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A critical reappraisal of the holotype of *Beothukis mistakensis*, a unique exceptionally preserved rangeomorph organism from Mistaken Point, Newfoundland, Canada

Reevaluación crítica del holotipo de Beothukis mistakensis, único organismo rangeomorfo excepcionalmente preservado en Mistaken Point, Terranova, Canadá

R.S. Taylor¹, J.B. Hawco¹, R. Nichols², D. McIlroy¹

¹Department of Earth Sciences, Memorial University of Newfoundland, St. John's, NL, Canada. Email: rodt@mun.ca;
ORCID ID: <http://orcid.org/0000-0003-3072-6040>, <http://orcid.org/0000-0001-9162-2013>, <http://orcid.org/0000-0001-9521-499X>

²Palaeocreations, Bristol, UK. ORCID ID: <http://orcid.org/0000-0001-8980-7297>

ABSTRACT

The holotype of *Beothukis mistakensis* in Mistaken Point, Newfoundland, is the only currently known specimen that can be definitely placed within the species. Morphological differences between the holotype of *B. mistakensis* and the well-constrained species *plumosa* suggest that the two are not congeneric and *Culmofrons plumosa* should be retained as a valid taxon as originally established.

Keywords: *Beothukis*; Rangeomorph; Mistaken Point; Ediacaran; Newfoundland.

RESUMEN

El holotipo de *Beothukis mistakensis* en Mistaken Point, Terranova, es el único ejemplar actualmente conocido que puede ser colocado definitivamente dentro de la especie. Las diferencias morfológicas entre el holotipo de *B. mistakensis* y la especie plumosa sugieren que ambas no son congéneres y que *Culmofrons plumosa* debería conservarse como un taxón válido tal como se estableció originalmente.

Palabras clave: *Beothukis*; Rangeomorfo; Mistaken Point; Ediacárico; Terranova.

Introduction

The Mistaken Point Ecological Reserve is a UNESCO World Heritage Site situated on the south-east coast of Newfoundland, Canada. It is home to

multiple localities preserving complex accumulations of a group of late Ediacaran fossils known as the Avalonian Assemblage (Waggoner, 2003). These fossiliferous sites represent whole communities of deepsea seafloor-dwelling organisms that

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were preserved as ‘snapshots in time’ through burial by volcanic ash (Clapham *et al.*, 2003; Ichaso *et al.*, 2007) ranging in age from 570.94 ± 0.38 to 566.25 ± 0.35 Ma (Pu *et al.*, 2016). *Beothukis mistakensis* (Fig. 1A) is one of the most recognizable Ediacaran fossils from Mistaken Point. It has been illustrated in numerous publications, although it represents an exceptionally small component of the total fossil assemblage. It is perhaps best known for its occurrence on the Mistaken Point ‘E surface’ in a small area colloquially known as ‘Seilacher’s Corner’, in close proximity to other well-known Ediacaran taxa (e.g. *Fractofusus*, *Charniodiscus*) in a highly photogenic portion of the surface.

Beothukis mistakensis was a uniterminal, frond-shaped organism with an oval to spatulate outline. Like all rangeomorphs, *B. mistakensis* is composed of a complex modular architecture, with each component unit being made up of similar but smaller units arranged in a fractal-like manner (Narbonne, 2004; Brasier *et al.*, 2012). The taxonomic status of

the genus *Beothukis* is currently uncertain: it has been amended to include specimens with a stem and basal disc (Brasier *et al.* 2012), although these features are not preserved on the holotype. Liu *et al.* (2016) reconsidered *Beothukis mistakensis* in the context of new discoveries of *Culmofrons plumosa* (LaFlamme *et al.*, 2012; Fig. 2). *C. plumosa* was considered to possess a frond with similar gross morphology to *Beothukis*, but also a stem and holdfast. *Culmofrons plumosa* was thus considered to be a junior synonym of *B. mistakensis*, thereby creating the new taxon *Beothukis (Culmofrons) plumosa*. Part of the rationale for this decision was on the basis that continuous characters (i.e., stem length) are unsuitable for genus-level differentiation of taxa (Liu *et al.*, 2016), the authors instead recommended utilizing gross architecture, the presence/absence of morphological features, and overall growth programme. The number of second order rangeomorph branches (8-12 in *B. (C.) plumosa* versus 5-8 in *B. mistakensis*) is an important feature used by Liu *et al.* (2016) to distinguish between the two

