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Palaeobiology of the reclining rangeomorph *Beothukis* from the Ediacaran Mistaken Point Formation of southeastern Newfoundland

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Abstract

Beothukis mistakensis from the Ediacaran System of Newfoundland, Canada demonstrates complex fractal-like morphology through the development of primary-, secondary- and tertiary-order Rangea-like units. The primary-order rangeomorph units observed in *B. mistakensis* are tightly juxtaposed, show no evidence of being independent of one another and are made up of chamber-like secondary-order – probably mesoglea-filled – units. The growth of these rangeomorph units demonstrates that the frond developed from the tip towards the basal region through ontogeny. The tertiary-order units of *Beothukis* are considered to represent surface morphology on the secondary-order units. This is in contrast to palaeobiological reconstructions of *Beothukis* that invoke three-dimensional fractal-like branches with independent units, which has been used to infer an osmotrophic mode of life. It is considered here that the fractal-like morphology of the lower surface of *B. mistakensis* was an adaptation to increase surface area to volume ratio. The quilted morphology of *Beothukis* proposed here is consistent with a sessile, reclining, phagocytotic and/or chemosymbiotic mode of life similar to that invoked for the reclining rangeomorph *Fractofusus*.

1. Introduction

The late Ediacaran fossil assemblages of Newfoundland, Canada preserve abundant, large, morphologically complex macro-organisms (Anderson & Misra, 1968; Narbonne, 2011; Liu *et al.* 2016) known as the Avalonian Assemblage (Waggoner, 2003), predominantly found on coastal exposures of the Avalon and Bonavista peninsulas (e.g. Narbonne, 2005; Liu *et al.* 2015). The most famous of these sites is the Mistaken Point Ecological Reserve, a UNESCO World Heritage Site located on the southeastern portion of the island of Newfoundland (Fig. 1). The original discovery of the Mistaken Point biota occurred on the D and E surfaces of the Mistaken Point Formation at Mistaken Point itself (Anderson & Misra, 1968; Misra, 1969). The fossil assemblage is interpreted to have been preserved *in situ* on the deep basin floor by smothering under an ash-laden turbidity current (Seilacher, 1992; Clapham *et al.* 2003; Wood *et al.* 2003; Ichaso *et al.* 2007), which has recently been dated at 565.00 ± 0.64 Ma (Matthews *et al.* 2020). The E Surface fossils are preserved as both positive and negative epireliefs cast by a fine silty mudstone that, in some cases, preserves very fine morphological details. The E Surface at Mistaken Point has the most abundant and diverse assemblage of Ediacaran macro-organisms found in Newfoundland, of which frondose taxa comprise approximately 50% of the total assemblage (Clapham, 2011). The most figured portion of the E Surface is known as 'Seilacher's Corner', which includes a number of similarly orientated fronds of *Charniodiscus procerus* (Laflamme *et al.* 2004) as well as abundant negative epirelief casts of the lower surfaces of the fusiform epibenthic recliner *Fractofusus* (cf. Gehling & Narbonne, 2007; Mitchell *et al.* 2015; Dufour & McIlroy, 2017) and also the lower surface of *Beothukis mistakensis* (Brasier & Antcliffe, 2009; Fig. 2a). Neither *Fractofusus* or *Beothukis* are consisitently orientated in the direction of the stems of *C. procerus* (Wood *et al.* 2003).

The Ediacaran biota of Newfoundland was dominated by the Rangeomorpha, named for the first described member of this clade, *Rangea schneiderhoehni* (Gürich, 1930; Pflüg, 1970, 1972; Jenkins, 1985; Grazhdankin & Seilacher, 2005). This broad clade consists of millimetre- to metre-scale soft-bodied organisms that are characterized by a unipolar to multipolar frondose morphology composed of several orders of self-similar units that resemble *Rangea* fronds in a range of orientations (e.g. Jenkins, 1985; Brasier & Antcliffe, 2004, 2009; Narbonne, 2004; Brasier *et al.* 2012). Some rangeomorphs have stems and/or basal discs and a range of growth programmes in the frondose portion that have created a diverse range of morphotaxa (Narbonne, 2004; Narbonne *et al.* 2009; Brasier *et al.* 2012; Laflamme *et al.* 2013; Liu *et al.* 2016).

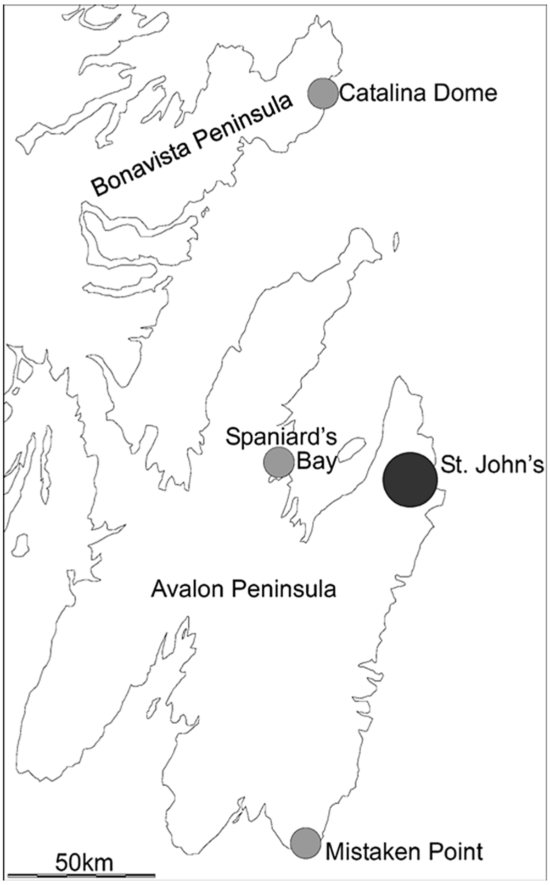

Fig. 1. Avalon and Bonavista peninsulas, southeastern Newfoundland, highlighting fossiliferous Ediacaran localities at Mistaken Point, Spaniard's Bay and the Catalina Dome.

A wide variety of terminology has been used to describe rangeomorph architecture (Pflüg, 1972; Jenkins, 1992; Laflamme & Narbonne, 2008; Brasier & Antcliffe, 2009; Narbonne *et al.* 2009; Brasier *et al.* 2012). The self-similar architecture of the Rangeomorpha is built around the basic rangeomorph unit, or 'branch', which is repeated at a range of scales (orders) in the frondose portion of the organism (Narbonne, 2004; Brasier *et al.* 2012). The primary-order branches are here considered to be the largest rangeomorph units that compose the rows on either side of a central stalk or axis. Small (higher-order) rangeomorph units can be determined within larger (low-order) rangeomorph units (Jenkins, 1985; Narbonne, 2004; Brasier & Antcliffe, 2009), although their precise three-dimensional organization is poorly known in many taxa.

It is generally accepted that all orders of rangeomorph units may be expressed in a number of different orientations and with variable degrees of rotation, openness and/or furling in different taxa (Brasier *et al.* 2012). Rangeomorph taxa have been established based on combinations of: (1) the architecture of the rangeomorph elements; (2) the postulated growth program (insertion versus inflation); and (3) the number of growth tips or poles, plus other characters such as the presence or absence of a stem and basal disc (e.g. Brasier *et al.* 2012). However, there is currently a lack of consensus concerning which morphological characters should be of significance at the genus and species level (e.g. continuous versus discrete branching characters; Liu *et al.* 2016; Kenchington & Wilby, 2017). Our re-examination of the type material of *Beothukis* has the potential to inform that debate by assessing the validity of the emended diagnosis of *Beothukis* (Brasier *et al.* 2012) that was broadened and inadvertently overlapped with the diagnosis of the simultaneously introduced genus *Culmofrons* (Laflamme *et al.* 2012).

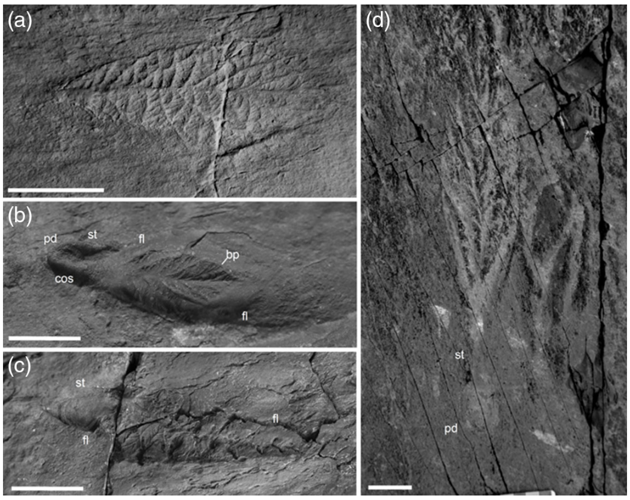

Fig. 2. (a) Holotype of *Beothukis mistakensis* from the 'E Surface' within the Mistaken Point Ecological Reserve. Scale bar, 5 cm. (b) Specimen previously attributed to *Beothukis mistakensis* from Spaniard's Bay, showing that the inferred pedal disc and stalk are actually related to obstacle scour and lie within a flute mark. bp – primary branch; cos – crescentic obstacle scour; fl – erosion within flute; pd – pedal holdfast; st – stalk. The current was from left to right. Scale bar, 2 cm. (c) Specimen previously attributed to *Beothukis mistakensis* from Spaniard's Bay showing a conical erosion on the up-current end of a shallow flute. fl – flute. The current was from left to right. Scale bar, 2 cm. (d) Holotype of *Culmofrons plumosa* from Lower Mistaken Point within the Mistaken Point Ecological Reserve. Scale bar, 3 cm.

