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Modularity and overcompensatory growth in Ediacaran rangeomorphs demonstrate early adaptations for coping with environmental pressures

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Abstract:	The first known diverse, complex, macroscopic benthic marine ecosystems (late Ediacaran, ca. 571-541 Ma) were dominated by the Rangeomorpha, an enigmatic group of extinct frondose eukaryotes that are candidate early metazoans[1,2]. The group is characterised by a self-similar branching architecture that was likely optimised for exchange, but nearly every other aspect of their biology is contentious[2-4]. We report locally-enhanced, aberrant growth ("eccentric branching") in a stalked, multifoliate rangeomorph - Hylaecullulus fordi n. gen., n. sp. - from Charnwood Forest (UK), confirming the presence of true biological modularity within the group. Random branches achieve unusually large proportions and mimic the architecture of their parent branch, rather than that of their neighbours (the norm). Their locations indicate exceptional growth at existing loci, rather than insertion at new sites. Analogous over-compensatory branching in extant modular organisms requires the capacity to orchestrate growth at specific sites, and occurs most frequently in response to damage or environmental stress, allowing regeneration towards optimum morphology[e.g. 5-7]. Its presence in rangeomorphs indicates a hitherto unappreciated level of control to their growth plan, a previously unrecognised form of morphological plasticity within the group, and an ability to actively respond to external physical stimuli. The trait would have afforded rangeomorphs resilience to fouling and abrasion, partially accounting for their wide environmental tolerance, and may have pre-adapted them to withstand predation, weakening this argument for their extinction. Our findings highlight that multiple, phylogenetically disparate, clades first achieved large size through modularity.

Modularity and overcompensatory growth in Ediacaran rangeomorphs demonstrate early adaptations for coping with environmental pressures

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Data: primary data is the casts housed at BGS Keyworth; dynamic imagery (RTI) files of casts of the holotypes and paratypes are stored under the following DOI: 10.5285/d4aa9ec5-7cd4-4c35-aada-e7c4a119b64c

Summary

The first known diverse, complex, macroscopic benthic marine ecosystems (late Ediacaran, ca. 571-541 Ma) were dominated by the Rangeomorpha, an enigmatic group of extinct frondose eukaryotes that are candidate early metazoans[1,2]. The group is characterised by a self-similar branching architecture that was likely optimised for exchange, but nearly every other aspect of their biology is contentious[2–4]. We report locally-enhanced, aberrant growth ("eccentric branching") in a stalked, multifoliate rangeomorph – *Hylaecullulus fordi* n. gen., n. sp. – from Charnwood Forest (UK), confirming the presence of true biological modularity within the group. Random branches achieve unusually large proportions and mimic the architecture of their parent branch, rather than that of their neighbours (the norm). Their locations indicate exceptional growth at existing loci, rather than insertion at new sites. Analogous over-compensatory branching in extant modular organisms requires the capacity to orchestrate growth at specific sites, and occurs most frequently in response to damage or environmental stress, allowing regeneration towards optimum morphology[e.g. 5–7]. Its presence in rangeomorphs indicates a hitherto unappreciated level of control to their growth plan, a previously unrecognised form of morphological plasticity within the group, and an ability to actively respond to external physical stimuli. The trait would have afforded rangeomorphs resilience to fouling and abrasion, partially accounting for their wide environmental tolerance, and may have pre-adapted them to withstand predation, weakening this argument for their extinction. Our findings highlight that multiple, phylogenetically disparate, clades first achieved large size through modularity.

Keywords: Palaeoecology, palaeobiology, Ediacaran, rangeomorph, overcompensatory growth, palaeontology, Charnwood Forest, damage response, evolution, ecology

Results

SYSTEMATIC PALAEONTOLOGY

Material

Six well-preserved specimens, all preserved in lateral aspect (Fig. 1), from the top surface of a single bedding-plane (Bed B of [8]) in the Bradgate Formation, Maplewell Group, Charnwood Forest, UK (Figure S1). Two co-occurring, poorly-preserved specimens (GSM106012 and GSM106034, Figure S2) are also assigned to the genus. All specimens are current-aligned with the other fossils on the surface, and are preserved as low epirelief impressions. Master moulds and casts are housed at the British Geological Survey, Keyworth, UK (nos. GSM105875, GSM105957, GSM105958, GSM105959, GSM106040 and GSM106112); original specimens remain *in situ*. Reflectance Transformation Imaging (RTI; [9,10]) files of specimen GSM105875 are available in the SI. For a description of rangeomorph terminology, see [4], SI Table 1.

Genus *Hylaecullulus* gen. nov.

Type species *Hylaecullulus fordi* sp. nov. by monotypy

The plastotype is designated as GSM105875 (Fig. 1a); GSM106040 and GSM106112 are designated as plastoparatypes.

Etymology. Named for the goblet-like shape of the organism (Gr. *Cullulus*, a goblet) and its occurrence in Charnwood Forest (Gr. *Hylaeos*, meaning from the woods)

Diagnosis

Rangeomorph comprising a disc and similarly-sized crown, connected by a straight and proportionally long and narrow stem. The disc typically has several concentric rings, and frequently includes a triangular feature at its junction with the stem. The stem is of uniform width along its length, and is longer than the crown. The crown has a sub-circular outline and is multifoliate, comprising numerous folia emanating from a single location at the distal end of the stem. The folia are displayed, unfurled or furled, unconstrained and show distal inflation. Primary branches are typically displayed, furled, radiating and unconstrained and show proximal inflation; unfurled branches may be locally present. Secondary branches are displayed, furled, radiating and unconstrained and show distal inflation. Tertiary branches are displayed, furled, constrained and show slight radiation and slight distal inflation. Branch axes of all orders are concealed, and opposing ones are offset along the length of their host branch. The folia, first and second order branches, at least, may bear eccentric branches at any point along their length; these conform to the branching pattern of the host branch, rather than their neighbouring branches of the same order.

Hylaecullulus fordi sp. nov.

2011 "dumbbell-like taxon", "dumbbell-like frond" [8] p. 656, fig. 2D; fig. 4.

2012 "multi-ringed impression", "unnamed species" [11], Supplementary Figure 3.

2017 "dumbbells" [4], Supplementary Figure 1a

Diagnosis – as per genus.

Etymology. Named for Trevor Ford, in recognition of his contribution to Ediacaran palaeontology.

Description

The heights of known specimens, from the base of the stem (i.e. centre of the disc) to the distal margin of the crown, range from 7.6 cm to 37.6 cm (SI Table 1). Disc diameter ranges from 2.7 cm to 27 cm, and increases proportionally with total height. The disc has a well-defined outer margin and a variable number (2—5) of prominent concentric rings. The stem is straight and of uniform width, except at its base where it expands abruptly into a triangular structure to meet the disc, and comprises between 58% and 69% of the total height of the organism. The triangular structure is approximately a third of the width of the disc, and overlays the disc. The stem of the largest specimen (GSM105875) displays fine, closely-spaced, parallel lineations along much of its length, interpreted as biostratinomic artefacts (Fig. 1a, b; cf. [12]).

The crown is broadly circular in outline, with a well-defined, scalloped distal margin (Fig. 1b). It is slightly wider than it is high, and its width has an almost 1:1 correlation (R^2 = 0.9737) with that of the disc. Its shape is maintained throughout known ontogeny. The crown consists of numerous partially-overlapping folia[4], all emanating from the terminus of the stem. Five folia are visible in the majority of specimens (Fig. 1), but only four are clearly preserved in the smallest (GSM105957). Additional (taphonomically overlying) folia are suggested by the frond's scalloped distal margin. The organism is interpreted to have had a goblet-shaped morphology (Figure S3) – the functional significance of its morphology is discussed in the STAR Methods (under "Method Details").

At least three orders of branching can be resolved within the folia of the best-preserved specimens (Figs 2, 3; SI Table 2), with a fourth suggested in the holotype (GSM105875, Fig. 3a). Folia are displayed, unconstrained, show median-distal inflation and are unfurled; in three specimens (GSM105959, GSM105957, GSM 105957; Fig. 1d, f, g), folia are locally furled at their bases. Primary branches are displayed, furled, radiating, unconstrained and show moderate proximal-median inflation. In two specimens (GSM105875 and GSM106040), some primary branches are unfurled. Secondary branches are displayed, furled, radiating, unconstrained and inflate moderately distally. Tertiary branches are displayed, furled, constrained and show moderate radiation and slight distal inflation.

Eccentric branches occur on folia, primary branches and (rarely) secondary branches of the three best-preserved specimens (Fig. 3); these include the two largest individuals (GSM105875 and GSM106040) and a comparatively small one (GSM106112). Eccentric branches are oversized relative to their neighbours on the same host branch, but occupy a normal branch position (rather than, for example, representing branches of a lower-order poking through; shown schematically in Figure S3). In all cases, their branching pattern mimics that of the host branch, rather than that of their neighbours (Fig. 2). Multiple examples are present in all three specimens (Figs 2, 3). Eccentric branches may occupy any position along the host branch and within the crown, with no clear bias for either distal or proximal end (Figs 2, 3). Clustering of eccentric branches is apparent on secondary branches, is less common on primary branches, and has not been observed on folia (Figs 2, 3).

