, the prevailing view is that many or most Ediacaran taxa represent extinct clades at a high taxonomic level along with some stem-group animals, including potential sponges and mollusks (Fedonkin et al., 2007; Xiao and Laflamme, 2009, Erwin et al., 2011; Sperling et al., 2011; Laflamme et al., 2013). Considerable controversy still exists for the affinities of many Ediacaran taxa.

Ediacaran fronds in particular were traditionally interpreted as pennatulacean cnidarians (e.g., Sprigg, 1947, 1949; Glaessner and Wade, 1966; Anderson and Conway Morris, 1982; Jenkins, 1985, 1992; Boynton and Ford, 1995) or ctenophores (Gürich, 1933; Dzik, 2002), but other interpretations have included fungi or fungigrade organisms (Peterson et al., 2003), elaborate colonies of prokaryotes (Steiner and Reitner, 2001), terrestrial lichens (Retallack, 1994, 2013), or organisms belonging to an extinct high-level clade, either at the kingdom level (Seilacher, 1992) or the phylum level within the Metazoa (Pflug, 1970, 1972; Buss and Seilacher, 1994). Interpretations of Ediacaran fronds as cnidarian or ctenophore filter feeders have been discarded due to the absence of openings large enough to accommodate filter-feeding polyps or other feeding structures (Narbonne, 2004). Interpretations that require photosynthesis have been discarded for all taxa found in Newfoundland on the basis of numerous sedimentological studies of the strata in which the fossils are found in that area, which conclude that the depositional environment was deep marine, well below the photic zone (Misra, 1971; Myrow, 1995; Wood et al., 2003; Ichaso et al., 2007; Mason et al., 2013). Geochemical evidence is not consistent with a chemosynthesis-based ecosystem (Canfield et al., 2007). The current leading hypothesis is that they are stem-group animals that represent an early 'failed experiment' in metazoan evolution (Narbonne, 2005; Xiao and Laflamme, 2009; Liu et al., 2015). This interpretation is supported by paleoecological analyses (Clapham and Narbonne, 2002; Clapham et al., 2003), which found that, in the census populations preserved in situ in the Mistaken Point area (Figs. 1, 2), the biota show epifaunal tiering and other ecological patterns similar to those observed in metazoan filter-feeding communities of the Phanerozoic (Narbonne, 2005).

The Mistaken Point area is exceptional for its abundance and diversity of deep-marine Ediacaran fossils preserved beneath ash beds. The vast majority of taxa found there have been studied and described in great detail (e.g., Gehling and Narbonne, 2007; Laflamme et al., 2007; Bamforth et al., 2008;

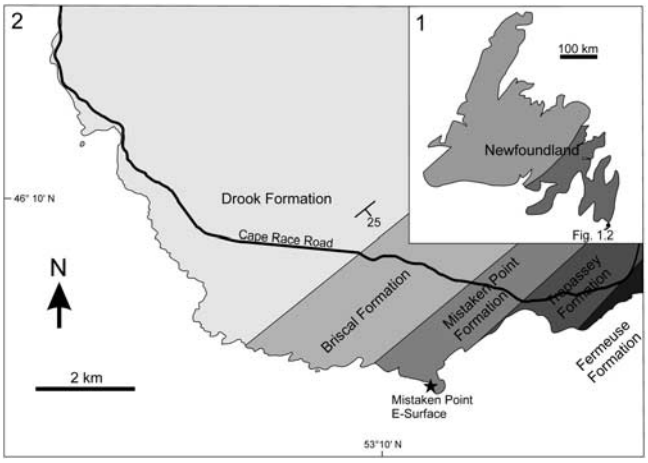

Figure 1. (**1**) Location map showing the study area in the southeast of the island of Newfoundland. The Avalon Terrane is in dark gray. (**2**) Geologic map of the Mistaken Point area, with the Mistaken Point E-surface marked with a star. The G-surface is exposed meters away from the E-surface. Adapted from Clapham et al., 2003.

Liu et al., 2011, 2015) and used in paleoecological studies (Clapham and Narbonne, 2002; Clapham et al., 2003; Darroch et al., 2013). However, many of the stemmed, small-frond fossils have previously received relatively little attention, which this study seeks to redress.

Ediacaran frond morphology

The frond body plan is common among Ediacaran assemblages all over the world (Laflamme and Narbonne, 2008b), including South Australia (Glaessner and Daily, 1959; Jenkins and Gehling, 1978), Namibia (Pflug, 1970, 1972; Narbonne et al., 1997; Vickers-Rich et al., 2013), the White Sea area of Russia (Fedonkin, 1985), central England (Boynton and Ford, 1995; Wilby et al., 2011), and eastern Newfoundland, Canada (Misra, 1971; Narbonne and Gehling, 2003; Laflamme et al., 2004, 2007; Hofmann et al., 2008; Narbonne et al., 2009). This paper follows the morphological terminology proposed by Laflamme and Narbonne (2008a, b).

Ediacaran fronds are generally composed of three main parts (Fig. 3): a basal holdfast, typically bulbous or disc-shaped; a stem and/or central stalk (the stalk being an extension of the stem into the petalodium); and a leaf-like, morphologically complex petalodium (Laflamme and Narbonne, 2008a, b), the ornamented leaf-like section generally composed of two or more 'petaloids' (Laflamme and Narbonne, 2008a, b), each composed of repeating modules arranged in branches attached to the stalk or stem. The petalodium, as the most morphologically complex and variable part of the frond, is most important for identification and classification (Jenkins and Gehling, 1978). The largest branches connected directly to the stem or stalk are termed primary branches; any smaller branches that emerge from those branches are termed secondary branches, and even smaller branches attached to the secondary branches are termed tertiary branches. The frond body plan characteristic of many Ediacaran taxa is likely an example of convergent evolution due to shared ecology—in this case, a common need to elevate above the substrate, the same reason that frond-shaped morphologies are