1.a. *The rangeomorph* Beothukis mistakensis

Beothukis is a uniterminal rangeomorph frond, with an oval to spatulate outline that has latterly been considered to have had a stem and holdfast (Narbonne *et al.* 2009; Brasier *et al.* 2012; Liu *et al.* 2016). The first mention of the taxon is under the moniker 'Flat Recliner' (Seilacher, 1992), and later as the 'Spatulate Rangeomorph' (Laflamme & Narbonne 2008). Formal description of *Beothukis mistakensis* (Brasier & Antcliffe, 2009) noted similarities in its mode of growth to that of *Charnia* and *Bradgatia*, with which it is commonly reported in the Newfoundland sections (e.g. Laflamme *et al.* 2007; Hofmann *et al.* 2008; Narbonne *et al.* 2009; Liu *et al.* 2015). The most spectacularly preserved material attributed to *Beothukis* comes from the Trepassey Formation, close to Spaniard's Bay (Narbonne *et al.* 2009), which has a smooth, bulbous structure at the base of the frond that has been called a 'pedal holdfast' and separated from the frondose portion by a short stem or sheath (Fig. 2b, c). The resultant reconstruction of *B. mistakensis* as an erect frond with holdfast and a short stem (Narbonne *et al.* 2009) has been accepted in all recent literature on the Mistaken Point biota (Liu *et al.* 2015, 2016; Mitchell *et al.* 2018), despite the recognition that the Spaniard's Bay fossils lie in flute marks and linear current scours (Brasier *et al.* 2013). The structures that resemble stems are likely to be current scours that originate from holdfasts that may not have been associated with the frond (see full discussion in Section 4.a).

1.b. *The* Beothukis/Culmofrons *problem*

The taxonomic status of the genus *Beothukis* is controversial due to an emendation of the original diagnosis (Brasier *et al.* 2012) to

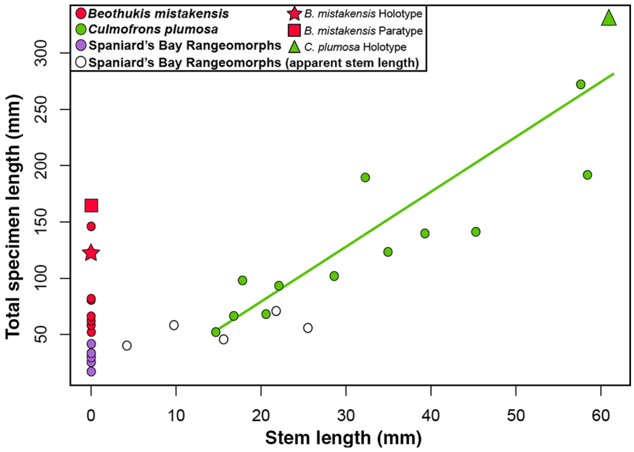

Fig. 3. Comparison of stem length versus total specimen length among specimens of *Beothukis mistakensis* (*n* = 10), *Culmofrons plumosa* (*n* = 13) and undetermined *Beothukis*-like spatulate rangeomorphs from Spaniard's Bay (*n* = 6).

include rangeomorphs with a basal disc (holdfast) and stem (Narbonne *et al.* 2009; Fig. 2b, c). The emendation occurred at around the same time as the creation of *Culmofrons plumosa* (Laflamme *et al.* 2012), which has a similar spatulate frond to that of *Beothukis*, but was differentiated from it by having a larger number of primary-order branches, subparallel secondary branches, and the presence of both a basal disc and stem (Laflamme *et al.* 2012; Fig. 2d). Subsequent review of this taxonomic issue concluded that stem length and number of branches might be ecophenotypic, characters that were inappropriate for differentiation of taxa at the generic level (Liu *et al.* 2016).

While stem length is undoubtedly variable in *Beothukis* and *Culmofrons*, stem length is problematic due to all the short-stemmed forms considered being controversial specimens from Spaniard's Bay (Narbonne *et al.* 2009; Fig. 3) discussed in detail in Section 4.a. The argument that *Culmofrons* should be considered a junior synonym of the emended concept of *Beothukis* – accepting that *Beothukis* could have a disk and stem – resulted in the creation of *B. plumosa* (Laflamme *et al.* 2012). This assertion is based on comparisons of stem length, the number of rangeomorph units and taphonomy, as well as the relative importance of continuous versus discrete characters.

At the species level, *Beothukis mistakensis* is distinguished from *B. plumosa* (Laflamme *et al.* 2012) (hereafter referred to simply as the species *plumosa*) on the basis of the latter having: (1) a zig-zagged and concealed axis (despite this morphology being considered to be a possible taphonomic artefact; Laflamme *et al.* 2007; Brasier *et al.* 2012; Liu *et al.* 2016); (2) a stem and disc; and (3) the fact that the more numerous (8–12) secondary-order rangeomorph units are commonly subparallel in the species *plumosa*, in contrast with the (5–8) radiating secondary-order rangeomorph units typical of *B. mistakensis*. However, this decision relies heavily on the validity of the emendation of the generic diagnosis to include the presence of a stem and disk in *Beothukis* (Narbonne *et al.* 2009), an assertion that is reassessed here.

The conclusion that continuous characters should not be included in generic diagnoses of the Rangeomorpha (Liu *et al.* 2016) has been contested through statistical analysis of the architecture of the rangeomorph *Primocandelabrum* from the UK, which can apparently have a range of types of rangeomorph units in branches of the same order within the same fossil (Kenchington & Wilby, 2017). The current view is therefore that a combination of continuous and discrete characters is required to diagnose rangeomorph genera and species (Kenchington & Wilby, 2017).

2. Material

Careful photography of the holotype of *Beothukis mistakensis* (OUMNH ÁT.410p; Fig. 4a), and other published material, under controlled lighting, forms the main basis of this work. When the holotype of *Beothukis mistakensis* is retrodeformed with reference to the closest discs, the shape is notably more elongate than previous retrodeformations (cf. Narbonne *et al.* 2009, fig. 8.1; online Supplementary Fig. S1, available at http://journals.cambridge.org/geo), but the fundaments of the branching pattern remain broadly unchanged. Older field photographs were also studied in order to assess the possibility that some features have been lost to weathering, since the holotype was first exposed in 1990 by removal of the overlying crystal tuff (Seilacher, 1992; Matthews *et al.* 2017; online Supplementary Fig. S1).

3. Results

3.a. *Morphological analysis of the type material of* Beothukis mistakensis

The holotype of *B. mistakensis* is beautifully preserved, and suitable for more detailed study than has been previously attempted. Previous illustrations have been tightly cropped and overlook some morphological elements as a result.

3.a.1. Primary-order units and frond outline

Of all of the fronds in the Mistaken Point type assemblages, *Beothukis mistakensis* is commonly considered to have some of the most complex fractal-like rangeomorph morphology. The type description of *B. mistakensis* focused on aspects of the self-similar rangeomorph elements without consideration of how those elements are distributed throughout the fossil (Brasier & Antcliffe, 2009, fig. 17c). The holotype of *Beothukis* consists of two rows of primary-order rangeomorph elements (Fig. 5a). On each side of the fossil there are eight primary-order rangeomorph units (L1–8 and R1–8; Fig. 5b). L4–8 are bound on their distal margin by a row of units with rotated, furled rangeomorph primary-order units (RFU L1) and R6–8 abut against RFU R1–2 (see Section 3.a.3 below; Fig. 5c).

Determining which of the rangeomorph units are of primary order can be challenging in material that is composed of self-similar elements such as those that characterize *Beothukis*: units of different orders can appear to be similar. It is considered here that in the holotype of *Beothukis* all successive branches of the same order in a series have increasing angles relative to the axis (Fig. 5; i.e. radiating).

In the original diagnosis and type description, the authors grouped our R5–8 as a single primary-order rangeomorph unit (Brasier & Antcliffe, 2009; Fig. 5b). We disagree with the original interpretation because their amalgamated primary-order unit: (1) does not clearly show the changing angle of sub-units within it that is characteristic of all the other primary-order units; and (2) would have an additional order of branching that is not seen in any of the other primary-order rangeomorph units. A consequence of this difference in interpretation is that the inferred glide-plane symmetry between the two rows of the holotype (Brasier & Antcliffe, 2009) breaks down (Fig. 5a, b). This helps to distinguish *Beothukis* from taxa such as *Charnia* that has a

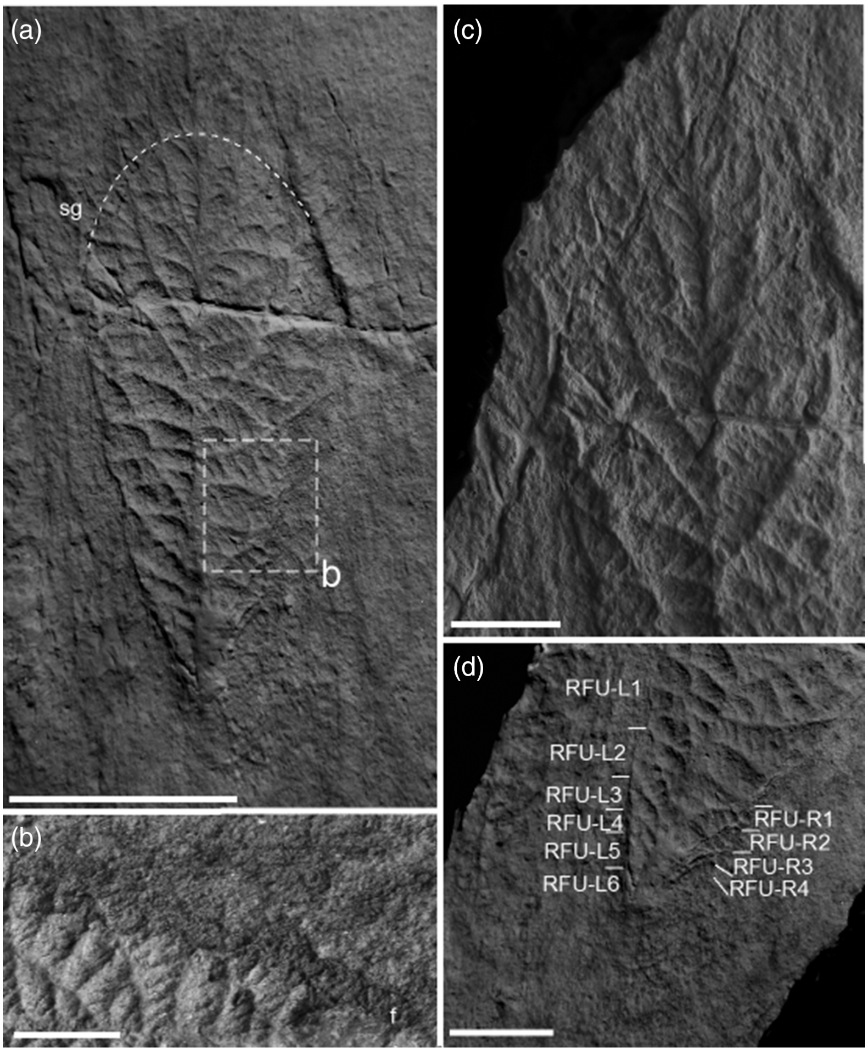

Fig. 4. Cast of the holotype of *Beothukis mistakensis* from the 'E Surface', Mistaken Point Ecological Reserve. (a) Complete holotype arc defines boundary between frond and zone of secondary growth (sg) in (c). (b) Fringe of secondary growth (f) at the margin of *Beothukis mistakensis* in a photograph of the holotype from around 2010 (courtesy of Liam Herringshaw). (c) Secondary growth at the tip of *Beothukis mistakensis* extending beyond what is normally considered to be margin of the spatulate frond. (d) Rotated, furled units (RFU) at the base of *Beothukis mistakensis* and the sharp proximal termination without evidence for a basal disc. Note the offset between the basal extent of the Rangeomorph units on each side of the centreline. Scale bars, 2 cm, except (a) which is 5 cm.

simple alternating succession of primary branches that creates the glide-plane symmetry (cf. Laflamme *et al.* 2007; Brasier *et al.* 2012; Dunn *et al.* 2018).