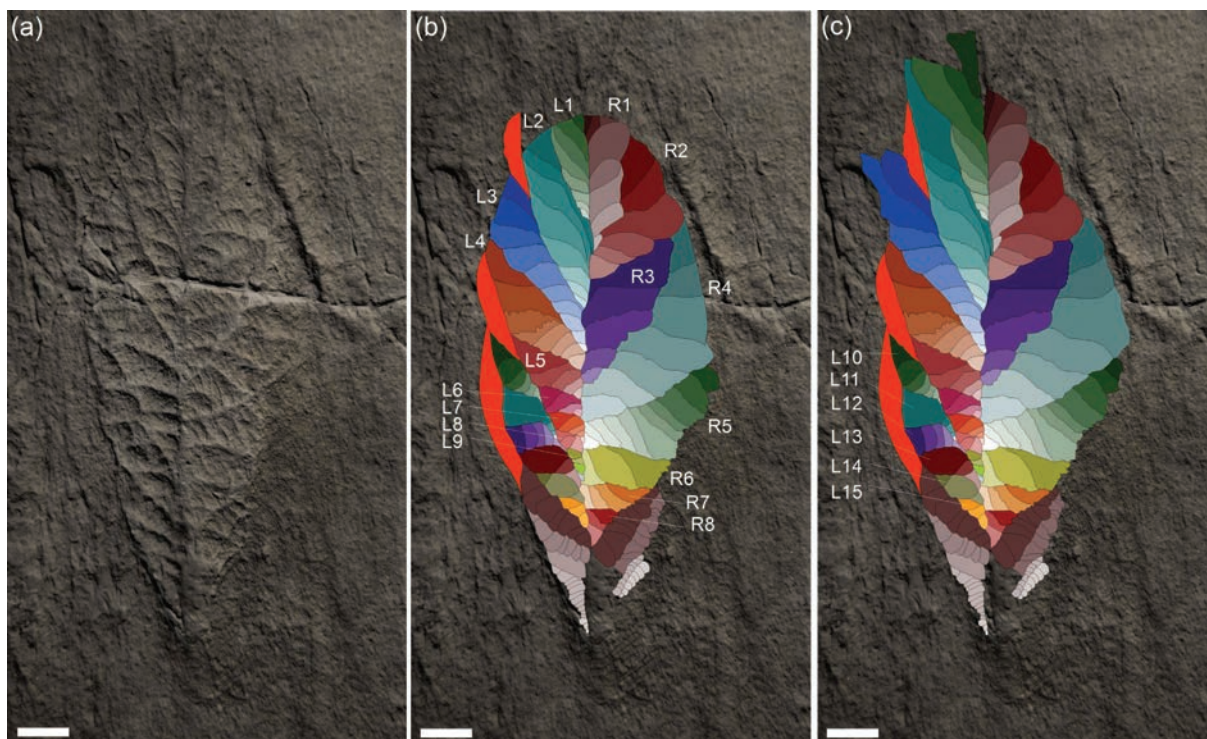


Figure 1.—A. Plastotype of the *Beothukis mistakensis* holotype, Mistaken Point Ecological Reserve. B. Interpretive drawing showing the first order units, labelled L1-9 and R1-8 (second order rangeomorph units are coloured so as to be progressively darker closer to the margin of the fossil); the orange coloured features are arcuate units with non-rangeomorph sub-units. (c) Secondary growth occurs at the tips of some first order units; the first arcuate unit on the left overgrows the secondary growths, implying its later development relative to secondary growth of unit L2. Scale bars = 1 cm.

