EDiacaran Rangeomorphs in the Mistaken Point Biota, Newfoundland

by

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Abstract

The Ediacara biota is a cosmopolitan assemblage of the first macroscopic multicellular soft-bodied fossil organisms (Late Neoproterozoic, 575 – 542 Ma). The Avalon Peninsula of Newfoundland preserves entire communities composed of hundreds of organisms in their natural life positions on decameter- to hectometer-scale bedding plane surfaces as impressions under a layer of ash. The communities are dominated by rangeomorphs, an extinct taxon with modular construction and fractal architecture.

*Bradgatia*, a multibranched rangeomorph initially studied from 7 specimens from England, is represented by >200 specimens from 8 surfaces on the Avalon Peninsula. The *Bradgatia* petalage is a radial array of up to eight rangeomorph petals with four visible orders of rangeomorph branching. The petalage changes throughout ontogeny from juvenile I- or V-shaped organisms to larger U-shaped specimens to the largest and oldest O-shaped specimens. Counts of the number of petals within each taphomorph suggest that a constant number of petals was maintained throughout ontogeny. There is no significant variation in the number of frondlets with petal length suggesting that petals maintained a constant number of secondary branches throughout ontogeny.

*Culmofrondis* new genus and species is a rangeomorph frond known from a single surface within the Mistaken Point Formation. It is constructed from non-rangeomorph primary branches which are subdivided by rangeomorph secondary and tertiary branches. The zigzagging central midline and non-rangeomorph primary branches are typical of *Charnnia*-type branching whereas its rangeomorph secondary branches and flexible primary branches are typical of *Rangea*-type branching.
Both *Bradgatia* and *Culmofrondis* were basally attached to the ocean floor by holdfasts suggesting they were sessile, epifaunal benthic organisms. Both were oriented parallel to contour current direction and display decreasing preservation distally along specimens. Additionally, *Bradgatia* overlies spindles and discs and *Culmofrondis* possesses a long stem further supporting an epifaunal suspension feeding lifestyle. *Bradgatia*’s multiple petals and lack of a stem would have maximized the surface area available for suspension feeding whereas the elevated petalodium of *Culmofrondis* would have accessed nutrients in a zone higher in the water column with lower competition.
Co-Authorship

This thesis is substantially my own work but has benefited from the supervision and guidance of my supervisor and colleagues. Chapter 2 has been published in the Canadian Journal of Earth Sciences and has been co-authored by Guy Narbonne (Flude and Narbonne, 2008). A modified version of Chapter 3 will be submitted to an international scientific journal and co-authored by Guy Narbonne and Marc Laflamme.
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Chapter 1

Introduction

1.1 Ediacara Biota

The Ediacara biota is a distinct group of centimetre- to metre-scale organisms which occur globally in rocks of the recently named Ediacaran period (635-541 Ma) and represent Earth’s oldest known complex multicellular life. The Ediacaran is the first period added to the geological time scale in over a century (Knoll et al., 2006). Its lower boundary is defined with the Global Boundary Stratotype Section and Point (GSSP) at the base of the Nuccaleena Formation cap carbonate in the Flinders Ranges of southern Australia, which directly overlies a diamictite of the Elatina Formation of the Umberatana Group and represents the end of the Marinoan glaciation. The top of the Ediacaran Period is defined by the GSSP marking the base of the Cambrian, on the Burin Peninsula, Newfoundland, which marks the first appearance of a biologically distinct trace fossil assemblage (*Treptichnus pedum*), and shortly after which is observed the first widespread and diverse skeletal fauna (Narbonne et al., 1987; Gehling et al., 2001; Knoll et al., 2006). The fossils of the Ediacara biota, for which the Period is named, are unique to this period and occur in the upper part of the period (575-543 Ma).

The Ediacara biota is an assemblage of impressions of soft-bodied organisms typically preserved as moulds and casts on the bases of siliciclastic and volcanioclastic event beds (Narbonne, 2005). The fossils are known from Ediacaran sediments on all continents except Antarctica but are virtually unknown from the Phanerozoic. The biota is
named for the Ediacara Hills in South Australia from where the fossils first gained widespread attention (Sprigg, 1947, 1949).

The affinities of the Ediacara biota remain contentious (Narbonne, 2005; Xiao and Laflamme, 2009). Originally they were interpreted as primitive Precambrian ancestors of Phanerozoic animal life (e.g. Sprigg, 1947, 1949; Glaessner, 1984). Seilacher (1984, 1985, 1989, 1992) subsequently proposed that they instead represented a separate Kingdom Vendozoa (renamed Vendobionta), which was composed of Pflug’s (1972) serially quilted Petalonamae and fractally quilted rangeomorphs. Following these suggestions, some or all of the fossils have been proposed as being classifiable within several different kingdoms and phyla, ranging from lichens (Retallack, 1994; but see Waggoner, 1995) to bacterial colonies (Grazhdankin and Gerdes, 2007) to protists (Steiner and Reitner, 2001; Seilacher et al., 2003) to fungi (Peterson et al., 2003). Most workers believe that some or all of the taxa were animals, a view supported by the presence of bilaterian burrows (Jensen et al., 2006) and animal-like embryos (Xiao et al., 1998; Xiao and Knoll, 2000) in Ediacaran strata. Some have been suggested to be representatives of stem- or even crown-group members of modern animal phyla including sponges (Gehling and Rigby, 1996), cnidarians (Gehling, 1988; Xiao et al., 2000; Chen et al., 2002), mollusks (Fedonkin and Waggoner, 1997), arthropods (Lin et al., 2006) and echinoderms (Gehling, 1987). Others, however, do appear to be more similar to each other than to modern taxa and are apparently unclassifiable within modern phylogenies (Seilacher, 1992; Brasier and Antcliffe, 2004; Narbonne 2004; Sperling et al., 2007).

The appearance of the Ediacara biota in the fossil record marks a significant milestone in the evolution of eukaryotic life, the first appearance of large and
architecturally complex eukaryotes. Pre-Ediacaran life was overwhelmingly dominated by cyanobacteria, with eukaryotic life being restricted to small single-celled or simple multi-cellular organisms. The timing of the first appearance of eukaryotes is uncertain and controversial, but probably occurred between 2.7 and 1.6 Ga (Brocks et al., 1999; Knoll, 2003; Knoll et al., 2006). The first widely accepted acritarchs, dated at about 1500 Ma, were documented from the Roper Group of Australia and have been classified as Tappania (Javaux et al., 2001, 2004). Multicellularity was first achieved in the algae several hundred million years before the origin of animals. Bangiomorpha, a crown-group red alga, appeared in the Hunting Formation of arctic Canada at 1.2 Ga and is the oldest-known eukaryote to possess true cellular differentiation and specialization (Butterfield, 2000). Bangiomorpha is similar to its modern sexually reproducing counterpart Bangia in possessing two distinct spore-producing phases, suggesting that it is also the first known eukaryote capable of sexual reproduction (Butterfield, 2000).

Earliest heterokonts are known from the Lakhanda Group, Siberia (Jankauskas, 1989; Herman, 1990) and date back to 1005 ± 4 Ma (Rainbird et al., 1998), and the oldest-known green algae were described from the 800 – 750 Ma Svanbergfjellet Formation of Spitsbergen (Butterfield et al., 1994). Divergence dates based on molecular evidence between the opisthokonts (eukaryotic superkingdom that includes animals, fungi, and several unicellular kingdoms) vary widely (Hedges et al., 2004; Douzery et al., 2004) and there is no unequivocal fossil evidence for their divergence prior to the Ediacaran.

A rise in the oxygen levels of the Neoproterozoic oceans has long been thought to have driven the sudden appearance of the large, complex Ediacaran organisms (Berkner and Marshall, 1965; Knoll and Walter, 1992; Knoll, 2003). The Gaskiers (580 Ma) is the
last of the widespread Neoproterozoic glaciations and closely precedes the appearance of Ediacaran organisms (Narbonne and Gehling, 2003; Narbonne, 2005; Xiao and Laflamme, 2009). Gaskiers and pre-Gaskiers sediments show ratios of reactive vs. unreactive iron that imply that the deep-ocean was anoxic and ferruginous whereas post-Gaskiers sediments were oxic and able to support life (Canfield et al., 2007, 2008).

The earliest occurrence of Ediacaran-type fauna are disc-like fossils from the Northwest Territories of Canada (Hofmann et al., 1990) in sediments deposited prior to the Marinoan glaciation, predating the Ediacaran Period. These are considered to be simple precursors to younger, more complex Ediacaran communities (Xiao and Laflamme, 2009) which occur globally shortly after the end of the Gaskiers glaciation (~580 Ma). Fossil embryos possibly belonging to cnidarians or bilaterians have been reported from the Doushantuo Formation of China (Fig. 1.1; Xiao et al., 1998; Xiao and Knoll, 2000). U-Pb dates on zircons suggest that they span from 635.2 ± 0.6 Ma to 551.1 ± 0.7 Ma (Condon et al., 2005). The Drook Formation (575 ± 1 Ma; isotope dilution thermal ionization mass spectrometry (ID-TMS) U-Pb, Bowring et al., 2003) of the Avalon Peninsula of Newfoundland directly overlies the glacial Gaskiers Formation (Fig. 1.2). It preserves two species of *Charnia*, the oldest, large, architecturally complex fossils yet discovered (Narbonne and Gehling, 2003).

Younger communities have been classified based on cluster analysis into three distinct assemblages which are considered to represent different evolutionary stages of the Ediacara biota (Waggoner, 2003). Fossils of the oldest Ediacaran assemblage, the Avalon assemblage (575 – 560 Ma), are examined in this thesis and are known from deep water sediments of the Conception and St. John’s groups of Newfoundland and from
Figure 1.1. Temporal and stratigraphic distribution of the three Ediacaran assemblages with representative fossil genera. The Marinoan and Gaskiers glaciations and Doushantuo biota are included. Reproduced from Xiao and Laflamme (2009).
Figure 1.2. Stratigraphy of the Ediacaran succession of the Avalon Peninsula of Newfoundland. U-Pb ages from Dunning in Benus (1988) and Bowring et al. (2002). Fossiliferous surfaces: SH, Shingle Head; SB, Spaniard’s Bay; G, E, D, Mistaken Point beds; GH, Green Head; BC, Bishop’s Cove; GRC, Gull Rock Cove; BrC, Bristy Cove.
Charnwood Forest in England. It is dominated by rangeomorphs and displays the lowest taxonomic richness (Fig. 1.1). The White Sea assemblage (560-550 Ma) occurs in shallow-water deposits worldwide, principally the White Sea coast of Russia and the Flinders Ranges of South Australia. It exhibits the highest taxonomic diversity of organisms, and new forms include trace fossils made by motile animals and probable stem-group bilaterian fossils (Fig. 1.1; Waggoner, 2003). The Nama assemblage (550-543 Ma) is characterized by the Kuibis and Schwartzrand subgroups of Namibia and the Khatyspyt Formation of Siberia and consists mainly of rangeomorphs, erniettomorphs, and of the oldest known biomineralizing organisms (Fig. 1.1).

Rangeomorphs, the group examined in this thesis, are constructed of centimetre-scale architectural elements called frondlets (Narbonne, 2004) which are self-similar over at least three fractal orders and are arranged as modules to form spindle-, lettuce-, frond and comb-like constructions. No such architecture and construction is known from any post-Ediacaran fossils or extant groups of organisms and thus rangeomorphs are considered to be a failed experiment in the evolution of life (Narbonne 2004).

Numerous feeding strategies have been assigned to rangeomorphs. McMenamin (1986) regarded the Ediacara biota as representing exclusively obligatory photo- and/or chemo-autotrophic organisms. Photo-autotrophy can be discounted as the fossiliferous sediments of the Avalon Peninsula contain no features characteristic of shallow-water deposits suggesting that they formed well below the photic zone (Misra, 1969; Landing et al., 1988; Wood et al., 2003; Ichaso et al., 2007), an interpretation that also applies to the Ediacara fossil assemblages of NW Canada (Aitken, 1989; Narbonne and Aitken, 1990; Dalrymple and Narbonne, 1996; MacNaughton et al., 1997) and Charnwood Forest in
England (Carney and Noble, 2007). Similarly, the Avalonian sediments also contain carbonate and sulphide concentrations several orders of magnitude lower than the minimum required to support chemo-autotrophic communities (Canfield et al., 2007). The fractal architecture of rangeomorphs creates divisions smaller than 1/10\textsuperscript{th} of a millimeter which would be too small to house any sort of organisms capable of filter-feeding (Laflamme and Narbonne, 2008b). It, however, maximises the surface area to volume ratio of organisms, creating a morphology well-suited to directly absorbing dissolved nutrients from the water column (Laflamme and Narbonne, 2008b), which is consistent with the views originally expressed by Seilacher (1984, 1985, 1989, 1992). The tiering structure of the communities of the Avalon assemblage is similar to that found in modern-day suspension-feeding communities (Clapham and Narbonne, 2002), implying that the rangeomorphs were probably most closely related to the animals. Sperling and Peterson (2007) noted the lack of any metazoan apomorphies, the fractal architecture, the heterotrophic community tiering and the absence of a water canal system in rangeomorphs and suggested that they may represent an opisthokont group which may have represented the last common ancestors between animals and fungi.

