

# **Ediacaran Fronds from South Australia and Newfoundland**

by:

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## ABSTRACT

The Ediacara biota (575-539 Ma) represents a seminal event in the evolution of life, the first abundant appearance of large, architecturally complex, soft-bodied organisms after three billion years of mostly microbial evolution. Fronds occupied all tiers of the Ediacaran ecosystem and were the first animals with a construction allowing them to partition the water column macroscopically resulting in a tiering ecosystem similar to Phanerozoic marine ecosystems in structure.

Elongate fronds were a rarity in the Ediacaran, one in particular, formally named *Rangea longa*, was defined in 1966 but has not been studied in detail since. The specimens of this elongate frond are disparate in appearance, which have resulted in their exclusion from global syntheses and assigned to five different genera since its formal designation. The specimens of the Mincham-Flounders collection constitute one species with four taphonomic variants that illustrate the 3D structure of this frond. *Akrophyllas longa* is an elongate rangeomorph bifoliate frond attached to a bulbous holdfast either directly or with a short stem. The primary branches consistently appear sigmoidal in shape with rectangular secondary branches oriented perpendicular to the primaries. These fronds can be assigned to the Rangeomorpha, an extinct clade near the base of animal evolution, but exhibit an architecture and a construction that differs significantly from all other rangeomorph genera yet described and are herein formally designated as a new genus.

Fronid dusters, small fronds never reaching more than 8 cm in height as adults, occur commonly in the Ediacaran of Avalonian Newfoundland but have not been extensively described. A new frond duster is described and named here that displays unique architecture, otherwise unknown from the Ediacaran biota and easily distinguished from all Ediacaran

macrofossils, justifying its erection as a new genus and species. This frond is a spatulate, feather-like frond with primary branches emerging from a single point at the base of the petalodium, complete with a bulbous holdfast with filamentous connections. Convergent evolution has resulted in numerous frond dusters sharing a similar body plan. We are slowly uncovering the diversity of fronds occupying the lowest tier of the Ediacaran ecosystem.

## STATEMENT OF CO-AUTHORSHIP

This thesis is substantially my own, original work, assisted by my supervisor and colleagues who have contributed to its completion. A modification of Chapter Two will be submitted to an international journal and co-authored by Guy M. Narbonne, James G. Gehling and Peter Trusler. Chapter Three will be submitted to an international journal and co-authored by Guy M. Narbonne, Nicole M. Heikoop and Alexander G. Liu. Order of authorship is indicative of each author's contributions.

## TAXONOMIC STATEMENT

The systematic paleontology of the new Ediacaran genera and reclassified species described in this thesis does not constitute the official description of these taxa in accordance with the International Code of Zoological Nomenclature (third edition). The official descriptions of *Akrophyllas longa* and *Plumumbra peniculiformis* will appear in a modified versions of Chapter Two and Three that will be submitted for publication in international journals.

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## LIST OF ABBREVIATIONS

**Ma** – Mega annum/Million years

**SAM** – South Australia Museum

**ROM** – Royal Ontario Museum

**UNESCO** – The United Nations Educational, Scientific and Cultural Organization

## **CHAPTER ONE:**

### **General Introduction**

## 1.1 The Ediacaran Period

The Ediacara biota (575-539 Ma) represents a seminal event in the evolution of life, the first abundant appearance of large, architecturally complex, soft-bodied organisms after three billion years of mostly microbial evolution (Linnemann et al., 2019; Matthews et al., 2021). The affinities of the Ediacara biota were formerly controversial, but a consensus is emerging that it consisted of a mix of extinct Neoproterozoic clades of early multicellular life forms unrelated to any living creatures, alongside stem-group animals that formed the root for the subsequent Cambrian explosion of animal life (Narbonne, 2005; Fedonkin et al., 2007; Xiao and Laflamme, 2009; Droser et al., 2017). Some of the most common and iconic Ediacaran images are fronds, and these were critical components in late Ediacaran ecosystems and communities (Ford, 1958; Jenkins and Gehling, 1978; Sun, 1986; Seilacher, 1992; Narbonne et al., 1997, 2009; Laflamme and Narbonne, 2008; Vickers-Rich et al., 2013; Laflamme et al., 2018; Dunn et al., 2018, 2019; Wang et al., 2020). Examining these fronds, their components, and determining their functions permits insight into their roles in the Ediacaran ecosystem and in animal evolution.

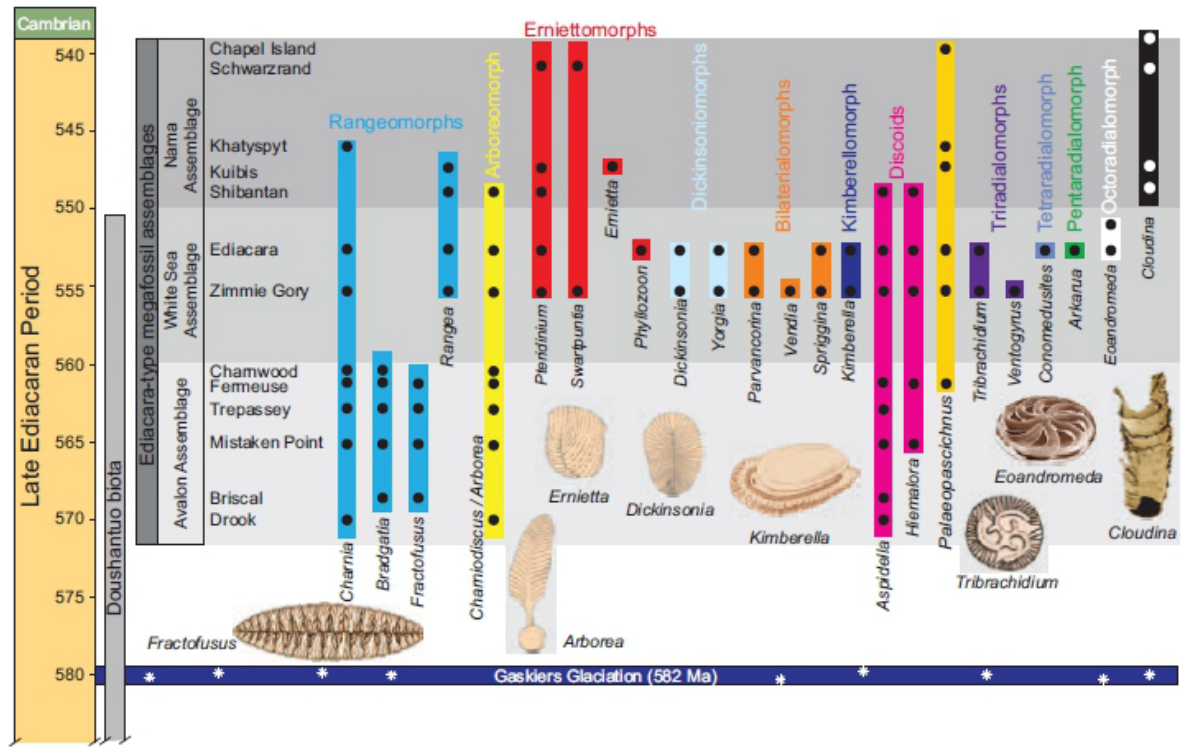


Figure 1.1. Temporal distribution and stratigraphic occurrence of key Ediacaran-type fossils. (From Xiao and Narbonne, 2020).

The Ediacaran Period was ratified in 2004, the first period-level addition to the geologic timescale in more than a century (Knoll et al., 2004, 2006; Xiao and Narbonne, 2020). The Global Stratotype Section and Point (GSSP) at the base of the Ediacaran marks the end of the last massive “snowball” glaciations, consisting of continental glaciers reaching tropical latitudes and the commencement of a definitive interval in Earth history (Hoffman et al., 1998; Hoffman and Schrag, 2002; Hoffman and Li, 2009). The end of the Ediacaran Period is marked by the initial GSSP of the Cambrian, marking another biologically distinct biota characterized by complex behaviour patterns as trace fossils, diverse skeletal fossils and bilaterian animals (Brasier, 1992; Valentine 2002; Marshall, 2006; Peng et al., 2020). For definition, the **Ediacara biota** which thrived before the Cambrian, are soft-bodied organisms preserved as impressions beneath event beds of Ediacaran age. **Ediacaran fossils** consist of all fossil organisms that lived during the Ediacaran Period, and in addition to the Ediacara biota carbonaceous compressions of algae, microfossils, stromatolites and early shelly fossils such as *Cloudina*. Fossils of the Ediacara biota (**Ediacara-type fossils**) occur as impressions of soft-bodied macrofossils preserved primarily on the soles of event beds of sandstone or volcanic ash.

## 1.2 Ediacaran fronds

The Ediacara biota represents the first morphologically, architecturally, and physiologically complex macroscopic organisms in Earth history ranging from centimeter- to meter-scale individuals (Jenkins and Gehling, 1978; Narbonne and Gehling, 2003; Butterfield, 2007). The frond morphoshape is a product of convergent evolution and a common feature in the history of

life, appearing in at least three kingdoms of extant life with a variety of lifestyles including light absorption, gas exchange, spore dispersal and filter feeding (Raven et al. 2005). The Ediacara biota have wide and diverse temporal and stratigraphic occurrences. The Ediacara biota contains an array of diverse morphology, but one body plan stands out among the rest, benthic epifaunal fronds that display an innovation that revolutionized the ecosystem. Fronds in the Ediacaran were the first to possess a construction that allowed them to be vertical and elevated, allowing them to have a feeding/trapping structure in the water column. By accomplishing this, fronds were able to partition the water column macroscopically, resulting in a tiering ecosystem that is similar to Phanerozoic marine ecosystems (Clapham and Narbonne, 2002), although more controversially in function (compare Ghisalberti et al., 2014 with Mitchell and Kenchington, 2018). Preservational features, including bending and overfolding, show that fronds were entirely soft bodied (Jenkins and Gehling, 1978; Seilacher, 1992; Narbonne et al., 2009). No evidence currently exists to suggest motility or active feeding. Fronds have been reconstructed as sessile, feeding by nutrient absorption through the body surface (Laflamme et al., 2009). This was disputed by Butterfield et al. (2020) who proposed a hydrostatic exoskeleton and semi-isolated digestion chamber capable of processing recalcitrant substrates. This architecture and construction defines the fronds and allowed them to commonly dominate assemblages, in particular at Mistaken Point and other Avalonian assemblages of early Ediacaran fossils.

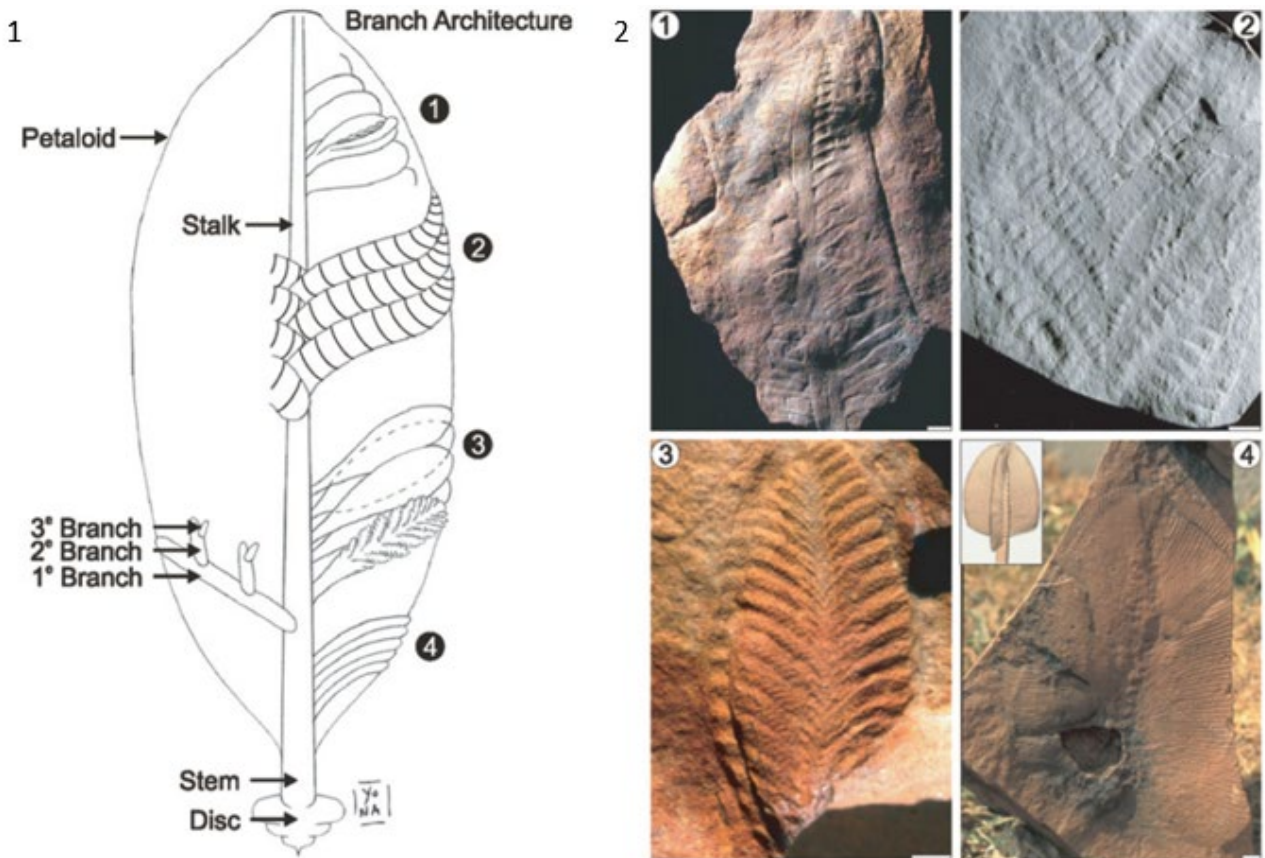


Figure 1.2. (1) Elements of an Ediacaran frond on an interpretative diagram displaying common features of fronds and showcasing four types of branching architecture. 1. *Arborea*-type branching consisting of pea-pod-like primary branches. 2. *Charnia*-type branching with zigzagging central axis and rectangular repetitive secondary elements. 3. *Rangea*-type branching with fractal repetitive branches and multifoliate petalodium. 4. *Swartpuntia*-type branching consisting of unornamented tubes in a multifoliate petalodium. (2) Photograph examples of the four branching types characterized on left. (From Laflamme and Narbonne, 2008).

Ediacaran fronds have become iconic representatives of the mainly soft-bodied life of the Ediacaran. The standard Ediacaran frond morphoshape has been divided into four branching architectures (Laflamme and Narbonne, 2008); *Arborea*-type branching, characterized by pea-pod like primary branching, which house several secondary branches within a protective sheath; *Rangea*-type branching, composed of several overlapping primary branches, which are self-similar and with multiple orders of fractal branching attached to a straight central stalk; *Charnia*-type branching, consisting of parallel, sigmoidal to rectangular primary branches which alternate and cross to form a central zig-zag axis. Primary branches contain secondary modular elements, which house tertiary branches and *Swartpuntia*-type branching, consisting of petaloids with unornamented tube-like primary branches (Laflamme and Narbonne, 2008) Dececchi et al., 2017) (Fig 1.2).

### **1.3 Ediacaran fronds of Newfoundland and Australia**

The two fronds discussed are from different localities and Ediacaran strata of different ages.

Chapter 2 discusses fronds from the eponymous region for the Ediacara biota, Ediacara in the Flinders Ranges of South Australia. The Flinders Ranges exhibits one of the best exposed and most complete successions of Neoproterozoic to early Paleozoic rocks in the world and contains the Global Stratotype Section and Point (GSSP) for the Ediacaran Period (Knoll et al., 2004, 2006). The fronds were first illustrated by Glaessner and Daily (1959), were named *Rangea longa* in the classic paper by Glaessner and Wade (1966) and have had relatively little attention ever since. These fronds differ from other, better-known, frondose taxa from Ediacara

in that they are highly elongate in contrast with the other frondose taxa which are mainly ovate; and that most specimens are preserved on the tops of beds rather than on bed soles that host most Ediacaran fronds worldwide. The present study shows that this fronds architecture and construction differ significantly from *Rangia*, and this frondose taxon is herein regarded as a new genus distinct from all other Ediacaran fronds.

