



ANATOMICAL AND ONTOGENETIC REASSESSMENT OF THE EDIACARAN FROND *ARBOREA ARBOREA* AND ITS PLACEMENT WITHIN TOTAL GROUP EUMETAZOA

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Abstract: Organisms in possession of a frondose body plan are amongst the oldest and most enigmatic members of the soft-bodied Ediacaran macrobiota. Appraisal of specimens from the late Ediacaran Ediacara Member of South Australia reveals that the frondose taxon *Arborea arborea* probably possessed a fluid-filled holdfast disc, the size and form of which could vary within populations. Mouldic preservation of internal anatomical features provides evidence for tissue differentiation, and for bundles of tubular structures within the stalk of the organism. These structures connect in a fascicled arrangement to individual lateral branches, before dividing further into individual units

housed on those branches. The observed fascicled branching arrangement, which seemingly connects individual units to the main body of the organism, is consistent with a biologically modular construction for *Arborea*, and raises the possibility of a colonial organization. In conjunction with morphological characters previously recognized by other authors, including apical-basal and front-back differentiation, we propose that to the exclusion of all alternative known possibilities, *Arborea* can be resolved as a total group eumetazoan.

Key words: Ediacaran, Eumetazoa, frondose, modularity.

Fossils of macroscopic, soft-bodied organisms are found globally in late Ediacaran rocks of ~570–541 million years in age. These fossils are considered to document a polyphyletic assemblage of diverse and morphologically complex marine organisms (Fedonkin *et al.* 2007; Budd & Jensen 2017; though see Hoyal-Cuthill & Han 2018). The Flinders Ranges of South Australia (Dunn *et al.* 2019, fig. S1) offer an exceptional record of these taxa within fine to coarse-grained sandstones of the Ediacara Member of the Rawnsley Quartzite (Droser *et al.* 2019). This unit documents a variety of shallow-marine and deltaic depositional environments (Gehling 2000; Gehling & Droser 2013; Callow *et al.* 2013; Tarhan *et al.* 2017) and contains the impressions of thousands of organisms representing at least 30 distinct macrofossil taxa. Although the precise mechanism by which these fossils are preserved is a matter of considerable debate (Gehling 1999; Retallack 2007; Tarhan *et al.* 2016, 2018; Bobrovskiy *et al.* 2019; Liu 2019), there is a general consensus that Ediacara Member palaeoenvironments were reasonably high-energy marine settings, and that the seafloor upon which the organisms

lived was covered by benthic microbial mat communities (Gehling & Droser 2009; Tarhan *et al.* 2017; Droser *et al.* 2019).

Fossil assemblages of the Ediacara Member are perhaps most widely known for possessing some of the oldest candidate bilaterian animals (Gold *et al.* 2015; Cunningham *et al.* 2017), including *Kimberella* (Gehling *et al.* 2014; Droser & Gehling 2015), *Parvancorina* (Paterson *et al.* 2017; Darroch *et al.* 2017; Coutts *et al.* 2017) and *Dickinsonia* (Evans *et al.* 2017; Hoekzema *et al.* 2017; Bobrovskiy *et al.* 2018; though see Sperling & Vinther 2010). Alongside these taxa, frondose organisms (Glaessner 1971) assigned to the unranked morphogroups Rangeomorpha and Arboreomorpha (Erwin *et al.* 2011) represent a comparatively little-studied component of the Australian Ediacaran assemblages. Frondose taxa are more typically known from older, deep-marine Ediacaran palaeoenvironments in Newfoundland (Canada) and England (Liu *et al.* 2015), but in the Ediacara Member they occur in shallow-marine facies interpreted to reflect deposition in delta front, sheet-flow and mass-flow

depositional environments (Gehling & Droser 2013; see also Tarhan *et al.* 2016). Frondose taxa represented in the Ediacara Member include *Charnia* (Gehling & Droser 2013), *Bradgatia* sp. (Droser & Gehling 2015) and *Pambikalbae* (Jenkins & Nedin 2007), and their facies distributions contrast with the shoreface and wave-base sand settings in which non-frondose taxa are most abundant (Gehling & Droser 2013). However, numerous discoidal impressions, initially interpreted as medusoids (Glaessner 1984) but more recently reinterpreted as holdfast structures of frondose organisms (Tarhan *et al.* 2015), may indicate that frondose taxa were reasonably abundant within all Ediacara Member palaeoenvironments. Taphonomic variation in disc expression currently precludes identification of original taxa in situations where the frond is absent (Gehling *et al.* 2000; Burzynski & Narbonne 2015; Tarhan *et al.* 2015).

The most common frondose taxon in the Ediacara Member is *Arborea arborea* (Glaessner & Daily 1959), the organism after which the morphogroup Arboreomorpha is named (Laflamme & Narbonne 2008; Erwin *et al.* 2011; Laflamme *et al.* 2018). *Arborea arborea* can be abundant on individual bedding surfaces within wave-base, sheet-flow and mass-flow facies (Laflamme *et al.* 2018; see *Charniodiscus* in Gehling & Droser 2013), and also occurs in low densities alongside more typical components of the Ediacaran biota (Coutts *et al.* 2016). Some *Arborea* specimens may have exceeded lengths of two metres (Dunn *et al.* 2019, fig. S2), making this one of the largest known Ediacaran macro-organisms. A detailed reassessment of frondose taxa in South Australia synonymized specimens previously assigned to *Charniodiscus oppositus*, *Charniodiscus arboreus*, *Rangea arborea*, *A. arborea*, and even some *Charnia* sp. within *A. arborea*, following determination of the three-dimensional structure of *Arborea* branches (Laflamme *et al.* 2018). That study diagnosed *Arborea* as a bifoliate frond with second order branches that lack rangeomorph sub-divisions (consistent with Laflamme & Narbonne 2008; Erwin *et al.* 2011; Brasier *et al.* 2012; Laflamme *et al.* 2018): an arrangement that is distinct from that observed in the type *Charniodiscus* material from the UK. We concur with these opinions, but to avoid confusion we resist drawing morphological comparison to arboreomorph taxa described from outside of Australia in this study. Whereas rangeomorph taxa have historically been assigned to multiple, often contradictory, phylogenetic positions within the