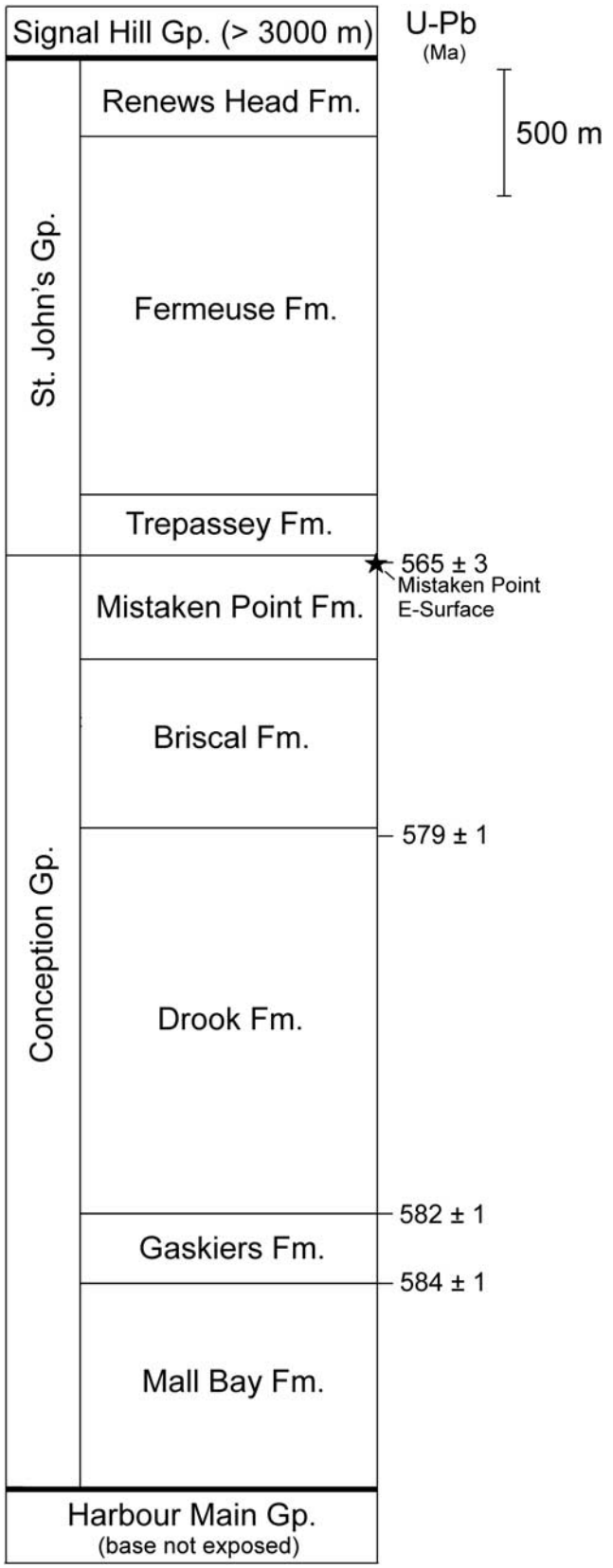

Figure 2. Ediacaran stratigraphy of the eastern Avalon Peninsula. The Mistaken Point E-surface is marked with a star. U–Pb dates from Benus (1988) and Narbonne et al. (2012b). Fm. = Formation; Gp. = Group.

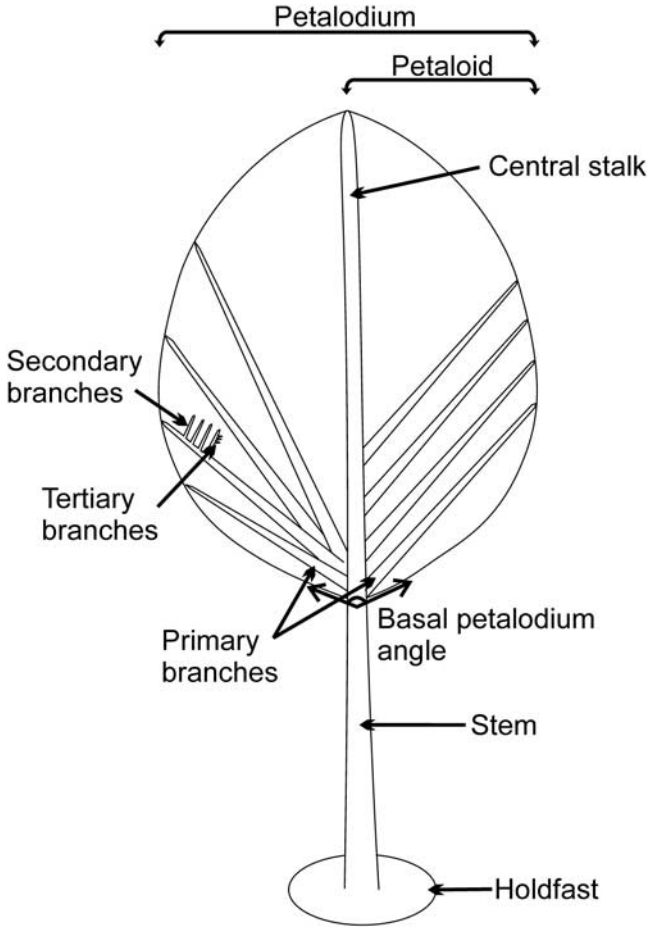

Figure 3. Generalized morphology of a stemmed frond. The three main components are the holdfast, stem, and the petalodium. Primary branches can be attached to a central stalk, as in the right half of the figure, or to the distal end of the stem, as in the left half of the figure.

observed today across several kingdoms (plants, animals, and fungi; Laflamme and Narbonne, 2008b). Laflamme and Narbonne (2008a, b) described four distinct branching architectures that they regarded as apomorphies for four high-level taxonomic groups within the Ediacara biota. Three of these are known from Mistaken Point: *Arborea*-type branching, which consists of parallel primary branches attached to a central stalk at right angles with teardrop-shaped secondary branches; *Rangea*-type branching, which has been called fractal—self-similar over at least three orders of magnitude, and constructed from individual 'rangeomorph frondlets'; and *Charnia*-type branching, which is subcategory of *Rangea*-type, composed of sigmoidal primary branches with a zigzagging central axis, and secondary modular elements that are composed of tertiary rangeomorph elements. The latter two belong to a high-level clade called the Rangeomorpha (Pflug, 1972; Jenkins, 1985; Narbonne, 2004; Laflamme et al., 2013), and the first constitutes a clade called the Arboreomorpha (Laflamme et al., 2013). Rangeomorphs, along with the arboreomorph genus *Charniodiscus* Ford, 1958, dominate the deep-sea Ediacaran assemblages of eastern Newfoundland (Narbonne, 2004; Hofmann et al., 2008; Narbonne et al., 2009) and central England (Boynton and Ford, 1995; Wilby et al., 2011; Liu et al., 2015), and are known sparingly from younger and shallower Ediacaran localities (Fedonkin et al., 2007).

Laflamme et al. (2009) concluded that Ediacaran fronds could have absorbed dissolved organic carbon osmotrophically, and that the fractal branching of rangeomorph elements would have increased surface-area-to-volume ratios sufficiently for this to be a viable strategy. This mode of feeding is used today mainly among bacteria, but a larger pool of available dissolved organic carbon in the Ediacaran combined with the high surface-area-to-volume ratio would have made this a viable feeding strategy for macroscopic Ediacaran organisms (Laflamme et al., 2009). It is therefore suggested that the tiering observed in the rangeomorph-dominated assemblages in eastern Newfoundland and central England evolved due to competition to take maximum advantage of the dissolved organic carbon in the water column of their environments, and that this was the ecological pressure that led to the convergent evolution of a frond body plan among multiple clades in the Ediacaran (Laflamme and Narbonne, 2008b).