While the equivalent primary-order units on either side of the centreline, considered to be a concealed axis (*sensu* Brasier *et al.* 2012), are somewhat similar in shape (compare outlines of L1 versus R1, L2 versus R2, etc.) and there is a degree of overlap onto the previous unit, their size and orientation are markedly different due to differing amounts of inflation of the primary-order units on the left- and right-hand side (Fig. 5b). The angle between the centreline and the boundary between the primary-order rangeomorph units – as measured in a series from the tip of the frond towards the base – is acute near the tip, becoming progressively steeper in angle in successive units in a series (Fig. 5a).

3.a.2. Secondary-order rangeomorph units in the holotype

The number of secondary-order rangeomorph units within the primary-order units of the holotype of *Beothukis mistakensis* varies from 3 to 11, with the primary-order units L3 and R5 containing the most secondary-order rangeomorph units (Fig. 5). It is noted that both L3 and R5 are at the maximum width of the holotype on their respective sides (Fig. 5). In all cases, secondary-order rangeomorph units systematically increase in angle from the frond margin to those closest to the centreline (Fig. 5a). Near the frond margin, the secondary rangeomorph units meet the boundary between primary-order units at an acute angle (*c.* 20°), whereas close to the centreline the secondary rangeomorph units are typically nearly perpendicular to the centreline of the frond (Fig. 5a). Diagnoses of the genus have all considered that the secondary-order units occur in radiating sets (Brasier & Antcliffe, 2009; Narbonne *et al.* 2009; Brasier *et al.* 2012; Liu *et al.* 2016); however, this contradicts the inclusion of specimens formerly attributed to *Culmofrons* within the genus, as the secondary-order units in that genus are subparallel and not radiating (Laflamme *et al.* 2012). The secondary-order rangeomorph units that make up a primary-order rangeomorph unit may have their maximum length and width either near the centre of the unit or near the margin of the frond.

The morphology of the secondary-order rangeomorph units is dependent upon their position in a series, with three distinct settings. (1) The smallest three to five secondary-order rangeomorph units closest to the centreline of the *Beothukis* frond are typically coincident with it, and have their distal margin constrained by the adjacent primary-order rangeomorph unit. Such secondary-order units are rotated and furled (*sensu* Brasier *et al.* 2012; Fig. 5a). (2) Secondary-order units that are bound at their proximal and distal margins by the adjacent primary-order rangeomorph unit are commonly displayed and furled (Fig. 5b). (3) Rangeomorph units

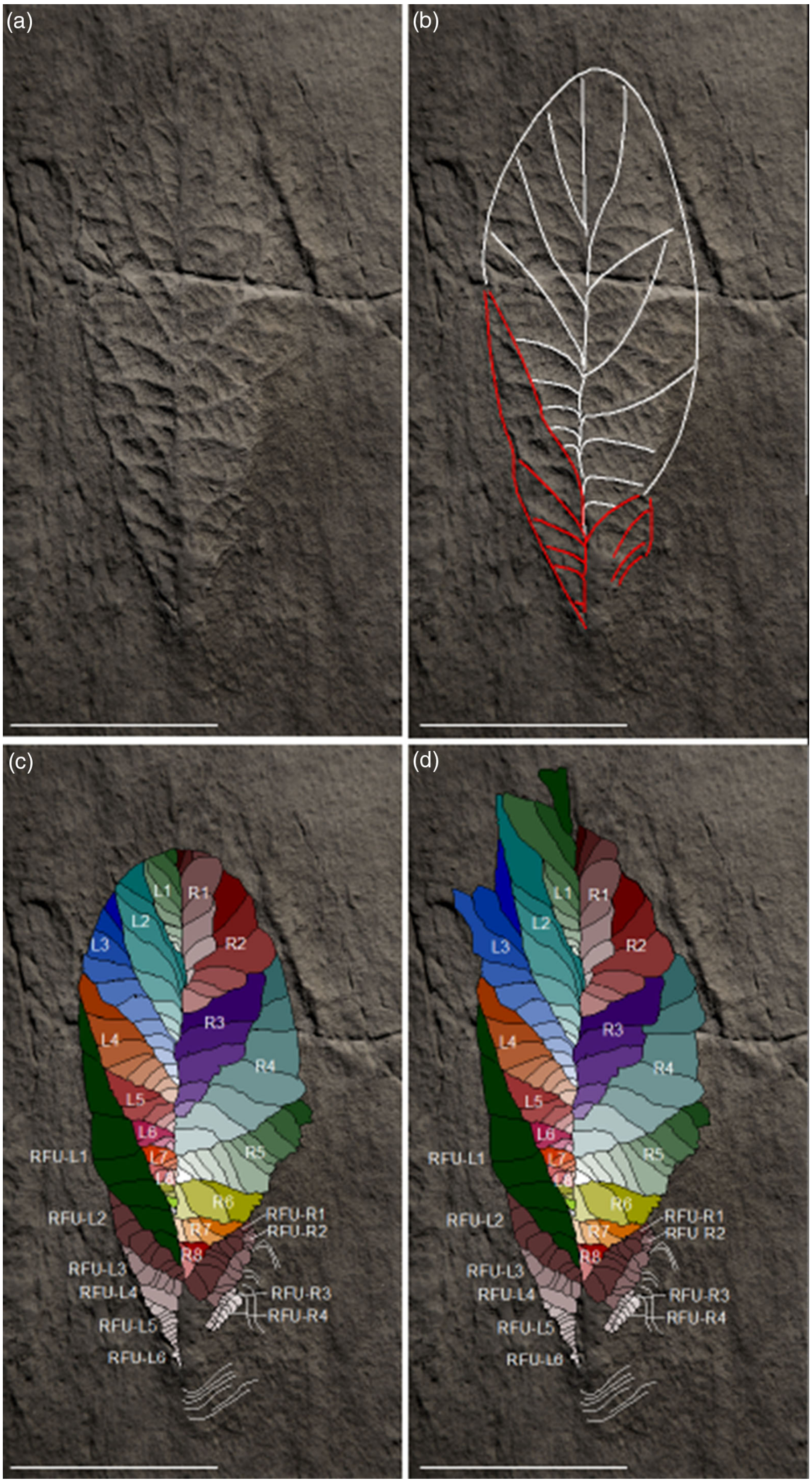

Fig. 5. Holotype of *Beothukis mistakensis.* (a) Cast of the holotype, carefully lit to show the maximum amount of morphological detail on the negative epirelief. (b) Holotype highlighting the margins of the primary-order rangeomorph units (white lines, excluding secondary growth at the tip, see (d)) and boundaries between rotated, furled primary-order units (red lines). (c) Interpretation showing the first-order units labelled L1–8 and R1–8; the second-order rangeomorph units within the first-order units are coloured to be progressively darker closer to the margin of the fossil. Tapering sets of rotated, furled primary-order rangeomorph units are present on each side of the basal region of the holotype (RFU L1–6 on the left and RFU R1–4 on the right; also Fig. 4d). (d) The holotype is prone to secondary growth from the tips of the first-order units (see L1–3, R1, R4; also Fig. 4c). Scale bars, 5 cm.

whose distal margin forms the outline of the *Beothukis* frond are variable in morphology, but are most commonly symmetrically displayed and furled. Secondary-order units with preservation beyond the 'normal' cuneate margin of the frond may also be unfurled (Fig. 5c), particularly in the paratype material.

3.a.3. Basal rotated, furled primary-order rangeomorph units

Tapering sets of progressively smaller primary-order units without clear rangeomorph architecture (cf. Jenkins, 1985; Brasier *et al.* 2012) are present on each side of the basal portion of the holotype of *Beothukis* (i.e. RFU L1–6 and RFU R1; Fig. 5c). It is unclear