Discussion

The late Ediacaran (ca. 571-541 Ma) was an interval of pronounced anatomical and ecological innovation, exemplified by the appearance of diverse assemblages of macroscopic, soft-bodied organisms (e.g. [1,3]). Collectively referred to as the "Ediacaran biota", these organisms are distinct from earlier macroscopic algae (see [2]) and may offer insights into the origination and early evolution of major clades[1], the assembly of benthic marine ecosystem (see [3], and the nature of the Ediacaran—Cambrian biotic transition[13]. The Rangeomorpha[14] are an important component of the Ediacaran biota, dominating early, deep-marine settings[3]. Their phylogenetic placement is contentious, but they have recently been placed within the Metazoa, based on their developmental biology[2]. They are characterised by fronds with a self-similar pattern of alternate branching, resolvable over up to four orders of subdivision; details of their branching architecture underpin their taxonomy and phylogeny [3,4,15–17]. Many taxa also possess a holdfast and a stem which acted to lift the frond clear of the substrate [18,19]. Their precise mode of feeding has generated particular interest because of its potential phylogenetic and ecological implications (e.g. [3]), but there is general agreement that their fronds functioned as exchange surfaces[3,4,20,21].

The preservation of rangeomorphs as external moulds[22] has necessarily meant that many aspects of their biology and ecology are inferred from indirect evidence, particularly from their growth and developmental characteristics[2]. A modular organisation has been assumed based on their self-similar branching architecture[17,20,23], but supporting evidence for their branches (modules) having had developmental or physiological independence from one another[24,25] has been lacking.

Rangeomorph construction

Rangeomorphs are considered to be fundamentally similar to each other, with relatively minor deviances from a common growth strategy accounting for anatomical differences (e.g. [17]). The morphology of *Charnia masoni* has been used as a model for rangeomorph growth. New branches differentiated from a generative zone at or near the distal tip on alternate sides of a central axis, and subsequently “inflated”[26]. The relative dominance of differentiation versus inflation varies between taxa (e.g. [2,15,27]) and, in certain species at least, varied during ontogeny and/or in response to environmental pressures(see [28]). Minor deviations from this model are poorly recorded but, where identified, are typically attributed to taphonomic effects and intra-specific variation(see [2,4]). However, there is suggestion that the growth strategy of *Charnia* (and so perhaps other rangeomorphs) was more complex than previously envisaged[2].

Eccentric branching subverts known rangeomorph growth programmes and indicates a hitherto unrecognised level of morphological plasticity (see [28]). It is distinct from the “subsidiary branching” recognised in *Bradgatia lindfordensis*[15] and the “subsidiary frondlets” in *Fractofusus misrai*[27], both of which record insertion at additional growth loci between normal branches, rather than aberrant, enhanced growth at existing sites. Consequently, we do not consider eccentric branching to be part of pre-determined growth architecture, but rather deviant growth. We find no instance of eccentric branching in known unifoliate fronds: none was found in well-preserved specimens of *Charnia masoni* from Charnwood Forest[28], or in *Beothukis, Vinlandia antecedens* and *Trepassia wardae* from Newfoundland[15,23]. However, we recognise eccentric branching in other multifoliate fronds – *Bradgatia* and *Primocandelabrum*[4] – from the same bedding-plane surface as *H. fordi*. Given the apparently random distribution of eccentric branches within the crown (Fig. 2), we consider them most likely a response to damage or abrasion, rather than growth in response to, for example, changing nutrient concentrations (cf. [21])

Implications for rangeomorph biology

New growth in response to damage which outpaces normal growth – termed ‘over-compensatory’ growth – is a phenomenon peculiar to truly modular organisms. A module is a group of elements whose interactions occur preferentially within the group, such that the activity of elements within a module may depend little on elements outside of it[24,25]. The expression of over-compensatory growth varies between groups. Some gorgonian octocorals exhibit a remarkably similar morphological response to *H. fordi*, with branches reverting to higher order states, and growing faster than normal[29]. Similar peripheral damage in plant leaves does not elicit similar results, and damage to the central stem does not result in overgrowth or repair, but rather the specification of new apical or sub-apical generative zones, with multiple new shoots borne from the vascular cambium (e.g. [30]). Bryozoans, which are the only extant colonial bilaterians that commonly produce an arborescent form, may repair the original structure or show little growth response (e.g. [31]), but show no over-compensatory response[5]. Regeneration in fragmented graptoloid colonies (monograptids) is generally marked by an abrupt change in thecae size and shape, and by the subsequent iteration of uniform thecae resembling typical distal thecae, rather than the normal astogenetic gradient of morphologies; where regeneration has taken place without a sicula (i.e. from a distal fragment), it additionally leads to development of a new branch (growth pole) in the opposing direction [32]. Rarely, the regenerated portion may show an abbreviated astogenetic succession[33]. Algae are less predictable, although broadly similar outcomes to eccentric branches may be generated. In the coenocytic chlorphyte *Caulerpa*, for example, rather than only branches appearing eccentric, complete fronds (including stem) can emerge from the middle of another frond (Fig. 4).

The clustering of eccentric branches in *Hylaecullulus fordi*, and their restriction to specific orders of host branch, strongly suggests an ability to target growth, and also perhaps that the pattern of higher order branches was fixed at inception – they did not have the capacity for eccentricity. These differences between branch orders contradict previous interpretations of simple and iterative growth in rangeomorphs (see [2,17,23]). Regardless of the trigger stimulus, the capacity to orchestrate enhanced growth at specific sites indicates either the ability to turn on local production of growth factor, or to target its delivery from a remote point. Both mechanisms indicate a greater level of control and complexity to the rangeomorph growth programme than previously assumed: while locally-controlled production of growth factor would suggest greater module autonomy, targeted delivery would suggest a high level of physical interconnectedness between modules. Based on the available specimens of *Hylaecullulus fordi*, there is currently no way to distinguish between these two alternatives, and previous reports of an unspecified "internal, semi-rigid, organic skeleton" within rangeomorphs[23] have subsequently been dismissed as taphonomic artefacts[see 22]. Consequently, the degree to which resources may have been shared between modules within a frond remains unknown. That individual branches within multifoliate fronds display over-compensatory growth, reverting to a lower-order branch architecture, and that they were able to respond and adapt independently to their environment indicates, for the first time, that they constituted true biological modules.

The apparent restriction of eccentric branching to multifoliate forms suggests that phenotypic plasticity, and potentially the presence of true modularity, varied within rangeomorphs, as it does in many extant groups (e.g. [34]). The absence of eccentric branching in *Charnia* would seem to suggest tighter controls on the autonomy of individual branches, consistent with its constrained architecture[2,28]. Eccentric branching may even have been selected against in unifoliate rangeomorphs because such branches would distort the outline of the frond and impact its efficiency (cf. [19]). In a similar vein, branching style and overall morphology of octocorals varies according to their degree of module integration (coloniality;[34]). The oldest known rangeomorphs are unifoliate, appearing several million years before multifoliate forms[3,35]. Hence, we speculate that the modularity in multifoliate forms may be derived. Any such move to true (or at least overt) modularity could be considered conceptually comparable to the independent shifts to coloniality (and thus modularity) seen in extant invertebrate groups. For example, the plesiomorphic condition for crown-group cnidarians was likely unitary, but successive transitions to colonialism are known in both the Octocorallia and the Hexacorallia[36]. Colonial bilaterian groups (e.g. bryozoans, entoprocts or rotifers) developed from unitary bilaterian ancestors[37,38]. Colonies are considered to develop by the weakening of zooid individuality in order to strengthen colony identity, conferring advantages to the colony as a whole[39]. Rangeomorphs could plausibly have developed modularity by greater integration (as with metazoans), or by the relaxation of integration and appearance of semi-autonomy (as with plants and algae); it is not yet possible to discriminate which.

Modularity may bestow a number of ecological advantages, including: increased overall size and complexity with limited changes in surface area to volume ratios; enhanced feeding efficiency, given the greater potential for at least one module being in an optimum position; greater plasticity and, consequently, adaptability; and increased resilience to damage, with the loss of one module not necessarily compromising the entire organism[40]. It is also a means of achieving large body size. Indeed, the three earliest groups to have achieved macroscopic size – algae, fungi and now rangeomorphs, did so through modularity. That rangeomorphs were able to respond to environmental stressors has significant ramifications for understanding of their ecology. Targeted growth in response to damage is a highly beneficial trait in extant sessile organisms, enabling them to maintain their optimum form and to better cope with environmental constraints[6,7,29]. By extension, this trait would likely have proved particularly advantageous for multifoliate rangeomorphs, whose unconstrained, overlapping branches would have been prone to abrasion by neighbouring ones and susceptible to fouling by suspended sediment. It potentially helps explain their successful invasion of both deep-water environments and shallower, more energetic, settings[3,28]. Such regenerative capabilities may have potentially acted as a pre-adaptation to withstanding predation, one of several proposed drivers of the extinction of Ediacaran organisms[13].