Geological setting

Much of eastern Newfoundland, including the Avalon, Bonavista, and Burin peninsulas, is part of the Avalon Terrane (O'Brien et al., 1983; Myrow, 1995; Fig. 1.1), which consists of Neoproterozoic and early Paleozoic strata that were deposited on and adjacent to the microcontinent Avalonia, a volcanic arc off the coast of Gondwana (Nance et al., 2002; Pisarevsky et al., 2011). Architecturally complex fossils have been found in three main locations in Ediacaran strata of the Avalon Terrane of eastern Newfoundland (Fig. 1): the Mistaken Point area on the southeastern tip of the Avalon Peninsula (see review by Narbonne et al., 2012b); the Spaniard's Bay area in the northwest of the Avalon Peninsula (Narbonne, 2004; Ichaso et al., 2007; Flude and Narbonne, 2008; Narbonne et al., 2009); and the Catalina Dome on the eastern coast of the Bonavista Peninsula (O'Brien and King, 2004; Hofmann et al., 2008; Mason et al., 2013). Ediacaran fossils occur commonly to abundantly in the Drook, Briscal, and Mistaken Point formations of the Conception Group, and the Trepassey and Fermeuse formations of the St. John's Group (Fig. 1.1, 1.2). The small frond specimens included in this study were found in the Mistaken Point Formation in the Mistaken Point Ecological Reserve, Avalon Peninsula.

The Mistaken Point Formation is the uppermost formation in the Conception Group, part of a deep marine siliciclastic succession that overlies the mainly igneous rocks of the Harbour Main Group (King, 1988, 1990). The Mistaken Point Formation is dominated by mudstone-rich, siliciclastic turbidites deposited at the toe-of-slope in a forearc basin (Misra, 1971; Wood et al., 2003; Ichaso et al., 2007; Mason et al., 2013). The turbidites are primarily Bouma $T_{(C)DE}$ beds (Bouma, 1962), with 'T_F' interturbidite, laminated mudstone deposits from the low energy intervals between turbidity currents (e.g., Hesse, 1975; Wood et al., 2003). The absence of wave-generated structures or evidence of exposure in several kilometers of stacked turbidites in the succession implies that the depositional environment was at great depth, from which it has been inferred that organisms living in that environment could not have relied on photosynthesis (Wood et al., 2003; Narbonne, 2005; Ichaso et al., 2007). In addition to the mudstone-rich siliciclastic turbidites,

the succession is punctuated by thin beds of volcanic ash from the adjacent island arc deposited within the T_F divisions, which are responsible for the preservation of the soft-bodied organisms beneath them (Seilacher, 1999; Wood et al., 2003; Ichaso et al., 2007) in what Narbonne (2005) termed 'Conception-style preservation.' Because ash layers are less resistant than the silicified mudstone, the rocks tend to weather along the planes of ash beds and expose the surface of the mudstone immediately underneath. The fossils are preserved as both positive and negative epireliefs on these surfaces (Narbonne, 2005). Frond-shaped organisms, which were tethered to the sea floor but otherwise were flexible in the water column, were typically oriented in a common direction with other fronds on the same rock surface, either parallel with the downslope direction inferred from Bouma T_C-division turbidite current ripples or in a contour-parallel orientation 90° counterclockwise from the downslope direction (Wood et al., 2003).

The Mistaken Point assemblage

The Mistaken Point Ecological Reserve, southeastern Avalon Peninsula, Newfoundland, is famous for its exceptional Ediacaran fossils that are exposed on numerous broad, flat surfaces along the coastal cliffs (Misra, 1971; Narbonne et al., 2007). These surfaces are effectively snapshots of the Ediacaran sea floor, with fossils of the soft-bodied biota preserved in relief by episodic burial by volcanic ash. The succession (Fig. 2) contains many significant fossil horizons, including the oldest known complex macroscopic fossils, found in the Drook Formation (Narbonne and Gehling, 2003), dated at 578.8 ± 0.5 Ma (van Kronendonk et al., 2008; Narbonne et al., 2012b). These include the rangeomorph fronds *Trepassia* Narbonne, Laflamme, Greentree, and Trusler, 2009 (see also Narbonne and Gehling, 2003); *Charnia* Ford, 1958 (see also Laflamme et al., 2007), and a possible specimen of *Charniodiscus* (see Liu et al., 2012); along with the possible early sponge (Sperling et al., 2011) *Thectardis* Clapham, Narbonne, Gehling, Greentree, and Anderson, 2004. The oldest known stemmed fronds, *Culmofrons* Laflamme, Flude, and Narbonne, 2012, are found in the overlying Briscal Formation, along with the branching rangeomorph *Bradgatia* Boynton and Ford, 1995 (see Flude and Narbonne, 2008) and the spindle-shaped rangeomorph *Fractofusus* Gehling and Narbonne, 2007. Above that, the Mistaken Point Formation is the most richly fossiliferous part of the succession, with diverse assemblages of rangeomorphs and other Ediacaran taxa preserved at Gull Rock Cove and Mistaken Point itself (Clapham et al., 2003; Wood et al., 2003), including the well-known and well-studied Mistaken Point E-surface, dated at 565 ± 3 Ma (Benus, 1988; Narbonne et al., 2012b), on which most of the fossils in this study are found. The overlying Trepassey Formation also contains fossil assemblages preserved by ash (Wood et al., 2003; Bamforth et al., 2008). Above that formation, ash deposition had ceased in this part of Newfoundland, so the taphonomic window allowing for preservation of architecturally complex Ediacaran fossils was closed (Gehling et al., 2000; Wood et al., 2003; Narbonne, 2005; Mason et al., 2013).

Over the last decade, numerous taxa have been described from the Mistaken Point area and the E-surface in particular, as well as elsewhere in the Ecological Reserve and elsewhere in Newfoundland. These have included taxa known from Charnwood Forest, England and new taxa, totaling 26 types (Narbonne et al., 2012a). Many of these taxa have been rangeomorphs: organisms constructed of numerous similar, fractally branching rangeomorph 'modules' assembled into a variety of different body plans (Narbonne, 2004), e.g., the reclining, spindle-shaped *Fractofusus* (Gehling and Narbonne, 2007), comb-shaped *Pectinifrons* Bamforth, Narbonne, and Anderson, 2008, bush-shaped *Bradgatia* (Flude and Narbonne, 2008), stemless elongate frond *Charnia* (Laflamme et al., 2007), and the stemmed, tulip-shaped frond *Culmofrons* (Laflamme et al., 2012). Mistaken Point taxa that do not belong to the Rangeomorpha include *Thectardis* (Clapham et al., 2004) and the stemmed arboreomorph frond with a discoid holdfast *Charniodiscus* (Laflamme et al., 2004). All known taxa were benthic and immobile, although Liu et al. (2010) reported a single level of putative trace fossils implying surficial locomotion from Mistaken Point.

Virtually all fossils in the Mistaken Point area have been named, with the notable exception of many of the small fronds. Many small fronds are simply juveniles of known taxa; Liu et al. (2012) reported the discovery of particularly tiny juvenile fronds from the Drook Formation, most of which can be identified as *Charnia, Trepassia,* or possibly *Charniodiscus*. However, some small fronds exist in the Mistaken Point Formation that bear little resemblance to any named taxa. Hofmann et al. (2008) described two distinctive small frond taxa from the Bonavista Peninsula—*Primocandelabrum* Hofmann, O'Brien, and King, 2008 and *Parviscopa* Hofmann, O'Brien, and King, 2008—which bear no resemblance to any larger Ediacaran taxa. In previous paleoecological work at Mistaken Point (Clapham and Narbonne, 2002; Clapham et al., 2003), many small, stemmed fronds were grouped together and informally called 'dusters,' but closer inspection finds significant disparity within that informal grouping, including representatives of the taxon *Primocandelabrum* from the Bonavista Peninsula.