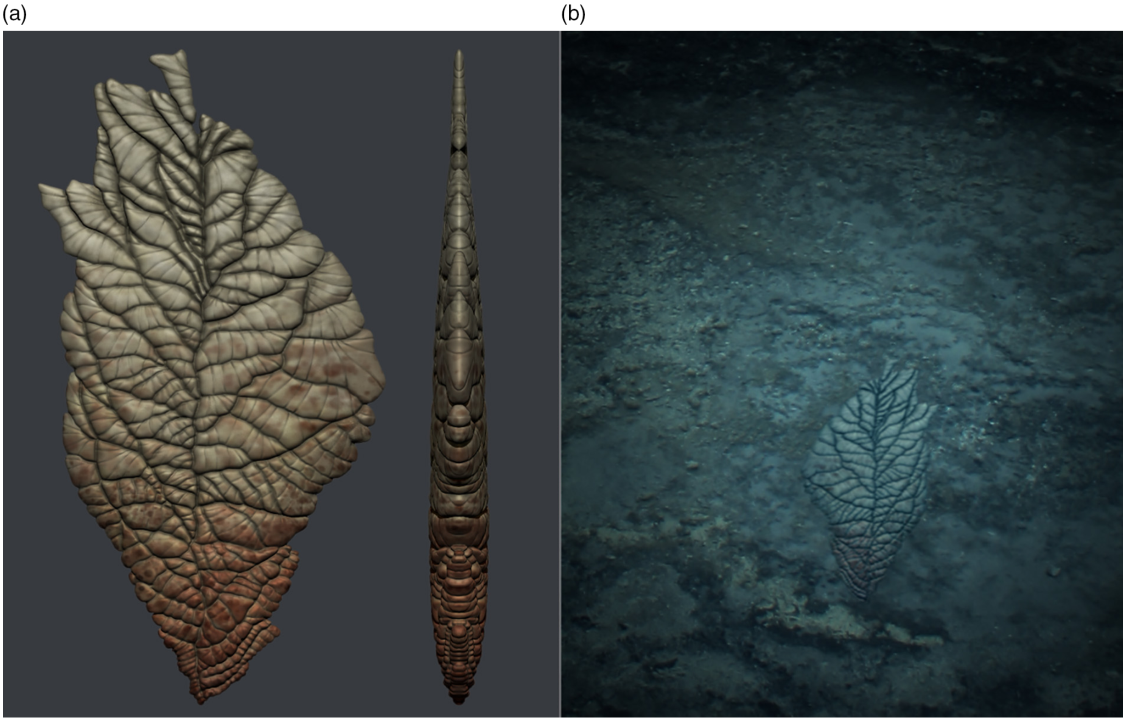

Fig. 6. (a) Surficial and (b) lateral reconstruction of *Beothukis mistakensis.* This reconstruction assumes symmetry between the upper and lower surfaces of *Beothukis mistakensis*. (b) Our reconstructed morphology of *Beothukis mistakensis* highlighting its sediment-reclining mode of life on a matground-dominated seafloor.

whether – in a more mature specimen – the component box-shaped (undivided) secondary-order rangeomorph units (*sensu* Brasier *et al.* 2012) might develop into the typical rangeomorph morphologies (displayed versus rotated, and unfurled versus furled; Brasier *et al.* 2012). Similar smooth second-order units have been proposed for *Hapsidophyllas* and *Charniodiscus* (possibly referring to *C. procerus*) by Brasier *et al.* (2012). The holotype of *B. mistakensis* is currently the only known specimen that shows such units at the base of a frond that has other more typical *Rangea*-like expressions (cf. Jenkins, 1985; Brasier *et al.* 2012). There is no indication of the likely presence of basal rotated, furled primary-order units in the material from Spaniard's Bay (Narbonne *et al.* 2009) or any other figured material of *Beothukis*. The basal region of the holotype of *Beothukis* is the most topographically high part of the fossil, but shows no evidence for the rotated and undivided primary-order units arising from a stem. The addition of these rotated, furled primary-order units to the outline of the holotype of *Beothukis mistakensis* changes the gross outline of the frond from spatulate to cuneate.

3.a.4. Secondary growth

While the outline of the type specimen of *Beothukis mistakensis* – as defined by the margins of the primary-order branches – is spatulate to cuneate, the tip and the basal portion of the frond are prone to the development of secondary growth. The tip of the type specimen was not figured in the type description (Brasier & Antcliffe, 2009), and is it not mentioned in the emended diagnosis (Brasier *et al.* 2012). Careful photography of the tip region (Fig. 4c) demonstrates that secondary growth was present around the fringe of the frond, including portions that are clearly displayed and unfurled.

The presence of secondary growth in the basal region is hinted at by the camera lucida drawings that accompany the type description (Brasier & Antcliffe, 2009, fig. 17b), but is not mentioned in the diagnosis. Photographs of the type specimen from around 2010 show the clear presence of a fringe of approximately heart-shaped elements adjacent to primary rangeomorph units R7–8 and RFU R1 (Fig. 4b, d).

3.a.5. Three-dimensional morphology of Beothukis *and other reclining rangeomorphs*

The Mistaken Point biota generally preserves only the lower surface of fronds and the upper surface of stems (e.g. Liu, 2016; but see Seilacher, 1992; Gehling & Narbonne, 2007). In our reconstruction of the morphology of *Beothukis* (Fig. 6), we are making the explicit assumption that the upper surface of reclining rangeomorph organisms was the same as the lower surface that is well preserved in the holotype. We are aware that need not be the case, and that the upper surface could have borne other tissues or even have been smooth, but we follow the current convention of assuming that the top is symmetrical with the lower surface for ease of illustration (Fig. 6) and to avoid needless conjecture.

3.b. Comparison of the holotype and paratypes of Beothukis

Superficially, the paratype material of *Beothukis* does not show close resemblance to the spatulate or cuneate holotype, being much more lanceolate without the same tightly constrained morphology, a greater abundance of displayed rangeomorph units and a very marked difference in the width of the two rows (Fig. 7). In the paratypes, the secondary-order rangeomorph units that are closest to the centreline show the displayed morphology, which is unlike the holotype. The more distal secondary-order rangeomorph units on the right-hand side of the paratype appear to be poorly organized, but clearly show the radiating pattern typical of the genus. We note that the paratypes are larger than the holotype (Figs 3, 7) and it is therefore possible that they show more unconstrained,

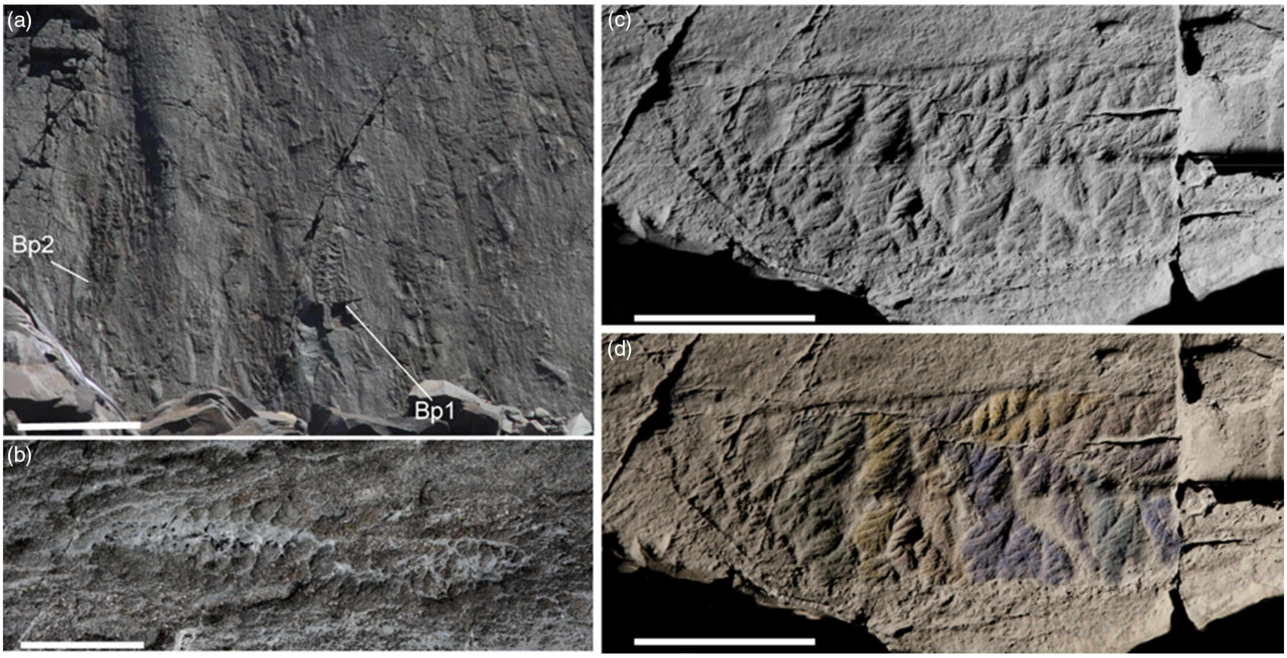

Fig. 7. Paratypes of *Beothukis mistakensis*. (a) Photograph of the 'E Surface' at Mistaken Point highlighting the locations of the *Beothukis mistakensis* paratypes (Bp1 and Bp2). (b) *Beothukis mistakensis* paratype 2. (c) *Beothukis mistakensis* paratype 1. (d) *Beothukis mistakensis* paratype 1, coloured to show primary branch structure. Note the eccentric, unconstrained distal growth, producing an erratic frond margin on the lower side of the image. Scale bars 5 cm, except (a) which is 20 cm.

eccentric growth during a senescent phase of their life cycle, giving them a more irregular outline and less-organized growth pattern, particularly the distal secondary-order branches that are unconstrained at the frond margin (Fig. 7b, c).

4. Discussion

4.a. Spaniard's Bay 'beothukids'

The description and diagnosis of *Beothukis* from Mistaken Point (Brasier & Antcliffe, 2009) shortly pre-dates the description of similar rangeomorphs from Spaniard's Bay (Narbonne *et al.* 2009). While it was originally suggested that the Spaniard's Bay assemblage was preserved within nodules (Narbonne, 2004), it has subsequently been determined that the fossils lie within obstacle scours and flute marks, probably caused by the action of currents around the stems of erect frondose organisms (Brasier *et al.* 2013). The deepest part of horseshoe-shaped obstacle scours is found on the up-current end due to undercutting by eddying (cf. Fig. 2b; Dzulynski & Walton, 1963; Dzulynski & Simpson, 1966; Sengupta, 1966). Similar erosional morphologies are found on the up-current end of some of the fossiliferous scours at Spaniard's Bay, including specimens attributed to *Beothukis mistakensis* (Fig. 2b). We therefore refute the assertion that the Spaniard's Bay material has associated basal discs and short stems, which had previously given the impression that there was a continuum between the type material of *Beothukis mistakensis* and other spatulate fronds with stems and discs (Liu *et al.* 2016). This is in agreement with Dececchi *et al.* (2018), who came to the same conclusion about the importance of the stem as a taxonomic character, although that study appears to accept the Spaniard's Bay material as *Beothukis*.

Some of the specimens identified as *Beothukis mistakensis* from Spaniard's Bay differ from the holotype in outline, being lanceolate rather than spatulate, and by having displayed secondary-order rangeomorph units that are not demonstrably radiating (Fig. 2c), which does not fit the diagnosis of the genus. That specimen also has a previously unfigured conical erosional structure (Fig. 2c) that lies up-current of the previously inferred spade-shaped holdfast (Narbonne *et al.* 2009, fig. 6.1), which is suggestive of both features being current-generated rather than being morphological characters.