Conclusions

Rangeomorphs are typically envisaged to have been simple and passive organisms. However, *Hylaecullulus fordi* gen. et. sp. nov. – a multifoliate rangeomorph from the Ediacaran strata of Charnwood Forest (UK) – provides evidence for considerable architectural complexity and a truly modular organisation, highlighting the importance of modularity in achieving large body size in phylogenetically disparate clades. Directed, enhanced growth in the form of eccentric branches illustrates their ability to respond to physical, external stimuli (such as damage), and conferred on them considerable environmental tolerance. Rangeomorph architecture was not immutable, and this plasticity has significant implications for the clade's taxonomy. The presence of over-compensatory growth demonstrates that rangeomorphs were not passive bystanders in a dynamic environment, but were able to actively adapt and recover, putting to rest the notion of a tranquil Garden of Ediacara.

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1. Erwin DH, Laflamme M, Tweedt SM, Sperling EA, Pisani D, Peterson KJ. (2011). The Cambrian Conundrum: Early Divergence and Later Ecological Success in the Early History of Animals. Science. *334(6059)*, 1091–7.

2. Dunn FS, Liu AG, Donoghue PCJ. Ediacaran developmental biology. Biol Rev. *93(2)*, 914–32.

3. Liu AG, Kenchington CG, Mitchell EG. (2015). Remarkable insights into the paleoecology of the Avalonian Ediacaran macrobiota. Gondwana Res. *27(4)*, 1355–80.

4. Kenchington CG, Wilby PR. (2017). Rangeomorph classification schemes and intra-specific variation: are all characters created equal? Geol Soc Lond Spec Publ *448*.

5. Cheetham AH, Hayek L-AC, Thomsen E. (1980). Branching structure in arborescent animals: Models of relative growth. J Theor Biol. *85(2)*, 335–69.

6. Järemo J, Palmqvist E. (2001). Plant compensatory growth: a conquering strategy in plant–herbivore interactions? Evol Ecol. *15(2)*, 91–102.

7. Shaish L, Abelson A, Rinkevich B. (2007). How Plastic Can Phenotypic Plasticity Be? The Branching Coral Stylophora pistillata as a Model System. PLoS ONE *2(7)*.

8. Wilby PR, Carney JN, Howe MPA. (2011). A rich Ediacaran assemblage from eastern Avalonia: Evidence of early widespread diversity in the deep ocean. Geology. *39(7)*, 655–8.

9. Hammer Ø, Bengtson S, Malzbender T, Gelb D. (2002). Imaging fossils using reflectance transformation and interactive manipulation of virtual light sources. Palaeontol Electron. *5(1)*, 1–9.

10. Kenchington CG, Harris SJ, Vixseboxse PB, Pickup C, Wilby PR. (2018). The Ediacaran fossils of Charnwood Forest: Shining new light on a major biological revolution. Proc Geol Assoc. *129 (3)*, 264-277.

11. Howe MPA, Evans M, Carney JN, Wilby PR. (2012). New perspectives on the globally important Ediacaran fossil discoveries in Charnwood Forest, UK: prequel to. Proc Yorks Geol Soc. *59(2)*, 137–44.

12. Tarhan LG, Droser ML, Gehling JG. (2010). Taphonomic Controls on Ediacaran Diversity: Uncovering the Holdfast Origin of Morphologically Variable Enigmatic Structures. PALAIOS. *25(12)*, 823–30.

13. Laflamme M, Darroch SAF, Tweedt SM, Peterson KJ, Erwin DH. (2013). The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat? Gondwana Res. *23(2)*, 558–73.

14. Pflug H-D. (1972). Systematik der jung-präkambrischen Petalonamae Pflug 1970. Paläontol Z. *46*, 56–67.

15. Brasier MD, Antcliffe JB, Liu AG. (2012). The architecture of Ediacaran Fronds. Palaeontology. *55(5)*, 1105–1124.

16. Dececchi TA, Narbonne GM, Greentree C, Laflamme M. (2017). Relating Ediacaran Fronds. Paleobiology. *43(2)*, 171–80.

17. Hoyal Cuthill JF, Conway Morris S. (2014). Fractal branching organizations of Ediacaran rangeomorph fronds reveal a lost Proterozoic body plan. Proc Natl Acad Sci. *111(36)*, 13122–6.

18. Laflamme M, Narbonne GM. Ediacaran fronds. (2008). Palaeogeogr Palaeoclimatol Palaeoecol. *258(3)*, 162–79.

19. Singer A, Plotnick R, Laflamme M. (2012). Experimental fluid mechanics of an Ediacaran frond. Palaeontol Electron. *15(2)*, 19A.

20. Laflamme M, Xiao S, Kowalewski M. Osmotrophy in modular Ediacara organisms. (2009). Proc Natl Acad Sci U S A. *106(34)*, 14438–43.

21. Hoyal Cuthill JF, Conway Morris S. (2017). Nutrient-dependent growth underpinned the Ediacaran transition to large body size. Nat Ecol Evol. *1(8)*, 1201–4.

22. Kenchington CG, Wilby PR. (2014). Of time and taphonomy: preservation in the Ediacaran. In: Laflamme M, Schiffbauer JD, Darroch SAF, editors. Reading and writing of the fossil record: preservational pathways to exceptional fossilization. Paleontological Research Institution; The Paleontological Society Papers; vol. 20. p. 101–22.

23. Narbonne GM. Modular Construction of Early Ediacaran Complex Life Forms. (2004). Science. *305(5687)*, 1141–4.

24. Eble GJ. (2005). Morphological modularity and macroevolution. Modul Underst Dev Evol Nat Complex Syst MIT Press Camb. p. 221–238.

25. Klingenberg CP. (2008). Morphological Integration and Developmental Modularity. Annu Rev Ecol Evol Syst. *39(1)*, 115–32.

26. Antcliffe JB, Brasier MD. (2007). Charnia and sea pens are poles apart. J Geol Soc. *164(1)*, 49–51.

27. Gehling JG, Narbonne GM. (2007). Spindle-shaped Ediacara fossils from the Mistaken Point assemblage, Avalon Zone, Newfoundland. Can J Earth Sci. *44(3)*, 367–87.

28. Wilby PR, Kenchington CG, Wilby RL. (2015). Role of low intensity environmental disturbance in structuring the earliest (Ediacaran) macrobenthic tiered communities. Palaeogeogr Palaeoclimatol Palaeoecol. *434*, 14–27.

29. Sánchez JA, Lasker HR. (2004). Do multi–branched colonial organisms exceed normal growth after partial mortality? Proc R Soc Lond B Biol Sci. *271(Suppl 3)*, S117–S120.

30. Brackmann K, Greb T. (2014). Long- and short-distance signaling in the regulation of lateral plant growth. Physiol Plant. *151(2)*, 134–41.

31. Bone EK, Keough MJ. (2005). Responses to damage in an arborescent bryozoan: Effects of injury location. J Exp Mar Biol Ecol. *324(2)*, 127–40.

32. Urbanek A. (2004). Morphogenetic gradients in graptolites and bryozoans. Acta Palaeontol Pol. *49(4)*, 485–504.

33. Urbanek A. (1973). Organization and evolution of graptolite colonies. In: Boardman RS, Cheetham AH, Oliver WAJ, editors. Animal Colonies Development and Function Through Time. Dowden, Hutchinson and Ross, Inc.. p. 441–514.

34. Bayer FM. (1973). Colonial organisation in Octocorals. In: Boardman RS, Cheetham AH, Oliver WAJ, editors. Animal Colonies Development and Function Through Time. Dowden, Hutchinson and Ross, Inc.. p. 69–93.

35. Pu JP, Bowring SA, Ramezani J, Myrow P, Raub TD, Landing E, et al. (2016). Dodging snowballs: Geochronology of the Gaskiers glaciation and the first appearance of the Ediacaran biota. Geology. *44(11)*, 955–8.

36. Zapata F, Goetz FE, Smith SA, Howison M, Siebert S, Church SH, et al. (2015). Phylogenomic Analyses Support Traditional Relationships within Cnidaria. PLOS ONE. *10(10)*, e0139068.

37. Philippe H, Brinkmann H, Copley RR, Moroz LL, Nakano H, Poustka AJ, et al. (2011). Acoelomorph flatworms are deuterostomes related to Xenoturbella. Nature. *470(7333)*, 255–8.

38. Cannon JT, Vellutini BC, Smith J, Ronquist F, Jondelius U, Hejnol A. (2016). Xenacoelomorpha is the sister group to Nephrozoa. Nature. *530(7588)*, 89–93.

39. Boardman RS, Cheetham AH, Oliver WA. (1973). Animal Colonies: Development and Function Through Time. Dowden, Hutchinson & Ross. pp. 622.