Interpretation of the small fronds has been problematic due to taphonomy. Because of the mode of preservation of the Mistaken Point biota, the resolution of the fossils is dependent upon the grain size of the ash beneath which they are preserved. This mode of preservation presents a problem for the study of the smallest fossils in the assemblage in particular, because their features are often obscured proportionally more than in larger specimens. Other Ediacaran fronds are classified heavily on the basis of their secondary and tertiary branching, which are not discernible in most small frond specimens. Because of this difficulty, the small fronds are some of the last fossils of the Mistaken Point E-surface to be described systematically, and only the best-preserved specimens can be identified with confidence.

Methods

Removal of fossils from the Mistaken Point Ecological Reserve is strictly prohibited, so paleontological study of the Mistaken Point biota relies heavily on field photographs, latex molds, and casts of the original fossils. A 70-m^2 cast of the Mistaken Point E-surface was made by Research Casting International in 2009 and 2010 in association with the provincial government of

Table 1. Measurements of retrodeformed specimens of *Plumeropriscum* and *Broccoliforma*. All measurements in centimeters except petalodium basal angle, which is measured in degrees.

Specimen number	Taxon	Figure	Surface	Holdfast diameter	Stem length	Stem width	Petalodium length	Petalodium width	Total frond length	Petalodium basal angle
1	*Plumeropriscum*	4.1, 4.3	E	1.18	2.87	0.29	5.51	5.00	9.11	133
2	*Plumeropriscum*	–	G	3.58	5.74	1.84	7.58	7.47	13.42	133
3	*Plumeropriscum*	4.5	E	1.31	3.16	0.46	5.08	5.24	8.09	107
4	*Broccoliforma*	4.2, 4.4	E	3.20	3.92	0.89	3.56	7.92	7.48	175
5	*Broccoliforma*	4.6	E	2.52	2.87	0.70	4.41	6.65	7.42	175

Newfoundland and Labrador, the Royal Ontario Museum, Johnson GeoCentre, Queen's University, and the University of Oxford. The complete cast is located in Research Casting International's facility in Trenton, Ontario, and this was an invaluable resource because it allowed thorough inspection of a large portion of the Mistaken Point E-surface—on which most of the small frond fossils included in this study are found—in a controlled indoor environment. Two hundred and fifty-one fossils were numbered and photographed from this cast, although many were too poorly preserved and ambiguous to be identified in this study. Additional field photographs were taken in Newfoundland of small fronds on parts of the E-surface that were not included in the casting project, as well as of two fossils from the G-surface. Dozens of latex molds of these and other fossils made by the authors and other Queen's University researchers were also used as resources and photographed for comparison. One original specimen (ROM 38641) that was previously collected from the E-surface by the Royal Ontario Museum was also included in this study.

Strata in the Mistaken Point area have been subjected to tectonic shortening of ~40% on most of the fossiliferous surfaces. This deformation is especially apparent in fossils with originally circular features, e.g., frond holdfasts, which are circular in every undeformed Ediacaran assemblage in the world (Ford, 1958; Jenkins and Gehling, 1978; Boynton and Ford, 1995; Wilby et al., 2011). In the Mistaken Point area, these fossils have become oblong, all in the same direction and the same amount on a given bedding surface, elongate in the direction of cleavage (Seilacher, 1999; Wood et al., 2003). To account for this deformation, each photograph was retrodeformed (i.e., stretched in the direction of shortening until oblong holdfasts became circular; Seilacher, 1999; Wood et al., 2003; Ichaso et al., 2007). In specimens without a holdfast to use as a direct indicator of the degree of shortening, an average retrodeformational ratio from across the surface was used.

Once retrodeformed, each specimen was measured for a variety of dimensions: holdfast diameter, stem length, stem width, petalodium length, petalodium width, frond length, and basal petalodium angle. Ratios between these measurements were compared to find morphometric differences in overall shape of the fronds. Petalodium branching architecture was also carefully observed in sufficiently well-preserved specimens.

Approximately 270 fossils in total were numbered and photographed. Many were identified as or tentatively assigned to known Ediacaran taxa, including *Charnia*, *Culmofrons*, *Bradgatia*, *Charniodiscus, Avalofractus* Narbonne, Laflamme, Greentree, and Trusler, 2009, *Beothukis* Brasier and Antcliffe, 2009, and *Primocandelabrum.* Others were too ambiguous to identify as either existing taxa or newly defined taxa. For many potential small frond fossils from the E-surface, only the holdfast and stem/stalk were preserved, with no evidence of the petalodium.

In all, five clear, well-preserved small fronds were determined to belong to two new monotypic genera. Measurements of these specimens are summarized in Table 1. Other small frond specimens with similar shapes might belong to these taxa, but due to poor preservation, such identifications are uncertain.

Systematic paleontology

Group Rangeomorpha Pflug, 1972
Genus *Plumeropriscum* new genus

2003 'Feather dusters,' Wood et al., fig. 9.
2005 'Feather dusters,' Narbonne, fig. 5e.

Type species.—*Plumeropriscum hofmanni* n. sp., by monotypy.

Diagnosis.—As per species.

Etymology.—From the Spanish 'plumero' meaning feather duster, and the Latin 'priscum' meaning old.

Plumeropriscum hofmanni new species
Figures 4.1, 4.3, 4.5, 5.1, 5.2

Holotype.—On the Mistaken Point E-surface. Plastotype on the E-surface cast at the Royal Ontario Museum, ROM 60065.1.

Diagnosis.—Cm-scale frondose fossil with a roughly deltoid petalodium attached to a bulbous or discoidal holdfast by a cylindrical stem. The petalodium consists of at least nine thin primary branches attached at the base of the petalodium extending upward distally from the base of the petalodium. Where well-preserved, rangeomorph architecture is subtly visible. No axial stalk is evident. Branches in the foreground can be seen in their entirety, but background branches are partially obscured beneath foreground branches, implying a bushy, mop-like shape of the organism before compaction.

Description.—The holotype (Figs. 4.1, 4.3, 5.1, 5.2), from the Mistaken Point E-surface, is a 9.1 cm-long frond with a small, bulbous holdfast, 1.2 cm in diameter, attached to a cylindrical stem (2.9 cm long, 3 mm thick). At the end of the stem, many (at least 12 visible in this specimen), thin (1 mm or less) primary branches emerge from the base of the petalodium, forming a deltoid petalodium (5.5 cm long, 5 cm wide) with a 133° angle at