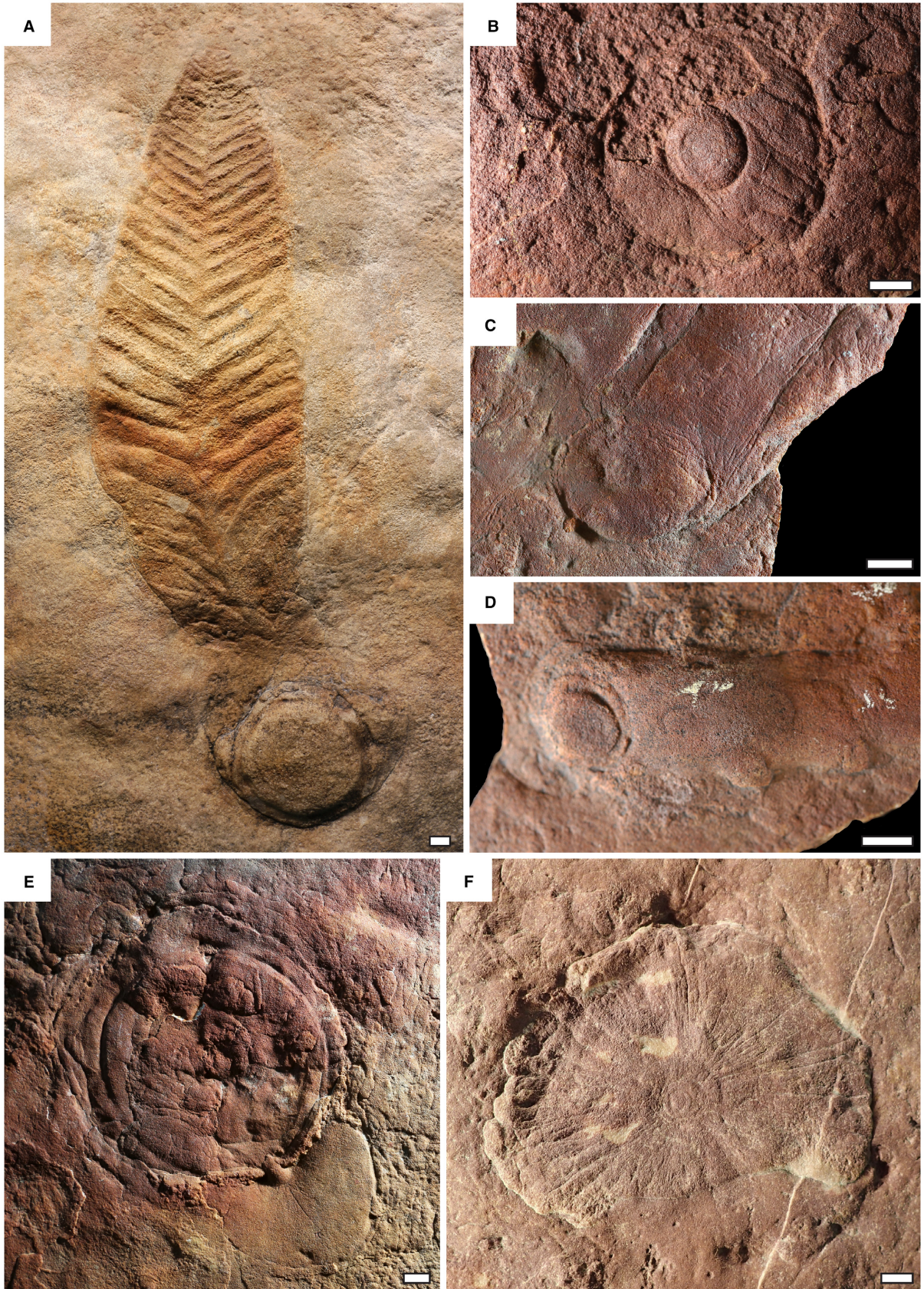
eukaryotes (summarized in Dunn *et al.* 2018), *Arborea* has only seriously been proposed to fall within either the hypothetical phyla Petalonamae (Pflug 1970, 1972; Hoyalcuthill & Han 2018) or Vendobionta (formerly Kingdom Vendozoa, more recently considered to be a class or order of rhizoid protists; Seilacher 1989, 2007; Buss & Seilacher 1994; Seilacher *et al.* 2003), or the Cnidaria (Jenkins & Gehling 1978). We here reassess the morphology of multiple *Arborea* specimens from South Australia, and build upon recent studies (Laflamme *et al.* 2018) to propose a new model for *Arborea* anatomy.

METHOD

We assessed 56 specimens that have either been historically assigned to *Arborea*, or recently synonymized with that taxon (Laflamme *et al.* 2018), in the collections of the South Australia Museum (SAM; Figs 1–5). Specimens were collected from South Australian fossil localities within the Ediacara Member of the Rawnsley Quartzite between 1957 and 2015; namely the Ediacara Conservation Park, the Flinders Ranges National Park, and National Heritage Site Nilpena (Dunn *et al.* 2019, fig. S1). Many of the studied specimens are incomplete, and when originally catalogued by their discoverers (who include M. Wade, M. Glaessner, W. Sun, R. Jenkins and J. Gehling), they were assigned to several different taxa. We follow recent synonymization (Laflamme *et al.* 2018) of these specimens, but note that we cannot categorically reject the possibility that some specimens may derive from a different taxon. Care has been taken to base the principal findings of this study only on specimens we are confident derive from a single taxon conforming to the most recent diagnosis of *A. arborea* (Laflamme *et al.* 2018).

Most of the studied specimens are preserved as positive hyporelief impressions on the bases of sandstone beds, but some reflect composite impressions of original external as well as internal anatomy. A small number of specimens are preserved in three dimensions, as sand-filled casts typically documenting external morphology (Laflamme *et al.* 2018), while one new surface (from Nilpena; Dunn *et al.* 2019, fig. S2) possesses very large specimens preserved in positive epirelief. These latter specimens remain *in situ* in the field. Key anatomical findings of Laflamme *et al.* (2018) include evidence for ‘dorso-ventral’ differentiation in *Arborea*, the inferred

FIG. 1. *Arborea arborea*, showing variability in the size and shape of *Arborea* holdfasts. All figured specimens are preserved as positive hyporelief impressions. A, complete specimen SAM P19690a, with an articulated holdfast. B, SAM P12888, with a single central boss and a stem whose width < holdfast diameter (stem is at bottom right). C, SAM P40332, holdfast with a stem with width = holdfast diameter. D, unlabelled specimen ‘52’, holdfast with a stem of width ≥ holdfast diameter. E, large holdfast, seemingly showing a fan of sediment (bottom right) emerging from the holdfast interior, SAM P40309. F, holdfast of a large frond (SAM P49366), with radially arranged striations. All scale bars represent 10 mm. Colour online.