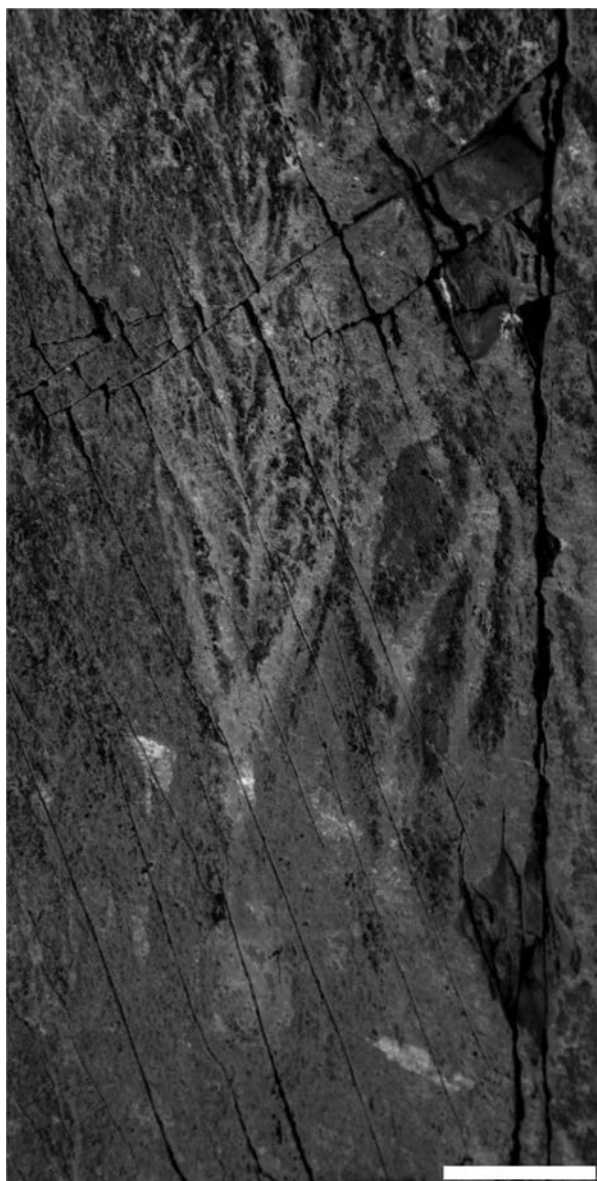


Figure 2.—Holotype of *Beothukis (Culmofrons) plumosa* from Lower Mistaken Point, Mistaken Point Ecological Reserve. Scale bar: 2 cm.

species. The objectives of this study are to re-assess the morphology of the holotype of *B. mistakensis*, and to re-examine the relationship between *B. mistakensis* and *B. (C.) plumosa*.

Results and discussion

Careful study of the *B. mistakensis* holotype reveals a considerably more complex morphology than previously recognized. The frond is

asymmetrical, with the left side being made up of nine primary order units (‘branches’) while the right side consists of only eight such units (Fig. 1B). Primary order units were added sequentially from the distal tip of the frond towards its base, our interpretation of the primary order units differs from earlier authors but is based on retention of equivalent number of orders of ‘branching’ within all primary order units. Although the overall outline of the organism is approximately symmetrical across the midline, the units making up the left and right sides show dissimilar sizes and orientations. The number of secondary order rangeomorph units within each primary order unit varies across the medial axis, compensating for the variability in size and shape of the primary units to maintain the overall frond shape. The angle of the primary order units relative to the midline increases from being acute at the distal tip of the frond to being approximately perpendicular near the base of the frond. Tertiary order rangeomorph branches are rotated and furled near the central axis but displayed and furled when bound proximally and distally by secondary growth. The tertiary units located at the lateral margin of the frond show variable morphologies.

Secondary growth occurs around the fringes of several of the first order units on the left side of the organism (Fig. 1C). Arcuate units without typical rangeomorph branching are also visible on the left-hand side of the holotype, in places overgrowing the secondary fringe growth. Several first order units without rangeomorph branching are located near the basal region of the organism, each composed of multiple rectangular second-order units and obliquely adjoining the frond’s central axis.

The paratype of *B. mistakensis* was also examined as a part of this study, revealing that there are 3 vanes of growth within the fossil. We thus determine that it is not congeneric with the holotype and thus needs to be reassigned to a different taxon. Of the many fossils previously described as *Beothukis*, none are morphologically comparable to the holotype, beyond perhaps having a spatulate outline. The other material is thus in need of reassessment, which is the focus of a separate morphometric study.

Several important morphological differences between *B. mistakensis* (Fig. 1A) and *B. (C.) plumosa* (Fig. 2) have been identified as a result of this study:

- The primary order branches of *B. mistakensis* are unequal and asymmetrical across a straight central axis, while the type specimen of *B. (C.) plumosa* possesses up to five pairs of equal but alternating primary order branches across its two rows, producing a zig-zag axis.
- The primary branches of *B. mistakensis* are small near the base and do not attach to a stem, while the primary branches are largest close to the stem in *B. (C.) plumosa* and attach directly to it.
- The largest second-order units in *B. mistakensis* are located close to the frond's edge and in the middle of the organism, while in *B. (C.) plumosa* the largest second-order units are situated near the axis and close to the base of the frond.
- The morphology of the third-order branches in *B. mistakensis* vary depending on their position within the frond, while in *B. (C.) plumosa* most of the tertiary branches appear to be rotated and furled.
- Lateral branches are found at the base of *B. mistakensis* but are not observed in *B. (C.) plumosa*.

Conclusions

The holotype of *Beothukis mistakensis* is the only currently known specimen that can be definitely placed within the species. Morphological differences between the holotype of *B. mistakensis* and the well-constrained species *plumosa* suggest that the two are not congeneric and *C. plumosa* should be retained as a valid taxon as originally established. We hope that further study of the Avalonian Assemblage in

Newfoundland will reveal more material belonging to *B. mistakensis*, and that morphometric analysis of the spatulate fronds will provide rationale for discrimination of the diversity within that morphospace.

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