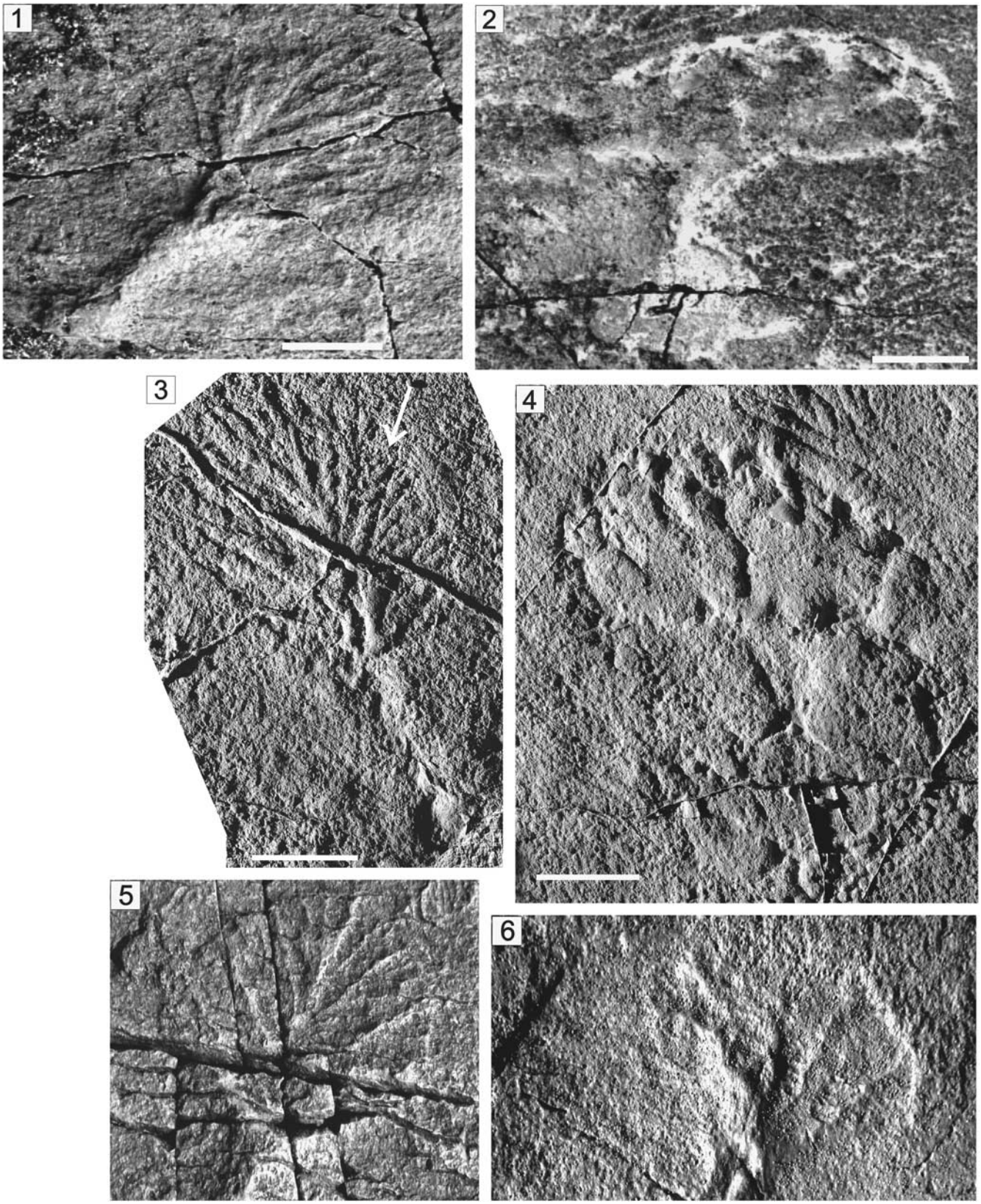

Figure 4. Light photographs of new small frond taxa. (**1**) Unretrodeformed holotype fossil of *Plumeropriscum hofmanni* n. gen. n. sp. from the Mistaken Point E-surface. (**2**) Unretrodeformed holotype fossil of *Broccoliforma alta* n. gen. n. sp. from the Mistaken Point E-surface. (**3**) Retrodeformed latex mold of the holotype of *Plumeropriscum hofmanni* n. gen. n. sp.; white arrow points to a primary branch with visible secondary branching. (**4**) Retrodeformed latex mold of the holotype of *Broccoliforma alta* n. gen. n. sp. (**5**) Retrodeformed field photograph of an additional specimen of *Plumeropriscum hofmanni* n. gen. n. sp. on the Mistaken Point E-surface. (**6**) Retrodeformed photograph of an additional specimen of *Broccoliforma alta* n. gen. n. sp. from the E-surface cast at the Research Casting International facility in Trenton, Ontario. Scale bars = 2 cm.