Some of the more spatulate material attributed to *Beothukis mistakensis* from Spaniard's Bay shows alternate branching across the centreline of the frond, but has biserial primary-order branches and rather narrow, radiating uniserial secondary-order rangeomorph branches (Fig. 8). There are several such *Beothukis*-like forms from the same locality that show an en échelon stacking of clearly independent rangeomorph branches angled towards the base of the frond, along with a single specimen from Australia (Narbonne *et al.* 2009, figs 5, 6). This morphotype with its two rows of radiating rangeomorph fronds clearly had independent branches, which would imply that it is closer to *Avalofractus* than *Beothukis* although the material is in need of full taxonomic treatment. It is this morphotype that has been identified from the Rawnsley Quartzite in South Australia (Narbonne *et al.* 2009, fig. 8.6). It seems likely that the morphotype comprises a separate genus within the Rangida, or perhaps a separate species within *Avalofractus*. For the purpose of this work, it is sufficient to exclude it from *Beothukis* s.s.

The exclusion of the Spaniard's Bay *Beothukis*-like taxa from the stem length data for *Beothukis* and *Culmofrons* demonstrates that there is a clear distinction between the stemless *Beothukis mistakensis* and the long-stemmed *Culmofrons plumosa* (Fig. 3). Further exploration of the idea that stem length may be an ecophenotyphic character in *Culmofrons* (Liu *et al.* 2016) requires careful consideration on a bed-by-bed basis and a more robust sedimentological framework. We consider that the generic diagnosis of *Beothukis* can be emended to exclude reference to a stem and disc.

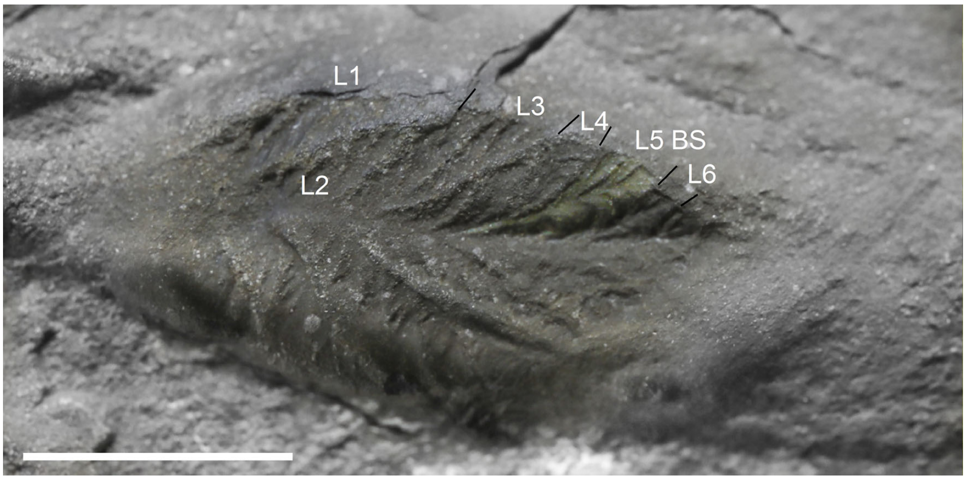

Fig. 8. Small specimen previously attributed to *Beothukis mistakensis* from Spaniard's Bay, excluded from the genus here. Note the presence of alternate branching across the frond centreline, with clear biserial (BS) primary-order branches on L6 (labelled following Narbonne *et al.* 2009) and the narrow, radiating uniserial secondary-order rangeomorph branches, some of which are also biserial (see L5). Note the marked erosion at the margins, particularly in the region of the frond tip. Scale bar, 1 cm.

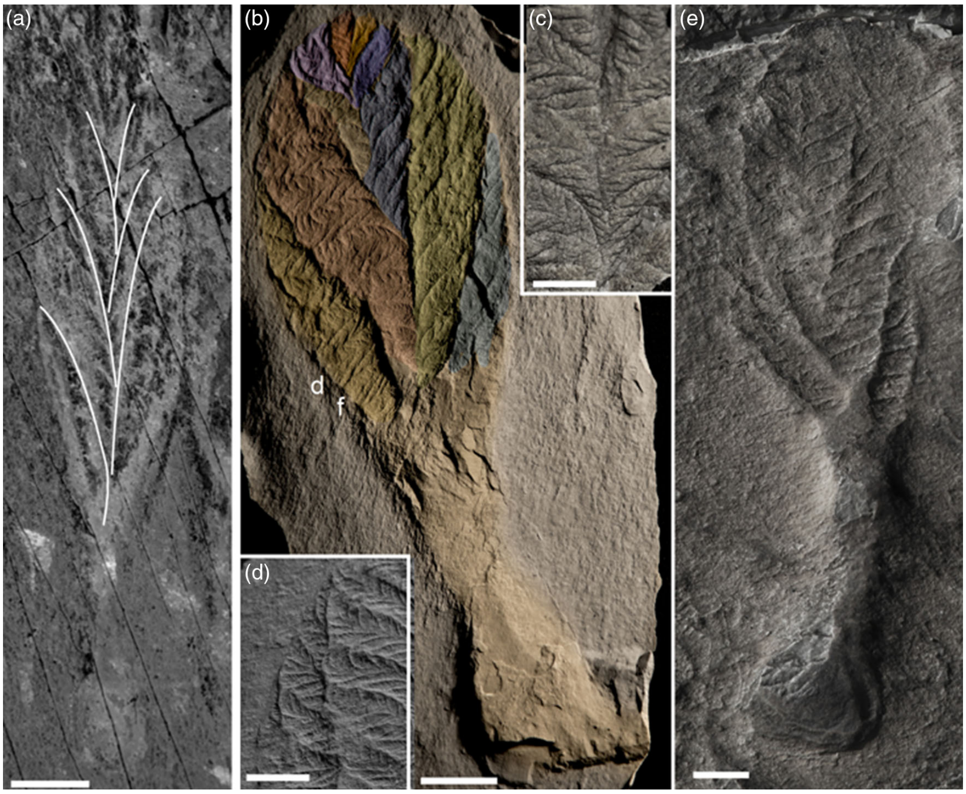

Fig. 9. *Culmofrons plumosa*. (a) Field photograph of *Culmofrons plumosa* holotype from Lower Mistaken Point, Mistaken Point Ecological Reserve, with alternating primary branches highlighted to emphasize the long-wavelength, low-amplitiude zigzagged medial axis. Scale bar, 5 cm. (b) Cast of *Culmofrons plumosa* from MUN surface, Catalina Dome, with primary branches artificially coloured to show the primary-order branching, revealing alternating branching including both displayed (labelled d) and proximal to the stem furled (labelled f) rangeomorph branching. Scale bar, 2 cm. (c) Close-up of secondary-order rangeomorph units close to the centreline of *Culmofrons plumosa* from MUN surface. Tertiary-order units within the secondary-order rangeomorph units are furled proximal to the centreline, but unfurled distally. Scale bar, 1 cm. (d) Close-up of the margin of *Culmofrons plumosa* from MUN surface, showing distally displayed second-order branch morphology not clearly seen in the type material. Scale bar, 1 cm. (e) Field photograph of *Culmofrons plumosa* from the MUN surface showing elongate subparallel second-order branches that appear to cross the boundaries between primary-order rangeomorph units and possible eccentric marginal growth extending beyond the frond margin on the right-hand side. Scale bar, 2 cm.

4.b. Comparison between Beothukis and the type material of Culmofrons

The type material of *Beothukis plumosa* (Laflamme *et al.* 2012) must be reconsidered as a result of the redescription of the holotype of *B. mistakensis* in Section 3.a above, and the exclusion of the forms previously interpreted to be *Beothukis mistakensis* with short stems and discs (Narbonne *et al.* 2009; Brasier *et al.* 2012; Liu *et al.* 2016).

4.b.1. Primary-order rangeomorph units

The primary-order rangeomorph branches of *Beothukis plumosa* (Laflamme *et al.* 2012) are alternate, describing the long-wavelength zigzagged axis to the frond (Laflamme *et al.* 2012; Fig. 9a, b). There are up to five primary-order branches in each of the two rows (Laflamme *et al.* 2012; Fig. 9a, b). The largest primary-order rangeomorph branches in *plumosa* are close to the frond–stem junction (Fig. 9a). These features are clearly different from the architecture of the holotype of *B. mistakensis*, which has a straight to slightly zigzagged axis, along which the primary-order rangeomorph units are arranged in a non-alternating manner (Fig. 5b, c). It is difficult to be sure of homologies between *Culmofrons* and *Beothukis* because of differences in their gross morphology. It could be argued that either the (up to) five primary-order units of *Culmofrons* are homologous with: (1) the more numerous primary-order rangeomorph units identified in the holotype here (i.e. L1–8 and R1–8; Fig. 5b, c); and (2) the two rows of rangeomorph elements in the holotype of *Beothukis* *mistakensis* (i.e. a single primary rangeomorph unit of *Culmofrons* would be equivalent to a complete row of rangeomorph units in *Beothukis*).

It is difficult to reconcile how the tightly constrained rangeomorph units that characterize *Beothukis mistakensis* might be modified during biostratinomy to create the distinctive strongly zigzagged axis diagnostic of *Culmofrons* (Laflamme *et al.* 2012; Fig. 9b); we therefore retain it as a useful diagnostic character to distinguish between *Beothukis* and *Culmofrons*.

4.b.2. Secondary-order rangeomorph units

The secondary-order 'branches' of *B. plumosa* (Laflamme *et al.* 2012) are numerous (8–12 in a series), subparallel to one another, subrectangular to trapezoidal in outline, and the largest in a series are either medial or distal (Fig. 9a, b). This contrasts with *Beothukis*, in which the largest secondary-order units are usually medial. Preservation in the type material of *plumosa* is comparatively poor at fine levels of detail, but many of the secondary-order branches would appear to be rotated and furled (Fig. 9a); the well-preserved MUN surface material (Liu *et al.* 2016) shows proximally furled and distally displayed second-order morphology (Fig. 9b, c). The *Culmofrons* from the MUN Surface locality near Port Union (Hofmann *et al.* 2008; Fig. 9d) have relatively well-preserved second-order morphology that appears to be predominantly furled, with some eccentric or 'overcompensatory' growth (Fig. 9d; cf. Kenchington *et al.* 2018). Within the limitations imposed by the relatively low-relief preservation of the type material of *plumosa*, it seems that there are significant differences in the shape, size and distribution of secondary-order rangeomorph units between *Beothukis mistakensis* and *plumosa*. Additionally, no specimens of the species *plumosa* have been found without a stem and disk.