1.2 Geographical and Geological Setting

The Conception and St. John’s groups of the Avalon Peninsula of Newfoundland contain the oldest known rangeomorphs (Fig. 1.2). Entire communities composed of hundreds of organisms are preserved in place on large bedding-plane surfaces exposed along the ocean’s coast making this an ideal location to study community paleoecology (Clapham and Narbonne, 2002; Clapham et al., 2003) as well as organism paleontology
(Gehling et al., 2000; Clapham et al., 2004; Laflamme et al., 2004, 2007; Narbonne and Gehling, 2003; Gehling and Narbonne, 2007; Bamforth et al., 2008).

Fossiliferous surfaces examined in this study occur on both the north and south coasts of the Avalon Peninsula of Newfoundland (Fig. 1.3, 1.4). Localities on the northern coast include Spaniard’s Bay in the Trepassey Formation of the Conception Group and Bishop’s Cove and Green Head in the Mistaken Point Formation of the Conception Group (Fig. 1.3). Localities on the southern coast include Bristy Cove of the Briscal Formation of the Conception Group, Mistaken Point and Gull Rock Cove of the Mistaken Point Formation and Shingle Head of the Trepassey Formation (Fig. 1.3, 1.4).

All specimens overlie a bed in the Drook Formation dated at 575 ± 1 Ma (Fig. 1.2; isotope dilution thermal ionization mass spectrometry (ID-TMS) U-Pb, Bowring et al., 2003). An ash bed directly overlying the E-surface of the Mistaken Point Formation is dated at 565 ± 3 Ma (Fig. 1.2; U-Pb; Dunning in Benus, 1988) precisely dating beds at Mistaken Point and providing a minimum age constraint on beds lower in the stratigraphy (Bristy Cove, Gull Rock Cove, Bishop’s Cove, Green Head).

The Briscal Formation is composed of grey, thick- to very thick-bedded, medium- to coarse-grained sandstones with minor amounts of interbedded greenish to grey mudstones (Narbonne et al., 2005). Ash beds are thinner and less common than in the Mistaken Point Formation. The gradation in the thinner beds contain partial to full Bouma sequences whereas the thicker beds are structureless except for common water-escape structures (Narbonne et al., 2005). Slump structures are unknown, suggesting that deposition took place on a flat surface. Current ripples infer that sediments were transported towards the northeast (Williams and King, 1979). Fossils are however
Figure 1.3. Locality map of the Avalon Peninsula, Newfoundland. Fossiliferous surfaces: SH, Shingle Head; SB, Spaniard’s Bay; MP Mistaken Point beds which include G,E,D from Fig. 1.2; GRC, Gull Rock Cove; GH, Green Head; BC, Bishop’s Cove; BrC, Bristy Cove.
Figure 1.4. Geological map of the southern Avalon Peninsula, Newfoundland outlining fossil localities and formation boundaries. Fossiliferous surfaces: SH, Shingle Head; D, E, G surfaces at Mistaken Point; GRC, Gull Rock Cove; Br.C, Bristy Cove; PC, Pigeon’s Cove. Modified from Clapham et al. (2003).
oriented towards the southeast (Narbonne, 2005). The Briscal Formation has been interpreted as coarse axial turbidite flows (Sala in Narbonne et al., 2001).

The Mistaken Point Formation conformably overlies the Briscal Formation and consists of medium- and thin-bedded turbidites with minor thick graded sandstones and debris flows punctuated by ash beds (Wood et al., 2003; Narbonne et al., 2005). Current ripples indicate deposition occurred toward the southeast but frondose fossils are oriented towards the northeast (Wood et al., 2003; Narbonne et al., 2005). This indicates that a weak contour current was active during intervals between the mass flow events (Benus, 1988; Benus in King et al., 1988; Narbonne et al., 2005). Rare debris flow beds are present and imply deposition in a slope environment (Fig. 1.5; Wood et al., 2003; Narbonne et al., 2005).

The Trepassey Formation conformably overlies the Mistaken Point Formation and consists of grey, thin- to medium-bedded siltstones, sandstones and mudstones (Wood et al., 2003; Narbonne et al., 2005). T_{de} and T_{(b)onde} turbidites are dominant. Current ripples indicate deposition towards the southeast. Very large scale soft-sediment deformation occurs in some sections indicating deposition on an unstable slope (Narbonne et al., 2005; Ichaso et al., 2007).

The Avalon Terrane, a late Proterozoic – early Paleozoic island-arc (Fig. 1.5), was a microcontinent probably located off the coast of West Africa (McNamara et al., 2001). During the Acadian orogeny at ~430 – 425 Ma, Avalonia was caught in a collision between Baltica and Laurentia. Parts of Avalonia can be found in modern-day Europe such as in Bradgate Park, Leicester, England as well as on the east coast of North America such as the Avalon Peninsula, Newfoundland.
Figure 1.5. Environmental setting of the Mistaken Point Formation. Modified from J.G. Gehling (1999).
The predominant form of preservation of the fossils is in both positive and negative relief under coatings of volcanic ash on top surfaces of interturbidite beds, described by Seilacher (1992) and termed Conception-style preservation by Narbonne (2005). Tissues more resistant to decomposition such as holdfasts, stems and stalks of fronds are preserved in positive epirelief whereas tissues less resistant to decomposition such as petalodia of fronds, petals of Bradgatia and modules of Fractofusus are preserved in negative epirelief (Seilacher, 1992; Narbonne, 2005). Ash coated organisms living on the ocean floor and labile minerals caused the ash to harden rapidly before the decomposition of the resistant tissues. Once the tissues had decomposed, mud was injected into the remaining void casting their top surfaces. Less resistant tissues, however, decomposed prior to the lithification of the ash and instead the ash coated and hardened over the impression left by tissues in the soft ocean floor mud, casting their bottom surfaces. Because fossilization occurs at the boundary between the ocean bottom sediment and ash layer, it largely excludes the preservation of both nektonic and infaunal organisms.

1.3 Materials and Methods

More than 200 specimens of Bradgatia from 8 localities across the Avalon Peninsula (Fig. 1.2) were examined and photographed in the field. 14 specimens of Culmofrondis were examined and digitally photographed from a single surface of the Mistaken Point Formation (Fig. 1.2). Latex moulds were collected of 51 of the best preserved specimens of Bradgatia and of 4 of Culmofrondis to be examined in the laboratory. No specimens were collected due to the protected nature of Mistaken Point as
an Ecological Reserve and as a candidate for a UNESCO World Heritage Site. Three specimens of *Bradgatia*, however, had been previously collected from the Briscal Formation at Bristy Cove (ROM 38647), from the Mistaken Point Formation at Mistaken Point (ROM36500) and from the Trepassey Formation at Spaniard’s Bay (NFM F-755). These were photographed and studied in the laboratory.

The paleodirections of *Bradgatia, Culmofrondis,* and other fronds on the same surfaces were measured using a Brunton compass. Orientations of *Bradgatia* were measured from the basal branching point of its petals to the distal end of the centrally branching petal. Orientations of *Culmofrondis,* were measured from the center of its basal disc to its distal tip. These measurements are represented within the contour of the rose diagrams within this thesis (eg. fig. 2.9, 3.5). Ripple marks within turbidite beds indicate the direction of turbidity currents (Wood et al., 2003; Ichaso et al., 2007) and are given as unidirectional arrows outside the contours of rose diagram. Fronds are typically unidirectionally oriented in a direction perpendicular to current ripples but parallel to the continental slope (Wood et al., 2003; Ichaso et al., 2007) indicating that the organisms lived under the influence of a contour current. No structures are found in contour current beds. Contour current direction as measured from fronds is also given as unidirectional arrows outside the contours of rose diagrams.

All surfaces have been tectonically deformed during the collision of Avalonia with Laurentia in the mid-Paleozoic (Murphy and Nance, 1989), with approximately 40% shortening perpendicular to cleavage. This is apparent through originally circular discs which have been shortened perpendicular to cleavage and now appear elongated in the direction of cleavage (Wood et al., 2003). *Bradgatia* and *Culmofrondis* have also
typically been shortened perpendicular to cleavage (see Fig. 1.6). Unless otherwise indicated, all photographs and measurements presented here have been retrodeformed using the methods of Wood et al. (2003) and Ichaso et al. (2007) to remove the effects of tectonic deformation (Fig. 1.6).

1.4 Purpose of Thesis

The main goal of this study is to describe two rangeomorph taxa from the Conception Group of the Avalon Peninsula to gain insight into the relationships between rangeomorph organisms.

The thesis begins with a detailed description of Bradgatia Boynton and Ford 1995 from the Avalon Peninsula of Newfoundland (Chapter 2). Bradgatia was initially described from 7 specimens on a single surface in Charnwood Park, Leicester, England but the more than 200 specimens from 8 different locations on the Avalon Peninsula provide a wealth of morphological and taphonomic information not apparent in the specimens from England. One locality, Spaniard’s Bay, yields exceptionally preserved three-dimensional specimens. The study notes the variation in taphonomy between specimens in relation to their size and determines a model for the growth of Bradgatia. Chapter 3 examines the morphology of a previously undescribed frond, Culmofrondis, known from only 14 specimens from a single surface of the Mistaken Point Formation and relates it to two distinct clades of rangeomorphs. The frond is described informally within this thesis.

The analysis of the morphological characteristics and growth patterns of rangeomorphs is essential to understanding the construction of Earth’s earliest life and to
Figure 1.6. *Bradgatia* from Bishop’s Cove, Avalon Peninsula, Newfoundland. A. Un-retrodeformed specimen. B. Specimen after retrodeformation. Scale bar divisions = 1cm.
help in determining the relationships between different rangeomorph species. The study of *Bradgatia* and *Culmofrondis* will help achieve this as well as provide further knowledge in the evolution of Earth’s earliest known complex multicellular organisms.
1.5 Glossary

**Bouma sequence:** the ideal series of structures in a turbidite deposit.

**Chemo-autotrophic:** acquiring energy by the oxidation of electron donating molecules.

**Cleavage:** foliation perpendicular to stress as a result of ductile deformation.

**Contour current:** current running parallel to the continental slope.

**Crown-group:** monophyletic group which includes all living members of a clade and their last common ancestor.

**Ediacara biota:** collection of the earliest known macroscopic architecturally complex organisms which lived during the Ediacaran Period.

**Epibenthic:** living on the ocean bottom.

**Erniettomorphs:** group of Ediacaran organisms which are not bilaterally symmetric and have biserially quilted tubes alternately arranged along a midline.

**Formation:** fundamental unit of lithostratigraphy consisting of a number of rock strata that have a comparable lithology, facies or other similar properties.

**Ga:** gigaannum, billions of years before the present.

**Group:** a succession of two or more contiguous or associated formations with significant and diagnostic lithologic properties in common.

**Heterokonts:** major group of eukaryotes which include haptophytes, cryptomonads and alveolates.

**Interturbidite bed:** sediments deposited as background sedimentation rather than by a turbidity current.

**Labile:** easily decomposed.

**Lagerstätte:** a fossil deposit known for its exceptional preservation of soft parts.

**Ma:** megaannum, millions of years before the present.
Ontogeny: description of the origin and development of an organism from the fertilised egg to its mature form.

Opisthokont: group of eukaryotes which include the animal and fungus kingdoms and the phyla Choanozoa and Mesomycetozoa of the protist clade.

Photo-autotrophy: the acquisition of energy from light.

Rangeomorph: Ediacaran organism with a fractal architecture and modular construction.

Retrodeformation: the process by which the original shapes and values of fossils which have been tectonically deformed are extrapolated.

Sessile: refers to an organism which is not able to move about.

Slope: the relatively steep portion of the sea floor extending from the outer edge of the continental shelf to the upper limit of the continental rise.

Stem-group: paraphyletic group of extinct lineages that lie outside a crown group but are more closely related to the crown group than to the crown’s living sister group.

Taphomorph: the apparent morphology of an organism as influenced by its degradation, burial, diagenesis and fossilization.

Taphonomy: the study of the degradation, burial, diagenesis and fossilization of organisms.