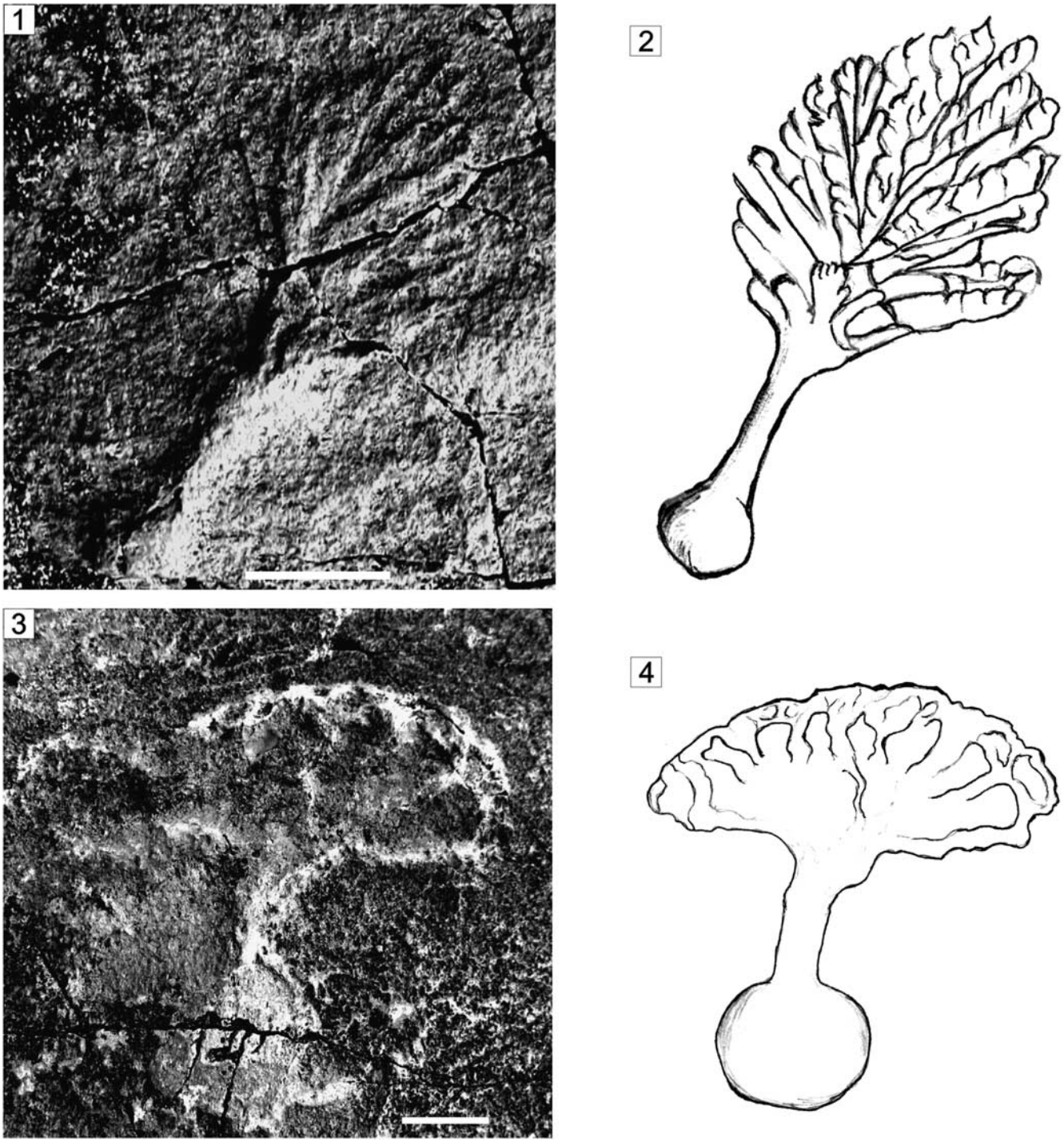

Figure 5. (**1**) Retrodeformed field photograph of the holotype of *Plumeropriscum hofmanni* n. gen., n. sp. (**2**) Sketch of the holotype of *Plumeropriscum hofmanni* n. gen. n. sp. based on numerous photographs of the fossil and latex molds under different lighting conditions. Secondary branching is visible in different areas of the fossil in different photographs depending on the light source. (**3**) Retrodeformed field photograph of the holotype of *Broccoliforma alta* n. gen. n. sp. (**4**) Sketch of the holotype of *Broccoliforma alta* n. gen. n. sp., based on numerous photographs of the fossil and latex molds. Scale bars = 2 cm.

the base, and an 80° angle at a pointed tip on the distal end of the petalodium. Additional primary branches emerge from behind the branches, with visible connections to the base. Subtle secondary branching is visible on several branches, which implies rangeomorph affinity.

In addition to the holotype, there are two more specimens that are well-preserved (Fig. 4.5): one also from the E-surface and the other from the slightly stratigraphically higher G-surface. Several other small frond fossils from Mistaken Point might belong to the species but are not preserved clearly enough to be certain. The G-surface specimen is somewhat larger than the two E-surface specimens, with a total length of 13.4 cm. Its holdfast, with a diameter of 3.5 cm, is also larger relative to its size. It is also the specimen of *Plumeropriscum hofmanni*

n. gen., n. sp. with the least number (9) of visible primary branches. However, it does have a very similar shape and overall morphology to the holotype. The third specimen is very similar to the holotype, only with a slightly shorter stem and a more acute basal petalodium angle (107°), unlike the other two specimens with angles of 133°. Both of the additional specimens are somewhat more rounded than the pointed, deltoid holotype. Secondary branching is not visible on either.

Etymology.—Named for the late Hans Hofmann who contributed greatly to our understanding of Ediacaran paleontology.

Comparisons.—*Plumeropriscum* is similar to *Primocandelabrum* in that all of the primary branches are connected to the stem at the base of the petalodium. However, the branches of *Plumeropriscum* are thinner and more numerous, and the petalodium shape is more deltoid with a point at the distal end, compared to the inverse triangle shape of *Primocandelabrum*. The branches of *Primocandelabrum* are arranged as a two-dimensional fan as opposed to the three-dimensional, mop-like shape of *Plumeropriscum*.

The petalodium of *Plumeropriscum* has some similarities to *Bradgatia* in that there are many primary branches all attached together at the base, but *Bradgatia* lacks the stem and holdfast of *Plumeropriscum* and shows a great deal more secondary and tertiary branching that forms individual 'petals' in a way that *Plumeropriscum* does not.

An as yet unnamed stemmed frond from the Ediacaran deposits of Charnwood Forest, central England, informally referred to as the 'dumbbell-like frond' (Wilby et al., 2011), shows some similarity to *Plumeropriscum,* with an orbicular petalodium attached to a stem with a holdfast. However, the dumbbell frond's holdfast is quite distinct from the small bulbous holdfast of *Plumeropriscum*; it is a large disc, larger even than the frond's petalodium, with many concentric rings. Within the dumbbell frond's petalodium, the branching pattern appears somewhat similar to that of *Plumeropriscum,* with no defined central axis and multiple primary branches attached at the base of the petalodium, but beyond that, the branching appears more complex in the dumbbell frond. It could be a closely related taxon.

Remarks.—The three-dimensional, mop-like architecture of *Plumeropriscum* makes it unique among the Mistaken Point biota. The 'mop' of primary branches that make up the petalodium would likely have been an effective means of straining flowing water for nutrients in a different but analogous way to other fronds.

Group uncertain
Genus *Broccoliforma* new genus

Type species.—*Broccoliforma alta* n.sp., by monotypy.

Diagnosis.—As per species.

Etymology.—From the Italian 'broccolo' referring to the vegetable, and the Latin 'formis' meaning shape.

Broccoliforma alta new species
Figures 4.2, 4.4, 4.6, 5.3, 5.4

Holotype.—On the Mistaken Point E-surface. Plastotype at the Royal Ontario Museum, ROM 62623.

Diagnosis.—Irregularly lobate, flabellate frond connected to a short cylindrical stem that attaches at the opposite end to a disk. Internal features consist of poorly developed lobes radiating in a semicircular, fan-shaped array from the center of the diameter, with an angle at the base of the petalodium near 180°.

Etymology.—From the Latin 'altus' meaning deep, referring to the deep marine environment of the organism.

Description.—The holotype (Figs. 4.2, 4.4, 5.3, 5.4), from the Mistaken Point E-surface, is a flabellate frond characterized by a large, bulbous holdfast (3.2 cm diameter), stem (3.9 cm long, 0.9 cm wide), and a roughly semicircular (3.5 cm long, 7.9 cm wide) petalodium. The flabellate petalodium has a sharp outer margin, and internal features of the petalodium consist of irregular, poorly developed lobes radiating in a fan-shaped array from the base of the petalodium where it attaches to the stem. The angle at the base of the petalodium is 175°, close to a horizontal line, and the petalodium itself is wider than it is long. Compared to other fronds, the holdfast, which appears as a thickened bulb continuous with the stem at its base, is notably large relative to the total length of the frond.

The other known specimen of *Broccoliforma alta* n. gen., n. sp. (Fig. 4.6), also from the E-surface, is slightly smaller but overall quite similar to the holotype. It also has a relatively large holdfast (2.5 cm), and thick stem (2.9 cm long, 0.4 cm wide). This specimen has similar overall petalodium morphology to the holotype, including the flabellate shape with a 175° angle of the base of the petalodium, and greater petalodium width than length (4.4 cm long, 6.7 cm wide).

Comparisons.—In contrast to most other fronds (with the exception of some *Primocandelabrum*), the petalodium of *Broccoliforma* is wider than long. Its petalodium has the widest basal angle of any Mistaken Point stemmed organism. Similar to a number of other Ediacaran fronds, including *Plumeropriscum* as well as *Avalofractus*, *Culmofrons,* and *Primocandelabrum*, *Broccoliforma* has a round, bulbous holdfast and a cylindrical stem. The stem is somewhat thick compared to that of other small fronds, and the diameter of the holdfast is relatively large compared to the total length. Unlike other Mistaken Point fronds, the petalodium of *Broccoliforma* does not exhibit modular construction or branching that is apparent even in poorly preserved frond fossils of a similar size. Instead, *Broccoliforma* has an irregular lobate morphology. Given the rough, radiating geometry of the lobes and the wide petalodium, it is possible that *Broccoliforma* is a taphomorph of *Primocandelabrum* in which the branches are not clearly preserved but other structures are, but until more specimens are found this is difficult to resolve.