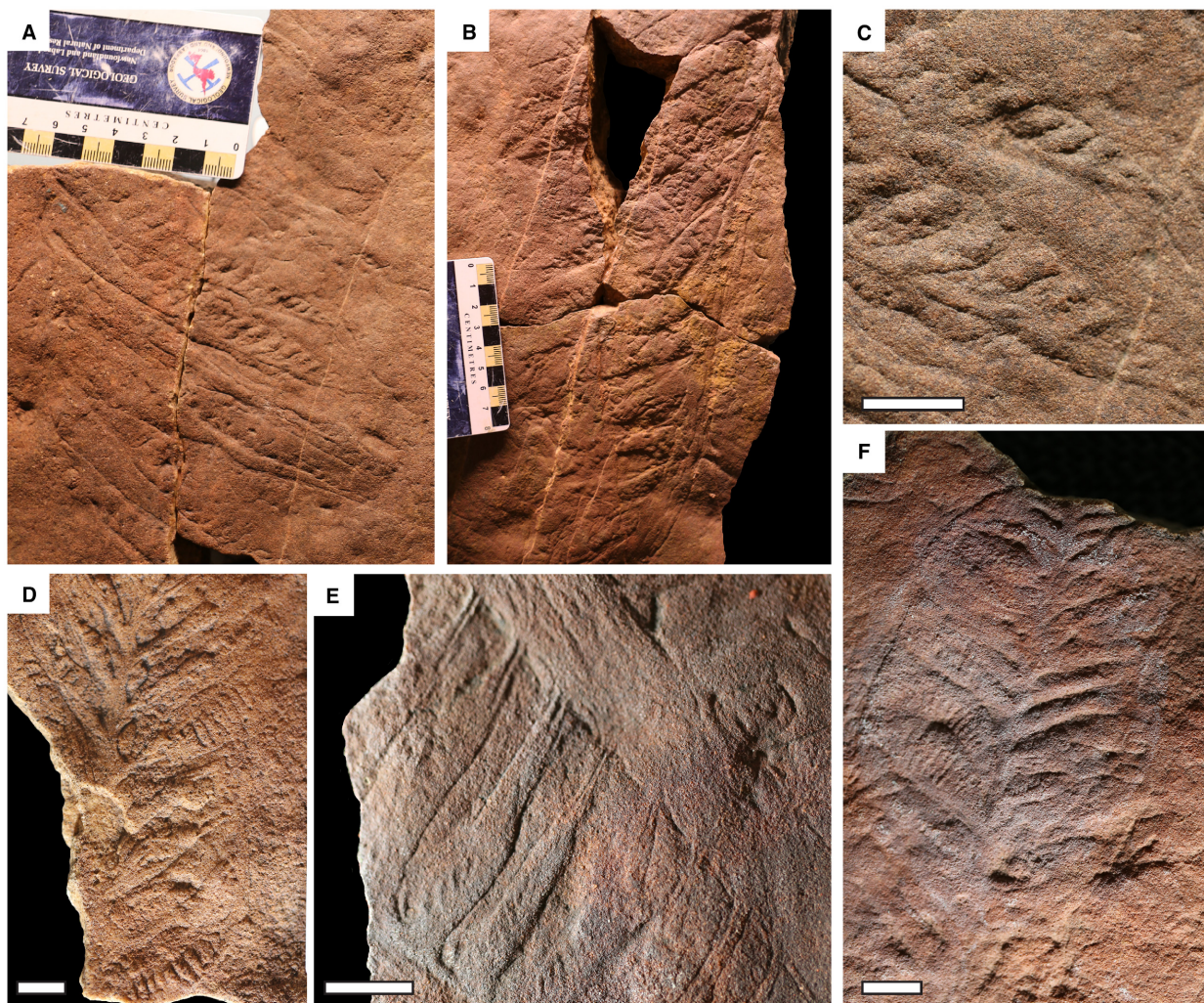


FIG. 2. Detailed lateral branch morphology in *Arborea* specimens demonstrating 'pod' and unit anatomy. A–C, SAM P40858, with lower order branches pointing upwards in A, but downwards in B on the opposite side of the frond, demonstrating that in life, these units were free to pivot along the branch axis; C, close up of lateral branches in A, with individual units showing comb-like sub-divisions. D, SAM P40952, lateral branches exhibiting units in the absence of 'pods'. E, SAM P42686, showing the connection between the 'pod' and the wide central stalk. F, SAM P40775, with units arranged on branches either side of a narrow stalk. All scale bars represent 10 mm. Colour online.

preservation of internal structures, and the ability for sediment to become incorporated within the specimens. We confirm those findings but interpret several additional anatomical observations to be biologically informative. We refrain from using phylogenetically loaded terminology in our description of *Arborea*, for reasons discussed in previous publications (Dunn *et al.* 2018).

RESULTS

Arborea arborea is composed of a holdfast, a stem, and an ovate, leaf-like frond comprising two rows of lateral

branches (following Runnegar 1995) emanating from either side of a central stalk (Fig. 1A). Each branch within the frond comprises smaller sub-divisions (here called units, previously referred to as second order branches) that appear to lie behind a covering structure, or 'pod' (*sensu* Laflamme & Narbonne 2008; Fig. 2). Known *Arborea* specimens range in size from complete specimens of just a few centimetres in length to incomplete fronds of over one metre (Dunn *et al.* 2019, fig. S2). The smallest studied specimen (SAM P40785; Fig. 3A) possesses ~19 lateral branches per row and is 3.5 cm in length, whereas specimens longer than ~4.5 cm in length (SAM P48727, Fig. 3E; or P19690a, Fig. 1A) often possess >30 lateral branches. One large incomplete frond possesses at

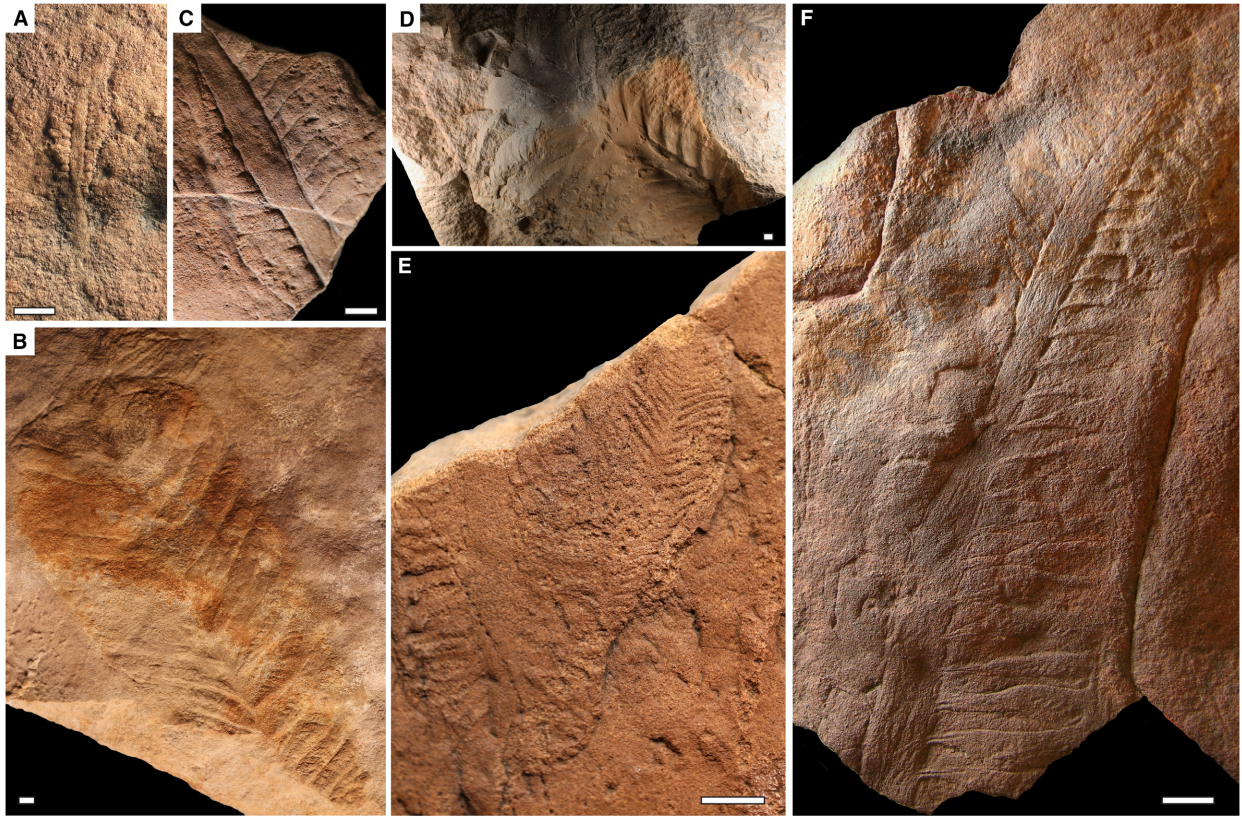


FIG. 3. The ‘sidedness’ of *Arborea*. A, SAM P40785, the smallest specimen studied, with no visible sub-division of lateral branches. B, SAM P19690b, the tip of the frond is over-folded revealing the two sides of the organism; the bottom of the frond shows ‘pods’ and units, and the tip of the frond (over-folded section) shows undifferentiated rectangular branches with no visible ‘pods’ or units. C–D, SAM P34499 and SAM P35704b respectively, exhibiting smooth rectangular panels interpreted as the ‘back’ of the organism. E, SAM P48727 with lateral branches visible in one of the smallest described specimens. F, SAM P42686, ‘pods’ and units clearly visible (interpreted as the ‘front’ of the organism), with rectangular undifferentiated branches absent. All scale bars represent 10 mm. Colour online.