40. Marfenin NN. (1997). Adaptation capabilities of marine modular organisms. Hydrobiologia. *355(1–3)*, 153–8.

41. Liu AG, Matthews JJ, McIlroy D. (2016). The Beothukis/Culmofrons problem and its bearing on Ediacaran macrofossil taxonomy: evidence from an exceptional new fossil locality. Palaeontology. *59*(1),45–58.

42. Boynton HE, Ford TD. (1995). Ediacaran fossils from the Precambrian (Charnian Supergroup) of Charnwood Forest, Leicestershire, England. Mercian Geol. *13*,165–82.

43. Hofmann HJ, O'Brien SJ, King AF. (2008). Ediacaran Biota on Bonavista Peninsula, Newfoundland, Canada. J Paleontol. *82*(1),1–36.

44. Mason SJ, Narbonne GM. (2016). Two new Ediacaran small fronds from Mistaken Point, Newfoundland. J Paleontol. *90(02)*, 183–194.

45. Gage JD, Tyler PA. (1992). Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. Cambridge, UK: Cambridge University Press. 524 p.

46. Baumiller TK. (1997). Crinoid functional morphology. In: Geobiology of Echinoderms. (Paleontological Society Papers; vol. 3). pp. 45–68.

47. Dade WB, Hogg AJ, Boudreau BP. (2001). Physics of Flow above the Sediment-Water Interface. In: Boudreau BP, Jorgensen BB, editors. The Benthic Boundary Layer: Transport Processes and Biogeochemistry: Transport Processes and Biogeochemistry. Oxford University Press, USA. pp. 4–43.

48. Dufour SC, McIlroy D. (2016). Ediacaran pre-placozoan diploblasts in the Avalonian biota: the role of chemosynthesis in the evolution of early animal life. Geol Soc Lond Spec Publ. *15*;448.

49. Laflamme M, Flude LI, Narbonne GM. (2012). Ecological Tiering and the Evolution of a Stem: The Oldest Stemmed Frond from the Ediacaran of Newfoundland, Canada. J Paleontol. *86*(2), 193–200.

50. Ghisalberti M, Gold DA, Laflamme M, Clapham ME, Narbonne GM, Summons RE, et al. (2014). Canopy Flow Analysis Reveals the Advantage of Size in the Oldest Communities of Multicellular Eukaryotes. Curr Biol. *24(3)*, 305–9.

51. Boudreau BP. Solute Transport above the Sediment-Water Interface. (2001). In: Boudreau BP, Jorgensen BB, editors. The Benthic Boundary Layer : Transport

Processes and Biogeochemistry: Transport Processes and Biogeochemistry. Oxford University Press, USA. p. 104–26.

52. Jorgensen BB. Life in the Diffusive Boundary Layer. (2001). In: Boudreau BP, Jorgensen BB, editors. The Benthic Boundary Layer : Transport Processes and Biogeochemistry: Transport Processes and Biogeochemistry. Oxford University Press, USA. p. 348–73.

53. Mitchell EG, Kenchington CG, Liu AG, Matthews JJ, Butterfield NJ. Reconstructing the reproductive mode of an Ediacaran macro-organism. (2015). Nature. *524*, 343–6.

54. Darroch SAF, Laflamme M, Clapham ME. (2013). Population structure of the oldest known macroscopic communities from Mistaken Point, Newfoundland. Paleobiology. *39(4)*, 591–608.

55. Gaylord B, Reed DC, Raimondi PT, Washburn L, McLean SR. (2002). A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. Ecology. *83(5)*,1239–51.

56. Thomson FJ, Moles AT, Auld TD, Kingsford RT. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. J Ecol. *99(6)*, 1299–307.

57. White P, Jentsch A. (2001). The Search for Generality in Studies of Disturbance and Ecosystem Dynamics. In: Esser K, Lüttge U, Kadereit JW, Beyschlag W, editors. Progress in Botany, vol. 62. Springer Berlin Heidelberg. pp. 399–450.

58. R Core Team. (2014). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.

59. Sebastien Le, Julie Josse, Francois Husson (2008). FactoMineR: An R Package for Multivariate Analysis. Journal of Statistical Software. *25(1)*, 1-18.

Figure 1. Specimens of *Hylaecullulus fordi* from Charnwood Forest.

A) GSM105875 (mould), the plastotype and largest known example; B) interpretive overlay (up to folium level detail) of GSM105875; dark blue area is the holdfast disc, with dark blue lines outlining its internal rings; medium blue is its stem, with red lines defining the "lineations" and "triangle"; bright blue outlines the folia; C) plastoparatype GSM106040 (mould); D) GSM105959 (cast); E) plastoparatype GSM106112 (cast); F) GSM105957 (cast), the smallest well-preserved example; G) GSM 105958 (cast). Scale bars = 2 cm; all moulds and casts are held at the British Geological Survey, Keyworth. Interpretative overlay is digitised from a camera lucida interpretation. Stratigraphic setting shown in Figure S1, additional specimens in Figure S2 and STAR Methods.

Figure 2: Detailed branching architecture of *Hylaecullulus fordi*.

A) GSM106040 (cast); B) close-up of a); C) interpretative overlay of b); D) GSM106112 (cast); E) close-up of d); F) interpretative overlay of e). Scale bars = 2 cm; all casts are housed at the British Geological Survey. Interpretative overlays are digitised from camera lucida interpretations, see STAR Methods.

Figure 3. Eccentric branching in *Hylaecullulus fordi*.

Increasingly higher magnification views of the outlined boxed areas; the final image is an interpretative overlay (digitised from camera lucida drawings) of the penultimate image. A) GSM106040 (cast); B) GSM106112 (cast); C) GSM105875 (cast). Scale bars = 2 cm; all casts are housed at the British Geological Survey, Keyworth. Artist's reconstruction shown in Figure S3, comparison to *Bradgatia* in Figure S4, and STAR Methods.

Figure 4. Aberrant growth in the chlorophyte, *Caulerpa*.

A) showing *Caulerpa prolifera* with aberrant fronds (frond emerging directly from another frond, as opposed to from the basal stolon) arrowed. B) a schematic of *Caulerpa prolifera* illustrating the variability of the aberrant fronds (arrowed).

STAR Methods

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Charlotte Kenchington (cgk27@cam.ac.uk). Access to the casts is controlled by the British Geological Survey, Nicker Hill, Keyworth, Nottingham NG12 5GG, UK.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The *Caulerpa* algae were collected from Bristol Aquarium, and were cultured at 21 degrees C in aerated open-system tanks, alongside other marine algae (*Galaxaura* and *Halimeda*), and sand anemones. Water salinity was 35 parts per thousand, and water pH was kept between 7.5 and 8.4. Nutrient addition was facilitated by addition of zooplankton every week, and nitrite and phosphate levels were tested every fortnight (using Salifert test kits). The algae were subject to diurnal cycles, with light provided by Aqua beam 1000 ultra HD marine lights

METHOD DETAILS

Analysis of fossil specimens

The original fossil specimens remain *in situ* on the bedding plane, as they cannot be removed and are protected under UK SSSI legislation. Silicone rubber moulds were taken from the bedding plane, and Jesmonite® resin casts produced from the moulds. The casts form the material presented in this study.

Analysis of fossil specimens was conducted through detailed examination using a palaeontological binocular microscope coupled with a directed light source (angle poise lamp). A camera lucida microscope and directed light source were used to make detailed line drawings of the fossils, which were then digitized in Adobe Illustrator. Measurements of specimen morphology were made with a ruler. High-resolution photographs were taken with a Canon EOS 7D Mark II and a Canon EOS 5D Mark III and were viewed through Adobe Photoshop.

Comparison to other known rangeomorphs

Rangeomorph taxonomy is currently in a state of flux[4, 41], but *Hylaecullulus* is readily distinguishable from all currently described taxa. It bears closest resemblance to *Bradgatia* Boynton and Ford[42] and *Primocandelabrum* Hofmann, O'Brien and King[43], both of which have a multifoliate construction and co-occur with *Hylaecullulus* on Bed B. However, *Bradgatia* lacks a stem and has a much smaller, bulb-shaped holdfast (Figure S4); its branching architecture is also distinct, being displayed, unfurled and radiating at all resolvable orders of branching (cf. [15]). While *Primocandelabrum* superficially resembles *Hylaecullulus* in its possession of a simple disc and a straight (albeit proportionally shorter) stem, its 'bushy' crown is notably triangular in preserved outline and its branches are coarser and arranged in a form resembling a candelabrum[43]. The poor preservation of the type specimens of *Primocandelbrum* from Newfoundland renders their finer branching architecture impossible to determine, but multivariate statistical analyses of specimens from Charnwood Forest consistently separates specimens of *Hylaecullulus* from *Primocandelabrum* ([4], their Fig. 4). Two small multifoliate fronds formerly described as "feather dusters" have recently been described from Mistaken Point, Canada, and assigned to the taxon *Plumeropriscum hofmanni*[44]. While these specimens appear superficially similar to *Hylaecullulus* and have been described as multifoliate, their primary branches appear to emanate along a central stalk ([44], their Figs 4 and 5(1)), they have smaller discs, proportionally much shorter stems, and a branching architecture that appears quite different to that of both *Hylaecullulus* and *Primocandelabrum*[41], but which remains to be fully described.