Chapter 3 discusses a new genus and species of frond dusters found in two localities in Newfoundland, Canada. The first is the famous Mistaken Point on the Avalon Peninsula and the second Little Catalina on the Bonavista Peninsula. Mistaken Point was named a UNESCO World Heritage Site (Thomas and Narbonne, 2016) and the Ediacaran localities of Bonavista Peninsula were designated as a UNESCO Global Geopark in 2020. Mistaken Point is home to more than 10,000 fossils spread over 146 hectares along the seacoast. Fossils preserved in volcanic ash are weathered to reveal large bedding surfaces with *in situ* fossilization of complete communities, allowing in depth community and ecosystem analysis. *Plumumbra peniculiformis* was previously grouped into an informal group known as “dusters” but is readily distinguishable from all other small and juvenile fronds. *Plumumbra* have been identified in the field but only rarely formally described. This group occupied the lowest tier of the Ediacaran marine ecosystem and is now being recognized as a diverse group of numerous organisms converging on a similar body plan. The present study helps to elucidate the nature of the basal tier of Ediacaran life in the deep-sea.

In depth study of these two species provides a more complete picture of the Ediacaran ecosystems. Uncovering a diversity that has not yet been realized and analysis of new modes of preservation allow for a more complete global analysis and synthesis of Ediacaran fronds. Studying Ediacaran fronds gives insight to the beginnings of macroscopic evolution and elucidates the importance of phylogeny versus convergence.

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## **CHAPTER TWO:**

### **Elongate Ediacaran fronds from the Flinders Ranges, South Australia**

## 2.1 Abstract

Elongate fossil fronds from Ediacara, Australia, were formally described as *Rangea longa* Glaessner and Wade, 1966, but the disparate nature of documented specimens has hindered their inclusion in global syntheses and has resulted in the taxon being assigned to five different genera since their discovery. Detailed study of the type material from Ediacara and subsequent collections elsewhere in the Flinders Ranges reaffirms that these specimens represent a single biological taxon, with the morphological variation between specimens now seen to reflect different preservational modes that collectively illustrate the three-dimensional structure of this complex frond. These studies also reaffirm the affinities of these fronds with the rangeomorphs but represent a new frond genus, herein named *Akrophyllas*. Preservation of these fronds almost exclusively on the tops of sandstone event beds may imply a slightly more buoyant composition than other Flinders Ranges fronds and would suggest an upright, epibenthic lifestyle for *Akrophyllas longa*.

## 2.2 Introduction

The Ediacara biota represents the first abundant morphologically, architecturally, and physiologically complex macroscopic organisms on Earth (Laflamme et al., 2013; Droser and Gehling, 2015; Droser et al., 2017). The Ediacara biota thrived 575 to 539 million years ago (Linneman et al., 2019; Matthews et al., 2021) and immediately predated the Cambrian

explosion of shelly and burrowing animals (Seilacher et al., 2003; Narbonne, 2005; Xiao and Laflamme, 2009).

The Ediacara biota comprises a diverse group of originally soft-bodied taxa that typically are preserved as impressions under event beds of sandstone or volcanic ash (Wade, 1968; Gehling, 1999; Narbonne, 2005). Fronds dominate many Ediacaran assemblages and were the first animals with a construction that allowed them to be vertical and elevated, permitting a feeding/trapping structure in the water column. Ediacaran fronds were able to partition the water column macroscopically, resulting in a tiering ecosystem that is similar to Phanerozoic marine ecosystems in structure (Clapham and Narbonne, 2002) and possibly also in origin (compare Ghisalberti et al., 2014 with Mitchell and Kenchington, 2018).

Traditional Ediacaran taxonomy emphasized unity of fronds as a high-level taxon (Glaessner, 1979), but more recent studies have suggested that frond morphology more likely represents convergent evolution resulting from competition for nutrients in the water column (Laflamme and Narbonne, 2008b; Dececchi et al., 2017). Differences in branching architecture provide a key to subdividing Ediacaran fronds into robust clades (Laflamme and Narbonne, 2008b; Xiao and Laflamme, 2009; Erwin et al., 2011; Brasier et al., 2012; Dececchi et al., 2017; Dunn et al., 2019b). Four distinct architectures have been recognized among Ediacaran fronds: 1) *Arborea*-type, characterized by specimens that contain pea-pod like primary branches and consist of parallel primary branches attached to a central stalk at right angles encased by a sheath (Laflamme et al., 2018; Dunn et al., 2019a); 2) *Charnia*-type branching, classified by a zigzagging central axis due to the overlapping of alternating sigmoidal primary branches and secondary modular elements that are composed of tertiary rangeomorph elements (Ford, 1958; Laflamme et al., 2007; Antcliffe and Brasier, 2008; Brasier et al., 2012; Dunn et al., 2019b); 3)

*Rangea*-type branching, composed of several overlapping primary branches, which are self-similar, fractal over at least three orders of magnitude and constructed from individual rangeomorph frondlets (Narbonne, 2004; Narbonne et al., 2009; Vickers-Rich et al., 2013); and 4) *Swartpuntia*-type branching, consisting of petaloids composed of unornamented tube-like primary branches (Narbonne et al., 1997; Ivantsov et al., 2016).

Glaessner and Daily (1959) first reported and illustrated abundant Ediacaran fronds from Australia, some of which have become iconic images of the Ediacara biota worldwide. Most Ediacaran fronds in Australia are specimens of *Arborea*, first described as *Rangea arborea* (Glaessner and Daily, 1959), a taxon that has been studied by numerous subsequent workers (Glaessner and Daily, 1959; Glaessner and Wade, 1966, 1966; Jenkins and Gehling, 1978; Jenkins, 1985; Laflamme and Narbonne, 2008b; Laflamme et al., 2018; Dunn et al., 2019a). Glaessner's original collection from Ediacara contained 15 slabs collected by V. H Mincham and B. Flounders in September 1957 and September 1958 that originally may have constituted a single broken bed (Glaessner and Daily, 1959; Wade, 1968; Jenkins and Gehling, 1978) and that is referred to as the "Mincham-Flounders collection" throughout this paper. The tops of these slabs include 13 specimens of an elongate frond that differs significantly from *Arborea* and was subsequently named *Rangea longa* (Glaessner and Wade, 1966). Ten additional specimens of this taxon have been collected from mostly unknown localities elsewhere in the Flinders Ranges (e.g. Sun, 1986), but no detailed studies of this taxon have been carried out in the more than 50 years since it was defined. This lack of a modern description and comparison has led to taxonomic confusion and has reduced the impact of "*Rangea*" *longa* in global compilations and analyses of Ediacaran fossils (Fedonkin et al., 2007; Erwin et al., 2011; Dececchi et al., 2017).

The present study evaluates these fronds from the Mincham-Flounders collection in light of recent developments in our understanding of Ediacaran paleobiology.

### **2.3 Geologic Setting**

The fossils reported in this study occur in the Ediacara Member, the most significant fossiliferous unit within the Pound Subgroup (Gehling, 2000; Tarhan et al., 2015; Reid et al., 2020) from the Flinders Ranges in the Neoproterozoic-middle Cambrian succession of the Adelaide Fold Belt of South Australia (Fig. 2.1). No radiometric dates are available from this succession, but the Ediacara Member occurs above the global Shuram-Wonoka-EN3 C-isotope anomaly (Xiao et al., 2016; Xiao and Narbonne, 2020) which elsewhere in the world ended at approximately 567 Ma (Canfield et al., 2020; Rooney et al., 2020) and occurs below the top of the Ediacaran which is elsewhere dated at approximately 539 Ma (Linnemann et al., 2019).

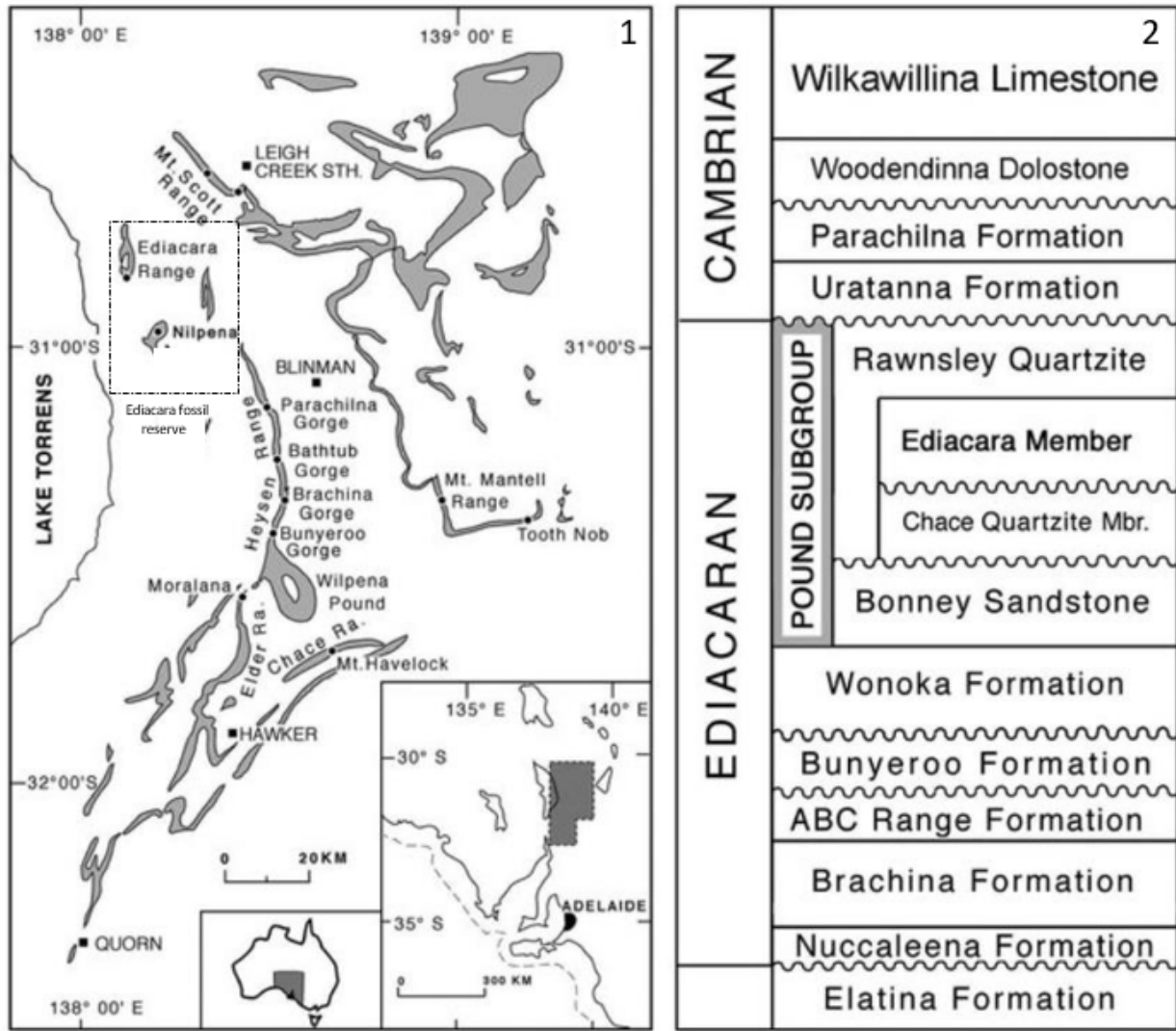


Figure 2.1. Location map (1) and stratigraphic section (2) of Ediacara and surrounding area. Ediacara fossil reserve indicated by a dotted black box. Modified from Gehling (2000) and Paterson et al. (2017).

Abundant and extraordinarily preserved fossil assemblages occur in the Ediacara Member of the Rawnsley depositional sequence and are limited by the stratigraphic distribution of facies suited to the preservation of non-skeletal organisms (Gehling, 2000). The Ediacara Member is a siliciclastic sequence of shallow marine and potentially delta-front environments deposited between storm- and fair-weather wave base (Gehling, 2020) or alternating non-marine and near-shore environments (McMahon et al., 2020). The Ediacara member occurs on an erosional surface of that cuts into the underlying Chace Quartzite Member of the Rawnsley Quartzite and Bonney Sandstone (Tarhan et al., 2015) with a relief ranging from 10 to 260m (Reid et al., 2020). The fossiliferous, ripple-laminated sandstone beds of the Ediacara Member are interpreted to represent storm sands (Gehling, 2000; McMahon et al., 2020). Preservation of Ediacara-type fossil impressions on these sandstone surfaces can be attributed to either or both of microbial casting of the organisms immediately following their death (Gehling, 1999; Liu et al., 2019a, b) and early silica diagenesis (Tarhan et al., 2016, 2017, 2018, 2019). Typical Flinders-style preservation of Ediacara-type fossil impressions exhibits a topologically complex surface with impressions of the bases of holdfasts, the tops of resistant epifaunal organisms such as *Dickinsonia* and non-resistant epifaunal organisms such as the petalodia of other frondose taxa typically preserved as positive impressions on soles (Gehling, 1999; Narbonne, 2005).

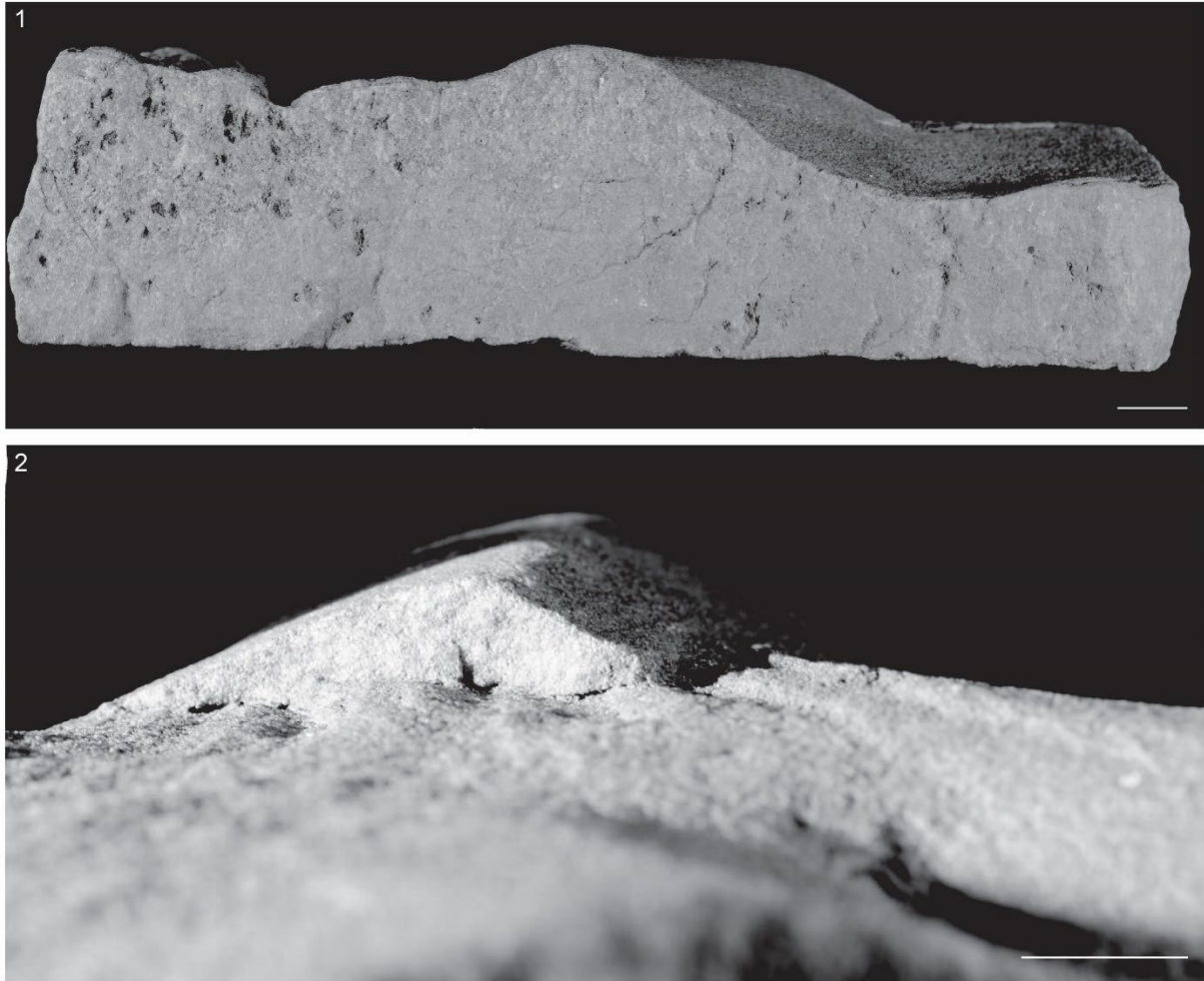
*Description of the Mincham-Flounders Collection.*—Frondose fossils of the Ediacara Member are typically preserved as impressions on the lower surfaces of sandstone beds (Glaessner and Wade, 1966; Wade, 1968; Gehling, 1999, 2000; Tarhan et al., 2010) but the Mincham-Flounders collection represents a preservational window in which all specimens are preserved on the upper surfaces (Fig. 2.2). Two specimens collected from unknown localities elsewhere in the Flinders

Ranges occur within the upper parts of event beds and a single specimen from Nilpena occurs on a sole (Fig. 2.2.3), but the vast majority of specimens throughout the Flinders Ranges occur on bed tops. Slabs of the Mincham-Flounders collection are typically well-sorted, fine- to medium-grained subarkosic arenites with fronds, scours, and abundant current ripplemarks on the tops of the beds (Figs. 2.2, 2,3). All frond petalodia are incomplete, lacking the base and in the majority of cases also the top of the frond. Every slab in the Mincham-Flounders collection shows fronds with a consistent orientation relative to each other, a relationship that is typical of current-aligned fronds attached to the sea bottom by discoidal holdfasts (Seilacher, 1999; Wood et al., 2003; Brasier et al., 2013), and these parallel arrays of fronds commonly include fronds that partly overlie other fronds on the same bed top (Fig. 2.2.2).