least 33 branches (SAM P40858), while a newly discovered specimen has >49 (Dunn *et al.* 2019, fig. S2). The frond outline transitions from tapering (in terms of branch length) at both tips in smaller specimens (fusiform), to tapering primarily at the apical tip. In a specimen ~4.5 cm in length (Fig. 3E) the basal-most branches are ~40% of the length of the longest branches, whereas in a specimen ~30 cm in length (Fig. 1A) the basal-most branches are ~78% of the length of the longest branch. The following description provides a model of the anatomy of *Arborea* (Fig. 6).

Arborea possesses a holdfast structure that may variously exhibit a small number of concentric rings (Fig. 1A, D), a prominent but smooth central boss (Fig. 1B; Dunn *et al.* 2019, fig. S3), or multiple radial grooves (Fig. 1F). Such structures have, when found in isolation, previously been referred to discoidal taxa such as *Aspidella* or *Eoporpita* (Wade 1972; Tarhan *et al.* 2017), but those are now largely interpreted as organ taxa, with much of the observed variation in discoid morphology asserted to be

taphonomic in origin (Tarhan *et al.* 2015; Burzynski *et al.* 2017). The holdfast connects at its centre to a single stem (Fig. 1), and varies in size relative to the width of the stem within the studied population, being of roughly equal diameter in some specimens (Fig. 1C, D), or 3–4 times larger in others (Fig. 1F). This variation does not appear to be directly correlated to specimen size (here measured as frond length), with a specimen of ~30 cm in length (SAM P19690a; Fig. 1A) possessing a holdfast of 108.6 mm diameter, while another >>74.45 cm (SAM P40858) possesses a holdfast of only 82.2 mm diameter. In one specimen, a holdfast is associated with an arcuate fan of sandy material (Fig. 1E). This fan does not exhibit any of the morphological characters typical of frond holdfasts (e.g. a central boss, or radiating striations), and a narrow projection of sand associated with the holdfast margin appears to connect the base of this disc to the ‘arcuate fan’ that lies stratigraphically above it. This relationship would be highly unusual in two overlapping discs. Together with its distinct morphology, this leads us to

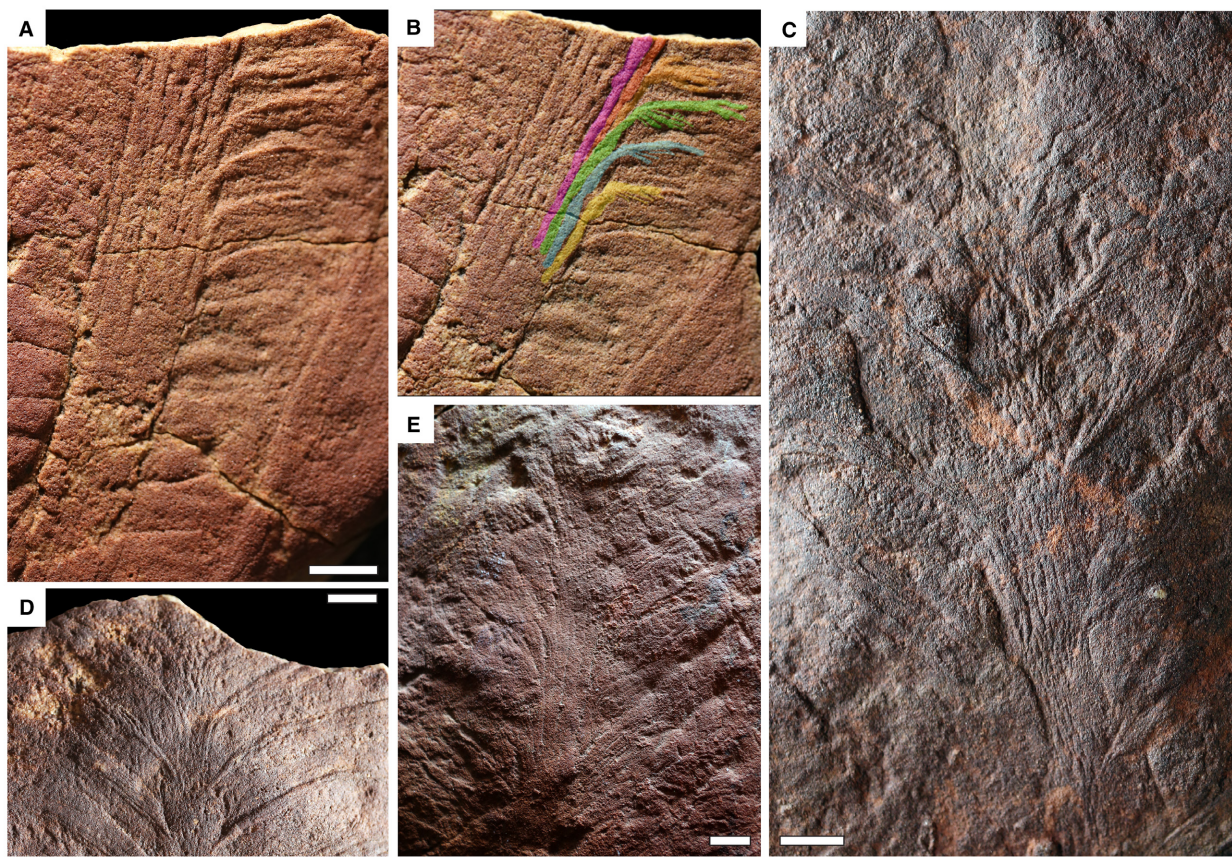


FIG. 4. The fascicled arrangement of branches in the stem of *Arborea arborea*. A–B, SAM P47800, individual tubular structures in the stem; A, tubular structures connecting in a one-for-one relationship to individual lateral branches, highlighted in B. These branches then either de-bundle or branch within the individual lateral branch. C–E, SAM P13801, SAM P47799 and SAM P51200 respectively, exhibiting the fascicled arrangement of tubular structures running up the stem and into individual lateral branches, where they divide further. All scale bars represent 10 mm.

postulate that this fan does not reflect the impression of a second holdfast. We instead suggest that the sediment fan represents fluidized sediment emanating from a break in the wall of the large holdfast. The sediment fan is similar in morphology to lobate structures produced by fluid escape in other late Ediacaran mat-bound sedimentary units (e.g. the Longmyndian Supergroup of the UK; Menon *et al.* 2016).