4.b.3. Significance of morphological differences between B. mistakensis *and* B. plumosa *(Laflamme* et al. *2012)*

There are a sufficient number of differences in the morphology and architecture of *Beothukis mistakensis* and the type material of *B. plumosa* (Laflamme *et al.* 2012) to determine that the two species are not congeneric. (1) The regular alternation of primary-order units of *plumosa*, which produces the strongly zigzagged axis, is fundamentally different to the asymmetrical distribution of primary-order rangeomorph units along the straight centreline of *B. mistakensis*. (2) Notwithstanding considerations of homology discussed in Section 4.b.1 above, there are comparatively few primary-order rangeomorph units in each row of *plumosa* (five), and the primary-order units uniformly increase in length towards the stem and disc (suggesting a distal growth tip). That is unlike the more numerous rangeomorph branches per row in the type material of *mistakensis*. (3) There is no indication of rotated, furled primary-order rangeomorph units at the base of the frondose portion of *plumosa* as there is in the type material of *B. mistakensis*. (4) The secondary-order branches in the type material of *plumosa* are more commonly subparallel than radiating, and many are rotated and/or furled in the type material, but in other material (e.g. Liu *et al.* 2016; Fig. 9a, b, e) they are commonly displayed and furled. (5) The fronds of the species *plumosa* are oval in outline, in contrast to the cuneate holotype of *B. mistakensis*. (6) All specimens of *plumosa* have a stem and disc (Laflamme *et al.* 2012; Dececchi *et al.* 2018), whereas no authenticated *mistakensis* have either (accepting that the Spaniard's Bay material is not attributable to *Beothukis*).

Notwithstanding differences in opinion regarding what should be considered to be genus- and species-level traits within the Rangeomorpha (Liu *et al.* 2016; Kenchington & Wilby, 2017), it is clear that the species *mistakensis* and *plumosa* are not closely related in terms of their morphology, architecture or growth. It is therefore considered that *plumosa* should be excluded from the genus *Beothukis*. The status of *Culmofrons* as a valid genus, that is, distinct from *Beothukis* (Laflamme *et al.* 2012), would appear to be justified at present and it should no longer be considered a junior synonym of *Beothukis*. The conclusion that stem length in *Culmofrons plumosa* may be an ecophenotypic character (Liu *et al.* 2016) remains to be tested through careful integration of sedimentology and morphological variability on a bed-by-bed basis. Since rangeomorph architecture finer than second order is conventionally considered to be of species-level taxonomic significance (cf. Liu *et al.* 2016), we do not currently distinguish between the displayed and undisplayed specimens of the genus *Culmofrons*.

4.c. Systematic palaeontology

4.c.1. Phylum Petalonamae Pflüg, 1972

Class. Rangeomorpha Pflüg, 1972
Order. Charnida Narbonne *et al.* 2009
Family. Charniidae Glaessner, 1979
Genus. *Beothukis* Brasier & Antcliffe 2009

Emended diagnosis. Unipolar spatulate to cuneate rangeomorph without visible stem and no basal disc, comprising two rows of undisplayed, radiating, uniserial primary-order rangeomorph units with medial inflation, arranged in a non-alternate manner across the weakly zigzagged centreline. Primary-order rangeomorph units comprise radiating uniserial secondary-order rangeomorph units with medial to distal inflation. Secondary-order rangeomorph units, that both abut against the axis and are constrained distally by an adjacent primary-order rangeomorph unit, are typically rotated and furled. Secondary-order rangeomorph units adjacent to the axis are typically displayed and furled, or may be displayed and unfurled where they extend beyond the – otherwise regular and smooth – frond margin. The narrow end of the frond may have radiating rows of primary-order box-like units without evidence of typical rangemomorph branching characteristics.

Species *Beothukis mistakensis* Brasier & Antcliffe, 2009
1992 'Flat recliner' Seilacher, pp. 608–9, figs 1–2 (*partim*).
1992 'Flat recliner' Seilacher, p. 609, fig. 3 (*partim*).
1999 'Other form' Seilacher, p. 98, fig. 3 (*partim*).
2004 Laflamme *et al.* p. 830, fig. 3.1 (*partim*).
[non] 2004 'Short stemmed rangeomorph frond' Narbonne p. 1143, fig. 3B-C.
2008 'Spatulate rangeomorph' Laflamme & Narbonne, p. 170, fig. 4.6–7.
2009 *Beothukis mistakensis* Brasier & Antcliffe pp. 383–3, fig. 17a–b; fig. 18a–b.
2009 *Beothukis mistakensis* Narbonne *et al.* pp. 507–15, fig. 8.1, 8.2, 8.4, 8.5.
[non] 2009 *Beothukis mistakensis* Narbonne *et al.* fig. 6–7, 8.3, 8.6.
[non] 2012 *Beothukis mistakensis* Dornbos *et al.* p. 58, fig. 5.2c.
2012 *Beothukis mistakensis* Brasier *et al.* p. 1116, fig. 5C–D.
2013 *Beothukis* Darroch *et al.* p. 596, fig. 2B.
2013 *Beothukis mistakensis* Laflamme *et al.* p. 562, fig. 2.2
[non] 2013 *Beothukis mistakensis* Laflamme *et al.* p. 562, fig. 2.1, 2.3, 2.4.
[?] 2013 *Beothukis* Macdonald *et al.* p. 257, fig. 6C.
2014 *Beothukis mistakensis* Hoyal Cuthill & Conway Morris p. 13 123, fig. 1.
2014 *Beothukis* Ghisalberti *et al.* p. 2, fig. 1e (*partim*).

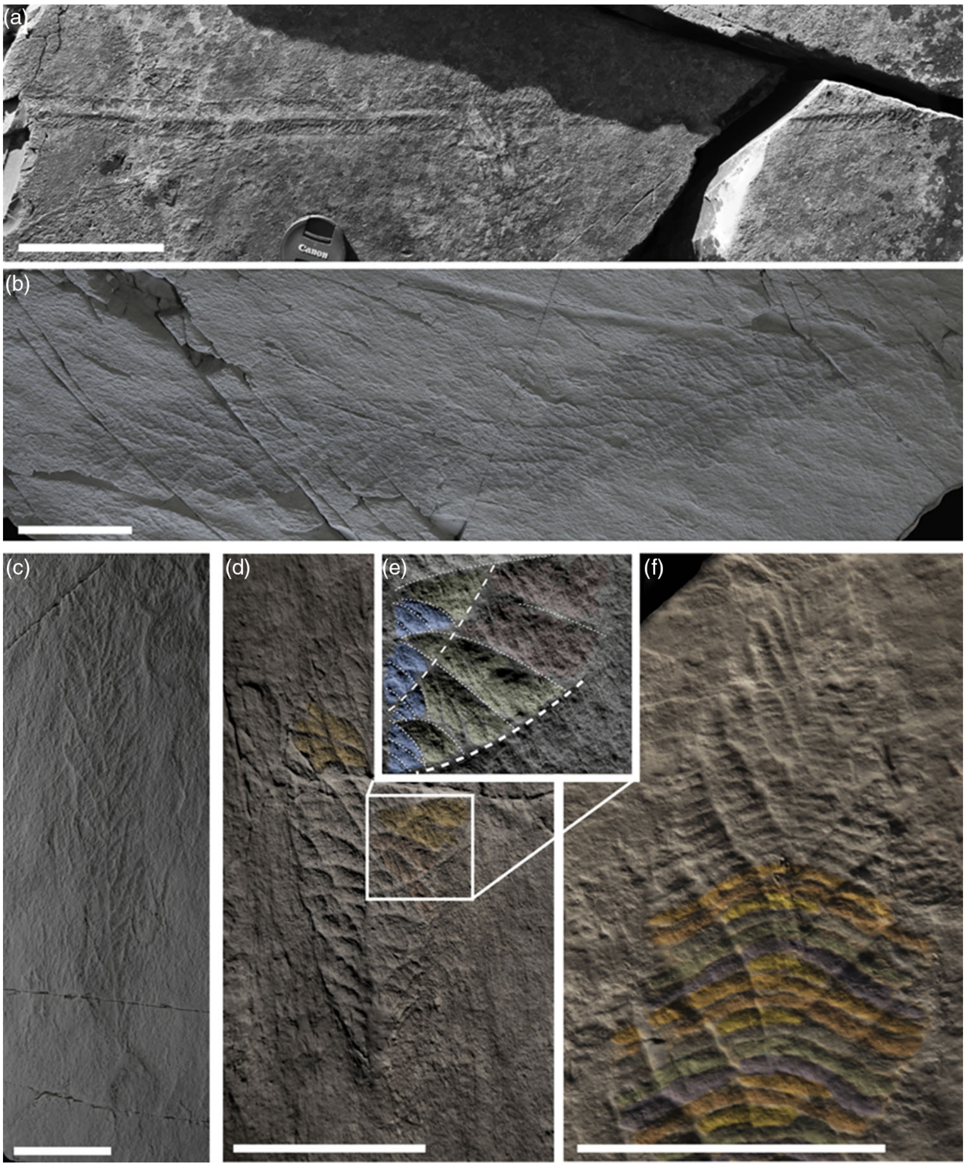

Fig. 10. Elongate and filiform rangeomorphs all with tightly constrained uniserial primary-order rangeomorph units (cf. the Charnida of Narbonne *et al.* 2009). (a) Field photograph of *Trepassia wardae* from the Drook Formation (MPER) showing radiating secondary-order rangeomorph units comparable to those of *Beothukis*. (b) Cast of an undescribed *Beothukis*- or *Trepassia*-like frond from Bonavista showing radiating secondary-order rangeomorph units. (c) Cast of *Vinlandia antecedens* from the Bonavista Peninsula showing tightly constrained, radiating, secondary-order rangeomorph units. (d) Cast of the holotype of *Beothukis mistakensis* artificially coloured to highlight evidence for arcs of secondary-order rangeomorph that cross both the boundaries between primary-order rangeomorph units. (e) Expanded portion of the holotype in *Beothukis* (boxed in (d)) showing three types of secondary-order rangeomorph units (Type 1, blue; Type 2, green; Type 3, purple; see text) separated by thin dashed lines that can be seen to cross the boundary between two primary-order units (heavier dashed line). (f) Cast of the holotype of *Charnia masoni* artificially coloured to highlight evidence for arcs of secondary-order rangeomorph that cross both the centreline and the boundaries between primary-order rangeomorph units. Scale bars 5 cm, except (a) which is 20 cm.