Functional morphology of Hylaecullulus fordi

Based on its morphology and taphonomy, we interpret the living *H. fordi* organism to have had an open, bowl-shaped crown which was held aloft on a long, naked (i.e. not bearing branches), comparatively stiff stem, and was anchored to the shallow substrate by a large, oblate holdfast (Main text Fig. 1). As such, it represents an early example of the tall, arborescent form that was subsequently converged upon in the Phanerozoic by a diverse range of deep-water, sessile organisms, including pennatulaceans, crinoids and bryozoans (see [45]).

The crown of *H. fordi* was composed of equi-sized, partially-overlapping folia. There is no evidence to suggest that it was able to pivot or flex to any significant degree about its junction with the stem (as in stalked crinoids; [46]), but each folium and primary branch was itself flexible. The net result was that a dense and near-continuous wall (both external and internal) of rangeomorph branches was presented to the water, enabling the crown to passively exploit currents from all directions equally. This made it particularly well-adapted to deep-water settings, where the direction and strength of benthic ambient flow may vary at any one location (e.g.[47]).

Rangeomorph fronds are generally considered to be feeding structures[20,21,48], and their stems are argued to be a response to competition for vertically-distributed resources (i.e. tiering; [49,50]). The long, naked stem of *H. fordi* would seem to support this interpretation; it would have placed the organism's crown in a region of the water column with higher flow, thereby likely increasing the efficiency of exchange across its surface (cf. [51,52]). However, the elevation of its crown overlaps with the fronds of most other taxa on the same bedding-plane surface, suggesting that it may have had an additional, or alternative, function to feeding. Rangeomorphs likely reproduced via waterborne propagules[53,54], whose dispersal distance might be expected to increase with the height of the parent frond (cf. [55,56]). Wide dispersal is particularly advantageous in disturbance-prone environments (e.g. [57]), such as the turbiditic settings occupied by *H. fordi* [28], and may have been the dominant driver of stem length in *H. fordi* and other frondose taxa with a naked stem.

QUANTIFICATION AND STATISTICAL ANALYSIS

The R statistical package was used for simple statistical analysis involving regression of morphological proportions against one another (results detailed in the Systematic Palaeontology section). The very low number of well-preserved specimens (n = 6) precluded further meaningful statistical analysis. Comparison of these fossil specimens with *Primocandelabrum* specimens was conducted using the R package FactoMineR[58,59], and is detailed in [3].

DATA AND SOFTWARE AVAILABILITY

Data: primary data is the casts housed at BGS Keyworth; dynamic imagery (RTI) files of casts of the holotypes and paratypes are stored under the following DOI: 10.5285/d4aa9ec5-7cd4-4c35-aada-e7c4a119b64c . R and the FactoMineR package are both open source[58,59].

Key Resource Table

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
dynamic imagery (RTI) files of casts of fossil specimens	dynamic imagery (RTI) files of casts of the holotypes and paratypes are stored under the following DOI: 10.5285/d4aa9ec5-7cd4-4c35-aada-e7c4a119b64c	GSM106112; GSM106958; GSM106957; GSM106959; GSM106040; GSM106875; GSM106012; GSM106034
Software and Algorithms		
R software package	https://www.r-project.org/	
Other		
Primary casts of fossil specimens	British Geological Survey, Keyworth, UK	GSM106112; GSM106958; GSM106957; GSM106959; GSM106040; GSM106875; GSM106012; GSM106034