Within the studied population, the stems can exhibit variable relative lengths (see Fig. 1A for a very short example), an observation that in other taxa has been considered functionally significant in terms of ecological tiering (Laflamme *et al.* 2012) or reproduction (Mitchell & Kenchington 2018). Stem length shows no clear relationship to frond size. Stems can be smooth and featureless (Fig. 1D), finely wrinkled (Fig. 1C) or composed of numerous grooves and ridges that run parallel to their length into the stalk (Figs 3F, 4). These structures distally taper in width, and do not branch or amalgamate within the stalk. They do not continue into the holdfast in any

studied specimen, and appear to record tubular structures extending up the stalk (Fig. 4). Along the length of the frond, individual tubes successively exit the stalk and become the primary axis for individual lateral branches (e.g. Fig. 4A). The tubes can connect to branches either at the margin of the stalk (Figs 2E, 4A, C), or closer to its centre (Fig. 4D).

The frond itself is composed of two rows of lateral branches (one on either side of the central stalk; Laflamme *et al.* 2018), which appear either bilaterally or alternately arranged across the midline. The longest branches are present in the middle of the frond, with branch lengths diminishing both apically and basally (Fig. 1A). *Arborea* has previously been described as possessing branches resembling ‘pea pods’ (Laflamme *et al.* 2018), with two sheet-like structures representing a continuation of the stalk wrapping up and around the serially-arranged units. Observed fronds typically show one of two possible branch variants. The first comprises solid, almost featureless rectangular blocks, which can

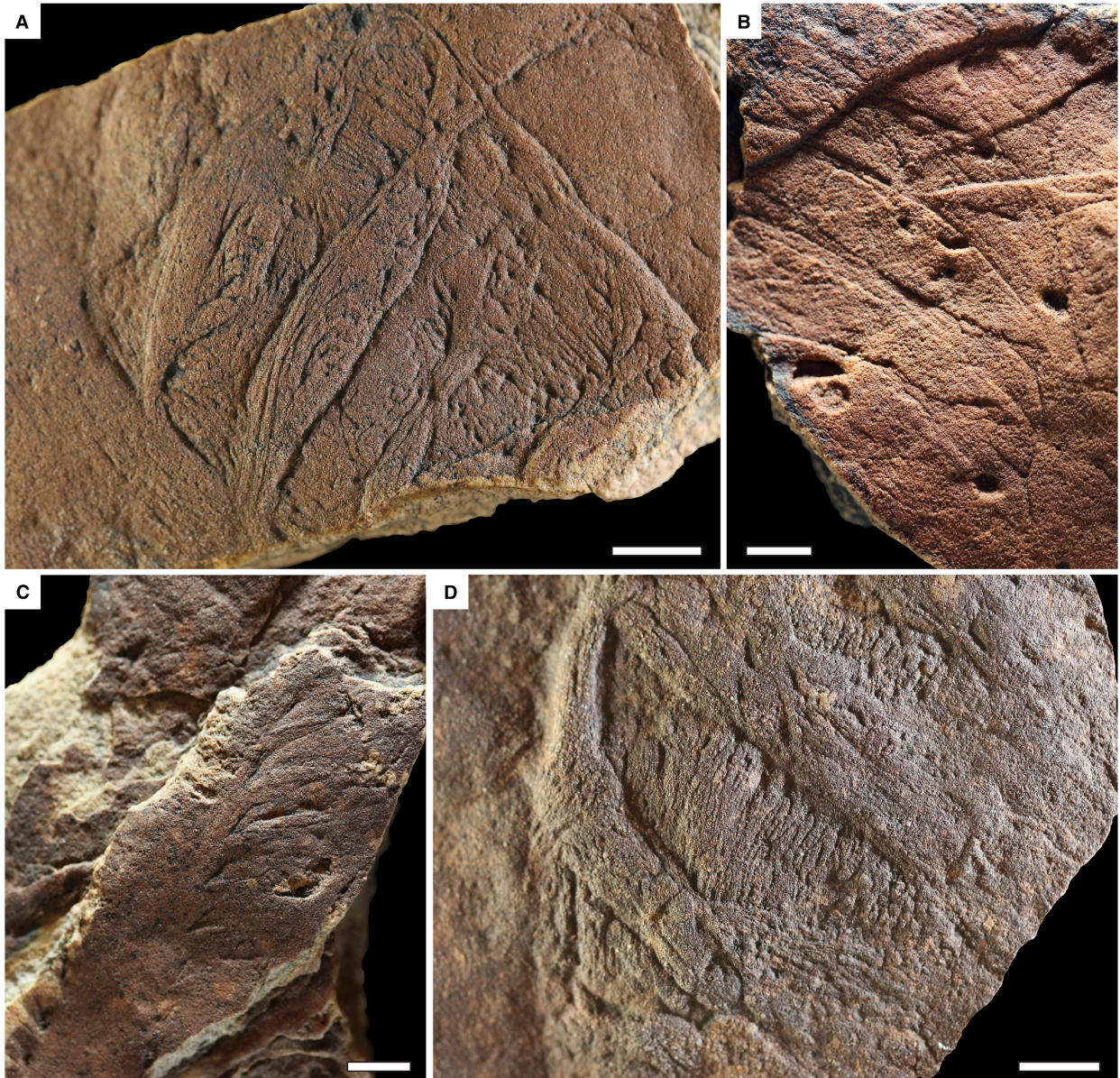


FIG. 5. The backing sheet and lateral margin of *Arborea*. A, SAM P40786, with lateral branches splitting off the stalk (at left), but also connecting to the lateral margin; linear striations running apico-basally between and seemingly beneath the lateral branches may indicate the presence of a wrinkled backing sheet underlying the branches. B, SAM P40772, exhibiting a striated surface, interpreted as the backing sheet, in between the lateral branches. C, SAM P40369, individual branches connecting to a lateral margin (at right). D, SAM P40773, revealing a striated backing sheet between the relatively smooth lateral branches. All scale bars represent 10 mm. Colour online.

occasionally exhibit transverse linear ornament. These abut one another to form a continuous smooth impression (e.g. Figs 1A, 3C). The second variant exhibits branches with a lenticular ‘pod’, partially covering a row of finely divided units along the length of the lateral branch (Fig. 2). In such cases, each lateral branch attaches to the central stalk via a single tubular structure (e.g. Figs 2D–E, 4). The distal end of each branch can also attach to the frond margin in some specimens, along

what has previously been termed an undivided or marginal rim (Glaessner & Daily 1959; Jenkins & Gehling 1978). The secondary units within individual lateral branches can be oriented either apically or basally even within individual specimens (compare Fig. 2A, B), suggesting that they could pivot along the branch axis. In the smallest specimens, lateral branches appear bulbous, with no units visible (Fig. 3A). Each unit is rectangular to tear-shaped and may exhibit one order of transverse sub-