Turbidite: deposit resulting from rapidly moving, sediment-laden water down a slope.
Chapter 2
Taphonomy and ontogeny of a multibranched Ediacaran fossil: Bradgatia from the Avalon Peninsula of Newfoundland

Abstract: Rangeomorphs, an extinct group of Ediacaran organisms with a fractal architecture and modular construction, occur abundantly in the Mistaken Point assemblage (575–560 Ma) of the Avalon Peninsula of Newfoundland. Bradgatia is represented by hundreds of specimens, collectively permitting analysis of its morphology, growth mode, and life habits. Bradgatia is a petalage that consists of a radial array of up to eight petals, each exhibiting up to four visible orders of rangeomorph branching. The taphonomy and ontogeny of Bradgatia are tightly linked by a change in preserved morphology, from juvenile I- to V-shaped specimens to larger U-shaped specimens, to the largest and ontogenetically oldest O-shaped specimens. Bradgatia probably maintained a constant number of petals that gradually spread out with age. The number of frondlets per petal does not correlate with length, suggesting either fractal or inflationary growth. Presence of a structure from which petals branch, abundance of contour-parallel specimens, differential preservation within specimens, and specimens overlying spindles and discs all imply that Bradgatia had an attached, epifaunal, suspension-feeding lifestyle. Bradgatia's multiple thin petals would have helped to filter water more efficiently, while its lack of a stem would have allowed for suspension feeding along the entire length of each petal.
2.1 Introduction

The Rangeomorpha (Pflug 1972; Jenkins 1985; Narbonne 2004) are a late Neoproterozoic clade of macroscopic, soft-bodied organisms characterized by a fractal architecture and modular construction. Rangeomorphs are globally distributed in Ediacaran fossil assemblages, especially in older and deep-water assemblages of this age, but have not been described from any Phanerozoic assemblages, including Cambrian Lagerstätten such as Chengjiang or the Burgess Shale. Rangeomorphs were originally regarded as primitive ctenophores (Gürich 1930, 1933; see also Dzik 2002) or cnidarians (Misra 1969; Glaessner 1984; Jenkins 1985; Runnegar and Fedonkin 1992; Boynton and Ford 1995). Most subsequent workers have pointed out that rangeomorphs do not resemble any living groups of organisms and have regarded the Rangeomorpha as an extinct Ediacaran clade (e.g., Pflug 1972; Seilacher 1992; Brasier and Antcliffe 2004; Narbonne 2004; Grazhdankin and Seilacher 2005; Gehling and Narbonne 2007; Sperling et al. 2007) that represents a “failed experiment” at a high taxonomic level. Similarity of rangeomorph communities with those of suspension-feeding animals (Clapham and Narbonne 2002; Clapham et al. 2003; Bambach et al. 2007) led Narbonne (2004, 2005) to regard the Rangeomorpha as stem-group animals, whereas the lack of features suggestive of the presence of a water vascular system led Sperling et al. (2007) to suggest that they may be even more primitive and represent stem-group opisthokonts, the superkingdom that includes the animals, fungi, slime molds, and several protistan kingdoms. Information on the construction, ecology, biology, and lifestyles of these organisms is, therefore, crucial to our understanding of the early evolution of megascopic life.
Rangeomorphs vary considerably in form, yet they all consist at the most basic level of “rangeomorph frondlets”, small architectural elements that consist entirely of self-similar branches, with these frondlets used as modules to construct larger structures and organisms (Narbonne 2004). Work on elucidating rangeomorph construction has thus far been restricted to the fronds Rangea (Jenkins 1985; Dzik 2002; Grazhdankin and Seilacher 2005) from Namibia and Charnia (Laflamme et al. 2007; Antcliffe and Brasier 2008) from Avalonian England and Newfoundland and the “spindle” Fractofusus (Gehling and Narbonne 2007) and the “pectinate” Pectinifrons (Bamforth et al. 2008) both from the Avalon Peninsula of Newfoundland. The taxon that gives the group its name, Rangea, is a multifoliate frond with at least four petaloids composed of parallel arrays of rangeomorphs diverging from a central stalk (Jenkins 1985; Dzik 2002; Grazhdankin and Seilacher 2005). The petalodium of Charnia is composed of a series of sigmoidal, overlapping and alternating primary branches and is attached directly to a basal holdfast (Laflamme et al. 2007). Fractofusus is fusiform in shape and is made up of at least two vanes, each consisting of a parallel array of plumose rangeomorph elements that branch from the central axis (Gehling and Narbonne 2007). Its typically excellent preservation implies that Fractofusus was an ocean-bottom recliner that was in full contact with the underlying sea-floor muds at the time of arrival of the volcanic ash that cast it (Seilacher 1992, 1999; Clapham and Narbonne 2002; Narbonne 2004; Gehling and Narbonne 2007). Pectinifrons is a multibranched rangeomorph that is constructed from a basal tubular pedicle rod from which stem two rows of alternately branching fronds in an opposite arrangement (Bamforth et al. 2008). Recent studies suggest that Fractofusus grew entirely by inflation (Gehling and Narbonne 2007), Charnia grew
mainly by addition of new branches at the tip of the frond (Antcliffe and Brasier 2008), and *Pectinifrons* grew by the addition of new fronds to both sides of the pedicle rod (Bamforth et al. 2008). Other rangeomorph constructions from Mistaken Point are currently under study at Queen’s University, Kingston, Ontario.

One of the most distinctive rangeomorph structures is the bush- or fan-like form, which commonly occurs in the Conception Group of the Avalon Peninsula, Newfoundland. These were originally reported by Misra (1969); subsequently mentioned by Anderson and Conway Morris (1982), Seilacher (1994), and Narbonne (2004, 2005); and recently reported from Bonavista Peninsula (Hofmann et al. 2008). Bush-shaped fossils occur abundantly on numerous bedding surfaces spanning >1 km of stratigraphy (Fig. 2.1), and specimens vary significantly in size and preservational style. This dataset permits analysis of the taphonomy and ontogeny of these bush-shaped fossils.

Our detailed study of >200 specimens of bush-shaped rangeomorph fossils from the most important localities of the Avalon Peninsula (Fig. 2.1) strongly suggests that all of these specimens represent ontogenetic and taphonomic variants of a single biological species. Among described taxa, the bush-shaped fossils from the Avalon Peninsula are most similar to *Bradgatia linfordensis* Boynton and Ford 1995, a monospecific genus that originally was defined on the basis of seven fossils on a bedding plane in Charnwood Forest in Avalonian England. Our specimens from the Avalon Peninsula of Newfoundland are smaller than the British forms but are similar to the type material from Britain, in that they are preserved in negative epirelief as oval impressions on bedding plane surfaces, are composed of stemless, highly fractal rangeomorph petals that radiate from a central branching point, and are further subdivided by frondlets that stem from the
Figure 2.1 Geographic and stratigraphic distribution of Bradgatia. (A) Locality map of the Avalon Peninsula, displaying the localities from which Bradgatia was studied. (B) Stratigraphy of the Ediacaran section of the Avalon Peninsula including published U/Pb ages on zircons (from Benus 1988 and Bowring et al. 2003). Abbreviations represent Avalon Peninsula localities from which Bradgatia was studied: BC, Bishop’s Cove; BrC, Bristy Cove; D, E, G, Mistaken Point beds; GH, Green Head; MP, Mistaken Point; SB, Spaniard’s Bay; SH, Shingle Head.
central axis of petals, secondary branches that stem from the central axis of frondlets, and third-order branches that stem from the central axis of secondary branches. Narbonne et al. (2001) and Hofmann et al. (2008) believed that this close similarity extended to the species level and regarded all Avalonian bush-shaped specimens as *Bradgatia linfordensis*, a view with which we concur. The type specimens of *Bradgatia* from Charnwood Forest in Britain are large and spectacularly exposed but are in urgent need of a modern redescription and high quality illustrations to elucidate the three-dimensional structure and range of variation of this taxon.

### 2.2 Geographic and stratigraphic setting

In this study, ~200 specimens of *Bradgatia* were studied in outcrops of the Mistaken Point Formation of the Conception Group (Fig. 2.1B) on the southern coast of the Avalon Peninsula (Fig. 2.1A) and at Conception Bay near Bishop’s Cove and Green Head (Fig. 2.1A). Specimens also occur rarely in the Briscal Formation (Fig. 2.1B) at Bristy Cove (Fig. 2.1A) and near the top of the Trepassey Formation near Shingle Head (Fig. 2.1A). A unique occurrence of small specimens, previously informally referred to as “plumose” or “leek-shaped” rangeomorphs (Narbonne 2004), is exquisitely preserved within a fine turbidite from the Trepassey Formation near Spaniard’s Bay (Fig. 2.1). The three-dimensional structure and preservation of morphologic details <0.1 mm in the Spaniard’s Bay specimens provides a unique insight into the morphology of *Bradgatia*, particularly into juvenile stages of its growth.

Age constraints on this section suggest that the Ediacaran assemblage of the Avalon is the oldest yet known (Narbonne 2005). All of the examined specimens overlie
an ash bed in the Drook Formation (Fig. 2.1B) dated at $575 \pm 1$ Ma (isotope dilution thermal ionization mass spectrometry (ID-TIMS) U–Pb zircon, Bowring et al. 2003), providing a maximum age constraint on the fossils. An ash bed immediately overlying the Mistaken Point E surface (Fig. 2.1B) has been dated at $565 \pm 3$ Ma (U–Pb, Dunning in Benus 1988), precisely dating fossils on the D, E, and G surfaces and providing a minimum age constraint on the fossils lower in the stratigraphy (Green Head, Bishop’s Cove, Bristy Cove).

The Mistaken Point Formation (Fig. 2.1B) at Mistaken Point (Fig. 2.1A) consists of medium- and thin-bedded, laminated siltstones interpreted as distal turbidites, primarily of $T_D^*$ and $T_E^*$ divisions of the classic Bouma Sequence (Wood et al. 2003). The presence of debris-flow deposits, extensive lateral continuity of bedding, and absence of channel and slump deposits and slump scars has been taken by Wood et al. (2003) as suggesting formation on a topographically smooth surface at the toe-of-slope. Similarly to Mistaken Point, turbidites at Bishop’s Cove (Fig. 2.1A) and Green Head (Fig. 2.1B) are medium-bedded, laminated mudstones and siltstones consisting primarily of the $T_{DE}^*$ divisions but dominated by the $T_E^*$ divisions of the classic Bouma sequence (Ichaso et al. 2007). These show excellent lateral continuity with the absence of large-scale erosional features, slumps, and debris flows (Ichaso et al. 2007). A lack of debris flows has been taken by Ichaso et al. (2007) as indicating that the Mistaken Point Formation at Bishop’s Cove and Green Head formed further down slope in the distal outer fan and basin plain.

The Briscal Formation (Fig. 2.1B) is primarily composed of thick to very thickly bedded turbiditic sandstones with few interbedded mudstones, which are interpreted as proximal $T_A^*$ and $T_{AB}^*$ turbidites that flowed down the basin axis (Wood et al. 2003). The
fossiliferous succession is entirely of deep-water origin, with a complete absence of any shallow-water features anywhere in the Conception and St. John’s groups (Wood et al. 2003; Ichaso et al. 2007).

Ediacaran fossils of the Conception Group are preserved on top surfaces of siltstone interturbidite beds under coatings of volcanic ash (Wood et al. 2003; Ichaso et al. 2007). This type of preservation was originally described by Anderson (1978) and Seilacher (1992) and later termed Conception-style by Narbonne (2005). As volcanic ash percolated through the water column, it covered the organisms, possibly contributing to their demise by smothering them. The ash lithified relatively rapidly owing to the presence of labile minerals. In the case of discs and stems of frondose organisms, the ash lithified prior to decomposition of tissue, molding their top surfaces, and mud from beneath was subsequently injected into the voids created during decomposition and cast an imprint in positive epirelief. Fronds, spindles, and other softer bodied organisms decomposed prior to ash lithification. Ash then hardened over the imprint left by the organism on the upper surface of the mud layer, producing molds in negative epirelief. *Bradgatia* is also preserved in negative epirelief and was thus fully composed of relatively labile tissue.

On the Avalon Peninsula, *Bradgatia* ranges from the middle part of the Briscal Formation to the top of the Trepassey Formation (Fig. 2.1). *Bradgatia* has recently been reported from the Fermeuse Formation of the Bonavista Peninsula of Newfoundland, slightly extending its stratigraphic range (O’Brien et al. 2006; Hofmann et al. 2008). One possible specimen has been reported but not yet figured from the Upper Miette Group of
British Columbia (Hofmann and Mountjoy 1998, 2001; Hofmann et al. 2008). All of these reports are from relatively deep-water settings.

2.3 Methods

Latex molds were taken of 51 specimens. All the fossiliferous surfaces except for the one at Spaniard’s Bay (Narbonne 2004) here have been tectonically deformed in the direction of cleavage. This is evident through originally circular discs, which are now elongated in the direction of cleavage (Wood et al. 2003). All measurements and photographs of specimens presented here have been retrodeformed using the methods of Wood et al. (2003) and Ichaso et al. (2007) to remove the effects of tectonic deformation from the images and measurements.

To determine the mode of growth of Bradgatia, radius and width (Fig. 2.2) of complete specimens were measured from both latex molds and field photographs of 68 individual specimens. Counts of the number of petals (Fig. 2.2), the number of frondlets (Fig. 2.2), and the number of secondary branches (Fig. 2.2) were also taken from those specimens preserved sufficiently well to exhibit such details.

2.4 Terminology

In the original description of Bradgatia, Boynton and Ford (1995) used the term “frond” to describe each of the largest independent units of Bradgatia. Laflamme and Narbonne (2008) condensed decades of different terms used to describe fronds into a terminology universally applicable to Ediacaran fronds, independent of their taxonomic affinities. In the terminology put forth by Laflamme and Narbonne (2008), “frond”
Figure 2.2 Labeled sketch of a Bradgatia petalage. Radius and petal length are typically approximately the same length. Scale bar divisions = 1 cm.
denotes a single entire organism, including a basal holdfast, stem, and petalodium. *Bradgatia*, however, is a multibranched fossil that consists of several of these frond-like units emanating from a common central point. There is no evidence for a disc or central stalk within any of the frond-like structures of *Bradgatia* in Newfoundland. Boynton and Ford (1995) did not use any further terms to describe smaller units of the highly fractal *Bradgatia*.