Figure 1

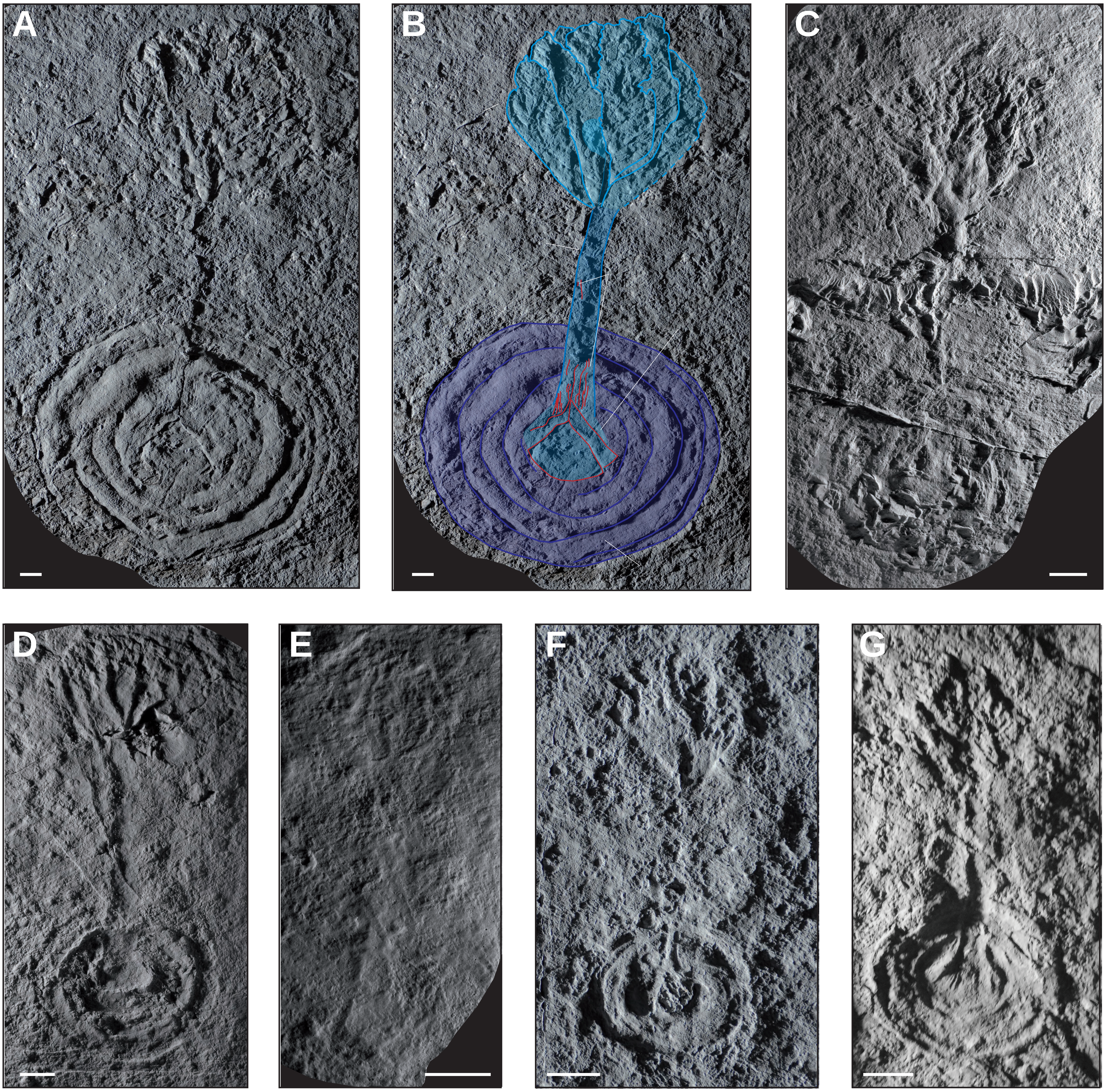


Figure 2

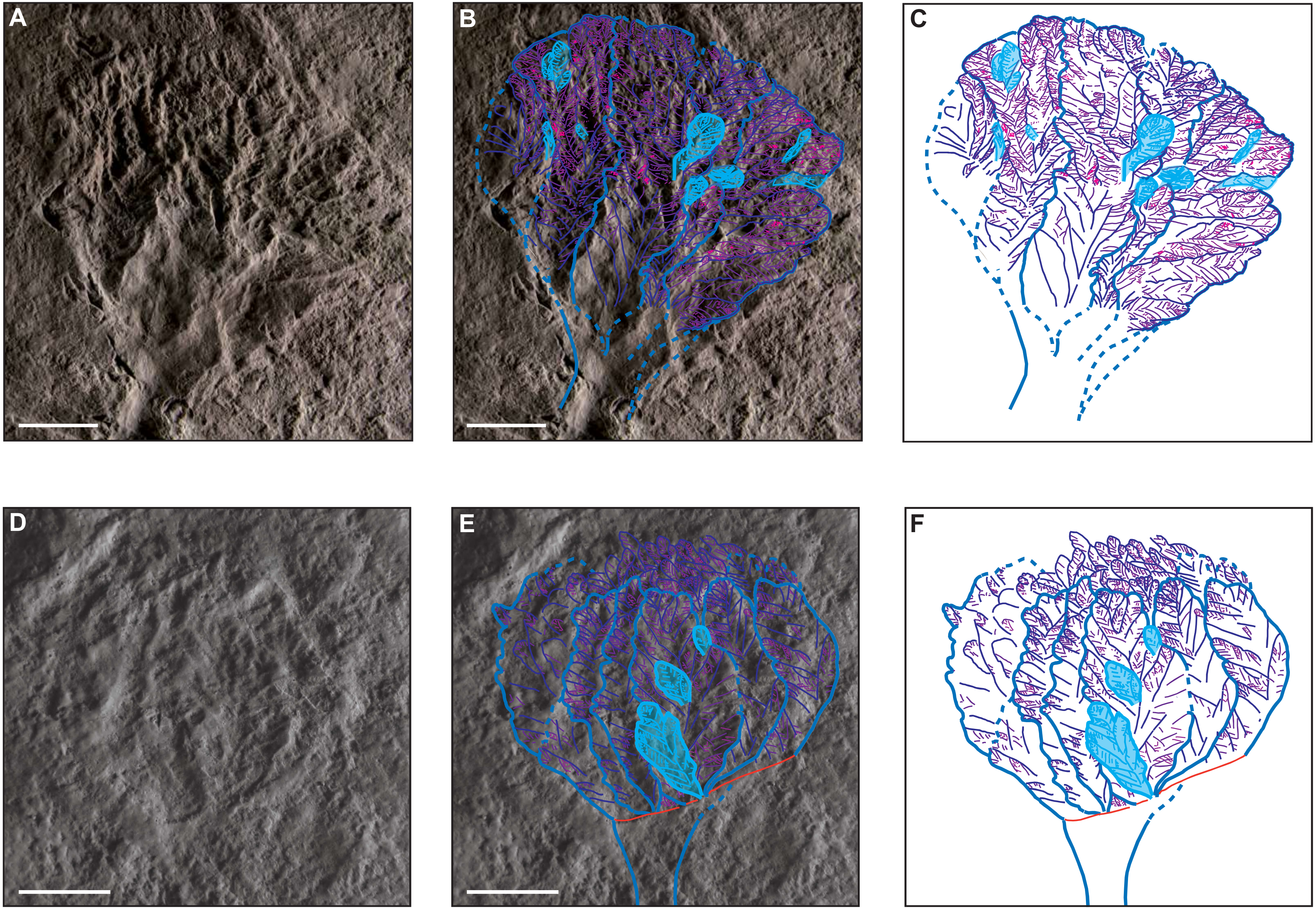


Figure 3

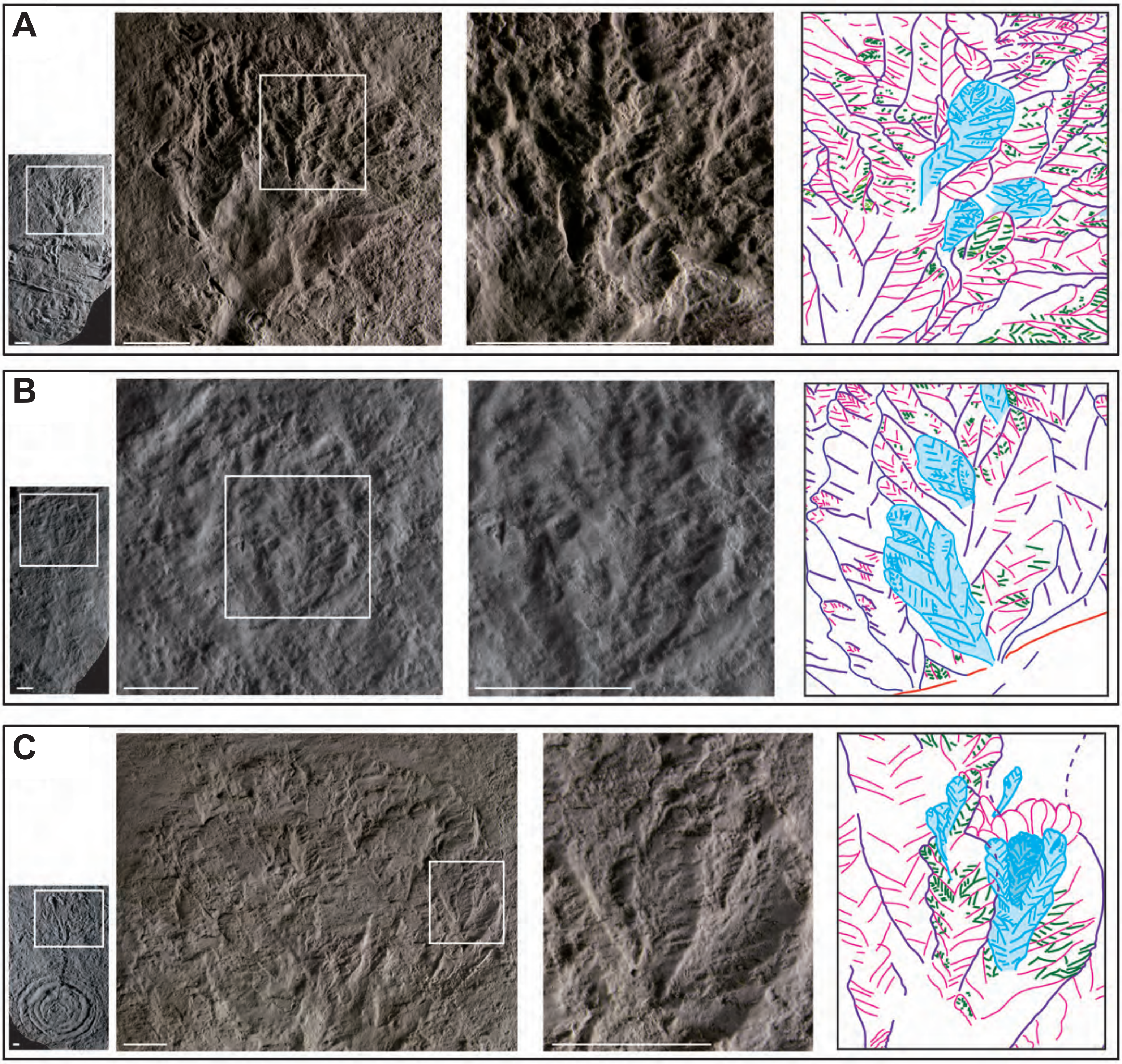
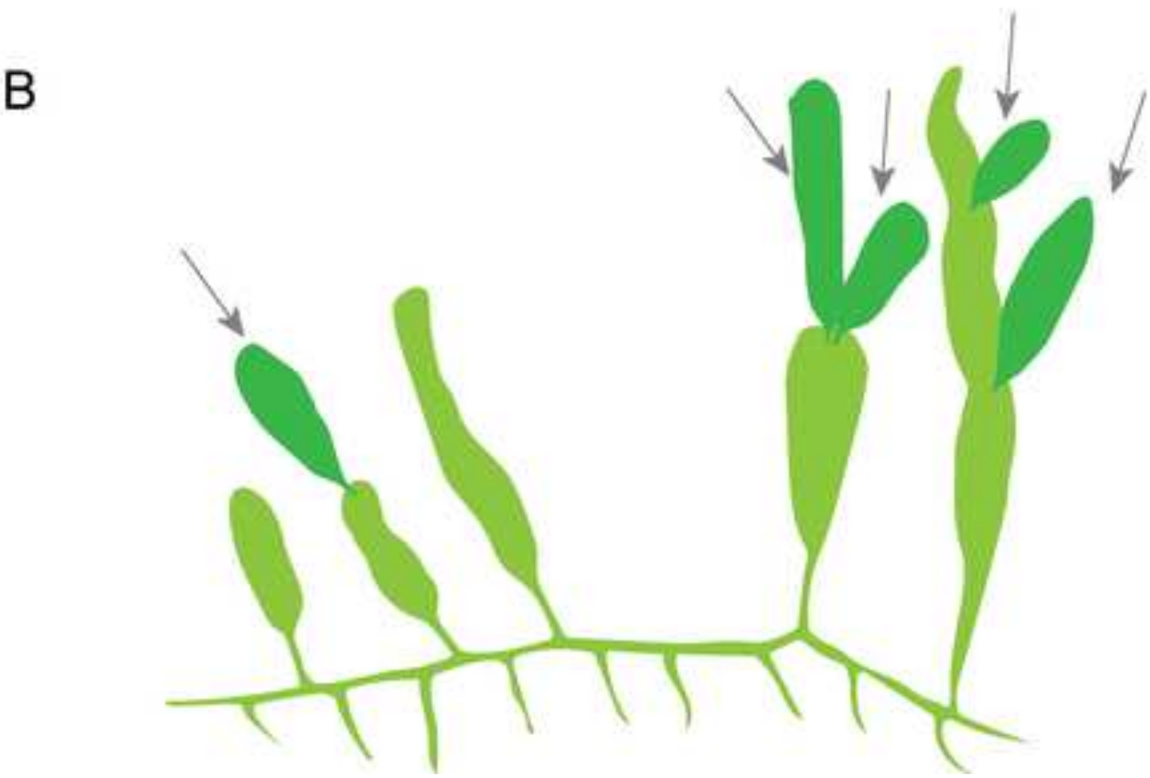