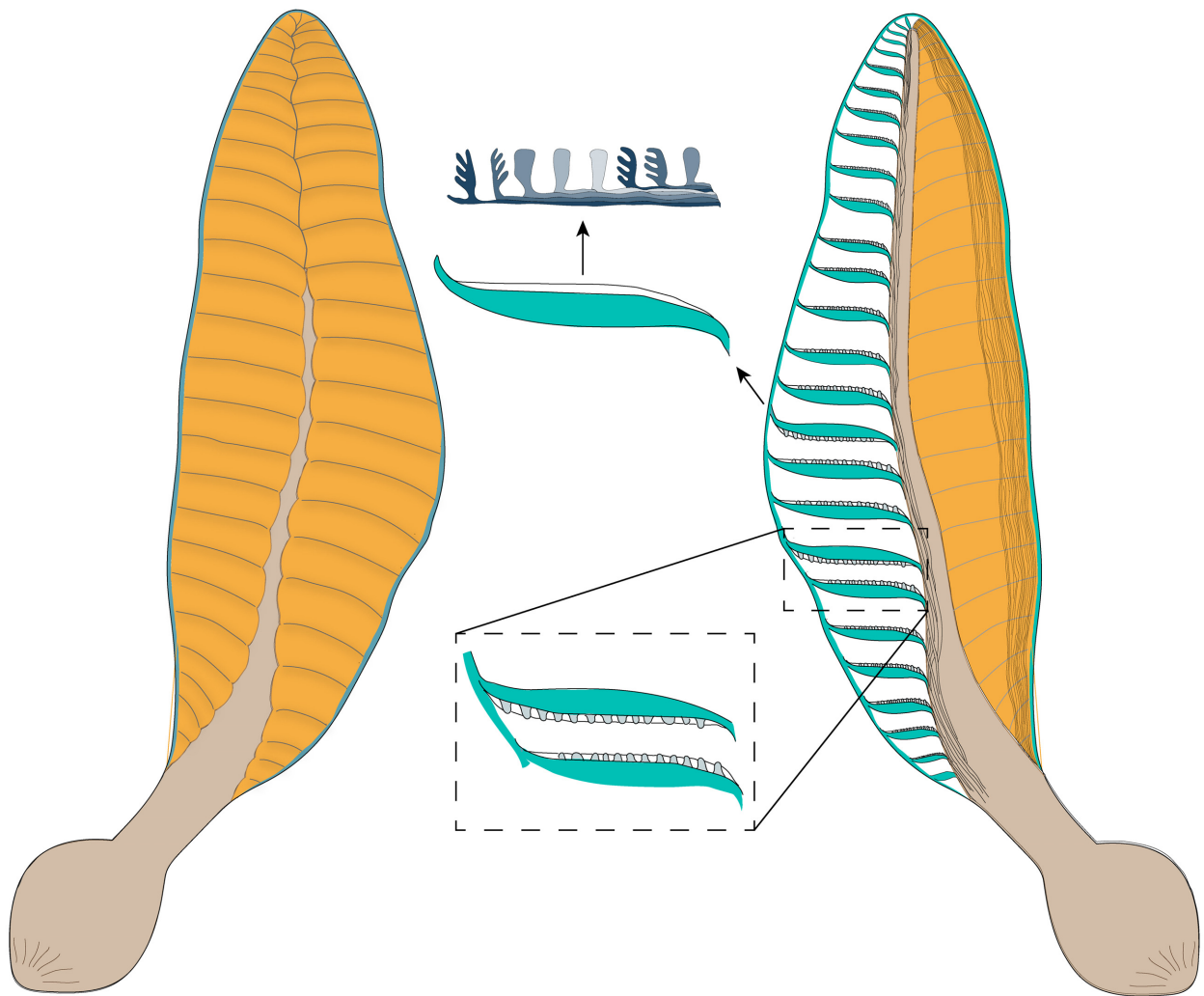


FIG. 6. An anatomical reconstruction of the Ediacaran frondose taxon *Arborea arborea*, based on the features discussed in this study. The 'back' (left) and 'front' (right) faces of the organism are shown. The right-hand side of the front shows the organism with the 'pods' and units (i.e. the branches) removed to reveal the underlying backing sheet. Inset: fine-scale arrangement of units within the 'pod'. Units are each connected to their own tubular, stolon-like structure running into the stalk. Note that pods (green) are free to pivot about the lateral branch axis.

divisions along its length (Figs 2A, 3B; termed striations by Hoyal-Cuthill & Han 2018). These subdivisions appear to emanate in a single direction, suggesting a comb-like morphology for individual units.

The tubular structures running along the stalk connect to individual lateral branches in a one-to-one, fascicled, arrangement (Fig. 4). They then divide and orient themselves perpendicular to the lateral branch, before branching further, or debundling, at regular intervals (Fig. 4A–C). Specimens only rarely exhibit both tubular structures and branch units. The tubular structures run up the lateral branches to their distal margin, dividing/debundling as they go to correspond, in a one-for-one relationship, with the expected positions of individual units that sit within the 'pod' (Figs 4A, C; 5A).

The lateral branches may additionally be underlain by a set of unidirectional linear striations arranged parallel (e.g. Fig. 5A, D) or oblique (Fig. 5B) to the marginal rim. These can be present across the entire width of the frond between the stalk and the lateral margin. This striated fabric may reflect a continuous sheet-like structure.

DISCUSSION

Model of anatomy

Holdfasts are rarely preserved in association with complete *Arborea* fronds, most likely due to both the large size of *Arborea* specimens and because in life much of

the holdfast may have been located beneath the sediment–water interface, and thus in a different plane of preservation (although preservation varies between beds; see Fig. 1A and Dunn *et al.* (2019, fig. S3) for examples of fronds and holdfasts preserved in the same plane). In the three clearest examples within the studied collection, where the complete frond and holdfast disc are articulated, there is no relationship between the size of the frond and the size of its associated holdfast, although the smallest specimen does possess the smallest holdfast structure. Laflamme *et al.* (2018) referred to one specimen (their fig. 2.2) as ‘deflated’. Our observation of variable holdfast size is consistent with this interpretation. The ability of holdfasts to deflate, either during life or upon burial, is consistent with the organism being able to control and modify its shape. This interpretation is supported by the specimen with a fan of what appears to be escaping sediment (Fig. 1E), which may imply fluid fill within such holdfasts, and thus a potential ability to hydrostatically control holdfast size. An ability to actively modulate holdfast shape and size would imply the presence of contractile (muscular?) tissue (Jenkins & Gehling 1978), though in the absence of further data, contraction due to dehydration could represent an alternative possibility. An absence of contraction rims or disturbed sediment surrounding the specimens may suggest that this is unlikely.

The stalk of *Arborea* was likely to have originally been cylindrical (Laflamme *et al.* 2018), as supported by observed variation in the position of branch connection points, and the presence of both alternating and bilaterally symmetrical branch arrangements amongst the studied population. We consider at least some of this variation to result from rotation of the branch connection points out of the plane of preservation prior to compression of the cylindrical stalk, followed by their composite moulding on to the stalk in their ‘rotated’ positions. It is difficult to determine whether lateral branches were originally arranged in an alternating or bilaterally symmetrical manner, since these two branching arrangements are observed in almost equal numbers within the studied population.

The fascicled arrangement of tubular structures in the stalk and within the lateral branches (Fig. 4) appears to document the connection of individual units along each branch to the central part of the organism. These tubular structures extend into the stalk beyond the position expected of branches, and since *Arborea* is only known to possess two rows of branches, we do not consider the tubes to represent overprints of other lateral branches. The consistent one-for-one relationship of the tubes with individual lateral branches in multiple specimens precludes taphonomic interpretations such as wrinkling of an epithelium or a similar soft-tissue structure. It is not

currently possible to determine whether these tubes were originally hollow or solid structures.