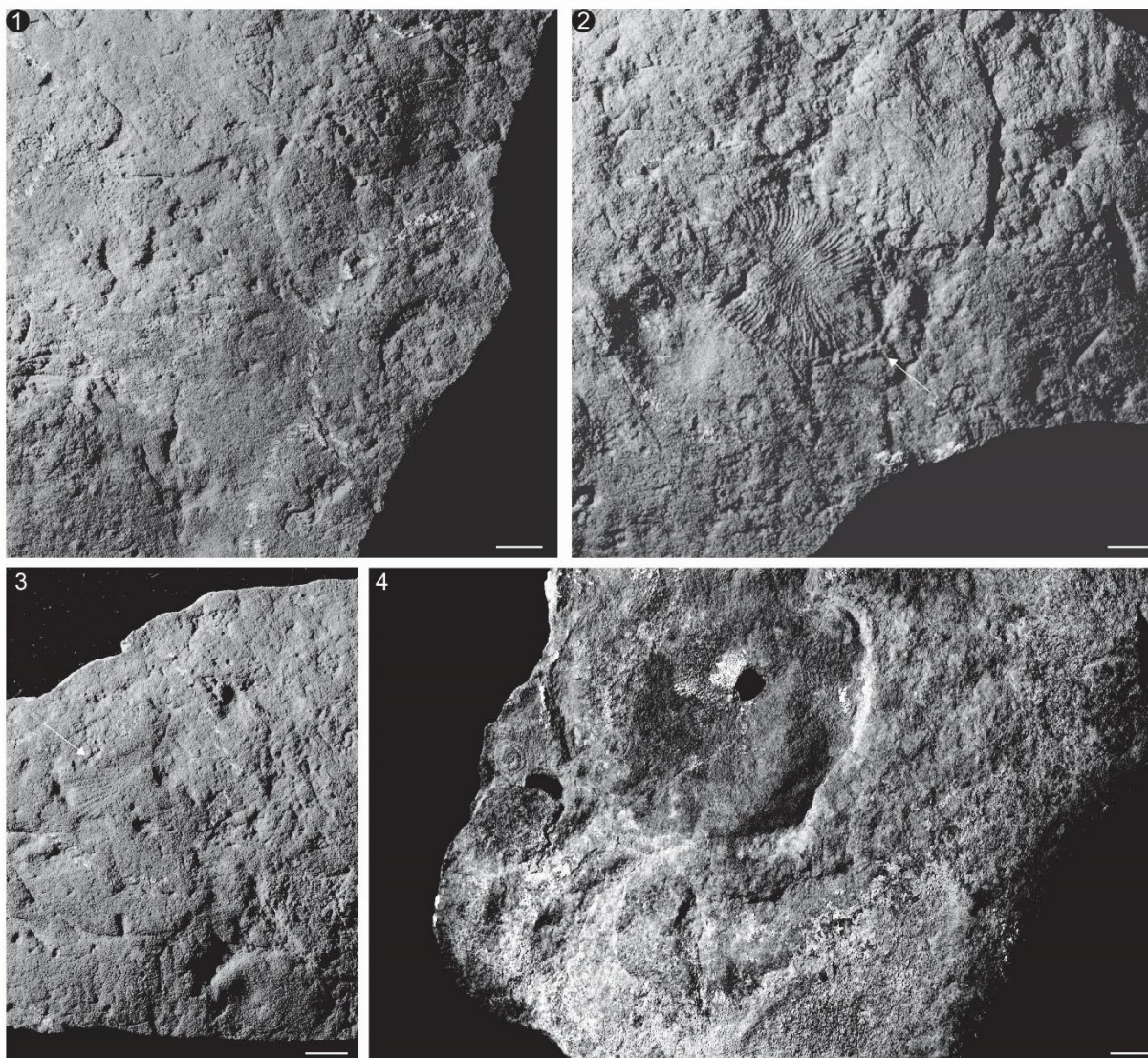
Basal surfaces of the slabs are sharp (Fig. 2.3) and commonly exhibit microbial textures (Fig. 2.4) typical of those previously described from the Ediacara Member (Gehling, 1999, 2000; Tarhan et al., 2010) along with typical Flinders-style sole preservation of Ediacaran megafossils including *Tribrachidium* (Fig. 2.4.1) and *Dickinsonia* (Fig 2.4.2, 2.4.3). *Aspidella*, interpreted by most modern workers as holdfast discs for fronds (Gehling, 2000; Burzynski and Narbonne, 2015; Tarhan et al., 2015; Droser et al., 2020) occur as impressions on the base of beds (Fig. 2.4.4) and hemispherical craters on the top of the beds (Fig. 2.2.2d). None of these *Aspidella* discs are visibly attached to any of the fronds on the top of the beds, but it may be significant that only a single species of frond is present in the Mincham-Flounders collection. All specimens of *Aspidella* in the Mincham-Flounders beds are interpreted as spheroidal holdfasts located at, or buried slightly, below the sediment-water interface.



*Figure 2.2.* Preservation of *Akrophyllas longa* specimens on top surfaces in the Mincham-Flounders collection and as a cleavage relief within a bed. **(1)** Elongate *Akrophyllas longa* with a gentle distal taper, preserved as a cleavage relief within a bed of coarse sandstone, SAM P24593. **(2)** Three current-aligned petalodia of *Akrophyllas longa* (a) smooth-style preservation, (b) deep-style preservation, (c) smooth-style preservation, (d) large *Aspidella* crater, SAM P12716. White arrows with no letters denote evidence of additional petalodia. **(3)** Parallel-sided petalodium of *Akrophyllas longa* preserved in deep-style, SAM P12721a. **(4)** Holotype of *Akrophyllas longa*, up to three orders of architecture are visible, preserved in holotype preservation, dusted with ammonium chloride, P13777. Scale bars for Figs. 2.2-2.4 and divisions on the scale bar in Fig. 2.1 = 1cm.

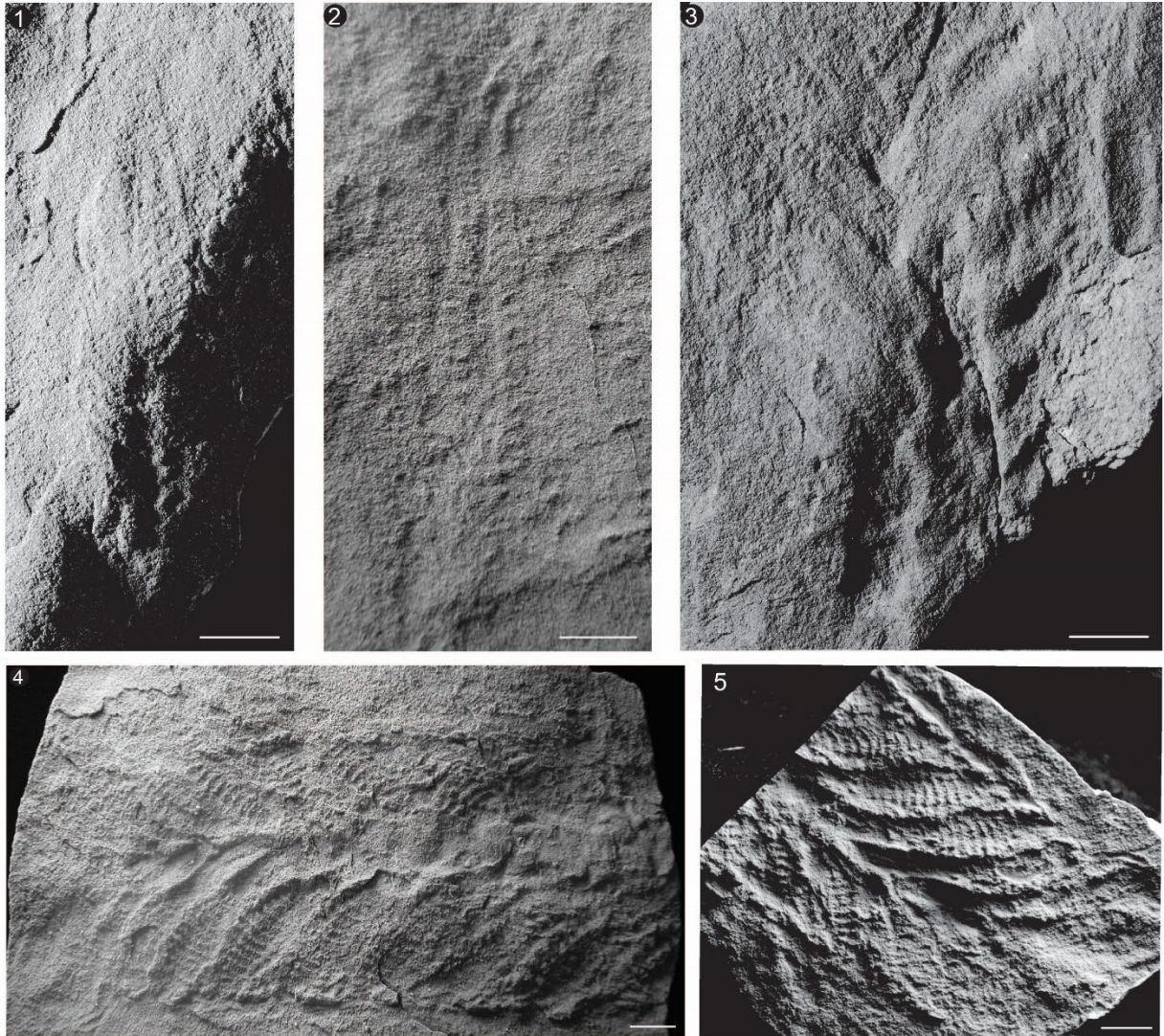


*Figure 2.3.* Cross sections of slabs exhibiting *Akrophyllas longa* specimens on their top surfaces. **(1)** Bed cross-section displaying a sharp base, scoured top, and lamination throughout, SAM P40445. **(2)** Close-up of a current ripple on the top of SAM P40445. All scale bars = 1cm.



*Figure 2.4.* Soles of beds with *Akrophyllas longa* specimens found on their top side. All of these sole surfaces show microbial mat textures. **(1)** *Tribrachidium*, SAM P12716 **(2)** *Dickinsonia* indicated by a white arrow, SAM P12730 **(3)** Incomplete specimen of *Dickinsonia* indicated by a white arrow, SAM P12721a. **(4)** *Aspidella* holdfast, SAM P12736. All scale bars = 1 cm.

Wade (1968) and Jenkins and Gehling (1978) postulated that the fronds in the Mincham-Flounders collection were gregarious, living in proximity to one another and included individuals of multiple sizes indicating multiple stages of growth shown by the 13 specimens represented on the 15 slabs collected. Wade (1968) reported that some slabs can be partly reconstructed into one bedding plane showing a surface strongly scoured by current action, which eddied around the fronds and gathered sand below them prior to burial so that the detail of external molds was impressed on an uneven surface. Fronds in the unidirectional current to rest in their own scour marks and were impressed on an uneven surface in a manner similar to that reported by Brasier et al. (2013) for Newfoundland fronds. Most specimens lie flat on the upper surface of the bed, but some were preserved at a gentle angle to the upper bedding surface (Fig. 2.2.4, 2.5.4, 2.5.5), providing oblique cross-sections through these fronds (Fig 2.6).



*Figure 2.5.* Distal tips and branching intersections in specimens of *Akrophyllas longa* from the Flinders Ranges and additional features of the holotype. All specimens coated with ammonium chloride. **(1)** Juvenile specimen exhibiting the distal tip of petalodium, preserved in smooth-style, SAM P12730a. **(2)** Latex of uncollectible juvenile specimen from Bathtub Gorge, preserved in smooth-style, SAM BT-D226. **(3)** Partial petalodium displaying detailed architecture and zig zag pattern created by insertion of primary branches into a cylindrical stalk that is lower than the plane of view, preserved in holotype style, SAM P12736b. **(4)** Holotype of *Akrophyllas longa* up to three orders of architecture are visible with a prominent central stalk and margin. From right to left petalodium and stalk changes from positive epirelief to negative epirelief. SAM P13777 **(5)** Oblique view of the holotype displaying petaloids representing bilaterally symmetrical rangeomorph elements that have been folded along their midlines. All scale bars = 1cm.

*Locality information.*—All specimens evaluated here are located in the repository of the South Australian Museum, North Terrace, Adelaide SA 5000, Australia (SAM). The Mincham-Flounders collection is from Ediacara, specimens are also known from nearby Nilpena, and other specimens are from unknown localities in the Flinders Ranges. All specimens are from the Ediacara Member of the Rawnsley Quartzite.

## **2.4 Materials and methods**

*Repository and institutional abbreviations.*—In the following section, a new description of *Akrophyllas longa* is based on 23 specimens from the South Australian Museum (SAM).

## **2.5 Systematic Paleontology**

Clade Rangeomorpha, Pflug, 1972

*Remarks.*—There is currently no universally accepted taxonomic hierarchy for Ediacaran biota above the rank of genus. The use of “clade” to indicate closely related Ediacaran taxa follows Erwin et al. (2011) and Laflamme et al. (2013, 2018). This paper follows the frond terminology proposed by Laflamme and Narbonne (2008a) and the rangeomorph terminology proposed by Brasier et al. (2012). “Proximal” refers to the part of the frond nearest its base and “distal” refers to the part of the frond nearest its tip. With the exception of specimens illustrated in Figures 2.2.1

and 2.2.3, all specimens including the holotype are preserved in positive epirelief on the tops of sandstone beds.

Genus *Akrophyllas* new genus

*Akrophyllas longa* Glaessner and Wade, 1966

Figure 2.2, 2.5, 2.7, 2.9

1959 *Rangea* sp. nov (*partim*) Glaessner, p. 1472-1473.