The lobate structure of the petalodium bears a resemblance to other lobate fossils from the Mistaken Point biota known as

ivesheadiomorphs (Liu et al., 2011), a group that includes the genera *Ivesheadia* Boynton and Ford, 1995 (see also Boynton and Ford, 1996), and *Blackbrookia* Boynton and Ford, 1995, although Liu et al. (2011) regarded all ivesheadopmorphs as taphomorphs of other taxa and therefore as variants of each other. The somewhat oblong shape and raised perimeter of the petalodium of the holotype are particularly reminiscent of the taxon *Blackbrookia,* which is primarily known from Charnwood Forest, England (Boynton and Ford, 1995; Wilby et al., 2011) and is also reported from Bonavista Peninsula (Hofmann et al., 2008). The frond morphology of *Broccoliforma,* in contrast with the irregular, unstructured shapes of *Blackbrookia* and *Ivesheadia,* could be useful in interpreting other lobate Ediacaran taxa.

Remarks.—The lobate, irregular Ivesheadiomorpha (Boynton and Ford, 1995; Liu et al., 2011) is a controversial group of taxa from the Ediacaran biota of eastern Newfoundland and Charnwood Forest. When Boynton and Ford first described them in 1995, they interpreted them as cnidarian-grade organisms, but this view has fallen out of favor. Three alternative explanations have recently been put forward: Laflamme et al. (2011) suggested that they are microbial colonies; Liu et al. (2011) argued that they are taphomorphs of other Ediacaran taxa representing advanced stages of decay; and Wilby et al. (2011) put forward the idea that they are the result of upright fronds causing sediment deposition beneath them during turbidity current flow.

Unfortunately, none of these explanations for ivesheadiomorphs can be used to interpret *Broccoliforma*. If the morphological similarity between *Broccoliforma* and *Blackbrookia* is homologous, the existence of a stem and holdfast attached to the lobate structure is inconsistent with the microbial interpretation of Laflamme et al. (2011) or the sediment deposition explanation of Wilby et al. (2011), which respectively require a simpler morphology, and an accumulation of sediment beneath an elevated frond's petalodium, not at the end of the stem of a horizontally felled frond. Similarly, the flabellate shape of the *Broccoliforma* is unique among Mistaken Point fronds, making it difficult to reconcile as a taphonomic degradation of some more common Mistaken Point frond as inferred for *Ivesheadia* by Liu et al. (2011). An alternative explanation is to echo the original interpretation of Boynton and Ford (1995) that ivesheadiomorphs are tissue-grade organisms themselves, albeit apparently lacking any of the apomorphies of the Cnidaria. This interpretation would suggest that perhaps another clade of Ediacaran organisms evolved convergently into a frondose body plan in order to extend higher into the water column to compete for nutrients.

Other small fronds at Mistaken Point

Apart from these two newly described small fronds, there are several other taxa that share a broadly similar morphology and that would have occupied the same ecological tier at Mistaken Point. These include juveniles of larger fronds present on the surface (i.e., *Charnia*, *Charniodiscus*, and *Beothukis*), as well as taxa only known as small fronds from elsewhere in eastern Newfoundland: *Primocandelabrum* (Fig. 6.2) from the Bonavista Peninsula (Hofmann et al. 2008), and *Avalofractus* (Fig. 6.1) from Spaniard's Bay. Some might be juveniles of the

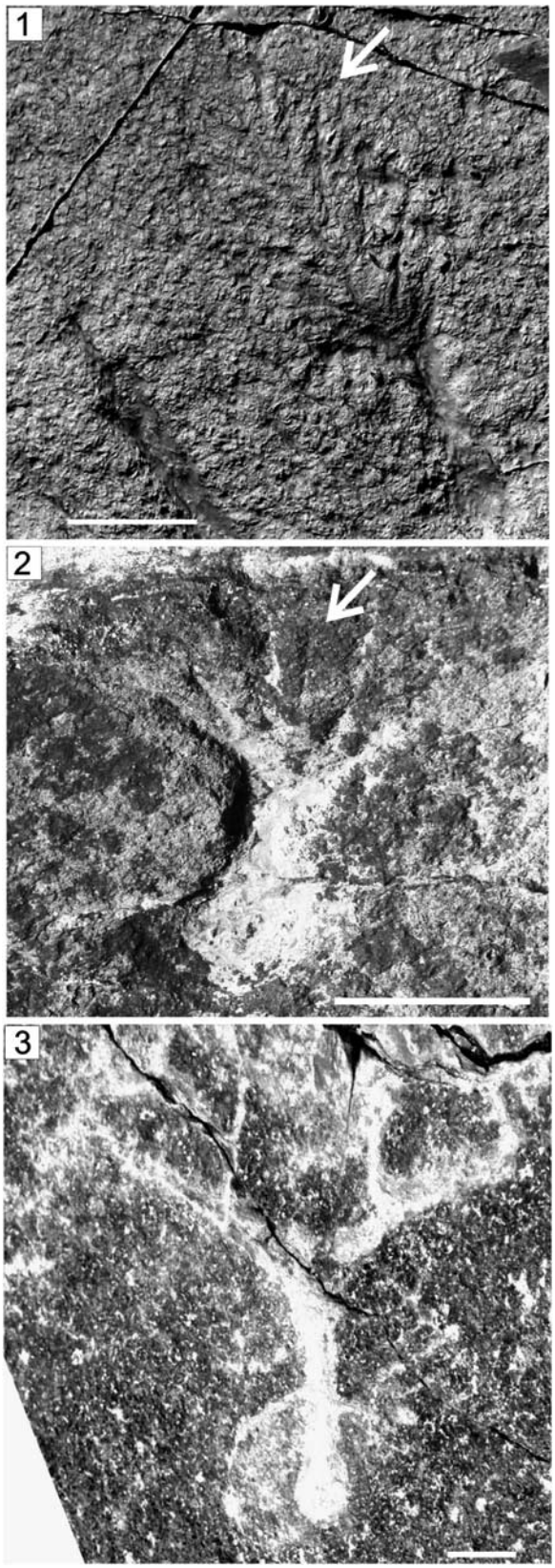

Figure 6. (**1**) *Avalofractus* from the Mistaken Point E-surface. White arrow points to a primary branch that shows secondary branching. (**2**) *Primocandelabrum* from the Mistaken Point E-surface. White arrow points to a primary branch that shows subtle secondary branching. (**3**) Large frond from the E-surface at Watern Cove; this fossil has a similar shape to other fossils identified as *Primocandelabrum*, but the two thick secondary branches are unique. Scale bars = 2 cm.

recently described *Culmofrons,* which is found lower in the succession in the Mistaken Point area (Laflamme et al., 2012). Many of the fossils that Clapham and Narbonne (2002) and Clapham et al. (2003) referred to as 'dusters' are now known to be *Primocandelabrum* or *Beothukis*, whereas others could be juvenile *Culmofrons.*