Since the tubular structures are most commonly observed when the pods and units assumed to reflect the exterior surface of the lateral branches are not preserved, we interpret the tubes as internal anatomical features. The relatively sharp boundary between these tubular structures and the smooth stem in some specimens (e.g. Fig. 4A) indicates that this difference is unlikely to be taphonomic in origin. Differential preservation of the smooth exterior of the stalk and these internal structures (Figs 3C; 4A, C) implies that they originally comprised different anatomical structures, suggestive of ‘tissue’ differentiation.

The tubular structures we report were documented and termed spicules by Glaessner & Wade (1966; see also Jenkins & Gehling 1978), an interpretation focusing on their sharp outlines and straight trajectories. However, their preservation as impressions rather than as biomineralized structures, the observation that they bend to extend into the branches, the presence of examples that curve and are clearly not straight within the stalk, and their ability to divide within the lateral branches (Fig. 4), lead us to question this hypothesis. True spicules in extant poriferans and cnidarians exhibit a variety of form. In cnidarians, calcitic spicules represent a derived condition, being present only in the Octocorallia. They are secreted by the mesoglea and are largely concentrated in the base of the colony, but may also be present in polyp leaves, or on anthocodia (Hyman 1940). In siliceous sponges, spicules are generally classified as either microscleres (smaller ‘flesh’ spicules) or megascleres (the main skeletal support elements). Megascleres are known to reach sizes of up to 3 m (and be up to 8.5 mm in diameter) in the basalia of *Monorhapis chuni*, where they function as a stalk (Müller *et al.* 2007). More commonly, microscleres are on the order of 1–60 µm, whereas megascleres are between 60–200 µm, and both can bundle and inter-weave (e.g. in the order Halichondrida; Hooper & van Soest 2004). The continuation of tubular structures up the stalk of *Arborea* and into its individual branches and units is an arrangement not seen in any extant spicular organism.

An alternative possibility, favoured here, is that the tubular structures in *A. arborea* represent non-mineralizing, stolon-like projections, consistent with their length, seemingly flexible nature, and one-to-one relationship with individual lateral branches and then units (Fig. 4). Stolons or stolon-like projections represent a derived condition in the Bilateria, but are nevertheless possessed by several invertebrate groups (e.g. the Bryozoa (Osborne 1984) and Entoprocta (Nielsen 2012, p. 201)) as well as many plants (de Kroons & Hutchings 1995) and algae (Ceccherelli *et al.* 2002), while fungal mycelia (Benjamin & Hesseltine 1949) may also produce thread-like projections. Horizontal creeping stolons are known in many land

plants (e.g. *Fragaria ananassa*; Savini *et al.* 2008) and in algae (e.g. *Caulerpa prolifera*; Ceccherelli *et al.* 2002). In the siliceous and calcareous sponges, stolons can take a variety of forms, including creeping stolons (e.g. the calcareous sponge *Leucosolenia*; Padua & Klautau 2016) and reinforced structural stolons (e.g. the carnivorous demosponge *Chondrocladia lyra*; Lee *et al.* 2012). Poriferan stolons are not known to bundle. Cnidarian clades exhibit stolons with morphological expressions that encompass horizontal creepers, and (particularly in the Hydrozoa) bundled vertical projections (Schuchert 2001), or fascicles. These fascicles may surround a ‘true’ stem but be encompassed by periderm (e.g. in the hydrozoan *Plumularia*; Hyman 1940 fig. 116) or may themselves comprise the stem (e.g. in the hydrozoan *Eudendrium*; Hyman 1940, fig. 116). Such fascicled branches provide the most similar extant analogue for the arrangement of tubular structures seen in *A. arborea*.

If the holdfast of *Arborea* was hydrostatically regulated, some form of hydraulic system would be expected. We find no firm evidence for any such system, but note that some extant hydraulic systems, such as the inhalant and exhalant siphonozooids of pennatulaceans (Williams *et al.* 2012) are unlikely to be expressed in known specimens of Ediacaran frondose taxa due to their position beneath branch attachment points along the stalk. Alternatively, the fascicled tubes may have been involved in hydraulic regulation, particularly if the individual units to which they connect were open to the water column.

The ‘backing sheath’ in *Arborea* (the apparent connective structure that joins the stalk with the marginal rim) may have anchored the lateral branches in place, though Laflamme *et al.* (2018) proposed that the rim could alternatively reflect folding of the distal tips of the lateral branches. The Russian frondose taxon *Charniodiscus yorgensis* has also been interpreted as having first-order branches that are constrained along their horizontal axes, but unlike *A. arborea*, *C. yorgensis* is reconstructed as exhibiting full branching units on both sides of the organism (Ivantsov 2016). No fascicled branching arrangement has been noted in *C. yorgensis* despite the pyritization of internal anatomical features.

The observation that ‘pods’ and units can be present or absent in *Arborea* specimens, even within individual specimens (Fig. 3B), is consistent with the suggestion that they are only present on one side of the organism, conferring front–back differentiation (Fig. 6; Jenkins & Gehling 1978; Laflamme *et al.* 2018). The ‘back’ of the organism comprises the backing sheath, subdivided into rectangular blocks defined by lateral seams. The linear striations observed running behind lateral branches in certain specimens (e.g. Fig. 5A) are interpreted to reflect either the inner surface of the backing sheath, or a distinct layer within the organism. In addition to the clear apico-basal

differentiation of the organism, this character could potentially assist in constraining phylogenetic affinities.

Lateral branches were attached to the stalk by both a tubular continuation of external tissue, and by the internal tubular projections (leading to apparent pairing of connections in some specimens; Gehling 1991). Lateral branches consist of two main elements: the ‘pod’, which was constructed of two lens-shaped sheets (not bound to each other at either their apical or basal margins) and the sub-rounded to comb-shaped units (Fig. 6, inset), which lay within the pod. Previous studies have considered subdivisions within second order units to reflect wrinkling of a soft tissue structure (Laflamme *et al.* 2018) but their consistent morphology both within and across specimens leads us to consider them biological features. We note that the first order branches of *Arborea*, being comprised of a lenticular ‘pod’ and subdivided units housed therein, differ fundamentally in architecture from the linear subdivisions seen in second and third order units. This distinction does not fit the ‘self-similar’ branching definition of the Rangeomorpha, and we therefore follow previous workers (e.g. Laflamme & Narbonne 2008) in considering branching arrangements in *Arborea* to be distinct.

If the pod does indeed surround the units, this has potentially interesting implications for the production of micro-eddies and flow disturbance around the units (which have previously been hypothesized to explain community dynamics in Ediacaran fronds; Singer *et al.* 2012; Ghisalberti *et al.* 2014) potentially aiding nutrient uptake in these regions. Laflamme *et al.* (2018) noted similarities between *Arborea* morphology and feeding in extant pennatulaceans.