[?] 2014 *Beothukis* cf. *Beothukis mistakensis* Narbonne *et al.* p. 215, fig. 6.
2015 *Beothukis* Zalasiewicz & Williams p. 144, fig. 13.
2015 *Beothukis* Liu *et al.* p. 1361, fig. 2B.
2015 *Beothukis* Burzynski & Narbonne, p. 37, fig. 4 A (*partim*).
[non] 2015 *Beothukis* Burzynski & Narbonne, fig. 5B (*partim*).
2016 *Beothukis mistakensis*, Liu *et al.* p. 9–10, fig. 4 A.
2019 *Beothukis mistakensis*, Matthews & McIlroy p. 2, fig. 2 (*partim*).
2017 *Beothukis mistakensis*, Matthews *et al.* p. 2, fig. 2c (*partim*).

Remarks. Previous works have assigned most foliose rangeomorphs with radiating displayed secondary-order 'branches' to *Beothukis* (Brasier & Antcliffe 2009; Narbonne *et al.* 2009; Brasier *et al.* 2012; Liu *et al.* 2016). In doing so, there is the implicit assumption that branching characters are of greater taxonomic importance than the presence or absence of major organs such as the basal disc and stem (Kenchington & Wilby, 2017). Here, we restrict the genus *Beothukis* to rangeomorphs with uniserial primary- and secondary-order branching – comparable to the Charnida of Narbonne *et al.* (2009) – and do consider the absence of a stem and disc to be of taxonomic importance (*contra* Liu *et al.* 2016). Superficially, *Beothukis*-like specimens with radiating, biserial, primary- and secondary-order rangeomorph (true) branches (e.g. Fig. 2b) should be considered to belong to the Rangida, probably within the genus *Avalofractus* of Narbonne *et al.* (2009). Material with uniserial primary- and secondary-order rangeomorph units, attached to a stem and basal disc, should be retained within the Charnida, specifically the genus *Culmofrons* since there is no demonstrable continuum of stem length between *Beothukis* and *Culmofrons* (Fig. 3; Dececchi *et al.* 2018).

Other elongate or filiform uniserial rangeomorphs with radiating primary- and secondary-order rangeomorph units that would seem to be taxonomically closer to *Beothukis* than *Charnia* include: *Trepassia* (Narbonne & Gehling, 2003; Narbonne *et al.* 2009; Fig. 10a), *Vinlandia* (Laflamme *et al.* 2007; Hofmann *et al.* 2008; Brasier & Antcliffe, 2009; Fig. 10b) and a recently documented un-named *Trepassia*-like frond (Liu & Dunn, 2020; Fig. 10c). None of the well-preserved mature specimens of these taxa have a well-developed stem or basal disc (Fig. 10a–c, e). The recent redescription of the holotype of *Charnia masoni* and

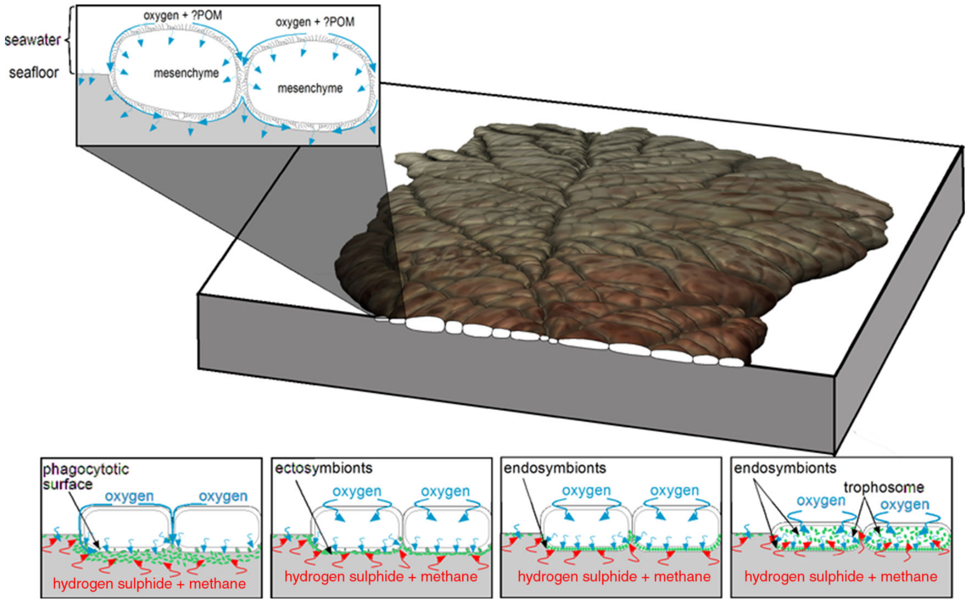

Fig. 11. Diagrammatic reconstruction of cross-section through *Beothukis mistakensis* showing the means by which the organism might have interacted with the underlying substrate, and its impact on the microbiotic productivity at the organism–sediment interface (based on Dufour & McIlroy, 2017). The localized redox gradient is likely to have stimulated microbial productivity, possibly part of a simple ectosymbiosis or endosymbiosis if the organism was capable of phagocytosing microbes on its lower surface.

other material from the type locality (Antcliffe & Brasier, 2008; Brasier & Antcliffe, 2009; Dunn *et al.* 2018) emphasizes the idea that *Charnia* is a rangeomorph with uniserial primary- and secondary-order rangeomorph units that are all rotated and furled (Jenkins, 1985; Brasier *et al.* 2012; Fig. 10d); however, even in large – presumably super-mature – '*Charnia grandis*' specimens they are never displayed.

4.c.2. Phylum Petalonamae Pflüg, 1972

Class. Rangeomorpha Pflüg, 1972
Order. Charnida Narbonne *et al.* 2009
Genus. *Culmofrons* Laflamme *et al.* 2012
Emended diagnosis. Unipolar ovate to obovate frond with stem and basal disc, comprising two rows of up to five undisplayed, radiating, uniserial primary-order rangeomorph units with medial to proximal inflation, arranged alternately across a strongly zigzagged axis. Primary-order rangeomorph units comprise subparallel to slightly radiating secondary-order rangeomorph units with medial to distal inflation that may be undisplayed or displayed.
Species *Culmofrons plumosa* Laflamme *et al.* 2012
2007 'Frond' Laflamme *et al.* p. 249, fig. 6d–e.
2012 *Beothukis* sp. Brasier *et al.* p. 1120, fig. 8b.
2012 *Culmofrons plumosa* gen et sp. nov. Laflamme *et al.* p. 196, figs 2.1–2.4.
[non] 2012 *Culmofrons plumosa* Laflamme *et al.* p. 196, figs 2.5–2.7.
2014 *Culmofrons* Kenchington & Wilby p. 105, fig. 2a.
2015 *Culmofrons plumosa* Liu *et al.* p. 1361, fig. 2e.
2016 *Beothukis plumosa* comb. nov. Liu *et al.* pp. 9–10, figs 2a, 4b–d.
Remarks. The re-establishment of *Culmofrons* as a valid genus is based upon reassessment of forms initially described as *Beothukis* (Narbonne *et al.* 2009) that appeared to bridge a gap between *Beothukis* and *Culmofrons* by having short, broad stems absent from the type material of *Beothukis*. That material is considered to belong to the Rangida rather than the Charnida, and additionally the stems and discs are considered to be erosional artefacts rather than real morphological features. The absence of a continuum of stem lengths between *Beothukis* and *Culmofrons*, along with the absence of specimens of stemless *Culmofrons plumose*, supports their separation into two genera within the Charnida of Narbonne *et al.* (2009), which encompasses taxa with uniserial secondary-order rangeomorph units.

Our field and laboratory observations of the type material of *Culmofrons* show that it is dominated by undisplayed secondary-order rangeomorph branching (Figs 2d, 9a). The material from the MUN surface of the Bonavista Peninsula (Liu *et al.* 2016) shows a continuum between displayed rangeomorph units near the tip of obovate forms that become progressively undisplayed towards the stem (Fig. 9b). This suggests that secondary-order rangeomorph units change in morphology through ontogeny, and are not a reliable taxonomic character (cf. Liu *et al.* 2016).

4.d. Palaeobiological implications

The basic building blocks of the Rangeomorpha (Pflüg, 1972; Narbonne, 2004; Brasier & Antcliffe, 2004; Brasier *et al.* 2012) are considered to be comparable in form to the gross-scale form of the eponymous *Rangea* (Pflüg, 1970), arranged in different combinations of scales and in a range of orientations to create a diverse morphogroup. The strongly three-dimensional nature of *Rangea* includes three orders of self-similar branches (Grazhdankin & Seilacher, 2005) and has been considered through detailed analysis of exceptionally preserved three-dimensional specimens to be multi-vaned (Dzik, 2002). Each vane comprised bilaminar sheets of frond-shaped elements, with the number of vanes now being demonstrated to be six (Vickers-Rich *et al.* 2013; Sharp *et al.* 2017). However, there do remain a number of important unresolved or poorly constrained gaps in our understanding of the palaeobiology of the Rangeomorpha.

4.d.1. Are rangeomorph fronds composed of truly fractal branches?

The architecture of the taxa now grouped under the Rangeomorpha has been a significant challenge to Ediacaran palaeontologists for many years (e.g. Narbonne, 2005; Gehling & Narbonne, 2007; Brasier & Antcliffe, 2009; Narbonne *et al.* 2009; Laflamme *et al.* 2012; Brasier *et al.* 2012). The model that the complex rangeomorphs of the deep-water palaeoenvironments of Avalonia were built of at least three orders of *Rangea*-like units in a range of orientations – which controls their appearance on bedding planes (Jenkins, 1985; Brasier & Antcliffe, 2009; Narbonne *et al.* 2009; Brasier *et al.* 2012) – has been highly influential and is the principle paradigm used in interpreting their morphology and palaeobiology.