The terms proposed here to describe *Bradgatia* were specifically chosen not to conflict with the terms used to describe fronds. The complete organism, which consists of several discrete frond-like structures emanating from a common base, is herein termed a “petalage;” and each individual frond-like structure attached to the base is termed a “petal” (Fig. 2.2). The basic unit of construction of each petal is the frondlet (Fig. 2.2), also recognized as such by Hofmann et al. (2008), and is similar to the rangeomorph frondlet of Narbonne (2004). Frondlets are further subdivided into secondary (Fig. 2.2), tertiary (Figs. 2.3C, 2.4), and quaternary (Fig. 2.4) branches.

Due to the highly fractal nature of *Bradgatia*, frondlets resemble secondary, tertiary, and quaternary branches. Frondlets, rather than secondary, tertiary, or quarternary branches, were however chosen as the basic building block of *Bradgatia* for two main reasons: first, they are the largest independent constituents of petals; second, picking the smallest visible branching order may not represent the actual smallest branching order of the organism. Also, the quality of preservation within each specimen dictates how many branching orders are visible.
2.5 Description

2.5.1 General features

*Bradgatia* from the Avalon Peninsula is constructed from a collection of independent stemless petals (Figs. 2.2, 2.4, 2.5B, 2.5D, 2.5F) that wrap around a basal spherical structure much like the leaves of a garden leek (Figs. 2.4A, 2.4C, 2.4D, 2.4E, 2.5B(f), 2.5D(h), 2.5F(d)). The minimum number of visible petals in any specimen is three and the maximum number is eight (mean = 5). Petals are elliptical with steeply tapering bases and gently tapering, rounded, distal ends (Figs. 2.2, 2.5). They typically overlap each other at left-hand sides of petals visible on the left-hand side of the specimen and right-hand sides of petals visible on right-hand sides of the specimen (Figs. 2.3A, 2.3B, 2.3C, 2.3E, 2.3F, 2.5A, 2.5C, 2.5E). Occasionally, full petals are exposed, which reveal that they are divided into two bilaterally symmetrical halves (Figs. 2.3D, 2.4A, 2.5C). They are further divided into three visible orders of rangeomorph branching, the largest of which are rangeomorph frondlets. Each petal is composed of five to ten (mean = 7) plumose frondlets (Figs. 2.2, 2.4A, 2.5B(e), 2.5F(a)). Frondlets are thin folia, ~1.5 mm thick as seen from one over-folded frondlet (Figs. 2.4A, 2.4B). They show a high degree of overlap with neighbouring frondlets with the distal ends of the basal frondlet typically being tucked under the distal ends of the distal frondlet (Figs. 2.3F, 2.4A, 2.4B, 2.5D). This pattern is consistent throughout the whole petal. No stalk has been preserved in any petal, but all proximal ends of frondlets meet alternately along a central axis. Frondlets emanate from the central axis of petals laterally and distally. Ends of frondlets closest to the central axis are not preserved. The angle at which frondlets diverge from the central axis of the petal becomes increasingly
Figure 2.3 Field photographs of taphomorphs showing the gradation from (A) V-shaped through to (B) transitional forms to (C–D) U-shaped through (E) transitional forms to (F) O-shaped of Bradgatia from the Mistaken Point Formation. (A) V-shaped taphomorph from Bishop’s Cove. (B) Transitional U–V-shaped taphomorph from the E surface of Mistaken Point. (C) U-shaped specimen exhibiting third-order branching (black arrow) and overlying a disc from Bishop’s Cove. (D) U-shaped specimen from Bishop’s Cove. (E) Transitional O–U-shaped specimen from Bishop’s Cove. (F) O-shaped specimen from Bishop’s Cove. Scale bar divisions = 1 cm.
Figure 2.4. Specimens of *Bradgatia* from Spaniard’s Bay. (A) Specimen NFM F-755 displaying petals diverging from a basal structure and one over-folded frondlet. (B) Enlarged view of the uppermost area of specimen NFM F-755 indicated in (A), displaying an over-folded frondlet. (C) Enlarged view of the lowermost of specimen NFM F-755 area indicated in (A), displaying the basal anchoring structure with proximal ends of petals wrapping around it. (D) Partial specimen displaying proximal ends of petals wrapping around a basal structure. (E) Specimen displaying seven rangeomorph petals, all wrapping around a basal structure. Note side-on view of some petals and plan view of others. (F) Specimen displaying three petals converging towards a basal location. (G) Poorly preserved specimen displaying three partial petals. Plate constructed by Marc Laflamme. Scale bar divisions = 1 cm.
Figure 2.5. Architecture and construction of *Bradgatia* from the Mistaken Point Formation. (A) Latex photograph and (B) interpretive line drawing of a V-shaped taphomorph from the E surface of Mistaken Point: (a–d) recognizable petals; (e) frondlet; (f) branching locus of petals. (C) Photograph and (D) interpretive line drawing of ROM36500, a U-shaped taphomorph from the E surface of Mistaken Point; thicker lines represent boundaries of frondlets, which make up petals; thinner lines represent outlines of secondary branches: (a–f) individual petals of ROM36500; (e) petal underlying (f) and (d) with only distal end visible and (d) note increasing acuteness of frondlets relative to the central axis; (g) secondary branches; (h) branching locus of petals; (i) unrelated specimen of *Thectardis avalonensis* underlying the specimen. (E) Latex photograph and (F) interpretive line drawing of an O-shaped specimen from Bishop’s Cove: (a) frondlets that make up petals; (b) frondlets of an exposed underlying petal; (c) secondary branches; (d) branching locus of petals, note decreasing distal preservation in petals. Scale bar divisions = 1 cm.
acute distally, being nearly perpendicular to the central axis at the basal end to being
closely in line with the central axis at the distal tip (Fig. 2.5D(d)). Frondlets are typically
sigmoidal but may be parallel-sided or basally tapering (Figs. 2.2, 2.4, 2.5B, 2.5D, 2.5E)
and are composed of plumose secondary branches (Figs. 2.2, 2.4, 2.5D(g), 2.5F(c)) that
alternately stem from the central axis of frondlets at an acute angle. Frondlets exhibit
four to nine secondary branches (mean = 6), which like frondlets may be parallel-sided,
basally tapering, or sigmoidal. The extent of preservation of rangeomorph orders
dePENDS MAINLY ON THE COARSENSNESS OF THE OCEAN BOTTOM MUD. Tertiary branches are
preserved on a few Bishop’s Cove specimens (Fig. 2.3C) but have not yet been observed
in the less well preserved specimens at Green Head and Mistaken Point. They are also
plumose and taper basally or are sigmoidal in shape and stem alternately from the central
axis of secondary branches. Plumose quaternary branches, which stem from the central
axis of tertiary branches, are visible only in the finely preserved specimens at Spaniard’s
Bay.

Two different preservational styles, preservation under an ash-fall (Conception-
style preservation; Narbonne 2005) and preservation within a turbidite, have fossilized
Bradgatia of the Avalon Peninsula. Conception-style preservation is by far the most
common preservational mode and is exhibited at all localities and on numerous
stratigraphic levels of the Avalon Peninsula, except at Spaniard’s Bay. Conception-style
Bradgatia is preserved virtually two-dimensionally as an impression of the structures that
lie at the boundary between the sediment and water. Spaniard’s Bay preservation is
known from a single occurrence on the Avalon Peninsula, which has yielded five
specimens of Bradgatia and numerous small fronds, all of them preserved in three
dimensions. *Bradgatia* preserved in each style reveals unique features described in the following section.

### 2.5.2 *Bradgatia* in Conception-style preservation

Conception-style specimens of *Bradgatia* exhibit a consistent pattern in their preservation with increasing age and size. Three taphomorphs (Figs. 2.3–2.5) differ primarily in the extent of the preservation of petals around their branching point and are termed by the characteristic shape they make on the bedding plane surface (Figs. 2.3–2.5). O-, U-, and V-shaped taphomorphs, as well as all transitions between these taphomorphs (Fig. 2.3), are known from the Avalon Peninsula.

Petals of O-shaped specimens (Figs. 2.3F, 2.5E, 2.5F, 2.6) fully surround a central branching locus at 360°. These petals are on average the largest taphomorphs ranging 9.2–20.6 cm (mean = 14.5 cm) in width and 8.3–20 cm (mean = 12.2 cm) in length (Table 2.1), and most closely resemble the type specimens of *Bradgatia linfordensis* from Charnwood Forest in England. In specimens transitional into U-shaped taphomorphs (Fig. 2.3E), petals projecting from one side are typically more complete lengthwise than those projecting from the opposite side. O-shaped specimens are found at Green Head and Bishop’s Cove.

Petals of U-shaped specimens (Figs. 2.3C, D, 2.5C, 2.5D, 2.6) project from a basal locus over a semi-circular area. This gives U-shaped specimens directionality with a clear distinction between a base located at their branching point (Fig. 2.5D(h)) and distal areas located at the ends of petals. Unlike O-shaped taphomorphs, no petals project basally. U-shaped specimens range from 2.0 to 17.3 cm (mean = 9.2 cm) in width and 2.2
Figure 2.6. Reconstuctions of Bradgatia taphomorphs from left to right of I-, V-, U-, and O-shaped taphomorphs showing the ontogenic and taphonomic progression of specimens. Drawing by Peter Trusler.
Table 2.1. Comparison of O-, U-, V-, and I-shaped taphomorphs

<table>
<thead>
<tr>
<th></th>
<th>O-Shaped Taphomorphs</th>
<th>U-Shaped Taphomorphs</th>
<th>V-Shaped Taphomorphs</th>
<th>I-Shaped Taphomorphs</th>
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</thead>
<tbody>
<tr>
<td>Specimen radius (cm)</td>
<td>8.3 - 20.0</td>
<td>2.2 – 15.0</td>
<td>1.6 – 10.6</td>
<td>4.9 – 6.5</td>
</tr>
<tr>
<td>Average specimen radius (cm)</td>
<td>12.2</td>
<td>8.3</td>
<td>3.9</td>
<td>5.6</td>
</tr>
<tr>
<td>Specimen width (cm)</td>
<td>9.2 - 20.6</td>
<td>2.0 – 17.3 cm</td>
<td>1.9 – 7.6</td>
<td>1.6 – 1.7</td>
</tr>
<tr>
<td>Average specimen width (cm)</td>
<td>14.5</td>
<td>14.5</td>
<td>3.8</td>
<td>1.6</td>
</tr>
<tr>
<td>Localities</td>
<td>Green Head, Bishop’s Cove</td>
<td>Green Head, Bishop’s Cove, E-Surface, D-Surface, Bristy Cove</td>
<td>Bishop’s Cove, E-Surface</td>
<td>Upper Island Cove</td>
</tr>
<tr>
<td>Arrangement of petals</td>
<td>Completely surrounding a central branching point</td>
<td>Radiating from a basal branching point over ~180 degrees</td>
<td>Radiating from a basal branching point over &lt;90 degrees</td>
<td>Projecting virtually linearly from a basal attachment point</td>
</tr>
<tr>
<td>Location of point from which petals branch</td>
<td>Central</td>
<td>Basal</td>
<td>Basal</td>
<td>Basal</td>
</tr>
<tr>
<td>No. of visible petals</td>
<td>6-7</td>
<td>4-8</td>
<td>4-5</td>
<td>3-7</td>
</tr>
<tr>
<td>Average number of counted petals</td>
<td>7</td>
<td>6</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Completeness</td>
<td>Most complete</td>
<td>Lacking basally projecting petals of O’s</td>
<td>Lacking basally projecting petals of O’s and most lateral petals of U’s</td>
<td>Lacking basally projecting petals of O’s and lateral petals of U’s and displaying a higher degree of petal overlap than in V’s</td>
</tr>
</tbody>
</table>
to 15 cm (mean = 8.3 cm) in length (Table 2.1) and are the most common forms found at all examined localities. In specimens transitional into V-shaped taphomorphs, lateral petals may be preserved on one side of the specimen but not on the opposite side (Fig. 2.5B).

V-shaped specimens (Figs. 2.3A, 2.5A, 2.5B, 2.6) are wedge-shaped with the angle between the outermost petals being acute. Unlike U-shaped specimens, the most lateral petals are not preserved. These petals tend to be the smallest *Bradgatia* taphomorphs and range in size from a length of 1.6–10.6 cm (mean = 3.9 cm) and a width of 1.9–7.6 cm (mean = 3.8 cm, Table 2.1).

### 2.5.3 Exceptional preservation of *Bradgatia* at Spaniard’s Bay

*Bradgatia* from Spaniard’s Bay takes the form of a unique I-shaped taphomorph, which does not occur elsewhere on the Avalon Peninsula. I-shaped specimens (Figs. 2.4, 2.6) are similar in length to V-shaped specimens elsewhere in the Avalon Peninsula, but strong current alignment during burial (Ichaso et al. 2007) has streamlined them into an I-shaped configuration, reducing their radius in comparison with Vs. Length ranges from 5.3 to 6.5 cm (mean = 5.6 cm) but width ranges from only 1.6 to 1.7 cm (mean = 1.6 cm, Table 1). Petals of *Bradgatia* have thus been extensively streamlined and have the highest degree of overlap of all *Bradgatia* taphomorphs (Figs. 2.4A, 2.4C, 2.4F, 2.4G). This makes *Bradgatia* petals appear more linear than those of Conception-style specimens.