1959 *Rangea arborea* (*partim*) Glaessner in Glaessner and Daily, p. 383, pl. 45, fig. 1 (only).

1962 *Charnia* sp.; Glaessner, p. 494, pl. 1, fig 5.

1966 *Rangea longa*; Glaessner and Wade, p. 614-615, pl. 100, fig 4.

1973 *Glaessnerina longa*; Germs, p. 5.

1978 *Charniodiscus longus*; Jenkins and Gehling, p. 351, 353-354.

1986 *Charniodiscus longus*; Sun, p. 367-369, fig. 3.

2007 *Charniodiscus longus*; Vickers-Rich et al., p. 266

2007 *Glaessnerina longa*; Vickers-Rich et al., p. 273.

2007 *Rangea longa*; Vickers-Rich et al., p. 285.

2020 *Charniodiscus longus*; Wang et al., Table 1.

*Type species.*—*Akrophyllas longa* new genus, by monotypy

*Etymology.*— *Akros* meaning “at the top” in Greek, in reference to its unusual preservation on the tops of beds. *Phyllas* meaning leaf in Greek, in reference to the overall leaf-like appearance of its petalodium and *longa* in reference to its unusually large size in comparison to the majority of the Ediacaran biota. “Long leaf at the top”.

*Holotype.*—SAM P13777 from Ediacara, Flinders Ranges, South Australia (Glaessner and Wade, 1966, pl. 100, fig. 4).

*Diagnosis.*—New. Decimeter-scale, strongly elongate, parallel-sided to gently tapering, bifoliate frond. Primary branches that appear sigmoidal to petaloid-shaped emanating at an acute angle in an alternate pattern from a central fold/crease or a central stalk. Primary branches display rotated furled, charnid-type rangeomorph architecture, composed of mm-scale secondary branches arranged perpendicular to the primaries and submillimetric tertiary branches arranged perpendicular to the secondary branches.

*Occurrence.*—Collected from an unknown level in the Ediacara Member at Ediacara, South Australia.

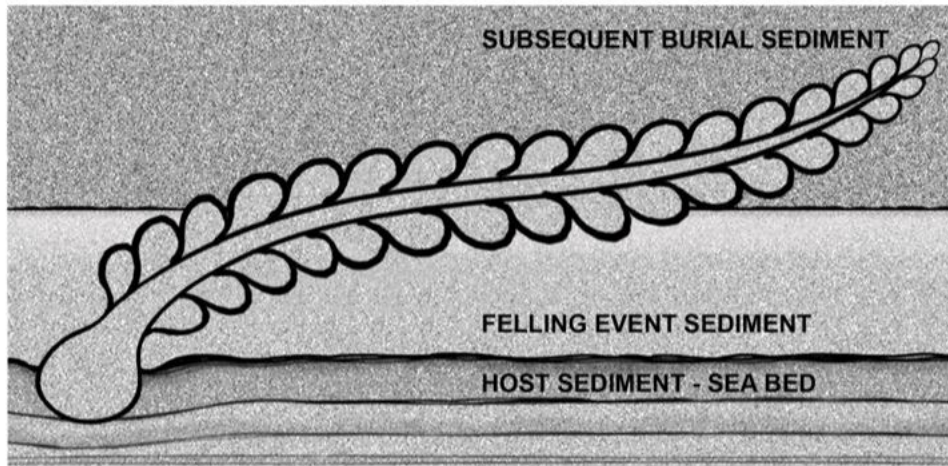
*Description.*—The holotype (P13777, Fig 2.2.4, 2.5.4, 2.5.5) is a bifoliate petalodium fragment that exhibits a prominent central stalk flanked on either side by primary branches with well-preserved microstructure. The holotype is incomplete at both its proximal and distal ends, with the preserved portion 150mm long with a width that tapers from 61mm at its proximal end to 45mm at its distal end. The primary branches appear sigmoidal in shape proximally passing into petaloid-shaped branches distally. Primary branches are approximately 10mm wide and 30mm long and are composed of 2mm wide linear secondary branches oriented perpendicular to the primary branches. Submillimeter-scale tertiary branches are oriented perpendicular to the secondary branches (parallel with the primary branches). Primary branches attach to a prominent central stalk in parallel rows forming a foliate sheet. Primary branches overlap with adjacent branches and are constrained at their distal tips by a prominent rim that stands in positive epirelief. Primary branches of the holotype show similar structures and arrangement but are better preserved on the left-hand side of the frond than the right-hand side.

The frond can be divided longitudinally into three preservational regions that reflect a slight inclination of the frond relative to the surface that preserves it (Fig. 2.6). The holotype grades from a proximal region with mainly positive epirelief, to a middle region of mainly negative epirelief, to a distal region exhibiting poor epirelief preservation (Fig. 2.5.4). The proximal region of the frond exhibits a central stalk that is preserved in positive epirelief with sigmoidal branches on the left-hand side of the frond preserved flat or in gentle positive epirelief; their preservation terminates sharply at the stalk and at the outside rim. The central region of the frond exhibits negative epirelief preservation of the central stalk and all of the branches on both sides of the stalk. Each branch consists of a petaloid-shaped element preserved in concave relief. Oblique views (Fig. 2.5.5) imply that these petaloids represent bilaterally symmetrical

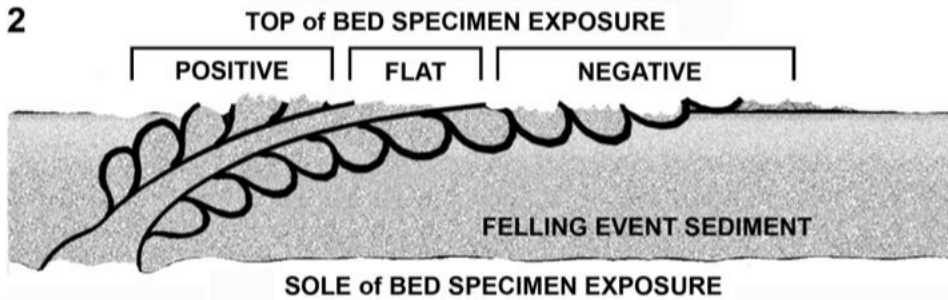
rangeomorph elements that have been folded along their midlines (rotated furled in the terminology of Brasier et al., 2012) to produce the proximal over distal imbrication of primary branches. The distal edge of each primary branch has imprinted through the branch that partly overlies it (Fig. 2.5.4, 2.5.5), permitting the size and shape of each rotated branch to be determined. The most distal region of the frond shows features that are increasingly poorly preserved.

Other specimens support and refine the description based on the holotype. All are incomplete specimens on broken slabs, with no frond base visible on any of the slabs. Most specimens are also incomplete distally, but five specimens preserve a sharply tapering distal tip (Fig. 2.2.1, 2.2.2a, 2.5.1, 2.5.2). Preserved fragments are strongly elongate, with moderate distal taper throughout the preserved portion of the petalodium (Fig. 2.2.2c) and rare specimens exhibit a linear form that is nearly parallel-sided (Fig. 2.7.2).

**1** SCHEMATIC AXIAL SECTION of DOUBLE-BRANCHED BIFOLIATE FROND.



**2**



*Figure 2.6.* Diagrammatic reconstruction of longitudinal (axial) section of buried specimen. **(1)** *Akrophyllas longa* during burial. **(2)** Resulting preservation on the bed surface reveals different layers through the specimens. Typified by the holotype in Figure 2.4 and Figure 5.4 where from right to left petalodium and stalk change from positive epirelief to negative epirelief. Illustration by P. Trusler (Melbourne).

All specimens are bifoliate with each petaloid consisting of a parallel series of branches that appear to emanate in an alternate pattern at either a zigzag central commissure (Fig. 2.2.2b, 2.5.3, 2.7.3) or a central stalk (Fig. 2.2.1, 2.2.4, 2.5.1, 2.5.2, 2.7.4). Most specimens at least locally exhibit a sharp outer rim constraining the outer edges of the primary branches in the petalodium (Fig. 2.2.1, 2.2.3, 2.2.4, 2.5.1, 2.5.4, 2.7.4). Three orders of architectural structure are visible on the best-preserved specimens. Primary branches are typically sigmoidal to petaloid in shape and are arranged in an imbricate pattern off both sides of the petalodium. Primary branches decrease in both length and width distally from 2-35mm (mean: 19mm) long and 0.70-12mm (mean: 5mm) wide, with a length:width ratio between 1.6 and 12.1 (mean: 4.6).

Primary branches meet at a central stalk 1-17mm (mean: 6.7mm) in diameter that runs the entire visible length of 12 of the 23 specimens (Fig. 2.2.1, 2.2.2c, 2.5.1, 2.5.2, 2.5.4). Individual primary branches overlap the stalk depicted clearly in Figure 2.7.4. The width of the petalodium/width of the stalk (at the same point) remains relatively constant between specimens (mean: 6mm). No central stalk is visible in the remaining specimens, and instead the primary branches meet at a central fold or crease (Fig. 2.2.2b, 2.5.3, 2.7.2). The direction of imbrication of the primary branches is proximal over distal in the holotype and in specimens illustrated in Figures 2.2.1 and 2.5.3, but distal over proximal in specimens illustrated in Figures 2.2.2b, 2.7.2, and 2.7.4.

*Materials.*—22 specimens from the South Australian Museum (SAM) + 1 latex of an uncollectable field specimen.

## 2.6 Comparisons

*Akrophyllas longa* is an elongate rangeomorph with charnid-type architecture. *Charnia*-type branching consists of a series of parallel, sigmoidal to rectangular primary branches, which alternate. Primary branches are composed of several secondary modular elements, which house tertiary branches interpreted as representing rangeomorph elements (Laflamme and Narbonne, 2008b). Over the 50 years since it was first reported, *Akrophyllas longa* has had a confused nomenclatural history that has seen it referred to four different rangeomorph genera and one arboreomorph genus.

*Rangea*.—*Rangea* Gürich, 1930 was the first Ediacaran frond described anywhere and remained the only described Ediacaran frond genus until Ford named *Charnia* and *Charniodiscus* in 1958, so it is not surprising that these fossils were originally compared with *Rangea* (Glaessner and Daily, 1959) and were later formally defined as *Rangea longa* Glaessner and Wade, 1966. The type species of *Rangea*, *R. schneiderhoehni* Gürich 1930, was first described from Namibia, where exceptional specimens preserved in three dimensions were documented by Vickers-Rich et al. (2013), and *Rangea* has now also been reported from the White Sea (Grazhdankin, 2004, 2014) and central China (Chen et al., 2014). *Rangea* is a multifoliate frond that consists of a hexaradial axial bulb that passes into an axial stalk extending the length of the fossil with six vanes arranged radially around the stalk; each vane consists of a bilaminar sheet composed of a repetitive pattern of double-sided rangeomorph elements, “rangid architecture” (sensu Laflamme and Narbonne, 2008b); “unfurled rangeomorph architecture” (sensu Brasier et al., 2012).

Essentially none of these features are present on the type material of “*Rangea*” *longa* in the Mincham-Flounders collection, supporting the view that this taxon cannot be referred to as *Rangea*.

*Charnia*.—Glaessner (1962, Pl. 1, fig. 5) pointed out the similarity between a specimen from the Mincham-Flounders collection (that was later designated as the type specimen of “*Rangea*” *longa*, Glaessner and Wade, 1966) and *Charnia*. *Charnia* is typified by its well-studied type species, *Charnia masoni* Ford, 1958, which has been described worldwide by numerous workers over more than 50 years (Ford, 1958; Brasier and Antcliffe, 2004; Grazhdankin, 2004, 2014; Laflamme et al., 2007; Hofmann et al., 2008; Narbonne et al., 2014; Dunn et al., 2019a). In the following discussion “*Charnia*” refers only to specimens identified as the type species, *C. masoni*.

*Charnia masoni* typifies charnid architecture with single-sided rangeomorph primary branches. The primary branches of *Charnia* change in shape along the frond from rectangular to sigmoidal with secondary modular elements and curved tertiary divisions which alternate to produce a zigzag central axis. The fronds in the Mincham-Flounders collection from Ediacara also exhibit charnid architecture showing single-sided-like rangeomorph primary branches but display sigmoidal to petaloid shaped primary branches with thin rectangular secondary branches and rectangular millimeter scale tertiary branches. Primary branches alternate and meet at a stalk to form a straight central axis.

The form of *Charnia masoni* remains constrained and primary branches do commonly stay tightly packed despite no specimen definitely attributable to *C. masoni* showing either a

stalk or a rim (Dunn et al., 2019a). Branches can dislocate from their neighbors suggesting that they have weak connection or stacked arrangement of non-conjoined branches bound together only at the central axis or alternatively attached to an axis independent of each other (Dunn et al., 2019a). Fronds in the Mincham-Flounders collection are strictly constrained at all levels with no change in architecture of primary, secondary, or tertiary branching throughout the frond, unlike *Charnia masoni*, which can have variable architecture throughout the frond. Branch dislocation is rare in *Akrophyllas longa* with only one known example (Fig 2.7.1), which dislocated from the stalk rather than from the rim.

*Charnia masoni* exhibits a holdfast, which is directly (Laflamme et al., 2007; Burzynski and Narbonne, 2015) or nearly directly (Dunn et al., 2019b) attached to a petalodium. First order branching is longest in the middle of the frond and shortest at its distal end, whereas in *Akrophyllas longa* primary branches are longest at the base in all cases and taper progressively towards the distal tip. *Akrophyllas longa* is elongate whereas *C. masoni* ranges from oval to moderately elongate. *Charnia masoni* lacks a stalk (Dunn et al., 2019a), but a prominent central stalk is visible in most specimens of *Akrophyllas longa*.

*Glaessnerina*.—Germis (1973) continued the comparison of “*Rangea*” *longa* with *Charnia* by specifically removing “*Rangea*” *longa* from *Rangea* and regarding it as a species in his newly erected genus *Glaessnerina*. The two species that comprise *Glaessnerina* show *Charnia*-style architecture but differ sufficiently in their construction that they would no longer be regarded as congeneric. The type species of *Glaessnerina*, *G. grandis*, Glaessner and Wade (1966) is represented by a single specimen that Runnegar (1992) regarded as a junior synonym of *Charnia*, a view with which we concur.

*Charniodiscus*.—The first Ediacaran frond named in Australia was *Rangea arborea* Glaessner in Glaessner and Daily (1959), a taxon that was later designated as the type species of *Arborea* Glaessner and Wade, 1966. Jenkins and Gehling (1978) regarded *Arborea* as a subjective junior synonym of *Charniodiscus* Ford, 1958, a decision later reversed by Laflamme et al. (2018) based on evidence that the holotype of *Charniodiscus* is multifoliate with possible fractal architecture (Brasier and Antcliffe, 2009). Based on an overall similarity of form, Jenkins and Gehling (1978) originally regarded *Rangea longa* as a species of *Charniodiscus*. However, subsequent work has emphasized the importance of architecture over shape in higher-level taxonomy of Ediacaran fronds (Laflamme and Narbonne, 2008b; Brasier et al., 2012; Dececchi et al., 2017; Dunn et al., 2019b). *Arborea*-type architecture consists of a parallel series of rectangular primary branches that, in well-preserved specimens, exhibit a peapod-like arrangement of oval secondary branches that lack modular subdivisions (Laflamme et al., 2018; Wang et al., 2020), whereas *Akrophyllas longa* displays charnid-type architecture. The ovate shape of the petalodium of *Arborea* (Glaessner and Wade, 1966; Jenkins and Gehling, 1978; Laflamme et al., 2018; Dunn et al., 2019a) further distinguishes it from the highly elongate shape of *Akrophyllas*.