The anatomical arrangement we describe is distinct from both the fractal rangeomorphs (Narbonne 2004), which diagnostically require three orders of identical branching (Erwin *et al.* 2011), and also from the latest Ediacaran erniettomorph *Swartpuntia germsi*, which is characterized by a multi-vented arrangement of featureless tubular branches (Narbonne *et al.* 1997). Recent studies suggesting a close phylogenetic relationship between the morphogroups Rangeomorpha, Arboreomorpha and Erniettomorpha (Dececchi *et al.* 2017; Hoyal-Cuthill & Han 2018) do not find support from our re-analysis of the anatomy of *Arborea*.

Growth

The anatomical organization described above permits inference of the morphogenetic strategy of *Arborea*, which is informative when considering organismal affinities. The smallest, assumed to be youngest, specimens of *A. arborea* possess fewer branches than larger specimens. This suggests that branch growth and differentiation actively

occurred during the frondose stage of the organism's life cycle, with new tubular structures presumably developing and terminally differentiating as the frondose organism grew (rather than undergoing a single event of terminal differentiation). We find no upper size limit to *Arborea*, and thus suggest that it may reasonably be interpreted to have displayed indeterminate (size) growth, with no known maximum number of branches. Significant branch differentiation appears to have occurred in small specimens, with the smallest known specimens (~3.5 cm) possessing ~19 lateral branches. *Arborea* also shows a determinate (i.e. consistent and predictable) form within the studied population, with no evidence for aberrant branches (branches that are unusually long or short, or do not conform to the expected branching architecture; e.g. Kenchington *et al.* 2018). That the frond outline appears to change as specimen size increases, with the basal-most branches becoming relatively larger despite continued branch differentiation, suggests that new branches in *Arborea* differentiated from a (sub)apical generative zone (as indirectly inferred by Hoyal-Cuthill & Han 2018). We find no evidence for further, lateral generative zones.

An ordered fascicled branching arrangement requires a unidirectional guidance and pathfinding system along both the apico-basal and front-back axes. Pathfinding refers to the ability of a cell or group of cells to locate their final destination: neurons, for example, are able to find their destination by growing in permissive substrates and binding to adhesive cues (Raper & Mason 2010). Differentiation of the tubular structures (fascicles) into both branches and units occurs only after they emerge from the stalk wall, suggesting either the removal of an inhibitory signal within the stalk, or the presence of a positive differentiation signal in the stalk wall. The strategy outlined above is consistent with morphogenesis of branches in *Arborea* having occurred by localized outgrowth, as opposed to regional apoptosis (from an undifferentiated sheet). This is in line with many other forms of branching growth in extant eukaryotes, for example that seen in the alga *Ectocarpus* (Katsaros *et al.* 2006), or the bilaterian tracheal network (Affolter *et al.* 2009).

Phylogenetic placement of Arborea

It is reasonable to assume that the anatomical complexity and large size of some *Arborea* specimens (~2 m in length) demonstrate that it was a multicellular organism, dwarfing even the largest multinucleate protists (xenophyophores). Indeterminate growth is compatible with several non-metazoan (e.g. Peterson *et al.* 2003) and metazoan (Sebens 1987) hypotheses of affinity, and is thus not considered an informative character here.

Arborea lacks the serially quilted arrangement that has been considered diagnostic of the Vendobionta, and inferred in some rangeomorph taxa (Seilacher *et al.* 2003; Seilacher 2007). The constrained form of *Arborea* within populations exhibits no aberrant branches, a lateral margin bounding the branches, and determinate changes in form (i.e. a transition from a fusiform to a distally tapering frond outline). This is inconsistent with the growth pattern of many extant modular groups (e.g. plant or algal groups), and some multifoliate rangeomorphs, which are characterized by a lack of constrained form (Kenchington *et al.* 2018). The differentiation of new branches as *Arborea* grew is also incompatible with a fungal affinity, where a fruiting body undergoes one round of terminal differentiation (Umar & Van Griensven 1997). We therefore consider that to the exclusion of extant non-metazoan comparators, *A. arborea* was a total group metazoan.

The constrained form, presence of two main body axes, and extensive body regionalization is incompatible with a poriferan affinity, but such an axial arrangement is compatible with a eumetazoan affinity. We recognize differential preservation of anatomical features in *Arborea*, with structures in the interior of the organism being preserved, and external structures being entirely or partially missing in different specimens. This implies that these structures were distinct, and potentially composed of different original materials, and could indicate tissue differentiation: a eumetazoan character. Possession of a fluid-filled holdfast, potentially indicating a capacity for hydrostatic regulation, is also compatible with, but not unique to, a eumetazoan affinity. On the basis of all available evidence, we therefore propose that *A. arborea* lies within the Eumetazoa. Such a phylogenetic position has been presented previously (Buss & Seilacher 1994; Hoyal-Cuthill & Han 2018; though we disagree with the monophyletic clade of Ediacaran organisms favoured by these authors) but this reassessment of *Arborea* provides developmental and anatomical support. Our current knowledge of anatomical characters in *Arborea* is insufficient to permit further constraint of its phylogenetic position.

The fascicled internal anatomy of *Arborea* suggests that each lateral branch grew independently of its neighbours, implying developmental independence and thus conforming to the definition of biological modularity. Such an arrangement is comparable with extant taxa that possess colonial organization (e.g. various hydrozoans; Hyman 1940) and it is therefore entirely feasible that *Arborea* could represent an Ediacaran colonial eumetazoan (*contra* Landing *et al.* 2018). Coloniality has previously been predicted to be the plesiomorphic condition for the Cnidaria, with *A. arborea* itself (then termed *Charniodiscus*) proposed to lie at the base of the cnidarian tree (Dewell 2000; see also putative stem-group colonial cnidarians

from Cambrian Series 3; Park *et al.* 2011). However, more recent work (Zapata *et al.* 2015; Kayal *et al.* 2018) would suggest that this scenario is unlikely, with coloniality only being known in derived cnidarian positions. Ctenophores are not known to be colonial (we favour the view that Porifera represents the earliest diverging animal clade; Simion *et al.* 2017; Fueda *et al.* 2017) suggesting that the Ur-eumetazoan was a unitary organism. Coloniality is also noted as a derived condition within the Bilateria, with the only truly colonial phylum being the Bryozoa. If our interpretation of *Arborea* as a potentially colonial organism is correct, this may suggest that coloniality in eumetazoans was present in early-diverging groups. With no current evidence to tie *Arborea* to any crown group, this character could feasibly be present in early-branching positions of the eumetazoan stem-lineage, suggesting further (perhaps derived) excursions into the colonial state were possible, thus broadening the possible permutations of the eumetazoan ancestor.

CONCLUSION

Reconstruction of the anatomy and developmental biology of *Arborea arborea* leads us to conclude that it represents a total-group eumetazoan. In addition to previously recognized morphological characters (Laflamme *et al.* 2018) we note a distinctive fascicled internal branching arrangement and a fluid-filled holdfast. The different taphonomic expressions of structures within the studied *Arborea* collection imply the possible presence of different tissue types, and thus tissue differentiation. We conclude that *Arborea* was a modular organism, and note that it displays characters consistent with (but not exclusive to) a colonial body-plan, something previously argued to have emerged in eumetazoans only in the Ordovician (Landing *et al.* 2018). Key differences between *Arborea* and rangeomorphs support morphological distinction between these frondose organisms, hinting at multiple independent excursions into frondose morphospace amongst early diverging animal groups.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8t8h54h>

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