Specimens from Spaniard’s Bay show strong architectural and constructional similarities with Conception-style *Bradgatia* that justify regarding both as taphonomic
variants of a single biologic taxon. Both are made up of a collection of independent petals, 4–8 in Conception-style specimens and 3–7 in Spaniard’s Bay specimens, that connect at a common base (Figs. 2.3–2.5). Petals in both Conception-style and Spaniard’s Bay specimens are typically overlapped by neighbouring petals and only display half petals but also complete petals may be rarely preserved (Figs. 2.3D, 2.4A, 2.5C). Furthermore, petals of Conception-style and Spaniard’s Bay specimens share the same arrangement of frondlets, secondary branches, and tertiary branches. Because of their exquisite preservation of four orders of rangeomorph branching, frondlets of Spaniard’s Bay specimens highlight the overlap of distal frondlets over neighbouring basal frondlets (Fig. 2.4A).

The differences between Spaniard’s Bay and Conception-style specimens stem mainly from the different style of preservation of each. Exquisite, three-dimensional preservation of Spaniard’s Bay specimens reveals a basal spherical structure preserved in negative relief on the surface, overtop of which proximal ends of petals are preserved and wrap around it in a similar fashion to leaves of a garden leek (Figs. 2.4A, 2.4C, 2.4D, 2.4E). This structure may have acted as an anchoring mechanism for Bradgatia and would thus have been buried and not preservable in Conception-style specimens in Charnwood Forest and the Avalon Peninsula. Preservation of the top surface of an overfolded frondlet (Figs. 2.4A, 2.4B) and the side-on view of petals (Figs. 2.4A, 2.4E, 2.4F, 2.4G) are also attributable to the preservational style of Spaniard’s Bay specimens. These features would not have made contact with the ocean-bottom sediments and would not have been preserved in two-dimensional Conception-style preservation.
2.6 Growth and taphonomy of *Bradgatia*

Although it may be tempting to infer that each end member of the *Bradgatia* continuum (i.e., I-, V-, U-, and O-shaped specimens) represents an independent species, the presence of a continuous gradation of forms intermediate between these end members (Figs. 2.3, 2.4) implies that this variation instead reflects ontogeny and taphonomy. Biometric analysis (Fig. 2.7A) reveals that Is and Vs are typically the smallest taphomorphs, Us span nearly the entire size range but tend to be intermediate in size, and Os are the largest, implying that there is a change in the preserved morphology of *Bradgatia* with age. The simplest explanation — *Bradgatia* added petals throughout ontogeny — superficially appears to be supported by a plot of the number of petals versus radius of *Bradgatia* (Fig. 2.7B), which shows that Is typically display three petals and Vs typically display four to five petals whereas Us have between four and eight (preservational constraints only allowed counts of the number of petals on two O-shaped specimens). However, the correlation between specimen size and number of petals is not strong, and some specimens of *Bradgatia* as small as 4 cm in radius already show the full adult complement of eight petals. Also, one small I-shaped specimen preserves seven petals.

Our preferred explanation involves a combination of ontogeny and taphonomy (Fig. 2.6). In this model, *Bradgatia* maintained a constant number of eight petals throughout ontogeny, but the petals gradually opened up with age. Is and Vs were the smallest with the most closely bundled collection of petals and thus were most prone to falling over. Petals were tightly bundled atop each other, but only those at the sediment—
Figure 2.7. Schematic illustrating the effects of taphonomy on *Bradgatia*. The black line represents the part of the organism that has been preserved as an impression. (A) Photograph of ROM36500, showing position of transects in (B); (B) Schematic representation of *Bradgatia* petals and frondlets, showing maximum preservational potential (black line at the sediment–ash interface). A–A’, lateral cross section through a *Bradgatia*, corresponding to transect A–A’ in the neighbouring picture, where each white ellipse corresponds to a petal. Note that any petals overlying those in contact with the ocean-bottom sediment are not preserved. B–B’, basal to distal transect through a petal, corresponding to B–B’ in the neighbouring picture, where each ellipse corresponds to a frondlet of a petal. Note the decrease in quality of preservation distally.
water interface could be preserved under the ash (Fig. 2.7A), creating the impression that Is and Vs have the fewest petals of all the taphomorphs.

Petals of U-shaped taphomorphs were more spread out than those of I- and V-shaped specimens, making them harder to fell. When felled, more petals were in contact with the muddy bottom sediments than in Vs and thus more of the petals could be preserved at the mud–ash interface (Fig. 2.7A). Petals of O-shaped taphomorphs were so spread out that they could not be felled, and most or all petals were in contact with the muddy sea bottom at the time of arrival of the volcanic ash that cast them.

Development is a key biological attribute that previously was underutilized in studies of Ediacaran paleobiology and growth by both inflation (*Fractofusus*, Gehling and Narbonne 2007) and addition (*Charnia*, Antcliffe and Brasier 2008; *Pectinifrons*, Bamforth et al. 2008) have been documented among different rangeomorph taxa. A graph of the length of petals against their number of frondlets (Fig. 2.8C) is effectively flat at seven (range 5–10) frondlets per petal, implying that *Bradgatia* did not grow by the addition of segments. This leaves two potential styles of growth for *Bradgatia*: growth by inflation or fractal growth. If *Bradgatia* grew by inflation, each segment would expand at a uniform rate and no addition of segments would occur. All specimens of *Bradgatia* would have a uniform number of fractal orders. In fractal growth, the most basic fractal order of a segment will expand until it reaches a critical size at which point it will turn into the second most basic fractal order. If *Bradgatia* grew fractally, the number of possible fractal orders would be infinite and there should be a theoretical maximum size to the smallest fractal orders. Due to taphonomic constraints, it is not yet possible to distinguish if *Bradgatia* grew fractally or by inflation. Only four fractal orders are
Figure 2.8. Biometric data for Bradgatia linfordensis from the Avalon Peninsula of Newfoundland. (A) Width of complete specimens against radius. Note the tendency for width and radius to increase moving from taphomorphs V to U to O while maintaining a similar width/radius ratio. (B) Number of petals per specimen against radius. (C) Number of frondlets per petal against petal length. See Fig. 1.2 for definition of attributes measured.
distinguishable in the most well-preserved specimens of *Bradgatia* from the Avalon Peninsula and, with this limited preservation, fractal growth would be indistinguishable from growth by inflation. Ripped petaloids reveal that their rangeomorph frondlets encompassed a single row of rangeomorphs ~1.5 mm thick (Fig. 2.4A), so growth of these elements would have been essentially two-dimensional and thus would have avoided the scaling problems inherent in three-dimensional fractal or inflationary growth.

### 2.7 Three-dimensional morphology of *Bradgatia*

*Bradgatia* has often been informally referred to as a bush-like fossil (Misra 1969; Boynton and Ford 1995; Brasier and Antcliffe 2004; Narbonne 2004). Jenkins (1992) described and reconstructed *Bradgatia* as a collection of fronds arranged in a conical circlet with a hollow centre. The high degree of overlap of all branching orders in *Bradgatia* led Hofmann et al. (2008) to suggest a high surface area to volume ratio more closely resembling a lettuce-like structure than a bush.

The three-dimensional morphology of *Bradgatia* changes throughout ontogeny as a result of petals spreading out with age. Small I- and V-shaped specimens have the most tightly bundled collection of petals. Is thus probably resembled leeks (Fig. 2.6) with their collection of at least eight petals projecting virtually linearly from a common spherical base around which they wrap. V- and U-shaped taphomorphs preserve petals projecting from only one side of a basal branching point, making it tempting to consider them fan-shaped organism; however, the more completely preserved O-shaped taphomorphs imply that, unlike a leek- or fan-shaped organism, petals fully surrounded a central branching point. The petals of Vs would have been slightly more spread out than those of Is,
resembling a head of romaine lettuce (Fig. 2.6). Petals of Us would have been considerably more spread out resembling a head of Boston lettuce (Fig. 2.6). O-shaped specimens have the most widely spread assemblage of petals with outer petals possibly touching the sediment–water interface, much like a head of butterhead lettuce (Fig. 2.6).

Specimens of Bradgatia may appear unconstrained in the field owing to overlapping and crossing branches of various rangeomorph orders; however, careful study of the number of frondlets per petal reveals that Bradgatia had a highly constrained order. Counts of frondlets are relatively consistent with a mode of seven, a minimum of five, and a maximum of 10 (Fig. 2.8C). No correlation exists between the number of frondlets and petal length (Fig. 2.8C), implying that each petal had a specific number of frondlets throughout ontogeny.

2.8 Orientation

O-shaped specimens are equidimensional in their two-dimensional expression and thus do not show any directionality in their orientation on bedding plane surfaces. U- and V-shaped taphomorphs from the Avalon Peninsula, on the other hand, have a clearly defined base and distal end and can, therefore, be used to analyze orientations of specimens. Results from such an analysis provide valuable information on the influence of currents on Bradgatia and thus also on the life habits of Bradgatia. I-shaped Bradgatia preserved within a turbidite bed at Spaniard’s Bay show a strong alignment with all other fronds in this bed and are oriented in the same direction as turbidite flow as determined from ripple marks in these beds (Ichaso et al. 2007; Fig. 2.3F). Bradgatia from Bishop’s Cove display strong unimodal alignment (Fig. 2.9A) that is in the same direction as felled fronds oriented by contour-parallel currents (Ichaso et al. 2007).
Figure 2.9. Rose diagrams showing the retrodeformed orientations of *Bradgatia* on various surfaces of the Mistaken Point Formation: (A) Bishop’s Cove, (B) G surface, (C) E surface, and (D) D surface.
*Bradgatia* orientations of the G surface of Mistaken Point West display a bimodal orientation with one mode in the contourite direction (Fig. 2.9B) and a second mode in the opposite orientation. The reason for the concentration of these specimens in directly the opposite direction to the predominant contourite currents remains unknown but is consistent with the wide diversity of bottom current processes and orientations common in modern deep-sea settings (p. 405, Stow et al. 1996). *Bradgatia* from the E surface is weakly oriented in the turbidite direction (Fig. 2.9C), which is the same as that shown by fronds on the same surface (Seilacher 1999; Wood et al. 2003). *Bradgatia* on the D surface shows no preferred orientation (Fig. 2.9D). Green Head is mainly populated by O-shaped taphomorphs, rendering measurements of *Bradgatia* orientation meaningless. In summary, four of the six main occurrences of *Bradgatia* show an alignment in the same direction as fronds on the same surface, suggesting that both lived under the influence of the same turbidity and contour currents.

### 2.9 Lifestyles of *Bradgatia*

#### 2.9.1 Life habit

*Bradgatia* was originally regarded as a nektonic organism (Boynton and Ford 1995). A single specimen from Charnwood Forest displays a large, ovoid, boss-like structure in very high positive epirelief in its central area, which Boynton and Ford (1995) considered a central float or anchoring structure; but it is not clear that this structure is a float or it is related in any way to the *Bradgatia* specimen that overlies it.
No specimens from Newfoundland display any similar structures and none shows any evidence for a nektonic life habit.

Several lines of evidence point to an epibenthic sessile life habit for specimens of *Bradgatia* from Newfoundland. *Bradgatia* typically shows alignment in the same direction as contour-parallel currents or turbidity currents (Figs. 2.9A, 2.9B, 2.9C), implying it inhabited a region within the influence of currents. Furthermore, well-preserved specimens from Spaniard’s Bay exhibit a structure to which petals attach that was tethered to the sea floor. Orientation in the same direction as paleocurrents has previously been used as compelling evidence in assigning an epifaunal erect lifestyle to Ediacaran fronds (Seilacher 1992, 1999; Laflamme et al. 2004, 2007).

*Bradgatia* is commonly preserved as an impression on sediment under an ash layer, in the same manner and on the same surfaces as other epifaunal benthic organisms of the Mistaken Point assemblage (Conception-style preservation; Narbonne 2005). This mode of preservation appears to be restricted to epibenthic organisms because preservation is restricted to the boundary between the ash and the sediment surface. Infaunal organisms would not be blanketed by a layer of ash and would thus not be preserved. Only those nektonic organisms that were already dead on the sediment surface at the time of arrival of the ash could be preserved, since any nektonic organisms that were killed by the ash fall would settle to the sea floor long after the denser ash, and this layer of ash would prevent their impression onto the ocean-bottom mud (Jenkins 1992).
There are no current accumulations of *Bradgatia* on any of the studied fossil horizons. Also, no impressions of *Bradgatia* flipped onto its distal end exist, further implying *Bradgatia* was strongly tethered to the ocean floor.

*Bradgatia* shows differential preservation within specimens, with distal ends of petals typically being more poorly preserved than proximal regions, indicating a concentration of ash under these regions (Fig. 2.7B). Proclined organisms would be expected to create relatively evenly and well-preserved impressions as is the case for “spindles” from Mistaken Point. *Bradgatia* is known to overlie spindles and discs (Fig. 2.3C). In these cases, spindles and discs are preserved preferentially, having been more firmly imprinted into the ocean-bottom mud before the arrival of the volcanic ash.