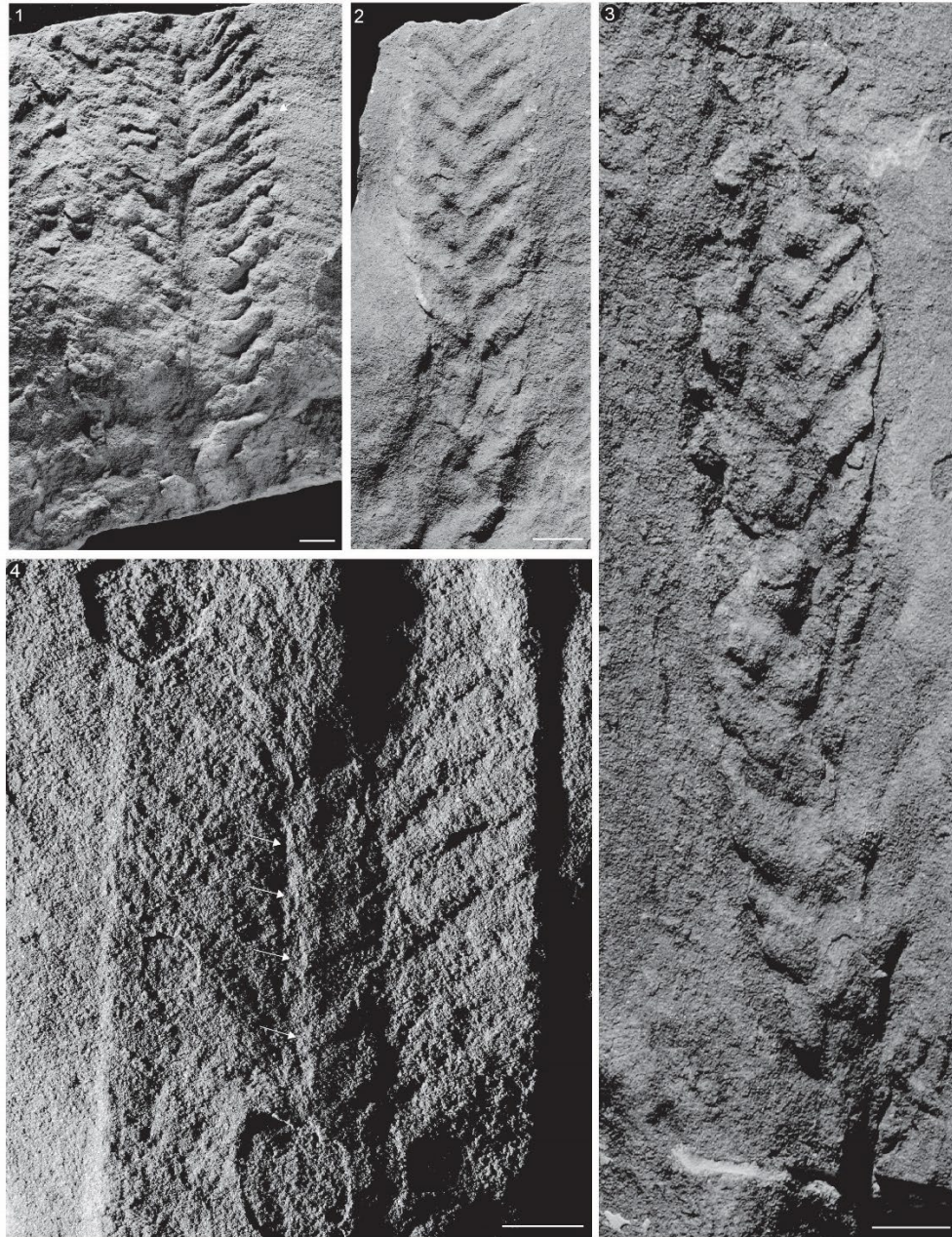
*Trepassia*.—Sun (1986) compared a specimen he regarded as *Charniodiscus longa* (re-illustrated in Fig. 2.2.1 of the present paper) with a similarly long frond from Newfoundland that had been figured but not named by Anderson (1978). The Newfoundland specimen was subsequently designated as the holotype of *Charnia wardi* Narbonne and Gehling, 2003 which later became the type species of the new genus *Trepassia* Narbonne et al., 2009. *Akrophyllas* and *Trepassia* are similarly highly elongate and both exhibit primary branches that alternate and meet to form a

straight central axis attaching to an internal stalk. In addition, there is little or no stem present irrespective of size in *Trepassia* and *Akrophyllas*.

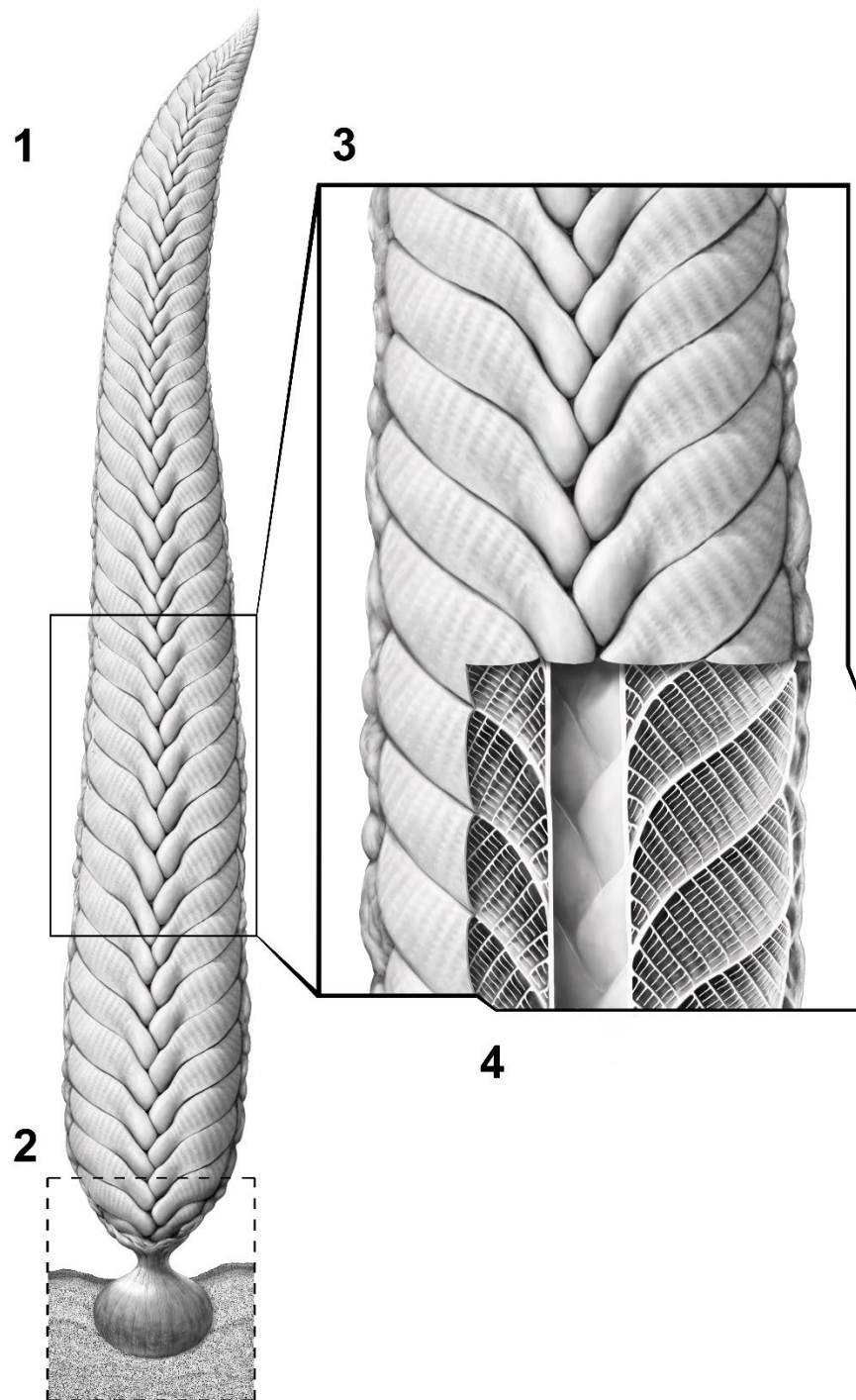
Despite these broad similarities in form, the branching architecture of *Akrophyllas* differs significantly from *Trepassia*. Branching is strictly rectilinear in *Akrophyllas*, with the 2<sup>nd</sup> order branches at right angles to the 1<sup>st</sup> order branches and the 3<sup>rd</sup> order branches strictly at right angles to the 2<sup>nd</sup> order branches, whereas both of these angles are considerably more acute in *Trepassia*. This greater degree of constraint also manifests in the 1<sup>st</sup> order branches, which in *Trepassia* are loosely constrained and do not end at a rim, whereas all 1<sup>st</sup> order branches are strictly constrained at both the stalk and the rim in *Akrophyllas*. This may be a result of how the ecology of fronds has affected their morphology. *Trepassia wardae* is present in a deep-water quiet environment with little to no turbulent wave action therefore not needing any constraint within its primary branches, whereas *Akrophyllas longa* is a large frond present in shallow water between storm and fair-weather wave base demanding a well-developed rim to withstand the more turbulent water.

Different adult growth strategies resulted in different shapes for the frond petalodia of these two genera. All adult specimens of *Trepassia wardae* are strictly parallel sided with tapering only at the distal end, which reflects adult growth entirely by distal insertion (Laflamme et al., 2007; Narbonne et al., 2009; Dunn et al., 2019a) whereas most or all specimens of *Akrophyllas longa* (all specimens if restricted to specimens in which both lateral margins are clearly visible) exhibit a gentle distal taper that reflects distal insertion of elements combined with an overall isometric inflation of the entire organism. Construction differs in the attachment of branches as the primary and secondary branches are attached to the central stalk in *Trepassia*

*wardae* whereas in *Akrophyllas longa* only the primary branches are directly attached to the central stalk.



*Figure 2.7.* Taphonomic variation in preservation of the internal stalk and the architecture of primary branches of *Akrophyllas longa*. **(1)** Primary branches emanating from the central stalk of a decaying frond in an alternate pattern and the only case of branch dislocation in *Akrophyllas longa*, SAM P12743b. **(2)** Smooth style specimen with some primary branch detail preserved, only known specimen preserved on the sole of a bed (SAM P40757). **(3)** Closeup of a three-dimensionally cast specimen (Fig. 2.2b) showing parallel series of branches emanating in an alternate pattern from a zigzag central commissure and the only known incidence of a possible stem in *Akrophyllas longa*, SAM P12716a+b. **(4)** Close-up of Fig. 2.2c highlighting primary branches with secondary architecture. Arrows indicate primary branches crossing over the central stalk and attaching to opposite side of stalk, SAM P12716c. All scale bars = 1 cm



*Figure 2.8.* Reconstruction of *Akrophyllas longa*. **(1)** Ventral view demonstrating gentle taper distally, prominent rim and attachment of primary branches. Primary branches are tightly constrained. **(2)** Interpreted bulbous holdfast buried below the sediment-water interface and short stem. **(3)** Close-up view of ventral side primary branches and attachment. **(4)** Ventral side of frond partly cutaway to reveal architecture of the elements and stalk. Illustration by P. Trusler.

## 2.7 Reconstructing *Akrophyllas longa*

Understanding of the morphology of *Akrophyllas longa* was formerly hindered by the disparate material in the collection made by Mincham and Flounders, which raised the question how many taxa are present in this collection. Our recognition that all of these specimens constitute taphonomic variants of a single frondose taxon, and that at least two specimens (SAM P13777: Fig. 2.2.4, 2.5.4, 2.5.5; and SAM P12716: Fig. 2.2.2b, 2.7.3) are preserved as highly oblique sections passing distally through the frond (Fig. 2.2.6), permits the first three-dimensional reconstruction of *Akrophyllas* (Fig. 2.2.8)

Three different preservational modes occur among the specimens in the Mincham-Flounders collection and a fourth mode is known from specimens subsequently collected from elsewhere in the Flinders Ranges. Smooth-style preservation displays a smooth convex epirelief with excellent preservation of the external microstructure on its surface (Figs. 2.2.2c, 2.5.1). Preservation of Ediacaran fronds in convex epirelief is rare among fronds from the Flinders Ranges (Wade, 1968; Gehling, 1999; Droser et al., 2020), but is common in *Dickinsonia* (Gehling, 1999) and among fronds from Avalonian Newfoundland (Seilacher, 1992; Laflamme et al., 2004, 2007; Liu et al., 2012), with hardening of the overlying bed before decomposition of the soft-bodied organism (Seilacher, 1992; Gehling, 1999; Narbonne, 2005). Smooth-style preservation of *Akrophyllas longa* shows the external shape of the outside of its folia, a well-developed external rim binding the individual branches that constitute the folia, and detailed impressions of their microstructure including primary, secondary, and very rarely tertiary branches. Internal features such as the stalk are visible through composite molding (Fig. 2.7.4).

Holotype-style preservation displays moderately to exceptionally well-preserved primary, secondary, and submillimetric tertiary branches (Fig. 2.2.4, 2.5.3, 2.5.4). Relief of the frond on the top surface of the bed ranges from positive epirelief to negative epirelief, occasionally within the same specimen (Fig 2.5.4) and the petalodium exhibits a sharp outer rim (Fig 2.8). Cleavage relief-style (Fig. 2.2.1) preserves the fossil fronds in part and counterpart between laminations within a bed of medium to coarse sandstone. These specimens are similar in appearance to holotype-style preservation but with poorer preservation due to the coarser grain size.

Deep-style preservation displays strongly cast primary branches but with no rim on the outside of the fossil (Fig. 2.2.2b, 2.7.1, 2.7.3). The specimen in Figure 2.2.2b and 2.7.3 sits in a scour on the top of the bed and appears to be nearly totally isolated from the underlying bed. This preservation is consistent with three-dimensional casting of the inside of the stalk and branches of this rangeomorph frond in a manner similar to that proposed by Brasier et al. (2013) and Butterfield (2020). Secondary branches and tertiary branches are rarely preserved on any specimens preserved in deep-style.

The features and relationships described above allow us to reconstruct the morphology of *Akrophyllas longa* as an elongate, bifoliate frond attached to a bulbous holdfast either directly or with a short stem (Fig. 2.7.3, 2.8.2). Current alignment of fronds of *Akrophyllas longa* (Fig. 2.2.2) implies that they were tethered to the substrate by means of a holdfast (see Seilacher, 1992, Wood et al., 2003). Holdfast structures are visible on the sole and top of the bed (Fig. 2.2.2d, 2.4.4), but the fragmentary nature of the slabs precluded seeing any connection between the base of any petalodium and its holdfast. The presence of a possible 1-cm-long stem in one specimen (Fig. 2.7.3) and the absence of any other stem impressions on any of the slabs suggest that the stem of *Akrophyllas longa* was short or the petalodium was directly attached to the

holdfast as shown in some Newfoundland rangeomorphs in which the holdfast was buried below the sediment-water interface and only rarely exhumed (Burzynski and Narbonne, 2015).

All four modes of preservation show that the primary branches were attached directly to an internal stalk (Fig. 2.8.1, 2.8.3). This stalk was cylindrical, as shown in cleavage relief style preservation (Fig. 2.2.1) and inferred from the high relief shown in some smooth style specimens (Fig. 2.2.2c, 2.7.4) and was similar in structure to the cylinder at the base of a specimen preserved in deep style (Fig. 2.7.3). Attached branches can give the cylindrical stalk a zigzag structure resembling a feather-stitch pattern where the branches join it (Fig. 2.2.3, 2.5.3, 2.7.3). A slightly displaced branch is visible in one specimen (Fig. 2.7.1), but the sharp rim on the outside of the frond (Fig. 2.2.1, 2.2.2c, 2.2.4, 2.5.1, 2.7.2, 2.7.4) and evidence of attachment to the internal stalk (Fig. 2.2.1, 2.2.2, 2.7.4) imply firm attachments at both ends of the branches but potentially a stronger attachment to the outer rim as the only known dislocation appears to have detached from the stalk rather than the rim despite the evidence for high-energy conditions during the burial of these tethered fronds.