Figure 4



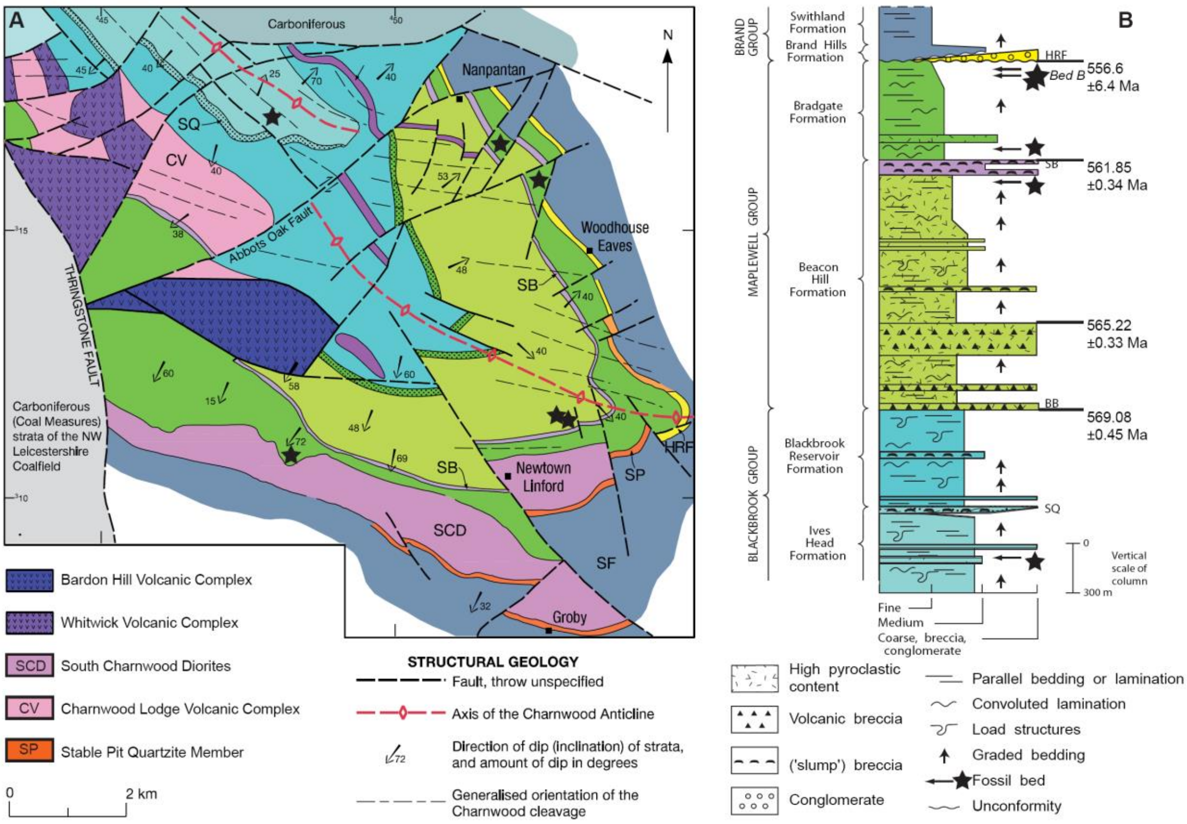


Figure S1. **Stratigraphic setting. Related to Figure 1.** A) Simplified geological map and B) generalised stratigraphic column of the Ediacaran—Cambrian succession of Charnwood Forest, modified after [S1]. Dates from [S2]. HRF = Hanging Rocks Formation; SB = Sliding Stones Breccia Member; BB = Benscliffe Breccia Member; SQ = South Quarry Breccia Member.

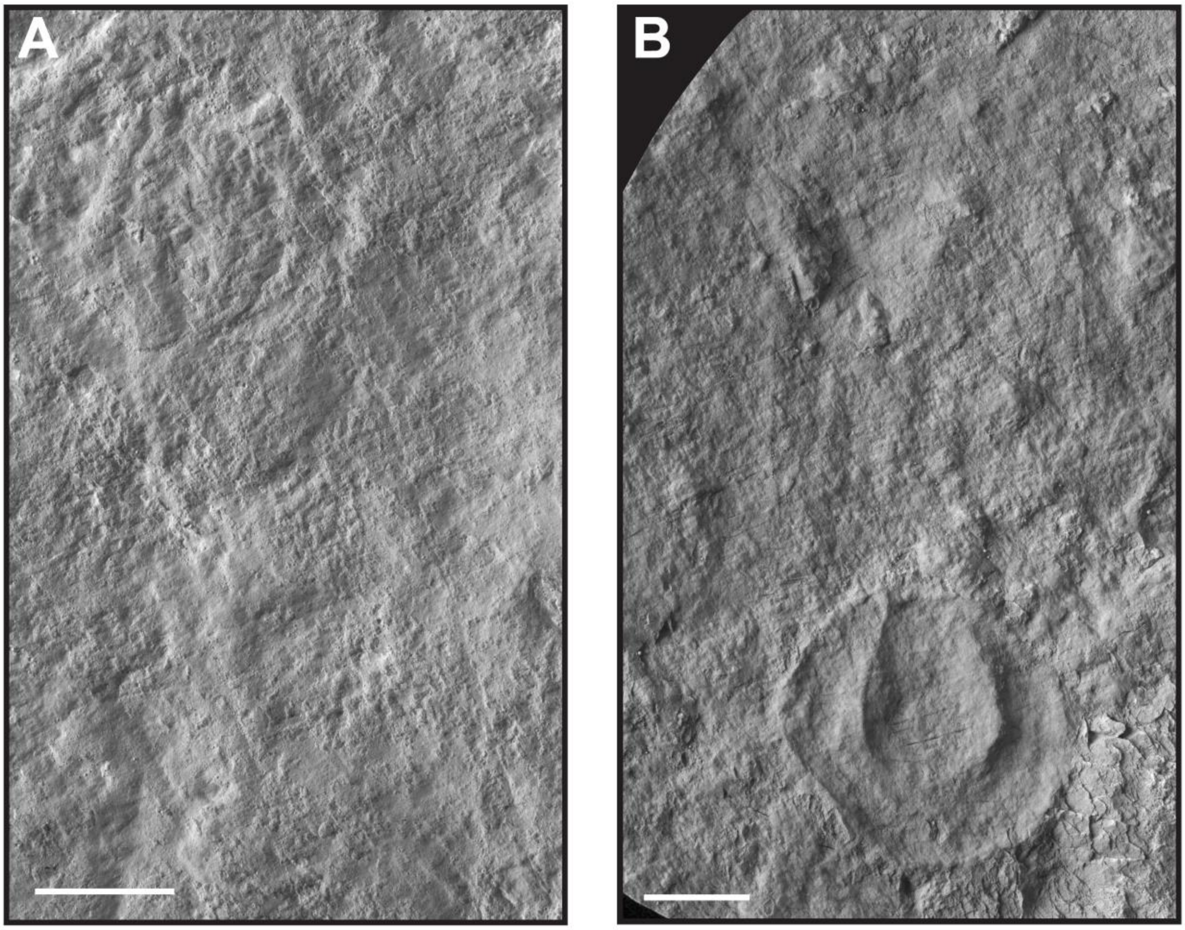


Figure S2. **Additional specimens assigned to *Hylaecullulus fordi*. Relates to Figure 1.** A) GSM106012 (cast) and B) GSM106034 (cast), poorly preserved specimens assigned to *Hylaecullulus fordi* on the basis of their morphological proportions and those branching characters that are discernible. Scale bars = 2cm