The lineations that demarcate the boundary between primary-order rangeomorph units have been called primary-order branch axes, and it has been considered that they are the locus of secondary-order 'branch' growth (Dunn *et al.* 2018). It has been proposed that, in some taxa (e.g. *Charnia*), the secondary- and tertiary–order 'branches' were free to move relative to the point at which they are tethered to the primary-order branch axis (Brasier *et al.* 2013; Dunn *et al.* 2018). This concept has been extrapolated to suggest that the modelled surface area of four orders of fractal branches might be sufficient to support an osmotrophic mode of feeding (Laflamme *et al.* 2009; Hoyal Cuthill & Conway Morris, 2014).

Contrary to the model of fully independent rangeomorph elements at all orders within the organism, the secondary-order rangeomorph units of *Beothukis* cross from one primary-order rangeomorph unit to the next (Fig. 10e), in the same way that the arcs of secondary-order rangeomorph units in *Charnia masoni* (Fig. 10d) cross the boundaries between primary-order branches. From this we infer that the secondary- and higher-order branches were not fully independent of one another, but were instead connected and closely juxtaposed. The lateral connectivity of the secondary-order branches, and the fact that units cross from one primary-order rangeomorph unit to another, opens up the possibility that the fronds of the Charnida may have grown from the tip towards the base (cf. Antcliffe & Brasier, 2008). The proposed mode of growth is consistent with variations on the quilted 'pneu construction' (Seilacher, 1989, 1992; Seilacher *et al.* 2003; Buss & Seilacher, 1994), and the conjugate branch margins of *Beothukis* noted by Brasier & Antcliffe (2009). This is at odds with the highly fractal and more independently branched plant or pennatulacean-like rangeomorph models of the Charnida (Narbonne *et al.* 2009; Hoyal Cuthill & Conway Morris, 2014). That is not to say that all rangeomorphs conform to this more rigid interconnected morphotype. It is clear that some of the Rangida, especially biserial forms, such as *Avalofractus* (Narbonne *et al.* 2009) and *Fractofusus* (Gehling & Narbonne, 2007), have clearly separated primary-order rangeomorph branches that were probably free from one another.

It seems unlikely that the tertiary-order rangeomorph units of *Beothukis* were three-dimensional independent tube-like branches, but are much more likely to simply constitute epithelial morphology. The rangeomorph morphology of the epithelium might therefore be an adaptation to increase the surface area of the *Beothukis* frond. While the increased surface area created by epithelial folds is significant, the surface area to volume ratio is not close to that of a truly three-dimensionally branching fractal frond (cf. Narbonne *et al.* 2009; Laflamme *et al.* 2009; Hoyal Cuthill & Conway Morris, 2014). Surface features, rather than constructional elements, are considered to be of low taxonomic importance (species-level) in many phyla. There is considerable potential for the surface texture to be generated in response to physical and chemical phenomena at the epithelium of *Beothukis* and potentially other rangeomorph organisms (cf. the tertiary-order rangeomorph units of *Charnia*; Dunn *et al.* 2018), as has been recently suggested for *Fractofusus* (Dufour & McIlroy, 2017, 2018).

4.d.2. *Was* Beothukis *an erect frond or a recliner?*

Most of the frond-like rangeomorph Ediacaran organisms from the deep-marine Avalon assemblage are currently accepted to have had an erect mode of life (e.g. Clapham *et al.* 2003; Narbonne, 2005; Mitchell & Kenchington, 2018; Kenchington *et al.* 2018). These fronds are inferred to have had a basal attachment to a microbe-rich substrate (e.g. a holdfast or holdfast disc; mat-stickers *sensu* Seilacher, 1999), many – but not all – of which are considered to have a stalk that held the frondose portion above the sediment–water interface (e.g. Jenkins, 1992; Seilacher, 1992; Laflamme *et al.* 2012; Liu *et al.* 2015, 2016; Dunn *et al.* 2018). The generally accepted exception to this mode of life among the Mistaken Point biota is the abundant frond *Fractofusus*, which is inferred to be a recliner as evidenced by the lack of a disc and stalk as well as the absence of current orientation (e.g. Seilacher, 1992; Gehling & Narbonne, 2007).

The lack of current orientation of the holotype of *Beothukis* in assemblages such as the E Surface of Mistaken Point provides strong evidence against an erect mode of life (e.g. Seilacher, 1992). In an erect mode of life, the spatulate to cuneate shape of *Beothukis* would have provided a large surface area and be likely to have been re-orientated by the sediment-laden current, but would also be expected to occasionally produce *Kullingia*-type scratch circles (cf. Jensen *et al.* 2018). The quality of preservation of the type material of *Beothukis* on the E surface is comparable only to that of the reclining taxon *Fractofusus*, in which the negative epirelief is inferred to be a cast of the lower surface that grew along and into the seafloor, below the ambient microbial mat (Seilacher, 1999; Gehling & Narbonne, 2007; Dufour & McIlroy, 2017, 2018). The negative epirelief preservation of *Beothukis* is also consistent with it being the cast of the lower surface of a reclining organism (cf. Seilacher, 1992; Fig. 6).

4.d.3. *What is the purpose of the high-order self-similar units?*

The highly divided, fractal-like, three-dimensionally branched model of *Beothukis* growth (e.g. Hoyal Cuthill & Conway Morris, 2014) has been used to support the inference of an erect osmotrophic mode of life for *Beothukis* and other rangeomorphs (Laflamme *et al.* 2009; Hoyal Cuthill & Conway Morris, 2014). Our reconsideration of *Beothukis* as a reclining frond with closely bound primary- and secondary-order rangeomorph units – rather than true fractal branching – is consistent with the phagocytotic and/or chemosymbiotic mode of life inferred for *Fractofusus*, another reclining taxon in the Mistaken Point assemblage (Dufour & McIlroy, 2017, 2018). If that mode of life were extended to *Beothukis*, the three orders of invaginations on the lower surface could then have been used as a surface for the exchange of oxygen with the underlying sediment, restricting the build-up of hydrogen sulphide (which otherwise would kill the cells on the lower surface), simultaneously creating an ideal sub-organism micro-environment for the growth of sulphur-oxidizing bacteria (Fig. 11). The enhanced microbial productivity at the organism–sediment boundary is likely to be consumed by phagocytosis across the epithelial membrane, as part of an ectosymbiotic relationship between the rangeomorph and sulphur-oxidizing bacteria (Dufour & McIlroy, 2017, 2018). This increased microbial activity may also, incidentally, increase the preservation potential of high orders of rangeomorph units in the reclining rangeomorphs by biological or authigenic stabilization of the sub-organism surface, although that assertion would need to be biogeochemically tested – using stable sulphur isotopes – should appropriately preserved material be discovered.

The systematically variable tertiary-order surface morphology of the lower surface of *Beothukis* has the highest surface area (displayed) secondary-order rangeomorph units closest to the margin, and the smaller, low-surface-area secondary-order rangeomorph units closest to the axis. We speculate that this variability in morphology might be an adaptation to reduce the surface area of the most central part of the frond (i.e. 'rotated-furled'-type rangeomorph surface morphology, *sensu* Brasier *et al.* 2012), whereas closer to the margin of the frond, the high-surface-area 'displayed-unfurled' rangeomorph morphologies are the norm. It also seems illogical for an erect organism with an osmotrophic or suspension-feeding lifestyle to have anything except a displayed-unfurled branch morphology. Furling would reduce feeding efficiency due to the decreased surface area to volume ratio; as such, future studies might consider that *Charnia* could also have been a *Beothukis*-like recliner. Reduction of rangeomorph surface area by furling might be an adaptation to reduce exposure to microbial hydrogen sulphide build-up. By decreasing the epithelial surface area, the amount of oxygen needed to prevent sulphide toxicity – which would otherwise cause cell death – is decreased. Oxygen could have been transported to the organism–sediment interface by either cilial irrigation or diffusion through the mesoglea or mesenchyme (Dufour & McIlroy, 2017; Fig. 11).

5. Conclusions

Through careful study of the type material of *Beothukis mistakensis* and *B. plumosa* (Laflamme *et al.* 2012), we have concluded that the two species are not congeneric, and that *Culmofrons plumosa* should instead remain valid. We do however agree with the recent assertion that the morphology of secondary- and higher-order rangeomorph units is probably inappropriate for use as a genus-level taxonomic trait within the rangeomorphs of the Avalon Assemblage (Liu *et al.* 2016; Dunn *et al.* 2018). The key observation that tertiary-order rangeomorph architecture in *Beothukis mistakensis* is not in the form of three-dimensional branching calls into question the surface area estimates that underpin the inference of an osmotrophic mode of life for the erect Rangeomorpha (e.g. Laflamme *et al.* 2009; Hoyal Cuthill & Conway Morris, 2014).

The discovery that the second-order branches cross the boundaries between primary-order rangeomorph units is important in that it strongly suggests that *Beothukis* grew from the tip towards the base. That mode of growth might also explain the – centreline crossing – arcs of secondary rangeomorph units in *Charnia*. The resultant architecture of the Charnida (Narbonne *et al.* 2009) is much more inflexible and much less pennatulacean-like in nature than previously considered, consistent with the rarity of non-idiomorphic specimens.

With our reassessment of the stems and discs of the Spaniard's Bay material previously attributed to *Beothukis mistakensis* as being erosional artefacts, there is no positive evidence that *Beothukis mistakensis* had an erect mode of life. However, there is evidence to support a reclining mode of life comparable to that of *Fractofusus* (Seilacher, 1992; Gehling & Narbonne, 2007; Dufour & McIlroy, 2017, 2018). These reinterpretations of the mode of life and classification of *Beothukis* and *Culmofrons* have knock-on implications for statistically based ecological, spatial and tiering analyses (e.g. Clapham *et al.* 2003; Clapham, 2011; Mitchell *et al.* 2015, 2018; Mitchell & Butterfield, 2018; Mitchell & Kenchington, 2018) that are beyond the scope of this paper. The likelihood of some frondose taxa being recliners rather than having an erect pennatulacean-like mode of life (cf. Glaessner, 1984) requires that the null hypothesis for interpreting Ediacaran fronds (and other taxa) must be that they lay on the seafloor, as we see them preserved in the field, until it is proven otherwise.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0016756820000941

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Conflict of interest. None.

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