Primary branches typically appear sigmoidal in proximal (mature) portions of the frond, but distal (younger) primary branches were more petaloid in shape, even in the different parts of the same specimen (Fig. 2.2.4, 2.5.4, 2.5.5). As with the rangeomorphs *Trepassia* (Narbonne and Gehling, 2003, fig. 3; Narbonne et al., 2009, figs 10.1) and *Beothukis* (Narbonne et al., 2009, fig. 5) from Newfoundland it seems likely that new branches were added as petaloids at the distal end of the frond. Petaloids are rotated and furled (terminology of Brasier et al., 2012), showing only on half of the full rangeomorph element (Fig. 2.5.5). Subsequent rotation, juxtaposition with adjacent primary branches, and preservation of these three-dimensional branches on a two-

dimensional surface makes them appear sigmoidal in more mature sections of the frond (Fig. 2.8.4).

Primary branches attach to the stalk in an alternate pattern on either side of the stalk and on both sides of the frond, which overlap the cylindrical stalk (Fig. 2.6.2, 2.6.3, 2.6.4, 2.8.3, 2.8.4). This pattern of attachment can create a zigzagging central crease where the branches alternate and are tucked underneath the previous branch, obscuring the stalk, and aiding in maintaining the structure of the petalodium (Figure 2.2.2, 2.2.3, 2.7.2). The branches continue outwards to the edge of the petalodium where they are attached a rim (Fig. 2.2.1, 2.2.2c, 2.2.4, 2.5.1, 2.5.2, 2.5.4, 2.5.5, 2.7.2, 2.7.4, 2.8.3, 2.8.4). The branches alternate attachment on either side of the stalk (Fig 2.8.2, 2.8.3), demonstrating monopodial attachment similar to other rangeomorphs such as *Avalofractus* (Narbonne et al., 2009) and *Rangea* (Vickers-Rich et al., 2013).

Casting of the primary branches in high relief in some specimens (especially Fig. 2.2.2b, 2.7.3) is consistent with Butterfield's suggestion that the inside of rangeomorphs were hollow and served as a hydrostatic skeleton and potentially as semi-isolated digestion chambers (Fig. 2.8.4). The rangeomorph architecture is interpreted to be visible externally, seen on the holotype (Fig. 2.2.4, 2.4.4, 2.4.5) but deep-style specimens in which primary branches were preserved by casting (Fig 2.2.2b, 2.7.2, 2.7.3) show nearly smooth surfaces with rare rangeomorph architecture which are interpreted to have preserved the inside of the frond. Exceptionally preserved specimens of *Rangea* showed well-developed rangeomorph architecture on the inside and outside of the frond (Vickers-Richer et al., 2013). A conundrum not yet resolved is whether the scarcity of rangeomorph architecture as seen in deep-style preservation of *Akrophyllas* is a true reflection of a smooth interior of primary branches in this taxon or whether taphonomic

conditions were not conducive to preserving rangeomorph architecture in these sandstone-cast specimens.

The central stalk is visible in most specimens, but typically only through composite molding of an internal stalk through the branches of the petalodium. A short cylinder is visible at the base of Figure 2.7.2, but no specimens preserve a naked stalk, suggesting that the stalk was internal and thus concealed during life. This internal stalk was likely fluid-filled and constructed of strong but flexible material that was collapsible as shown by its variable degree of fill among different specimens and in different parts of the same specimen (Fig. 2.2.1, 2.2.2, 2.2.4), attributes that are similar to stalks in other Ediacaran taxa (see Seilacher, 1989; Narbonne et al., 1997; Narbonne and Gehling, 2003; Laflamme et al., 2007; Laflamme and Narbonne, 2008a; Bamforth and Narbonne, 2009).



*Figure 2.9.* Reconstruction of *Akrophyllas longa* on the Ediacaran seafloor. Illustration by P. Trusler.

With the exception of multifoliate fronds, Ediacaran fronds are broadly similar on their “front” and “back” sides, but detailed study has shown consistent differences in the two sides of *Charnia* (Grazhdankin, 2014; Dunn et al., 2018) and *Arborea* (Dunn et al, 2019a). The direction of imbrication of the primary branches in *Akrophyllas* is proximal over distal in three specimens (Fig. 2.2.1, 2.2.4, 2.5.3) but distal over proximal in two specimens (Fig, 2.7.2, 2.7.4). The presence of both types of imbrication among approximately equal numbers of specimens is consistent with *Akrophyllas* being a bifoliate frond with proximal over distal imbrication on the “front” side of the frond and consequently distal over proximal imbrication on the “back side” (as illustrated by looking at both sides of a venetian blind). The central stalk is only visible in the fossil due to composite molding through the overlying branches, implying that the stalk was totally internal, and this raises the question whether *Akrophyllas* might be multifoliate like *Rangia* (Vickers-Rich et al., 2013) or the specimens questionably referred to *Trepassia* by Narbonne et al. (2009). A backing set of petaloids would effectively hide the stalk between them but would result in both the front and back of *Akrophyllas* showing the same pattern of imbrication irrespective of how they landed on the sea floor upon death. Similarly, although there is abundant evidence for overlapping specimens in accumulations of this gregarious frond (see arrowed specimens in Fig. 2.2.2), no evidence of a third folium was found in any specimen. Based on presently available evidence, the best model for *Akrophyllas* is an elongate, bifoliate frond with highly constrained rangeomorph architecture and a prominent internal stalk.

Eighteen of the 23 known specimens of *Akrophyllas* occur on the tops of beds, with four specimens known from laminations within the sandstone event bed (Fig. 2.2.1) and only one known from any bed sole (Fig. 2.2.3). This strong domination of epirelief preservation among specimens of *Akrophyllas* is in strong contrast with the taphonomy of other Ediacaran fronds in

Australia, which dominantly occur on bed soles or within beds and only very rarely on the tops of event beds (Gehling, 1999; Droser et al., 2020). This conundrum might be explained if *Akrophyllas longa* had a slightly higher concentration of gas in its hydrostatic skeleton and/or tissues that kept it upright in the water column and this made it less prone to sediment cover during storm events (Figure 2.9).

## 2.8 Conclusions

A gregarious assemblage of elongate fossil fronds from Ediacara originally named *Rangea longa* Glaessner and Wade, 1966 has had a confused taxonomic history due to the rather disparate morphology of the specimens that constitute the type material collected by Mincham and Flounders in the late 1950s. Our detailed studies confirm the view of Glaessner and Wade that all of these specimens are conspecific, and further suggest that they represent different preservational modes that collectively elucidate the three-dimensional morphology of this fossil frond. These specimens differ in both architecture and construction from all described rangeomorphs and are herein designated as the new genus *Akrophyllas*, an elongate, bifoliate frond with highly constrained rangeomorph architecture and a prominent internal stalk. Its widespread occurrence on the tops of event beds rather than the sandstone soles on which most Ediacaran fronds occurred may reflect a lower specific gravity of this taxon that made it slightly less likely to be buried by sand during storm events.

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## **CHAPTER THREE:**

**A new Ediacaran frond duster from Mistaken Point and Catalina Dome, Newfoundland**

### 3.1 Abstract

FronD dusters, small fronds never reaching more than 8 cm in height as adults, occur commonly in the Ediacaran of Avalonian Newfoundland but have not been extensively described.

*Plumumbra peniculiformis* new genus and new species is a frond-duster that is locally common in Ediacaran deep-water deposits from the Catalina Dome in the Bonavista Peninsula and near Mistaken Point in the Avalon Peninsula. It can be distinguished from all other Ediacaran fronds by the presence of lobe-like primary branches that, in the best-preserved specimens exhibit a feathery pattern consisting of a multitude of secondary branches attached to the base of the petalodium. *Plumumbra peniculiformis* is unrelated to either rangeomorph and arboreomorph fronds, providing further evidence that the lowest tier of the Ediacaran marine ecosystem was diverse, with numerous unrelated taxa converging on similar body plans.

### 3.2 Introduction

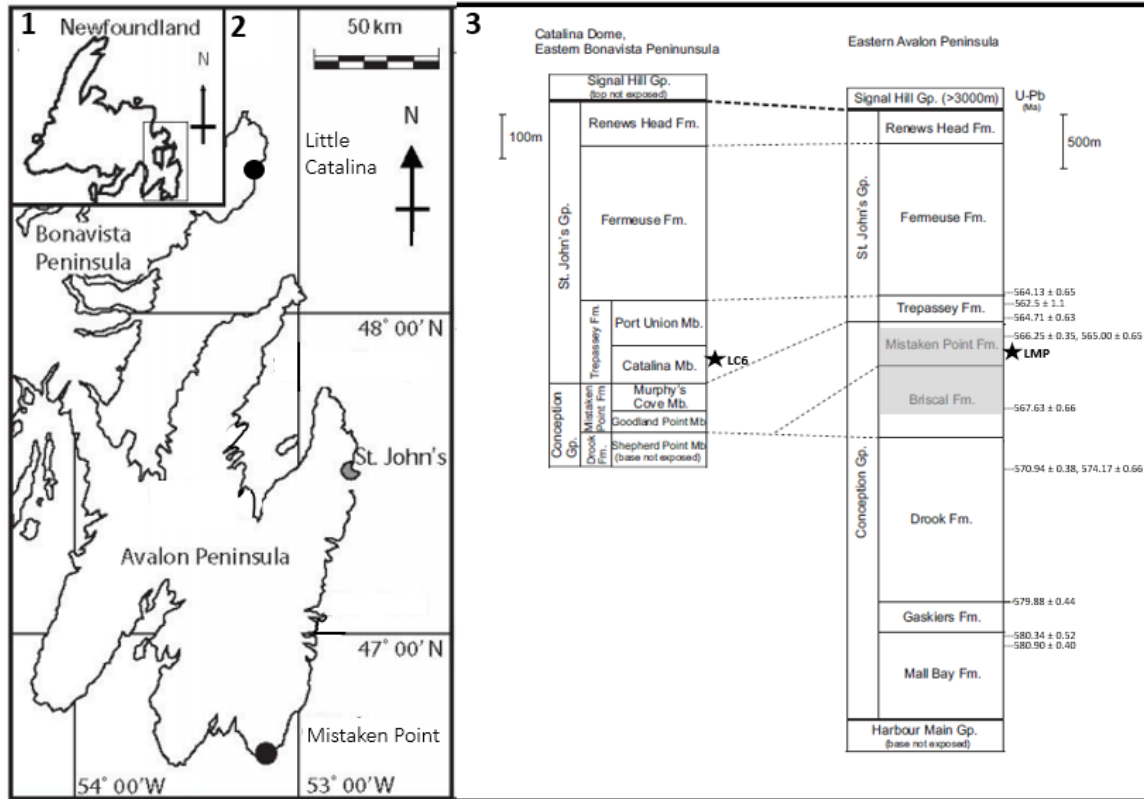
The Ediacara biota, impressions of soft bodied organisms on the bases of event beds, are the oldest known macroscopic, architecturally complex organisms in the fossil record (Laflamme et al., 2013; Droser and Gehling, 2015). Ediacaran fronds are entirely soft bodied and most frequently preserved as casts or molds of organisms buried beneath event beds. These conditions record a snapshot of Ediacaran life 575 to 539 million years ago (Linnemann et al., 2019; Matthews et al., 2021; Rooney et al., 2020) from localities all around the globe (Narbonne, 2005; Fedonkin et al., 2007; Xiao and Laflamme, 2009; Erwin et al., 2011). Their disappearance may

represent the first mass extinction event amongst macroscopic organisms (Darroch et al., 2015, 2018; Schiffbauer et al., 2016; Muscente et al., 2019).

Ediacaran fronds are critical components to the Ediacara biota and a popular area of research. Fronds dominate the oldest, deep-marine assemblages of Ediacaran macrofossils in Avalonian Newfoundland (Clapham and Narbonne, 2002), the Mackenzie Mountains of NW Canada (Narbonne, 1994), and Charnwood Forest, UK (Kenchington et al., 2018). Ediacaran fronds were the first organisms to partition the water column macroscopically, resulting in a tiered ecosystem that is similar to Phanerozoic marine ecosystem structure (Clapham and Narbonne, 2002) but with continuing discussion as to the details and function of tiering in the Ediacaran (Ghisalberti et al., 2014; Mitchell and Kenchington, 2018; McIlroy et al., 2021). Differences in branching architecture are key to understanding and categorizing Ediacaran fronds into robust clades (Laflamme and Narbonne, 2008; Brasier et al., 2012; Dececchi et al., 2017; Dunn et al., 2019). Fronds are found throughout all tiers, including the basal tier which extends from 1–8 cm above the sea floor (Clapham and Narbonne, 2002). Two types of fronds occupy the basal tier: juvenile fronds that have not yet reached their full adult height and frond dusters that never grew more than 8 cm high even in adulthood. Juvenile fronds are well described from the Mistaken Point biota and include juvenile representatives of *Charniodiscus* (Laflamme et al., 2004), *Charnia* (Laflamme et al., 2007, Liu et al., 2012), *Trepassia* (Narbonne et al., 2009; Liu et al., 2012), *Culmofrons* (Laflamme et al., 2012) and *Beothukis* (Narbonne et al., 2009, McIlroy et al., 2020, Hawco et al., 2020) all of which also occupied upper tiers as adults. Three taxa of frond dusters have previously been reported from the Mistaken Point assemblage: *Avalofractus abaculus* Narbonne et al., 2009; *Plumeropriscum hofmanni* Mason and Narbonne, 2016; and *Broccoliforma alta* Mason and Narbonne, 2016; and herein we describe a fourth taxon of frond

duster *Plumumbra peniculiformis* from Mistaken Point and Trepassey formations of Newfoundland.

### 3.3 Geologic setting



*Figure 3.1.* (1) Newfoundland, eastern Canada. (2) The Avalon and Bonavista peninsulas, Little Catalina and Mistaken Point study sites indicated with black circles. Modified from Liu et al., (2015). (3) Stratigraphic column of eastern Bonavista Peninsula and eastern Avalon Peninsula regions, modified from Mason et al. (2013). LC6 and LMP indicated by black stars. The gray box indicates the position of the Shuram-Wonoka-EN3 anomaly (Canfield et al., 2020). Drook (basal and upper), Mistaken Point and Gaskiers formation dates from Pu et al. (2016); Fermeuse, Trepassey (basal), Mistaken Point, Briscal, Drook (upper) formation dates from Matthews et al. (2021); Trepassey (upper) Formation date from Canfield et al. (2020). Where two dates appear for same bed, first stated dates are from Pu et al. (2016) and second from Matthews et al. (2021). All dates in this figure are more completely described in Matthews et al. (2021).

Specimens of this study occur on two surfaces, the Lower Mistaken Point (LMP) surface on the Avalon Peninsula and LC6 on the Bonavista Peninsula, in eastern Newfoundland, Canada (Fig 3.1.1, 3.1.2).

The Mistaken Point Formation (Williams and King, 1979) is a deep-marine succession of fine-grained, thick-medium bedded turbidites, contourites and siliciclastic-volcaniclastic rocks reliably bracketed by U-Pb dates of 564-567 Ma from ashes located above and below the formation (Pu et al., 2016; Matthews et al., 2021). Slumped units, debris flows, the low dispersion of turbidity current paleoflow directions, and the absence of wave-generated structures supports the interpretation of a deep-water environment below both the photic zone and storm wave base (Wood et al., 2003). Within the Mistaken Point Formation, a diverse range of Ediacara-type fossil impressions are preserved *in situ* beneath volcanic ash layers. The LMP surface (Clapham and Narbonne, 2002; Clapham et al., 2003; Bed 3 in Wood et al., 2003) contains the rangeomorph *Fractofusus andersoni* Gehling and Narbonne, 2007 and the most diverse assemblage of Ediacaran fronds in Avalonian Newfoundland, including *Trepassia wardae* Narbonne and Gehling, 2003, *Charniodiscus spinosus* Laflamme et al., 2004; *Frondephyllas grandis* Bamforth and Narbonne, 2009, *Beothukis mistakensis* Brasier and Antcliffe, 2009; and is the type locality for *Culmofrons plumosa* Laflamme et al., 2012 and the new genus and species *Plumumbra peniculiformis*. Ripple-cross-laminae with adjacent turbidites show that this deep-water slope dipped to the south-east (in present coordinates); all fronds on the LMP surface were strongly oriented to the present-day north-east by an interpreted contour current (Wood et al., 2003).