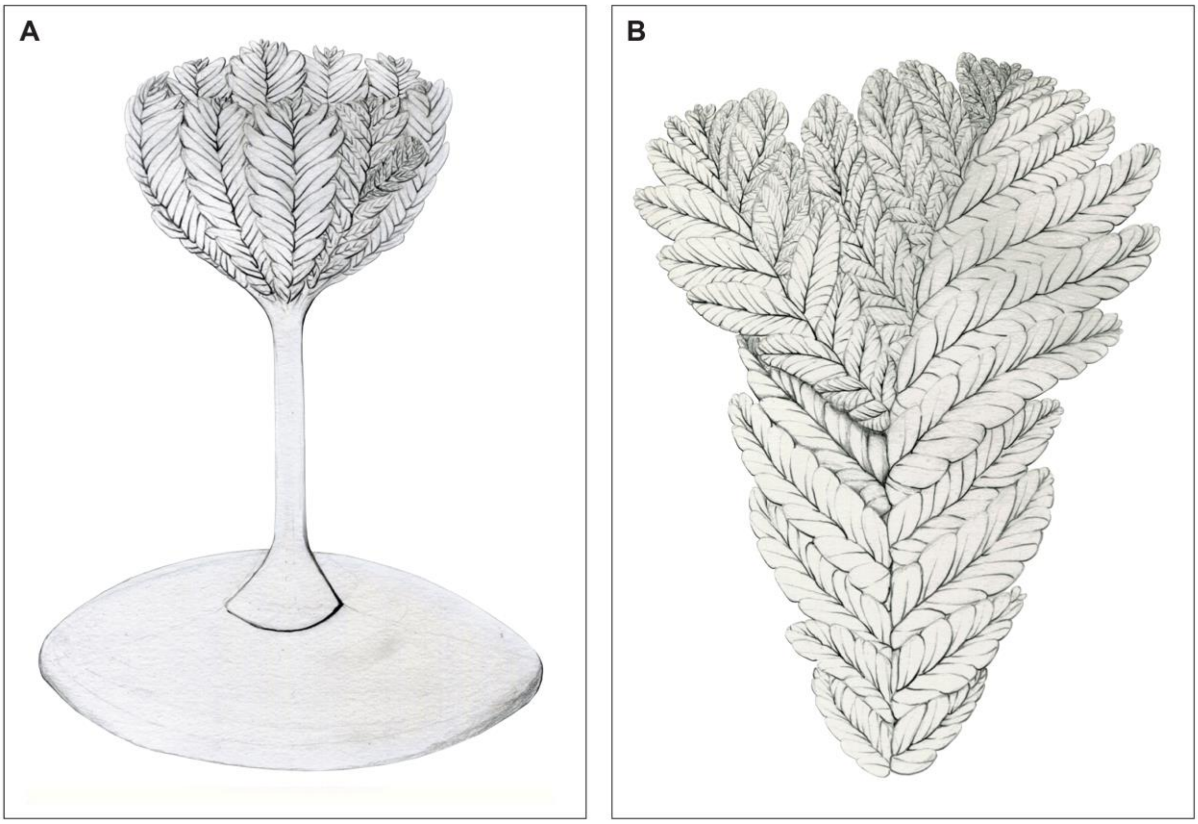


Figure S3. Reconstruction of *Hylaecullulus fordi*. Relates to Figure 3. A) Entire organism, with single eccentric branch illustrated; B) individual folium with an emanating eccentric branch. The architecture of the eccentric branch matches that of the host branch (the folium) rather than its neighbouring primary branches; finer architecture shown for some regions.

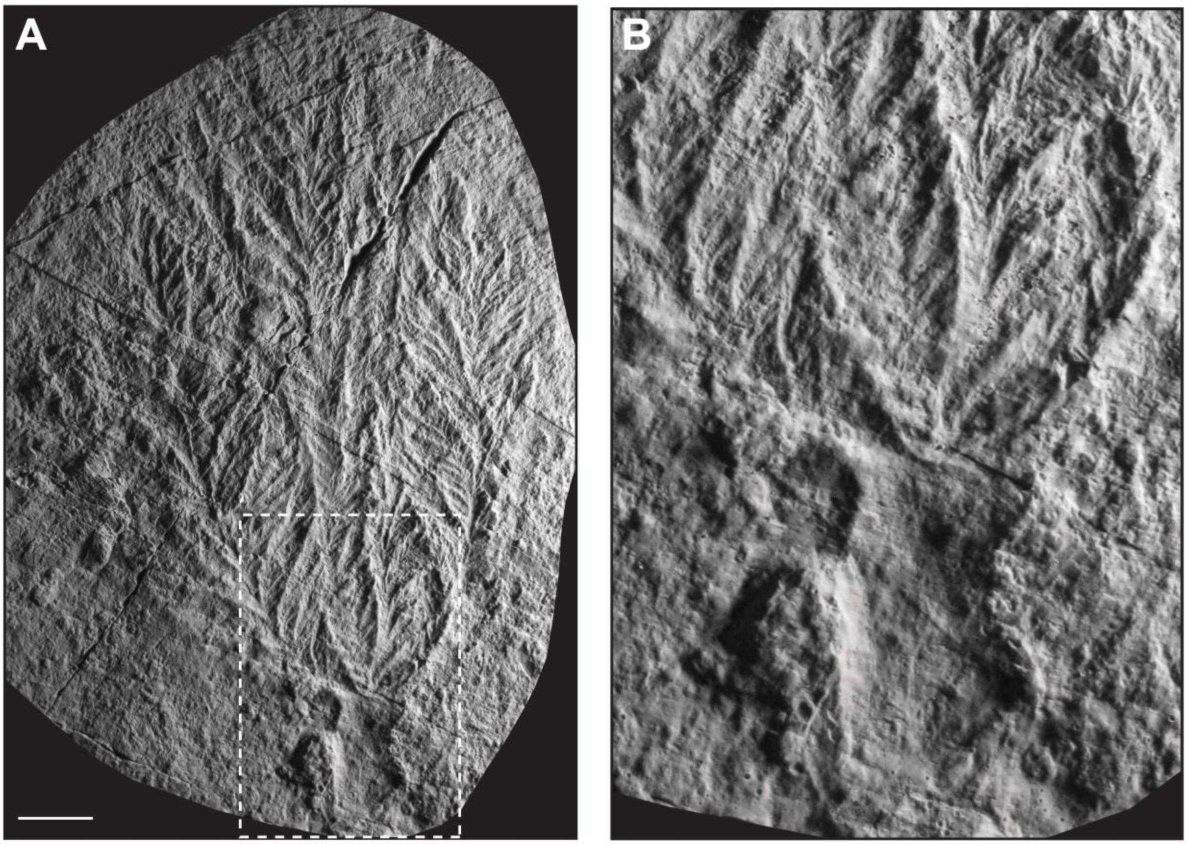


Figure S4. *Bradgatia*, GSM105873, relates to Figure 3. A) Whole specimen, showing bulbous holdfast and typical unfurled, displayed branching architecture; B) inset of A), showing the folia clearly emanating from a shared central point.

Specimen GSM	Total height (mm, to centre of disc)	Disc width (mm)	Disc height (mm)	No. complete rings	No. partial rings	Stem height (mm, centre of disc to point of inflection)	Stem height (mm, centre of disc to base of branches)	Stem width at inflection (mm)	Crown width (mm)	Crown height (mm)	Length left (mm)	Length right (mm)
106112	114	31	23			76	79	6	37	37	23	29
105958	124	77	67	3	2	75	79	13	42	40.5	38.5	30
105957	129	58	44	2	3	65		27	46	60	44	39
105959	210	112	97	3	2	135	145	9	73	80	64	72
106040	224	114	99	3	2	142	152	25	87	87	70	73
105875	376	270	219	5	4	211	219	35	178	162	131.5	123
106012	755	360	30			37	49	5	39	38	29	30
106034	120	560	54			68	76	14	40	54	30	31

Table S1. Quantitative measurements for *Hylaecullulus fordi* specimens on Bed B of Charnwood Forest. Related to Systematic Palaeontology and Figure 1.

Specimen GSM	Folia Displayed/ Rotated	Folia Un-/ Furled	Folia Inflation	Folia Un-/Concealed	Primary Displayed/ Rotated	Primary Un-/ Furled	Primary Radiating/ Parallel	Primary Inflation	Primary Un-/ Concealed	Secondary Displayed/ Rotated	Secondary Un-/Furled	Secondary Radiating/ Subparallel	Secondary Inflation	Secondary Un-/ Concealed
106112	displayed	unfurled		concealed	displayed	furled	radiating	proximal	concealed	displayed	furled	radiating	distal	concealed
105958	displayed	furled		concealed	displayed	furled	radiating		concealed					concealed
105957														
105959	displayed	furled		concealed	displayed	furled	radiating		concealed					concealed
106040	displayed	furled		concealed	displayed	furled	radiating	proximal	concealed	displayed	furled	radiating	distal	concealed
105875	displayed	unfurled	distal	concealed	displayed	furled	radiating	proximal		displayed	furled	radiating	distal	concealed
106012	displayed	unfurled		concealed	displayed	unfurled			concealed			radiating	distal	concealed
106034				concealed	displayed				concealed					concealed

Table S2. Detailed identification of the branching architecture of the *Hylaecullulus* specimens on Bed B of Charnwood Forest. Related to Systematic Palaeontology and Figure 1.

Supplemental references

S1. Carney JN. (1999). Revisiting the Charnian Supergroup: new advances in understanding old rocks. Geol Today. *15(6)*, 221–9.

S2. Noble, Stephen R.; Condon, Daniel J.; Carney, John N.; Wilby, Philip R.; Pharaoh, Timothy C.; Ford, Trevor D. (2015). U-Pb geochronology and global context of the Charnian Supergroup, UK: constraints on the age of key Ediacaran fossil assemblages. Geological Society of America Bulletin. *127 (1-2)*, 250-265