Primocandelabrum is a stemmed frond with a petalodium shaped like an inverted triangle constructed by a few thick primary branches attached at the base of the petalodium. It was first described from the Mistaken Point and Trepassey formations of the Bonavista Peninsula (Hofmann et al., 2008). Hofmann et al. (2008, p. 212) proposed that many of the small fronds at Mistaken Point represent specimens of *Primocandelabrum* sp. but did not illustrate or cite any specific specimens attributed to this taxon. The tentaculate holdfast of the species *Primocandelabrum hiemaloranum* Hofmann, O'Brien, and King, 2008 has not been observed at Mistaken Point, but one specimen from the Mistaken Point E-surface shows subtle secondary branches attached to its thick primary branches, suggesting rangeomorph architecture (Fig. 6.2). On the Mistaken Point E-surface at Watern Cove, there is a large frond that resembles *Primocandelabrum* (Fig. 6.3) with two thick primary branches attached at the base of the petalodium, but uniquely to this specimen, each of these branches also has a thick secondary branch attached that points inward toward the central axis at an ~60° angle. The total length of the frond is 12.7 cm, with a particularly wide petalodium, measuring 5.6 cm long and 12.3 cm wide. This specimen might be a separate species of *Primocandelabrum*, or considering its greater size than most *Primocandelabrum*, perhaps a more mature specimen.

Beothukis has a spatulate shape that in some specimens makes it appear as if it might have a stem between the holdfast and the petalodium, which allows for confusion with the true *Plumeropriscum* 'dusters,' especially in specimens that are small and poorly preserved. Other stemmed small fronds on the Mistaken Point E-surface bear a resemblance to *Culmofrons* from Lower Mistaken Point and the Briscal Formation, but they are not sufficiently well-preserved to classify them definitively to this genus. Juvenile *Charnia* and *Charniodiscus* fronds also share this low tier.

Discussion

When Clapham and Narbonne (2002) and Clapham et al. (2003) first studied the paleoecology of Mistaken Point, many of the taxa included in their analysis were still undescribed and unnamed, but most, such as the 'spindle' (now called *Fractofusus*) and the 'pectinate' (now called *Pectinifrons*), were nonetheless readily discernible due to their unique constructions. However, the smaller taxa were more problematic when approached informally, and a wide variety of small frond fossils that share a broadly similar organism-scale shape were grouped together as 'dusters,' including these two new taxa, *Plumeropriscum* and *Broccoliforma,* as well as the relatively recently described *Primocandelabrum*, *Beothukis*, *Avalofractus*, and *Culmofrons.*

Consequently, it is worth noting that the lower tier occupied by the small fronds has more diversity than previously realized in paleoecological analysis. At Mistaken Point, there are a number of different small fronds, many of which are not known as larger

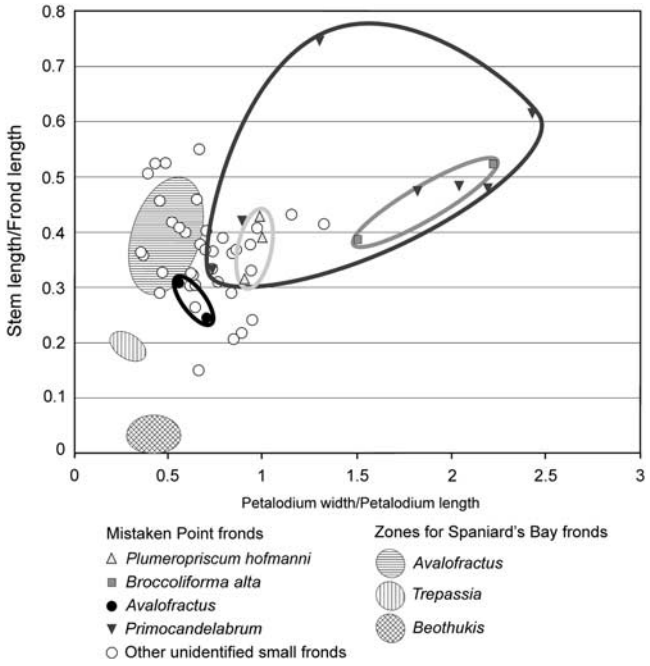

Figure 7. Comparison of the morphometric distribution of Mistaken Point small, stemmed fronds with the small fronds described by Narbonne et al. (2009) in the Spaniard's Bay area. Distribution of Mistaken Point taxa on the chart is represented by empty ellipses; distribution of Spaniard's Bay taxa is represented by patterned ellipses. Mistaken Point taxa show significantly more overlap, meaning that the overall body shape of the fronds shows convergence across multiple frond architectures.

taxa, and most of which have a broadly similar overall body shape. Small fronds from the E-surface show significant overlap in terms of stem length versus total frond length, and petalodium length versus width (Fig. 7). This observation is in contrast with Spaniard's Bay, where the various types of small fronds are distinct from each other based on the same criteria (Narbonne et al., 2009). The Spaniard's Bay types plot into three distinct groups, whereas the Mistaken Point taxa show significant overlap, which makes differentiating and identifying the numerous poorly preserved specimens challenging. *Primocandelabrum* in particular has a large morphometric range that both *Plumeropriscum* and *Broccoliforma* fall within, although their unique constructions allow them to be differentiated. Although there is not great disparity in the overall shape of the small, stemmed fronds, there is considerable diversity in petalodium architecture. It can therefore be concluded that this tier was a competitive one, with significant convergent evolution of multiple taxa.

In addition to the small fronds that were lumped together as 'dusters,' other, less similar taxa also share the same tier, slightly elevated from the substrate, adding to its biodiversity. These taxa include the bush-like rangeomorph *Bradgatia* (Flude and Narbonne, 2008), the triangular potential sponge *Thectardis* (Clapham et al., 2004; Sperling et al., 2011), and the comb-like rangeomorph *Pectinifrons* (Bamforth et al., 2008), as well as juveniles of taxa such as *Charniodiscus* and *Charnia*.

Conclusions

Although the small frond fossils of Mistaken Point are difficult to interpret and to identify due to the limitations of their

taphonomy and overall similarity in first-order shape, two new taxa have been described on the basis of their unique petalodium constructions: the mop-like *Plumeropriscum hofmanni* n. gen., n. sp., and lobate, flabellate *Broccoliforma alta* n. gen., n. sp.

With description of the small frond fossils previously informally referred to together as 'dusters,' the last major gap in the taxonomic description of the known Mistaken Point assemblage is filled, excluding fossils that are currently too unclear and poorly preserved to describe meaningfully. Future discoveries of similar fossils with better preservation in Newfoundland, England, or elsewhere, could shed light on remaining unnamed fossils at Mistaken Point, and on the two taxa described in this study based on a small number of specimens with suboptimal preservation. Now that the decade-long endeavor to describe all of the major fossils of the Mistaken Point assemblage is essentially complete, it could be enlightening to revisit detailed paleoecological study of the Mistaken Point biota, keeping in mind the greater taxonomic disparity and competition now known to have existed at this tier of the ecosystem.

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