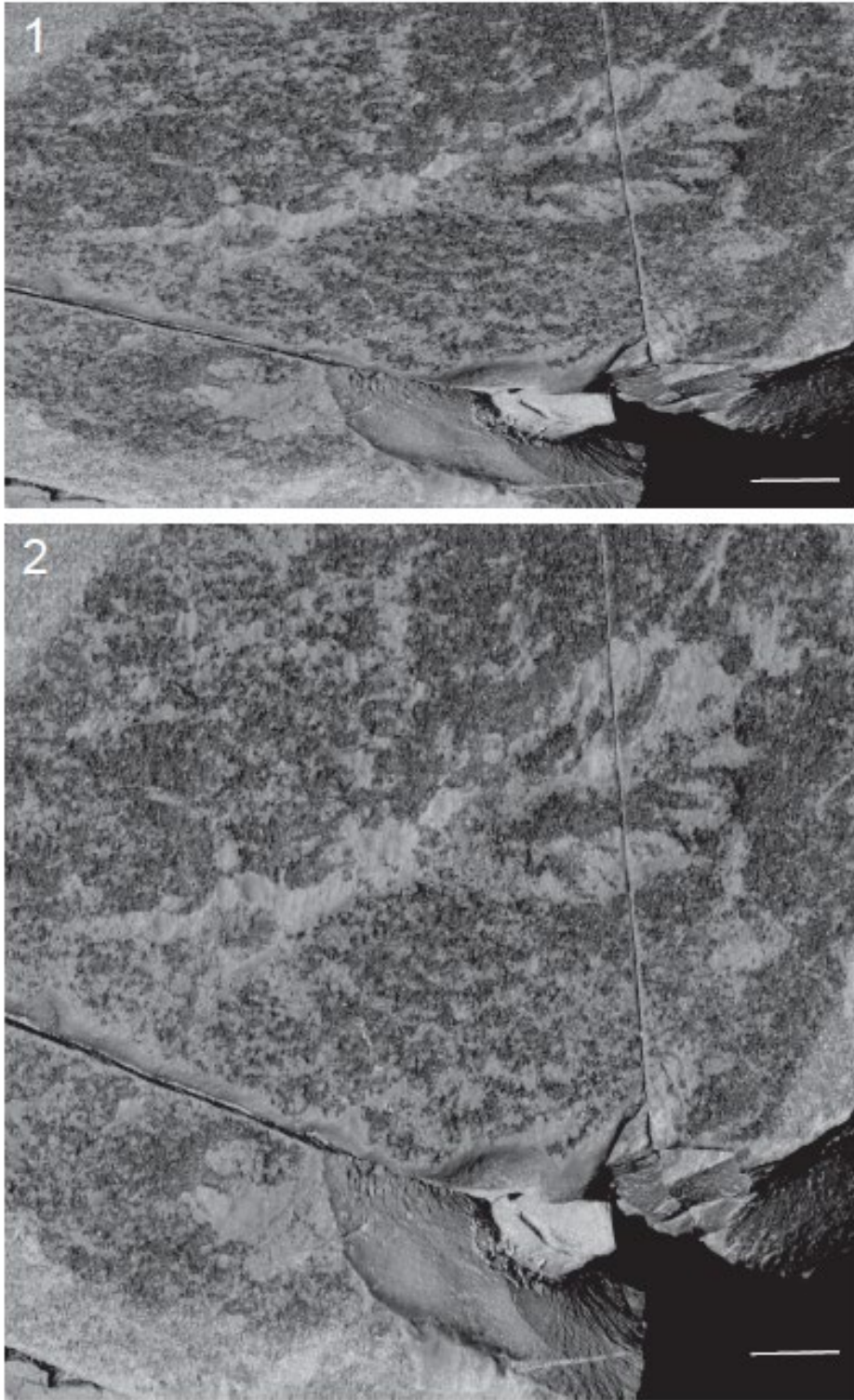
Exposed Ediacaran strata in Catalina Dome of eastern Newfoundland comprise a thinner but otherwise broadly similar succession to that documented at Mistaken Point in the southern

Avalon Peninsula (Fig. 3.1.3). Most of the Ediacaran succession in Catalina Dome comprise fine-grained turbidites with sporadic thin laminae and beds of volcanic ash. Ediacara-type fossil impressions are preserved on the tops of mudstone beds underneath volcanic ash (Hofmann et al., 2008; Mason et al., 2013). Sedimentary features similar to those in the Mistaken Point area support the interpretation of the Catalina Dome succession as having accumulated in a deep marine depositional environment (Mason et al., 2013). The newly described fossils occur on the LC6 surface in the Trepassey Formation (Dunn et al., 2019; Liu and Dunn, 2020), along with the arboreomorph frond *Charniodiscus*, and the rangeomorph fronds *Charnia* and *Primocandelabrum*. There is evidence of current flow from strongly aligned fronds on the LC6 surface, which implies that the fronds were tethered to the substrate by their holdfasts (Liu and Dunn, 2020, Fig. 2). Framboidal pyrite veneers which are associated in the death mask model of preservation are documented on Ediacaran fossil-bearing surfaces around the world (Fedonkin and Waggoner, 1997; Gehling, 1999) including the study site of LC6 (Liu, 2016). The pyrite is interpreted to have formed via microbial processes in hours to weeks following burial of benthic communities. LC6 documents oxidation of original pyrite framboids to iron oxides within an individual thin section (Liu, 2016).

### **3.4 Materials and methods**

The removal of fossils from the Mistaken Point Ecological Reserve (now a UNESCO World Heritage Site) is strictly prohibited and so paleontological study of the Mistaken Point biota is dependent on field photographs, latex molds, super-hydrophilic impression material, and casts of the original fossils. All studied sites are protected by provincial legislation and lie under the

jurisdiction of either the Parks and Natural Areas Division of the Department of Environment and Conservation (for Mistaken Point Ecological Reserve; MPER), or the Department of Business, Tourism, Culture and Rural Development (elsewhere in the Province, as outlined in Regulation 67/11 of the Historic Resources Act 2011).



*Figure 3.2. Plumumbra peniculiformis* holotype from LMP. **(1)** Specimen as it presently appears in the rock. **(2)** Specimen after retrodeformation to restore the fossil to its original size and shape. All scale bars = 1 cm.

Tectonic shortening events have affected the strata in the Mistaken Point area, subjecting the fossiliferous surface to ~40% shortening. The LC6 surface of the Bonavista Peninsula underwent a range of 14-42% shortening across the surface with an average of 28%. This deformation is evident particularly in circular elements like frond holdfasts, which are circular at nearly every known Ediacaran locality worldwide (Glaessner, 1984; Narbonne, 2005; Fedonkin et al., 2007). In the Mistaken Point and Bonavista peninsulas the holdfasts have become tectonically deformed from circular to elliptical, with all ellipses on a bedding plane oriented with their long axes in the same direction and exhibiting a similar degree of shortening. Following standard procedure (Seilacher, 1999; Wood et al., 2003; Gehling and Narbonne, 2007), all fossils were photographically restored to their original shape through the process of retrodeformation (Fig. 3.2.1, 3.2.2). After retrodeformation, each specimen was measured using ImageJ software to obtain the inner holdfast diameter, outer holdfast diameter, stem length and width, petalodium length and width and total frond length. Not every feature listed could be measured accurately in every specimen. All measurements in this chapter are from retrodeformed specimens.

### **3.5 Systematic Paleontology**

Group uncertain

*Remarks.*—There is currently no universally accepted taxonomic hierarchy for Ediacaran biota above the rank of genus. This paper follows the frond terminology proposed by Laflamme and Narbonne (2008).

Phylum, Class, Order, Family indeterminate

Genus *Plumumbra* new genus

*Diagnosis.*— As per species

*Type species.*— *Plumumbra peniculiformis* new species, by monotypy

*Etymology.*— The genus name is from the Latin word “Pluma” meaning feather and Latin word “Umbra” meaning shadow.

*Plumumbra peniculiformis* new species

2002 ‘Ostrich Feather’, Clapham and Narbonne, fig. 3.

2003 ‘Ostrich Feather’, Clapham et al., fig. 8.

2005 ‘Ostrich Feather’, Narbonne, fig. 2h.

2006 ‘Ostrich Feather’, Bottjer and Clapham., fig. 6A.

2008 ‘Ostrich Feather’, Hofmann et al.

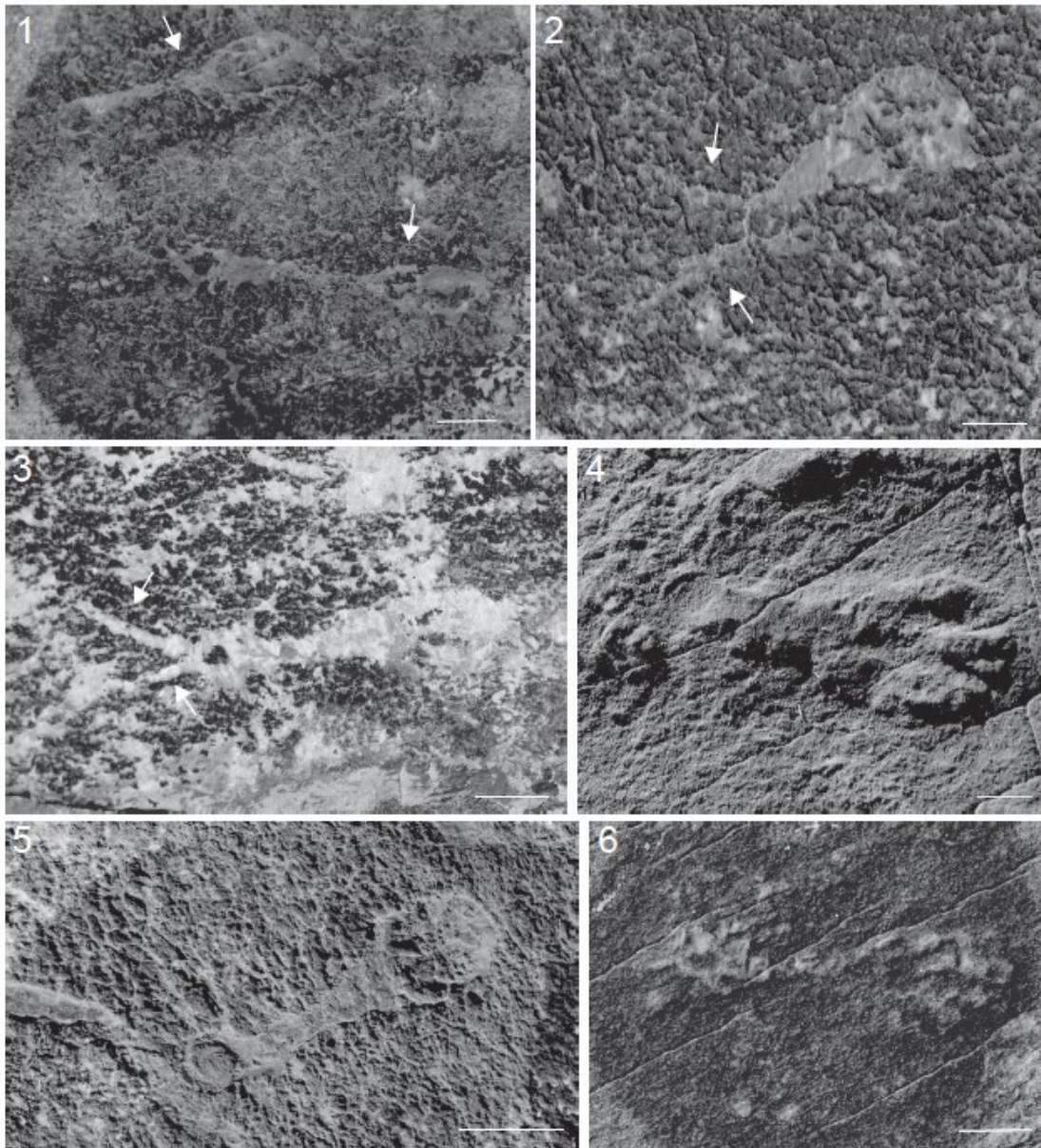
2011 ‘Ostrich Feather’, Clapham.

2015 ‘Ostrich Feather’, Liu et al.

2018 ‘Ostrich Feather’, Mitchell and Kenchington.

2019 ‘Ostrich Feather’, Mitchell et al.

2020 ‘Ostrich Feather’, Liu and Dunn., fig 4,e.



*Figure 3.3. Plumumbra peniculiformis.* All specimens have been retrodeformed. (1) Two current-aligned *Plumumbra* specimens from the LC6 surface, indicated by white arrows. (2) Specimen from LC6 displaying slight feather-like morphology and filamentous connections indicated by white arrows. (3) Specimen from LC6 displaying the lobed morphology of the petalodium and filamentous connections indicated by white arrows. (4) Three-lobed specimen of *Plumumbra* with well-preserved holdfast and no filamentous connections from Lower Mistaken Point. (5) *Plumumbra* specimen displaying a lobed morphology with well-preserved stem and holdfast, concentric rings within holdfast visible and filamentous connections. (6) Specimen from Lower Mistaken Point displaying five lobes and multiple radially arranged filamentous connections. All scale bars = 1 cm.

*Holotype.*—Following standard procedures for designating uncollectable holotypes of fossils in Mistaken Point Ecological Reserve (Laflamme et al. 2007; Brasier and Antcliffe, 2009; Bamforth and Narbonne, 2009; Laflamme et al., 2012; Mason et al., 2016) the holotype is designated as a specimen that remains in the field. The holotype is located *in situ* on the Lower Mistaken Point surface (“LMP” in Clapham et al., 2003; “Bed 3” in Wood et al., 2003). A plastic mold (currently labelled LMP17; Specimen number 16 in Table 1) will be repositied in “The Rooms” museum in St. John’s.