### 2.9.2 Feeding strategy

Numerous proposals as to the feeding strategies of rangeomorphs have been put forward, notably photo- and chemo-autotrophy (McMenamin 1986), nutrient absorption from the water column (Sperling et al. 2007), and suspension feeding (Jenkins and Gehling 1978; Seilacher 1989; Clapham and Narbonne 2002; Laflamme et al. 2004; Laflamme et al. 2007). Photo-autotrophy can be discounted as the Mistaken Point assemblage inhabited deep waters, well below storm wave base and the photic zone (Wood et al. 2003; Ichaso et al. 2007). Chemo-autotrophy remains an unlikely source of nutrients as carbonate and sulfide concentrations in the sediments are several orders of magnitude lower than the minimum for sustaining chemotrophic communities (Canfield et al. 2007). The Mistaken Point assemblage exhibits a tiering structure and other ecological features similar to that of nutrient-absorbing and filter-feeding communities.
Bradgatia is composed of multiple petals. As in Charnia, the absence of a stem permitted feeding along the entire length of each petal (Laflamme et al. 2007). The presence of multiple petals would have allowed for more extensive harvesting of nutrients from the water column than that of a single frond.

2.10 Conclusions

Bradgatia is constructed from at least four visible orders of rangeomorphs arranged into a minimum of eight thin, overlapping petals attached at a single basal to central locus to form what is herein termed a “petalage.” The first order of rangeomorph branching (the frondlet) emerges from the central axis of each petal. Frondlets are further subdivided by second-order elements, which stem from the central axis of frondlets. Third-order branches stem from the central axis of second-order branches and fourth-order branches stem from the central axis of third-order branches.

Three intergradational taphomorphs of Bradgatia occur: (1) O-shaped taphomorphs are most completely preserved with petals surrounding a central branching point and are typically the largest taphomorphs; (2) U-shaped taphomorphs do not preserve the basally projecting petals; and (3) V-shaped taphomorphs do not preserve the lateral branches that are seen in U-shaped taphomorphs and are typically the smallest taphomorphs. This transition is interpreted as representing the gradual opening of Bradgatia individuals with increasing ontogenetic age. A fourth taphomorph, the I-shaped taphomorph, is found only at a single locality, Spaniard’s Bay. Specimens are
similar in length to V-shaped taphomorphs but exhibit strikingly smaller widths owing to strong current alignment of their petals.

A graph of specimen size against the number of petals per specimen shows only slight correlation, implying that Bradgatia had a constant number of petals throughout ontogeny. Counts of frondlets per petal reveal no correlation with petal length, implying Bradgatia either grew fractally or by inflation.

Several lines of evidence suggest Bradgatia was an attached, sessile, epifaunal organism. Bradgatia branches attached to a distinct basal structure preserved in Spaniard’s Bay specimens, which was firmly anchored to the sea floor. In most cases, Bradgatia is oriented in the same direction as contour-parallel currents. No current accumulations of Bradgatia or flipped Bradgatia are preserved, further suggesting a firm attachment to the substrate. The decrease in the quality of preservation distally within specimens indicates that only the base of Bradgatia was in contact with ocean-bottom mud. In the cases where Bradgatia overlies a disc or a spindle, Bradgatia is invariably more poorly preserved, indicating it was felled overtop the disc or spindle.

Tiering structure at Mistaken Point is typical of that of a nutrient-absorbing or filter-feeding community (Clapham and Narbonne 2002). Bradgatia petals are stemless, implying Bradgatia could feed over the entire length of each petal. Multiple petals per organism allowed for more thorough filtering of the water column.
Chapter 3

Culmofrondis plumosis: a new Ediacaran fossil from the Mistaken Point Assemblage, Avalon Zone, Newfoundland

Abstract

Culmofrondis plumosis new genus and species is a stemmed rangeomorph frond from the Ediacaran (ca. 565 Ma) Mistaken Point Formation of the Avalon Peninsula, Newfoundland. The construction of its petalodium with a zigzagging central midline and non-rangeomorph primary branches are typical of fronds exhibiting Charnia-type branching whereas its rangeomorph secondary branches and flexible primary branches are typical of organisms exhibiting Rangea-type branching. The long stem of Culmofrondis served to elevate the petalodium into the water column to avoid competition in the lower tiers and the flexible branches of Culmofrondis could easily adapt to changing water currents.

3.1 Introduction

The Ediacara biota is a distinctive collection of the oldest complex soft-bodied macroscopic (mm to m scale) organisms. It spans the latter part (575-542 Ma) of the newly named Ediacaran Period (Knoll et al., 2006) and is known from approximately 30 different localities from five continents (Narbonne, 1998, 2005). Localities which yield the most diverse assemblages are known from Ediacara in Australia, the Avalon Zone of Newfoundland, the White Sea region of Russia, Ukraine in eastern Europe, Namibia in southern Africa and the Wernecke and Mackenzie Mountains in NW Canada. Some forms bear morphological features comparable to existing phyla and may represent stem-group and possibly even crown-group members (Gehling, 1987, 1991; Gehling and
Rigby, 1996; Fedonkin and Waggoner, 1997; Gehling et al., 2005). Others have no known modern counterparts or counterparts within the fossil record past the Ediacaran Period and may represent failed experiments in the evolution of life (Seilacher, 1992; Narbonne, 2004, 2005).

The Mistaken Point assemblage, found on the Avalon Peninsula of Newfoundland, is dominated by representatives of an extinct clade, the rangeomorphs. They have a modular construction from centimeter-scale architectural elements called frondlets which are self-similar over three fractal orders (Narbonne, 2004). Frondlets are arranged as modules to form frond-, bush-, spindle- and comb-like constructions (Narbonne, 2004; Gehling and Narbonne, 2007; Laflamme et al., 2007; Bamforth et al., 2008) that dominated the first 15 million years of Ediacaran evolution (Bottjer and Clapham, 2006). Rangeomorphs have been assigned to many different groups. Originally, they were considered primitive ctenophores (Gürich, 1930, 1933; see also Dzik, 2002) or cnidarians (Misra, 1969; Glaessner, 1984; Jenkins, 1985, Runnegar and Fedonkin, 1992; Boynton and Ford, 1995) but were later found to have no existing morphological features characteristic of any clade of living animal and were regarded as their own extinct clade, the Rangeomorpha (Pflug, 1972; Seilacher, 1992; Narbonne, 2004; Brasier and Antcliffe, 2004; Grazhdankin and Seilacher, 2005; Gehling and Narbonne, 2007; Sperling et al., 2007; Laflamme and Narbonne, 2008a,b). Narbonne (2004, 2005) recognized ecological similarities between rangeomorph and modern communities which led him to consider the Rangeomorpha as stem-group animals, a view largely supported by Xiao and Laflamme (2009) based on morphological features. Sperling et al. (2007) noted the absence of features suggestive of a water-canal system.
and suggested that they may represent stem-group opisthokonts, the superkingdom which contains both animal and fungus kingdoms. Rangeomorphs date back to the very beginnings of complex multicellular life and their study is critical in understanding the early evolution of megascopic life.

Some of the most characteristic organisms of the Ediacaran are fronds and include Rangea (Gürich, 1929; Jenkins, 1985) Charniodiscus (Ford, 1958; Laflamme et al., 2004), Charnia (Ford, 1958; Laflamme et al., 2007) Swartpuntia (Narbonne, 1997) and Primocandelabrum (Hofmann et al., 2008). They all consist of a basal holdfast and a feeding structure – the petalodium (Laflamme and Narbonne, 2008a, b). Charniodiscus, Rangea, Primocandelabrum and Swartpuntia possess a stem which served to elevate the petalodium into the water column, whereas the stemless petalodium of Charnia extended directly from its holdfast. They all differ, however, in the construction of the petalodium which is the most complex and diagnostic structure of the frond (Laflamme and Narbonne, 2008a, b). Charnia and Rangea differ from all other described fronds in being constructed from rangeomorphs and they differ from each other in their arrangement of rangeomorph branches within the petalodium. Charnia is composed of sigmoidal to rectangular primary branches which alternate along a central axis to create a zigzagging midline (Laflamme et al., 2007). Primary branches are composed of secondary modular elements which are arranged acutely to almost perpendicularly to primary branches and contain rangeomorphs at their limit of resolution (see Fig. 3 in Laflamme and Narbonne, 2008b for an illustration of the arrangement of rangeomorph building blocks within different forms). Rangea on the other hand is constructed from prominent rangeomorphs
arranged in a series of parallel arrays diverging from the central stalk of at least four petaloids (Jenkins, 1985).

Here we describe a rangeomorph frond, *Culmofrondis plumosis* new genus and species, from the Mistaken Point Formation of the Avalon Peninsula, Newfoundland. This taxon is informal within this thesis. The description leads to an interpretation of its three-dimensional morphology, a comparison to other described fronds and an analysis of its life habits.

3.2 Geologic and Stratigraphic Setting

The fossiliferous surface of the Mistaken Point Formation of the Conception Group examined in this study outcrops along the southernmost coast of the Avalon Peninsula, Newfoundland. Fourteen specimens of *Culmofrondis* were examined from a surface at Gull Rock Cove (Fig. 3.1); the only surface on which *Culmofrondis* has yet been discovered.

The Mistaken Point Formation is composed of thin- to medium-bedded turbidites primarily of the $T_E$ division of the Bouma sequence (Wood et al., 2003). $T_{DE}$ turbidites are second most common and outnumber $T_{(B)CDE}$ turbidites by an average of 3:1 (Wood et al., 2003). No channelized deposits are present and debris-flow deposits are not volumetrically significant (Wood et al., 2003). The presence of debris-flow deposits indicates that the Mistaken Point Formation accumulated on a marginal slope rather than in a mid- to distal- fan setting and the absence of channel deposits indicates that it was deposited downslope of mid-slope (Wood et al., 2003). The excellent lateral continuity of bedding and the absence of slump deposits and slump scars further suggest that the
Figure 3.1. Geographic and stratigraphic distribution of *Culmofrondis plumosis*. A. Locality map of Newfoundland displaying the locality map from which *Culmofrondis* was studied. A close up of the highlighted area on the map of Newfoundland is illustrated in the box. B. Stratigraphy of the Ediacaran section of the Avalon Peninsula including published U/Pb ages on zircons (from Benus, 1988 and Bowring et al., 2003).
Mistaken Point Formation formed on a topographically smooth surface (Wood et al., 2003). This led Wood et al. (2003) to interpret the Mistaken Point Formation as a toe-of-slope accumulation.

The Gull Rock Cove surface was discovered by Queen’s University in 1998 and has been included in paleoenvironmental analyses (Wood et al., 2003) as well as paleoecological studies (Clapham and Narbonne, 2002, Clapham et al., 2003) and has been an important stop on international fieldtrips (Narbonne et al., 2005). Clapham and Narbonne (2002) and Clapham et al. (2003) referred to this surface as Lower Mistaken Point. It occurs in the lower Mistaken Point Formation just above the boundary with the Briscal Formation. The thick (m-scale) olive-grey rocks of the Briscal Formation are abruptly, yet conformably overlain by the 0.5 -1 m thick red-purple rocks of the Mistaken Point Formation. The strata are composed of thin- to thick-bedded turbidites interbedded with very thin laminated contourites and debris flows (Narbonne et al., 2005). Contourite beds are typically 1-2 cm thick and overlain by very thin black or dark grey/green ash layers (Narbonne et al., 2005).

The surface is 14 m² and preserves 304 fossils (Clapham et al., 2003) which are dominated by fronds. Culmofrondis is labelled as Charnia Type B in Clapham et al. (2003) study. Charnia, including Culmofrondis, are the most common fossils, followed by “ostrich feathers”, Charniodiscus, unnamed fronds, and “dusters” (Clapham et al., 2003; Narbonne et al., 2005). Rarer fossils include Fractofusus, lobate discs, and Hiemalora (Clapham et al., 2003; Narbonne et al., 2005). Similarly to other surfaces of the Mistaken Point Formation, fronds display a strongly preferred felling orientation.
towards the NE, which is interpreted as representing alignment by a contour-parallel
current (Wood et al., 2003; Narbonne et al., 2005).

The Mistaken Point Formation at Gull Rock Cove lies between an ash bed in the
Drook Formation dated at 575±1 Ma (Fig. 3.1B; ID-TIMS U-Pb zircon, Bowring et al.,
2003) and an ash bed directly overlying the E-surface of the Mistaken Point Formation
west of Mistaken Point dated at 565±3 Ma (Fig. 3.1B; U-Pb, Dunning in Benus, 1988).

3.3 Materials and Methods

Of the 14 specimens on the Gull Rock Cove surface, 3 are large, complete, and
relatively well preserved (Fig. 3.2A, Fig. 3.3), 3 are poorly preserved small specimens
that do not reveal clear secondary features, 1 is a partially preserved petalodium of a
frond of which the base was cleaved off the surface but which reveals detailed smaller
structures, and the remainder are partially preserved large specimens which all preserve a
disc and stem but differ in the extent of preservation of the petalodium. Field
photographs were taken of all specimens. Latex moulds of all 3 complete specimens, the
partial petalodium and 1 small specimen were taken for further examination in the
laboratory. No specimens have been collected due to the protected nature of Mistaken
Point as an Ecological Reserve and as a candidate for a UNESCO World Heritage Site.