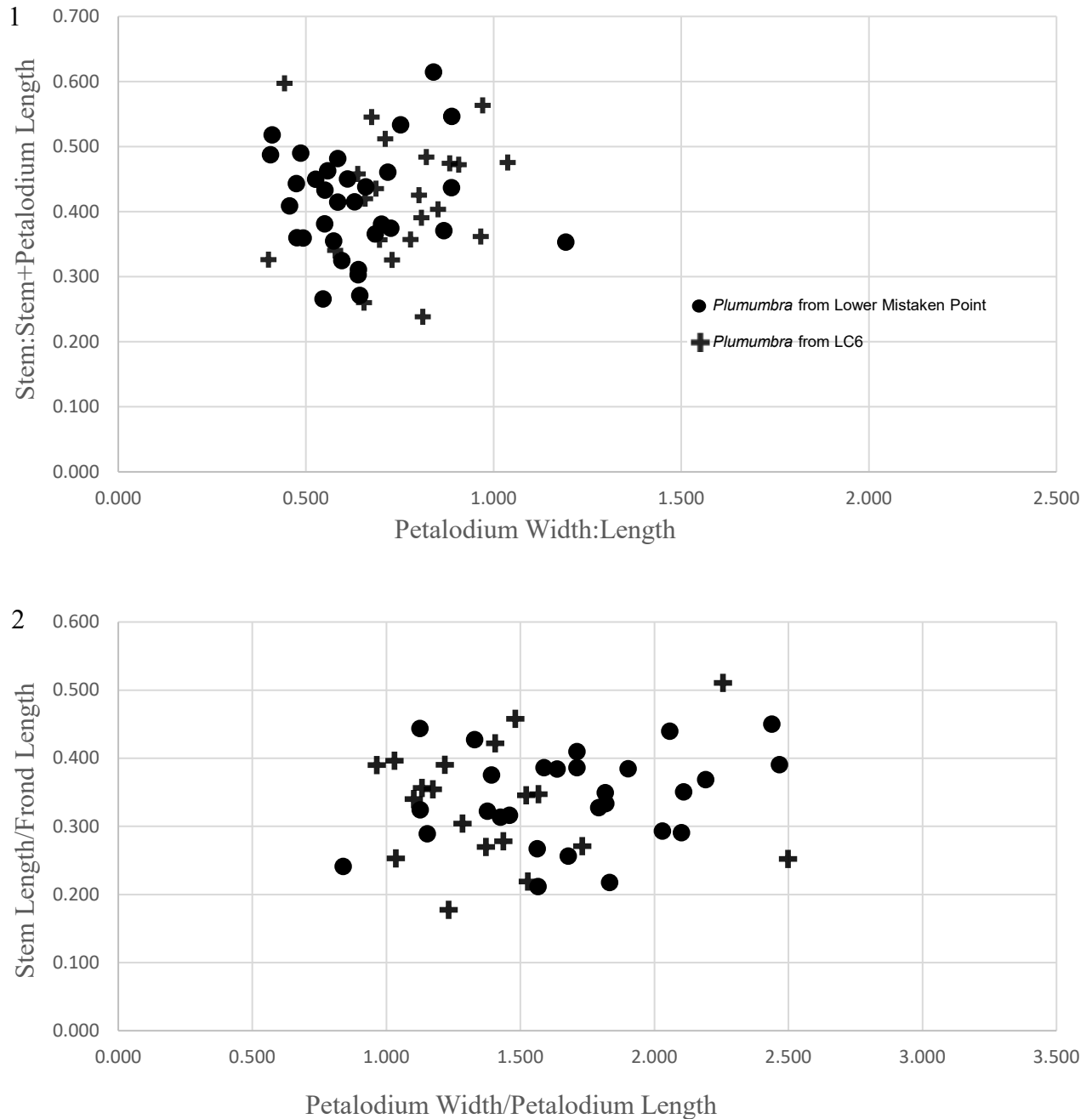
*Diagnosis.*— Cm-scale frondose fossils with a spatulate petalodium attached by a cylindrical stem to a bulbous or discoidal holdfast, commonly with filamentous connections. The petalodium consists of three feather-like primary branches that are nearly parallel typically preserved as 2-5 lobes.

*Description.*— The holotype (Fig. 3.2) is a 6.4 cm-long frond with a small bulbous holdfast, 0.5 cm in diameter attached to a cylindrical stem (1.4 cm length, 0.3 cm width). The stem passes into a spatulate petalodium (3.9 cm length, 1.6 cm width) at an angle of approximately 150° between the stem and the petalodium and consists of multiple feather-like primary branches that typically form three distinct lobes. Primary branches/lobes emerge from the distal end of the stem at the same point, splitting distally into subtle secondary branches visible in several areas.

Other specimens support and refine the description based on the holotype (Fig. 3.3-3.4; Table 3.1). The bulbous holdfast diameter ranges from 0.3-1.8 cm (n=54) with a mean of 0.8 cm. The stem width ranges from 0.2-1.1 cm (n=58) with a mean of 0.4 cm, the stem length ranges from 0.7-2.1 cm (n=60) with a mean of 1.4 cm (Fig. 3.3.1-3.3.5). The petalodium width ranges

from 0.6-2.8 cm (n=64) with a mean of 1.3 cm and length ranges from 2.7-6.9 cm (n= 65) with a mean of 4.2 cm. Almost all specimens are complete with an attached holdfast, which typically consists of concentric rings (Fig. 3.3.4, 3.3.5). All specimens display a consistent spatulate petalodium and a stem that comprises an average of 30% of the frond's length. Specimens either display a unique petalodium with architecture of feather-like primary branches with small similarly feather-like secondary protrusions (Fig. 3.2.2, Fig 3.3.2) or 2-5 lobe-like primary branches at the attachment point to the stem (Fig. 3.3.1, 3.3.3-3.3.6). 17 specimens display filamentous rays extending radially from their holdfast (Fig. 3.2.2, 3.3.2–3.3.6). Specimens from the LMP surface at Mistaken Point and the LC6 surface on Bonavista Peninsula show strikingly similar morphology (Fig. 3.2-3.3), proportions (Fig. 3.4), and sizes (Table 3.1).

*Etymology.*— The species name is from Latin, meaning “in the shape of a feather duster”.



*Figure 3.4.* Morphometric plots of complete, well-preserved specimens of *Plumumbra peniculiformis* from surfaces LMP and LC6. All ratios are derived from measurements listed in Table 1 and reflect the retrodeformed frond as it would have appeared on the seafloor. **(1)** Morphometric plot of *Plumumbra*, the y-axis reflects increasing relative stem length and the x-axis reflects increasing circularity of the petalodium. **(2)** Comparison of the morphometric distribution of *Plumumbra*. The two localities of *Plumumbra* show significant overlap demonstrating they are all members of the same species.

### 3.6 Comparisons

The distinctive feather-like architecture of the primary branches emerging from the end of the stem has not previously been described Ediacaran fronds (Fig. 3.2.2). *Plumumbra peniculiformis* is a small frond with distinctive feather-like architecture in the best-preserved specimens and 1-5 lobes in the majority of specimens (Fig 3.3.1, 3.3.3-3.3.6). Specimens consistently show a spatulate petalodium with the majority of specimens having three primary branches typically preserved as lobes, a cylindrical stem and a bulbous holdfast. The quality of preservation is limited by the size of particles underlying the ash layer which preserves large scale morphologic features well but reaches a limit for finer scale. The preservation of *Plumumbra* is superior to other described frond dusters *Broccoliforma alta* and *Plumeropriscum hofmanni* (Mason and Narbonne, 2016) but not as remarkable as *Avalofractus abaculus* (Narbonne et al., 2009).

The standard Ediacaran frond morphoshapes are divided into four main branching architectures; *Arborea*-type branching, characterized by pea-pod like primary branching which house several secondary branches within a protective sheath; *Rangea*-type branching, composed of several overlapping primary branches which are self-similar and fractal with multiple orders of branching attached to a straight central stalk; *Charnia*-type branching consisting of parallel, sigmoidal to rectangular primary branches which alternate and cross to form a central zig-zag axis; *Swartpuntia*-type branching, consisting of petaloids with unornamented tube-like primary branches (Laflamme and Narbonne, 2008; Dececchi et al., 2017). The architecture of *Plumumbra* has no parallels with any described Ediacaran frond taxon.

Fronde dusters commonly share a similar overall size and construction but possess drastically different architecture from one another. *Avalofractus abaculus* Narbonne et al. 2009 is a small, bifoliate, cm-scale rangeomorph that is self-similar over four fractal scales. Each fractal scale of *Avalofractus abaculus* is represented by a double-sided rangeomorph element (displayed, unfurled element, Brasier et al., 2012) that is only constrained at its attachment point which passes off a central ridge and were free to rotate and pivot relative to other branches (Narbonne et al., 2009). *Broccoliforma alta* Mason and Narbonne, 2016 is an irregularly shaped lobate, flabellate frond connected to a short cylindrical stem that attaches at the opposite end to a disk. Its internal features are poorly preserved lobes radiating in a semicircular fan-shaped array from the center of the diameter at an angle of approximately 180° with no architecture resembling the feather-like characteristics of *Plumumbra*. Although poorly preserved specimens of *Plumumbra* resemble the lobe structure of the primary branches of *Broccoliforma alta* and grow to similar maximum height, they are readily distinguishable. *Plumeropriscum hofmanni* Mason and Narbonne, 2016 is a cm-scale frondose fossil with a deltoid petalodium, bulbous holdfast, and cylindrical stem. Well-preserved rangeomorph architecture is locally visible in specimens of *Plumeropriscum*.

*Plumumbra peniculiformis* does not bear likeness to any known large Ediacaran frond, and unlike all known fronds at Mistaken Point is neither a rangeomorph nor an arboreomorph. *Plumumbra* therefore cannot be classified as a juvenile of any known species.

### 3.7 Conclusions

Formal designation of frond dusters like *Plumumbra peniculiformis* helps to fill in the lowest tier of Mistaken Point communities. *Plumumbra* is one of the few remaining Mistaken Point taxa to be formally described, and exhibits an architecture not previously described from any frondose taxon. Despite the unique architecture and construction shown in *Plumumbra*, convergence has led to a broadly similar in overall shape to the rangeomorph frond dusters *Plumeropriscum* and *Avalofractus* and juvenile specimens of the arboreomorph *Charniodiscus*. There is still an abundance to uncover in the Avalon assemblage, with more small frond species being recognized and described in detail information is becoming available to discover how these frond dusters interacted and divided the lower tier of the Ediacaran marine ecosystem with their niche small frondose body plan.

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**Table 3.1.** Distance measurements of specimens of *Plumumbra*. All measurements in centimeters. N/A refers to elements of the frond that were poorly preserved and unable to be counted/measured. All measurements were taken on retrodeformed specimens to adjust for tectonic shortening. \* indicates holotype.

Specimen numbers	Surface	Holdfast diameter	Stem length	Stem width	Petalodium length	Petalodium width	Total frond length
1	LMP	0.6	1.1	0.5	2.1	1.8	3.9
2	LMP	1.7	2.0	N/A	4.1	3.0	7.5
3	LMP	1.1	1.7	1.0	3.5	2.5	6.2
4	LMP	0.9	1.4	0.5	2.5	1.7	4.9
5	LMP	0.6	1.4	0.4	1.6	1.4	4.0
6	LMP	0.5	2.0	0.5	1.3	0.6	3.9
7	LMP	N/A	2.0	0.6	1.9	1.4	4.7
8	LMP	N/A	N/A	N/A	2.4	1.4	N/A
9	LMP	1.0	1.7	0.6	2.3	1.5	4.8
10	LMP	0.9	1.5	0.6	2.3	1.9	N/A
11	LMP	0.6	1.5	0.5	1.6	1.7	3.8
12	LMP	0.7	1.3	0.3	1.4	1.1	3.3
13	LMP	0.6	1.7	0.4	2.5	2.1	4.8
14	LMP	0.3	1.5	0.3	2.0	1.6	N/A
15	LMP	1.0	1.6	0.6	2.9	2.3	5.3
16*	LMP	1.0	1.5	0.7	4.3	2.8	6.9
17	LMP	1.2	1.7	0.5	3.4	1.9	6.4
18	LMP	1.4	1.5	0.6	3.1	1.2	6.0
19	LMP	0.7	1.3	0.4	2.0	N/A	3.9
20	LMP	N/A	1.7	0.5	1.4	1.2	N/A

21	LMP	0.8	1.2	0.4	0.9	0.9	3.0
22	LMP	0.5	1.5	0.3	1.3	0.9	3.3
23	LMP	N/A	1.0	0.4	1.3	0.9	N/A
24	LMP	0.8	1.7	0.4	2.0	1.3	5.0
25	LMP	1.3	0.9	1.1	2.9	2.3	5.1
26	LMP	0.6	1.1	0.4	1.3	1.1	3.3
27	LMP	0.5	0.7	0.3	1.3	1.3	2.9
28	LC6	N/A	N/A	N/A	2.3	1.3	N/A
29	LC6	0.9	1.8	0.7	2.5	2.2	4.9
30	LC6	0.5	0.9	0.4	1.1	1.0	2.7
31	LC6	N/A	0.9	0.4	2.2	1.4	4.5
32	LC6	1.0	1.2	0.6	2.0	1.5	3.8
33	LC6	0.6	1.5	0.5	2.5	1.4	4.6
34	LC6	N/A	0.9	0.2	1.2	0.8	N/A
35	LC6	1.1	1.8	0.9	3.0	2.6	6.1
36	LC6	0.6	1.2	0.5	1.6	0.9	3.5
37	LC6	1.7	0.9	0.5	1.7	2.0	3.8
38	LC6	N/A	0.9	0.4	1.8	1.1	3.4
39	LC6	0.8	1.2	0.6	2.2	1.2	N/A
40	LC6	0.4	1.2	0.3	1.0	0.9	2.7
41	LC6	0.9	1.7	0.4	2.4	1.4	4.4
42	LC6	0.6	1.5	0.2	1.9	0.9	4.3
43	LC6	N/A	0.9	0.3	2.3	1.5	N/A
44	LC6	0.5	1.2	0.3	1.5	0.8	3.8
45	LC6	0.5	1.1	0.3	2.0	1.0	3.9
46	LC6	0.4	1.6	0.4	1.0	0.9	N/A
47	LC6	0.7	1.2	0.3	2.1	1.0	4.1
48	LC6	0.5	1.2	0.4	2.1	1.4	3.8
49	LC6	0.6	2.1	N/A	2.3	1.3	5.1
50	LC6	0.7	1.7	0.2	1.8	0.7	4.3
51	LC6	0.8	1.8	0.3	1.6	1.2	4.2
52	LC6	0.7	1.4	0.5	2.0	1.3	3.7
53	LC6	0.5	1.2	0.5	1.9	1.3	3.7
54	LC6	0.5	0.8	0.3	2.3	1.2	3.8
55	LC6	0.5	1.3	0.2	1.5	1.1	3.4
56	LC6	0.5	1.8	0.3	1.7	0.7	4.0
57	LC6	0.5	1.6	0.2	1.9	1.0	4.1
58	LC6	N/A	N/A	N/A	1.4	1.0	N/A
59	LC6	0.2	1.7	0.1	1.8	0.9	3.9
60	LC6	0.7	1.6	0.4	1.9	1.2	4.0
61	LC6	0.6	N/A	N/A	2.1	1.1	3.2
62	LC6	0.6	1.5	0.2	2.1	1.0	3.9
63	LC6	0.7	1.0	0.5	2.2	1.4	3.7

## **CHAPTER FOUR:**

### **General Conclusions**

## 4.1 Conclusions

Originally described more than 60 years ago as “*Rangea*” *longa*, the critical examination of the Mincham-Flounders collection and the greater understanding of *Rangea* worldwide, shows that this material cannot be referred to *Rangea* or any other known genus and is herein designated as a new genus of Ediacaran fronds. *Akrophyllas longa* is an elongate large frond that occurs in the Flinders Ranges of South Australia. The frond consists of a strongly elongate petalodium with moderate distal taper and apparent sigmoidal to petaloid shaped primary branches with rectangular secondary branches creating distinct rangeomorph elements. Comprehensive study of these exceptional fossils confirms they comprise a single biological taxon. Four taphonomic variants collectively illustrate the three-dimensional structure of this frond. The preservation of *Akrophyllas longa* almost exclusively on the tops of sandstone event beds could imply a slightly more buoyant composition, and is consistent with an upright, epibenthic lifestyle for this frond.

*Plumumbra peniculiformis* new genus, new species is an Ediacaran frond duster <7 cm high that occurs in the Mistaken Point and Trepassey formations in the Avalon and Bonavista peninsulas of eastern Newfoundland. *Plumumbra* displays a distinctive architecture of lobe-like primary branches that, in the best-preserved specimens, exhibit a feathery pattern attached to the base of the petalodium, this architecture is otherwise unknown from the Ediacaran biota. Many taxa of the larger Ediacaran fronds like *Charniodiscus*, *Charnia* and *Beothukis* also preserve juveniles on the bedding planes, but *Plumumbra* is one of four genera that occurs solely as frond dusters occupying the lowest tier of the Ediacaran ecosystem. Convergent evolution has resulted in several unrelated genera of small fronds sharing a similar body plan of a petalodium attached to a stem to a bulbous holdfast, we are slowly uncovering that these frond dusters had a significant diversity within this body plan.

The two fronds studied here provide a more complete picture of the Ediacaran biota. Analysis of new genera and species allow further insight into Ediacaran ecosystems, distinguishing between phylogeny and convergence. Both species studied here have been victim to this debate as *Plumumbra peniculiformis* was a member of an informal group of species that had converged on a similar body plan and *Akrophyllas longa* had been assigned to five genera based on largely taphonomic features rather phylogeny. Describing new species offers a new understanding of the true diversity of each tier of the Ediacaran community. Reanalysis of existing species and analysis of new modes of preservation allow for a more complete global analysis and synthesis of Ediacaran fronds.