The Gull Rock Cove surface has been shortened 37% in the direction of cleavage
as observed through originally circular discs which are now elongated perpendicular to
the direction of cleavage (Wood et al., 2003). All photographs and measurements
presented here have been retrodeformed by the methods described in Wood et al. (2003)
and Ichaso et al. (2007) to remove the effects of tectonic deformation.
Figure 3.2. Field photograph of *Culmofrondis* (A) alongside its labelled line drawing (B). B. Thickest lines in the petalodium represent margins of primary branches, lines of intermediate thickness represent outlines of secondary branches and thinnest lines represent outlines of tertiary branches. Divisions on the scale bar = 1 cm.
Figure 3.3. Field photographs (A, B, C) of *Culmofrondis* from the Mistaken Point Formation at Gull Rock Cove. Scale bar divisions = 1cm.
3.4 Taphonomy

Fossils of the Mistaken Point Formation are preserved on the top surfaces of interturbidite beds under a layer of volcanic ash. Coatings of volcanic ash covered the organisms living on the top surfaces of interturbidite beds, also possibly smothering and felling them. Labile minerals aided in rapidly lithifying the ash which either cast the top surface of the organism itself, or its basal impression in the sea-floor mud. In the case of tissues least resistant to decomposition, such as petalodia of fronds, spindles and Bradgatia petals, tissues left an imprint in the ocean bottom sediments prior to decomposition. Ash subsequently fell into the remaining impression and cast it in negative epirelief. This is the mode of preservation for the petalodium of Culmofrondis. Tissues less prone to decomposition, such as discs and frond stems and stalks, were coated by a layer of ash which solidified prior to their decomposition. After they decomposed, ocean bottom mud was injected into the void and molded by the hardened layer of ash producing positive epirelief casts as is the case for the discs and stems of Culmofrondis. This style of preservation was described by Seilacher (1992) and termed Conception-style preservation by Narbonne (2005).

All three large, completely preserved specimens of Culmofrondis are equally well-preserved along the length of the specimens (Fig. 3.3). The specimen figured in 3C preserves secondary rangeomorph branches in its uppermost primary branch. However, only the discs, stems and basal portion of petalodia of seven partially preserved specimens were preserved. Given the exceptional preservation of the three complete specimens, it is likely that they were felled prior to the ash-fall so that no ash could fall between the fossil and the sediment to impede preservation. The seven partially
preserved specimens however decrease in preservational quality distally along the frond suggesting a layer of ash was able to accumulate between the distal portions of the frond and the sediment before the frond was felled. This degradation of preservation distally in fronds has also been noted in *Charniodiscus* and *Charnia* from the Mistaken Point Formation (Laflamme et al., 2004, 2007).

### 3.5 SYSTEMATIC PALEONTOLOGY

The systematic paleontology below is informal until published in a refereed scientific paper.

Group RANGEMORPHA Pflug, 1972

Genus *CULMOFRONDIS* new genus

*Type species.* – *Culmofrondis plumosis* new species, by monotypy

*Diagnosis.* – As per species.

*Etymology.* – From the Latin “culmus” meaning stem and “frondis” meaning frond, in reference to the long stem of the frond.

*CULMOFRONDIS PLUMOSIS* new species

Figures 2, 3 and 4

*Diagnosis.* – Stemmed, elliptic frond composed of up to 4 overlapping sigmoidal primary branches per petaloid alternating along a gently zigzagging central axis. Primary branches subdivided by a series of trapezoidal to plumose rangeomorph frondlets
arranged acutely to almost perpendicularly to the primary branches. Basal disc
commonly large.

Description. – *Culmofrondis plumosis* is a 3.6-31.9 cm (mean = 16.6 cm; n = 6) long
frond with a 1.4-10.7 cm (mean = 7.2 cm; n = 13) long stem and a disc with a large
surface expression ranging in diameter from 0.6-5 cm (mean = 3.5 cm; n = 13). Both
stem and disc are preserved in low positive epirelief. The petalodium is preserved in
negative epirelief, is typically elliptic and ranges in length from 2.2-23.6 cm (mean =
11.1 cm; n = 6) and in width from 1.7 to 9 cm (mean = 4.8 cm; n = 6). Well preserved
petaloids are composed of 4 sigmoidal primary branches (Fig. 3.2B) which alternately
stem at acute angles from a central axis creating a subtly zigzagging midline. Primary
branches become more acute distally (Fig. 3.2B) with the typically larger proximal
branches diverging from a central axis at 19° to 35° and the typically smaller distal
branches at 1° to 6°. The distal portion of primary branches is incomplete and tucks
under the distally neighbouring primary branch. Primary branches are divided into 1-11
(mean = 7) visible plumose secondary rangeomorph branches (Fig. 3.2B) which stem
from a location on primary branches overlapped by the neighbouring distal branch. Basal
secondary branches branch at almost perpendicular angles to the central axis of primary
branches but the branching angle becomes more acute distally along the primary branch.
Proximal primary branches typically display a higher number of visible secondary
branches (8-11) whereas distal branches display significantly fewer (1-3). Tertiary
rangeomorph branches visible in well-preserved specimens are typically plumose and
stem on either side of the central midline of secondary branches.
Discussion. – Three small specimens of Culmofrondis occur on the Gull Rock Cove surface. They are typically not well preserved and do not display the extent of detail which is visible in large specimens but the same characters are still decipherable. Both possess a disc with high surface expression and a long stem and alternating primary branches. Smaller structures such as secondary branches are not visible in small specimens due to poor preservation.

The petalodium of the three well-preserved specimens of Culmofrondis (Fig. 3.3) are of about the same length (20-23.6 cm; Table 3.1; Fig 3.3) but differ significantly in width (6.4-9.0 cm; Table 3.1; Fig. 3.3). The width of each petaloid within the petalodium of a specimen may also be different (Fig. 3.2A, 3.4). This suggests that the width of Culmofrondis petalodia is not fully dictated by the length of the petalodium. Measurements of primary branch angles indicate that the width of the petalodium as well as that of individual petaloids is dependent on the degree at which the primary branches diverge from a central axis (Fig. 3.4). This suggests that primary branches had a broad breadth of lateral motion and are thus only attached at their bases. The extent of overlap with underlying branches is dictated by the branching angles of primary branches and thus the sizes of primary and secondary branches differ throughout the specimen (Fig. 3.4) and represent a taphonomic rather than morphological trait.

Despite differences in primary branching angle, no evidence for a second half to primary branches exists to create bilaterally symmetrical double-sided branches. This suggests that primary branches may either be double-sided bilaterally symmetrical branches which have been folded in half or single-sided branches.
Table 3.1. Petalodium lengths and widths of complete large specimens of *Culmofrondis* from the Mistaken Point Formation.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Petalodium length (cm)</th>
<th>Petalodium width (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>20.4</td>
<td>6.4</td>
</tr>
<tr>
<td>B</td>
<td>23.6</td>
<td>8.0</td>
</tr>
<tr>
<td>C</td>
<td>20.0</td>
<td>9.0</td>
</tr>
</tbody>
</table>
Figure 3.4. Idealised line drawing of *Culmofrondis* drawn to its second order of branching illustrating the effects on the shape of the petalodium between highly angled branches (<20°) to the left and low angled branches (<55°) to the right. Thicker lines in the petalodium represent boundaries of primary branches and thinner lines represent boundaries of secondary branches. The dashed line represents the termination of the petaloid at <55°.
There is a large difference in the number of secondary branches per primary branch with the most basal primary branches typically displaying the highest number of secondary branches and the most distal primary branches typically displaying the fewest secondary branches. This is likely a taphonomic feature which is due to the distally increasing primary branch overlap brought about by increasing distal branch angles.

Comparisons.– Laflamme and Narbonne (2008a, b) classified fronds into four distinct groups based on their branching architecture: Arborea-, Charnia-, Rangea-, and Swartpuntia-type branching. They believed that each of these groups reflect distinct taxonomic clades.

Both members of Arborea- and Swartpuntia-type branching are not constructed from rangeomorph frondlets. Secondary and tertiary branches of Culmofrondis, however, are constructed of rangeomorphs suggesting that Culmofrondis belongs to neither of these groups. Furthermore, Swartpuntia-type branching displays only 1 branching order whereas Culmofrondis displays at least 3. No known specimens displaying Swartpuntia-type branching are known from the Avalon Peninsula. Charniodiscus, which displays Arborea-type branching is commonly found on the Avalon Peninsula as well as at Gull Rock Cove. It can be further distinguished from Culmofrondis by its complex disc with a central ring which may display annulae or radial ridges but which is surrounded by a smooth outer ring. Culmofrondis displays a smooth disc with no internal ornamentation.

Rangea- and Charnia-type branching are both subdivisions within the Rangeomorpha. In Charnia-type branching a series of parallel, sigmoidal to rectangular primary branches alternate and cross over the central midline to form a zigzagging central axis (Laflamme and Narbonne, 2008a, b; Ancliffe and Brasier, 2008). Primary branches
are subdivided by secondary modular elements which are further divided into rangeomorph tertiary branches (Laflamme and Narbonne, 2008a, b; Antcliffe and Brasier, 2008). Similarly to organisms displaying Charnia-type branching, Culmofrondis consists of sigmoidal primary branches which also cross over the central midline and create a zigzagging central axis. In Culmofrondis both secondary and tertiary elements are rangeomorph branches. Culmofrondis also preserves a large disc and long stem not typically seen in specimens exhibiting Charnia-type branching. Charnia wardii is common on the Lower Mistaken Point surface. Unlike Culmofrondis, its petalodium is long and parallel-sided and exhibits no stem.

Rangea-type branching consists of at least three self-similar branching orders of highly repetitive fractal rangeomorph elements. It is typified by Rangea schneiderhoheni and is the predominant branching structure in organisms from the Conception Group, notably Bradgatia linfordensis (Chapter 2), Fractofusus (Gehling and Narbonne, 2007), Pectinifrons abysallis (Bamforth et al., 2008) and a collection of unnamed fronds. In Culmofrondis, secondary branches are rangeomorph branches and are divided into tertiary rangeomorph branches. No further detail in branching is visible due to limited preservational detail. Primary branches of Culmofrondis are similar to primary branches in organisms exhibiting Rangea-type branching in that they have a broad range of movement.

Culmofrondis displays characteristics of both Rangea- and Charnia-type branching (Table 3.2). The branching pattern of Culmofrondis is similar to that of organisms displaying Charnia-type branching in that sigmoidal primary branches overlap
Table 3.2. *Charnia*-like and *Rangea*-like branching characteristics of *Culmofrondis* from the Mistaken Point Formation.

<table>
<thead>
<tr>
<th><em>Charnia</em>-like</th>
<th><em>Rangea</em>-like</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alternating sigmoidal primary branches</td>
<td>Primary branches move freely</td>
</tr>
<tr>
<td>Primary branches overlap the central axis to create</td>
<td>Plumose rangeomorph secondary branches</td>
</tr>
<tr>
<td>a zigzagging midline</td>
<td></td>
</tr>
<tr>
<td>Primary branches are single-sided</td>
<td></td>
</tr>
</tbody>
</table>
a central axis creating a zigzagging central midline. Primary branches do not exhibit
typical, double-sided rangeomorph structure. The importance of rangeomorph elements
in *Culmofrondis* is more similar to organisms displaying *Rangea*-type branching than to
those exhibiting *Charnia*-type branching. Both secondary and tertiary elements are
rangeomorphs in *Culmofrondis*, whereas only tertiary elements are rangeomorphs in
organisms displaying *Charnia*-type branching. Both *Culmofrondis* and organisms
displaying *Rangea*-type branching share primary branches with a broad breath of motion.

Organisms classified as having *Charnia*- or *Rangea*-type branching are members
of two separate rangeomorph clades (Laflamme et al., 2008a, b). The similarity of
*Culmofrondis* to both suggests one of 3 possibilities: 1. *Culmofrondis* is a common
ancestor to both rangids and charnids, 2. *Cumlofrondis* is an evolutionary intermediate
form between rangids and charnids, or 3. *Culmofrondis* is nested firmly within the
rangids or charnids but exhibits some features convergent with the other taxon.

As an interpreted common ancestor to both rangids and charnids a distinct clade
of *Culmofrondis*-like organisms may precede both rangids and charnids in the fossil
record. As an intermediate form between rangids and charnids, a temporal segregation
should occur between the first appearances of rangids and charnids within the fossil
record. Ediacaran fossils, however, appear too sparsely over too large a time scale to
accurately time their first and last appearances within the fossil record (eg. Strauss and
Sadler, 1989; Marshall, 1990; Knoll et al., 2006).

The hypothesis that *Culmofrondis* is nested firmly within the rangids or charnids
but exhibits some features convergent with the other taxon is less likely. Features are
unlikely to have evolved twice within the same clade and the features of *Culmofrondis*
similar to both charnids and rangids are basic defining characteristics of each taxon. *Culmofrondis* cannot be classified purely within either the rangids or the charnids based on its morphology.

*Primocandelabrum*, described by Hofmann et al. (2008) from the Bonavista Peninsula of Newfoundland, has not yet been classified into any of the categories of Laflamme and Narbonne (2008a, b). In all known specimens, its petalodium is only partially preserved, limiting the extent to which branching structure can be examined. Like *Culmofrondis*, *Primocandelabrum* preserves a large disc and long stem. Appendages also radiate from the holdfast producing a *Hiemalora*-like disc (see Fig. 12 in Hofmann et al., 2008). No appendages radiate from the discs of any *Culmofrondis* specimens (Fig. 3.3), but specimens of *Hiemalora* are preserved on the Lower Mistaken Point surface. This suggests that the lack of appendages on *Culmofrondis* holdfasts is probably not due to preservational limitations. Visible microstructure in the petalodium of *Primocandelabrum* shows rows of ridges diverging from the base of its petalodium (see Fig. 12 in Hofmann et al., 2008). No rangeomorph elements are apparent in any specimens. This is different than what is seen in even partially preserved *Culmofrondis* petalodia in which the basal outlines of primary branches are typically visible.

**Occurrence and stratigraphic range.** – *Culmofrondis* occurs at a single stratigraphic level in the lower part of the Mistaken Point Formation at Gull Rock Cove referred to as surface F3 in Wood et al. (2003).

**Etymology.** – *Plumosis* refers to the feather-like shape of the frond as well as the plumose nature of the rangeomorph branches within the petalodium.
*Holotype.* – Plastotype QG0115 from the Mistaken Point Formation, Conception Group at the type locality Gull Rock Cove, southeast Newfoundland.

*Three-dimensional Reconstruction.* – The nature of Conception-style preservation is such that originally three-dimensional organisms are preserved two-dimensionally on bedding plane surfaces beneath beds of volcanic ash. Taphonomic clues provide insight into the original three-dimensional form of the fossil impressions. Features preserved in positive epirelief such as discs and stems indicate tissues more resistant to decomposition (Seilacher, 1992; Narbonne, 2005). They also maintain some degree of form of the original structure and suggest that discs were spherical and stems were cylindrical.

In two dimensions, the petalodium appears to be a simple sheet-like structure but taphonomic features suggest otherwise. The difference in primary branching angle in specimens dictates the shape of the petalodium (Fig. 3.4). Petalodia of specimens with high primary branching angles appear elongated (Fig. 3.3A, 3.4) whereas specimens with lower primary branching angles appear wider (Fig. 3.3C, 3.4). This implies that primary branches were only attached at their bases and had a high degree of lateral motility. The apparent shape of primary branches changes with the differing amounts of overlap and is governed by primary branching angles. In three-dimensions, primary branches within and between specimens would have maintained the same shape. Primary branching angle also dictates the extent to which secondary branches are revealed in two-dimensions and thus their apparent shape. More highly angled primary branches create a higher degree of overlap with neighbouring branches which obscures a larger surface area of the secondary branches (Fig. 3.3). No bilaterally symmetrical second side to primary branches is apparent in any specimens despite the variations in branch angle.
3.6 Lifestyle

3.6.1 Infaunal vs. Epifaunal

Specimens of *Culmofrondis* show strong unimodal alignment in the same direction as 32 other felled fronds of the same surface that have been oriented by contour-parallel currents (Fig. 3.5; Wood et al., 2003). *Culmofrondis* also has a disc and a stem, a morphology unique to epifaunal fronds (Laflamme and Narbonne, 2008a, b). This suggests that *Culmofrondis* lived within the influence of currents, not prone on the sediment surface or within sediment, and was strongly tethered to the ocean floor by its basal holdfast.

Further evidence for an epifaunal erect lifestyle includes its preservation at the interface between an underlying mudstone and the overlying ash-fall tuff. All fossils of the Conception group are exclusively preserved in this manner. The quality of preservation of *Culmofrondis* also typically decreases along the length of the specimen suggesting that ash had time to accumulate between the distal parts of the specimen before it was completely felled. This suggests that *Culmofrondis* stood upright in the water column.

3.6.2 Feeding

A variety of feeding strategies have been proposed for the Ediacara biota including photo-autotrophy and chemo-autotrophy (McMenamin, 1986), and suspension feeding (Jenkins and Gehling, 1978; Seilacher, 1989; Clapham and Narbonne, 2002; Laflamme et al., 2004; Laflamme et al., 2007, Sperling et al., 2007). The presence of meter-thick turbidites and the complete absence of shallow-water features anywhere in the Conception and overlying St. John’s Group suggest that the depth at which these
Figure 3.5. Rose diagram illustrating the orientations of *Culmofrondis* specimens on the Gull Rock Cove surface of the Mistaken Point Formation relative to contourite direction, measured by the felling direction of other stalked fronds and turbidite directions from current ripples (Wood et al., 2003).
organisms lived was far below the euphotic zone, making photo-autotrophy an unlikely source of nutrients (Wood et al., 2003). The tiering structure also does not resemble that of a marine photo-autotrophic community such as a modern “kelp forest” in which organisms grow preferentially towards the surface and can reach lengths of >40 m (Foster, 1975; Raven et al., 2005). The elevated concentrations of sulphides and carbonates needed to support chemo-autotrophic communities do not occur in the sediments of the Mistaken Point Formation (Canfield et al., 2007). The tiering structure of Mistaken Point communities is strikingly similar to that of Phanerozoic filter-feeding or nutrient-absorbing communities (Clapham and Narbonne, 2002).

Bottjer and Ausich (1986) analysed the tiering structure of Phanerozoic suspension feeders and characterised them according to their relationship with the seafloor. The bodies of epifaunal primary tierers intersect the seafloor whereas epifaunal secondary tierers are epibionts which live upon primary tierers. Primary tierers are further subdivided by their style of suspension feeding. Primary colonial tierers, such as tabulate corals and bryozoans, feed along the entire length of their body. Primary solitary tierers, such as crinoids, elevate a feeding structure into the water column and grow upwards occupying different tiers throughout ontogeny.

*Culmofrondis* can be compared to Phanerozoic primary solitary tierers with its long stem which elevates its feeding structure, the petalodium, into higher tiers of the water column. All complete large specimens of *Culmofrondis* occur in the 22-35 cm tier of Clapham and Narbonne (2002) and only extremely rare taller organisms exist. *Charnia* and *Charniodiscus* also commonly occur in this tier (Clapham and Narbonne, 2002). *Charniodiscus*, like *Culmofrondis*, can be compared to primary solitary tierers of
the Phanerozoic. *Charnia* is stemless with a petalodium which extends to its disc and can be compared to primary colonial tirers of the Phanerozoic with the ability to suspension feed along its entire length.

The primary branches of *Culmofrondis* are flexible, much like organisms displaying *Rangea*-type branching, allowing it to adapt to changing currents. *Charniodiscus* is one of the only other organisms from the Mistaken Point assemblage which constructs a long stem, is of a similar height to *Culmofrondis* and also either filter fed or absorbed nutrients from the water column suggesting they occupied the same ecological niche. It was more successful than *Culmofrondis* in that it is found on most fossiliferous surfaces of the Mistaken Point Formation and ranges into the Trepassey Formation. Unlike *Culmofrondis*, its primary branches were attached to an outer rim surrounding its petalodium (Laflamme et al., 2004) not allowing for any independent movement within them.

Ecological succession is evident on fossiliferous surfaces of the Mistaken Point Formation with individual beds providing snapshots of communities in different stages of ecological succession (Clapham et al., 2003). The Gull Rock Cove surface is typical of a late succession stage community with a lower diversity and eveness than seen in mid-succession communities and non-random multispecies patterns and vertical partitioning of the water column is well-developed (Clapham et al., 2003). The surface is dominated by fronds and displays a tolerance model of succession where organisms adapted to higher resource levels are progressively replaced by those adapted to lower resource levels (Clapham et al., 2003). *Culmofrondis* is typical of a late succession stage frond...
being rare and only found on the Gull Rock Cove surface. This suggests that is was adapted to lower resource levels.

3.7 Conclusions

*Culmofrondis plumosis* is a rangeomorph frond with a long stem and disc with a high degree of surface expression. The petalodium is divided into up into four primary branches which alternate along a central midline creating a mildly zigzagging central axis. Primary branches are further divided into secondary plumose to trapezoidal secondary branches which stem from primary branches at nearly perpendicular to acute angles.

The petalodium of *Culmofrondis* shares branching characteristics with organisms displaying both *Rangea* - and *Charnia*-type branching. Similarly to *Rangea*-type branchling, *Culmofrondis* displays flexible primary branches with rangeomorph secondary branches. Like in *Charnia*-type branching, primary branches are not bilaterally symmetrical double-sided rangeomorph branches but only display half branches which create a zigzagging central midline. These similarities with both branching type end-members suggest that *Culmofrondis* was either an ancestral form from which *Rangea* - and *Charnia*-type branching evolved or that it is a form intermediate between organisms displaying *Rangea* - and *Charnia*-type branching. A less probable hypothesis is that *Culmofrondis* was nested firmly within the rangids or charnids but shared convergent characteristics with the other taxon.

*Culmofrondis* lived epifaunally attached to the ocean floor feeding off suspended particles in the water column. Its long stem elevated its petalodium higher into the water column, similar to primary solitary suspension feeders of the Phanerozoic (Bottjer and
Ausich, 1986), into less tapped nutrient sources and its flexible primary branches allowed for adaption to changing currents.
Chapter 4
Conclusions

4.1 Summary

This study examined the construction of two Ediacaran rangeomorphs from the Conception Group of the Avalon Peninsula, Newfoundland. *Bradgatia linfordensis*, formerly known from seven specimens from Charnwood Forest in England, occurs abundantly across the Avalon Peninsula and approximately 200 specimens from the Briscal, Mistaken Point and Trepassey Formations were studied. *Culmofrondis plumosis* is an endemic species known from 14 specimens from a single locality of the Mistaken Point Formation. The focus of this project was on the three-dimensional reconstruction of these flattened fossil impressions in order to elucidate the construction and growth of some of the earliest large and architecturally complex eukaryotes known anywhere.

*Bradgatia* is constructed almost entirely of rangeomorph frondlets that are arranged to form a lettuce-like petalage. Eight independent elliptical petals wrap around a spherical basal or central structure much like the leaves of a garden leek. Each petal is made up of 10 independent plumose, sigmoidal or parallel-sided frondlets which stem perpendicularly to acutely from either side of the central axis of each petal. Frondlets are similarly subdivided into plumose, sigmoidal or parallel-sided secondary branches which stem on either side of their central axis. Secondary branches are subdivided into plumose tertiary branches and tertiary branches are subdivided into a plumose fourth order of branching. The petalage of *Bradgatia* changed throughout ontogeny from juvenile I- or V-shaped organisms to larger U-shaped specimens to the largest and oldest O-shaped specimens, but the number of primary branches in each individual remained constant.
despite these changes in size and shape of the organism. This is interpreted as reflecting inflationary or fractal growth of the organism, with gradual opening of the petalage with increasing ontogenetic age.

*Culmofrondis plumosis* new genus and species is a rangeomorph frond with a long stem and large disc. Its petalodium is bifoliate with up to four independent primary branches on each petaloid. Primary branches alternately branch acutely from a central midline, creating a zigzagging central axis. Branching angles of primary branches vary significantly, producing petalodia of different widths and apparent shapes suggesting that branches were only basally attached at a single locus. Primary branches are constructed from a series of plumose double-sided rangeomorph secondary frondlets which are arranged at perpendicular to acute angles to the primary branches. Plumose rangeomorph tertiary branches stem on either side of the central midline of secondary branches.

**4.2 Paleobiological Implications**

Both *Culmofrondis* and *Bradgatia* show strong evidence for maintaining an epibenthic sessile lifestyle strongly tethered to the ocean floor. The presence of a holdfast structure, alignment with paleocurrents, preservation under a layer of ash and a lack of current accumulations and flipped specimens indicate that both *Bradgatia* and *Culmofrondis* lived epifaunally attached to the sea floor. *Bradgatia* is additionally known to overlie discs and *Fractofusus*. Both probably were suspension feeders that filtered suspended particles and/or directly absorbed organic materials from the water column (Clapham et al., 2002; Bottjer and Clapham, 2006; Bambach et al., 2007; Sperling et al., 2007).
Tiering, the vertical subdivision of space above the seafloor within a community, is well-developed in the Ediacaran communities of the Mistaken Point Formation (Clapham et al., 2002). *Bradgatia* and *Culmofrondis* each have distinct styles of suspension-feeding which enable them to occupy different divisions in tiering hierarchy. *Bradgatia*’s multiple stemless petals allowed for feeding along the entire length of each, whereas *Culmofrondis* developed a long stem throughout ontogeny to elevate its feeding structure above the seafloor. In Phanerozoic communities, *Bradgatia*’s style of suspension feeding is mimicked by colonial primary tierers (eg. tabulate corals and bryozoans) which feed along the entire length of the organism (Bottjer and Ausich 1986; Clapham and Narbonne, 2002). *Culmofrondis* is similar to solitary primary tierers such as crinoids which elevate their feeding structure above the seafloor to filter water from higher tiers with less competition (Bottjer and Ausich, 1986; Clapham and Narbonne, 2002).

Evidence for ecological succession is also present in the communities of Mistaken Point (Clapham et al., 2003). Communities exhibiting early stages of succession are typically populated by low-level feeders (eg. *Fractofusus* and *Pectinifrons*) whereas later stages are dominated by fronds (Clapham et al., 2003). *Bradgatia* typically inhabited communities in early to middle stages of succession, especially in middle stages of succession. Late stage succession was dominated by tiered filter-feeders, including several taxa not present in earlier successional stages (Clapham et al., 2003). *Culmofrondis* is known only from the late succession community preserved at Gull Rock Cove, where it occupies the middle and upper suspension-feeding tiers.
References


