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THE ARCHITECTURE OF EDIACARAN FRONDS

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Abstract: Ongoing discoveries of new rangeomorph fossils from the Ediacaran of Avalonia allow us to put forward a unified and approachable scheme for the description and phylogenetic analysis of frondose genera and their species. This scheme focuses upon the branching morphology of rangeomorph units. Our system has the advantage of being applicable at all visible scales of subdivision and is suitable for the study of isolated fragmentary specimens. The system is also free from hypothesis about biological affinity and avoids tectonically influenced features such as shape metrics. Using a set of twelve character states within this unified scheme, we here present emended diagnoses for *Beothukis*, *Avalofractus*, *Bradgatia*, *Hapsidophyllas*, *Fractofusus*, *Trepassia* and *Charnia*, together with a more extensive taxonomic treatment of the latter genus. For those forms that fall within the morphological spectrum between *Trepassia* and *Beothukis*, we introduce *Vinlandia* gen. nov. It is hoped that this scheme will provide a robust framework for future studies of rangeomorph ontogeny and evolution.

Key words: Ediacaran, rangeomorph, architecture, morphology, taxonomy, *Vinlandia*, Avalonia.

EDIACARAN fossils from the Avalon terrane represent some of the earliest known macroscopic fossil assemblages, ranging from *c.* 580 to 560 million years old (Brasier and Antcliffe 2004; Narbonne 2005). Interpretation of these and other Ediacaran fossils as multicellular animals ancestral to the Cambrian explosion of Metazoa has excited much interest (e.g. Glaessner 1966, 1984; Pflug 1971; Fedonkin 1985, 2003; Gehling 1991; Runnegar 1992; Fedonkin *et al.* 2007). However, this view currently rests in the balance; alternative affinities including fungal (Peterson *et al.* 2003) and protozoan (Pflug 1972*a*, *b*; Zhuravlev 1993; Seilacher *et al.* 2003) relationships have been proposed, while doubt has also been cast on suggested direct relationships with crown group Metazoa (Antcliffe and Brasier 2007*a*, 2008).

Over the last decade, there has been a concerted effort to document occurrences of frondose (adj. meaning to possess a frond; see Table 1) Ediacaran fossils on bedding planes in both England and Newfoundland, making use of conventional approaches (Narbonne and Gehling 2003; Laflamme *et al.* 2004, 2007; Hofmann *et al.* 2008; Laflamme and Narbonne 2008; Narbonne *et al.* 2009), as well as new technologies including high resolution laser scanning and digital mapping (e.g. Antcliffe and Brasier 2008; Brasier and Antcliffe 2009), and large-scale casting programs (e.g. Edwards and Williams 2011; Wilby *et al.* 2011). These recent efforts have brought forth remarkably preserved fossils that reveal, in unprecedented detail, the architecture and structure of several Ediacaran taxa. New observations made on these and other fresh materials have the potential to lead us to a better understanding of the construction of rangeomorph organisms (*sensu* Narbonne 2004), and their rules for growth (cf. Brasier and Antcliffe 2004).

Below, we set out broad constructional rules and a clear, coherent taxonomic scheme to describe the rangeomorph architectures found within frondose Ediacaran fossils. Although there have been prior attempts at such an endeavour (e.g. Pflug 1972*a*, *b*; Jenkins 1992; Laflamme and Narbonne 2008; Narbonne *et al.* 2009), newly emerging details of Avalonian fossils arguably permit a much more complete understanding of the architecture of frondose organisms than was previously possible. Prior terminology was often influenced by questionable views about biological relationships (e.g. use of cnidarian terms such as 'rachis'; Jenkins 1985). Laflamme and Narbonne (2008) have done much to help rationalise the terminology of the field, and their significant contribution in that regard is welcomed. In recent papers, we have gone further, and argued for a fresh approach to ontogeny and evolution (e.g. Brasier and Antcliffe 2004, 2009). This requires terminologies that are appropriate to the study of self-similar

TABLE 1. A glossary of terms useful for the description and analysis of frondose rangeomorphs.

Alignment: the orientation of *branches* with respect to the *growth axis* and to each other (Fig. 2B–D; see also *subparallel*, *irregular* and *radiating units*).

Apical growth tip: distal tip of a *frond* that contains the main generative zone. It helps to define the *polarity* of a *frondose organism* (Fig. 1A–F).

Apical insertion: addition of new *branches* at the *apical growth tip*, with inferred gradual displacement of these down the *growth axis* as new *branches* are added at the apex.

Basal disc: disc or bulb that anchors the organism to the substrate. If present, it occurs at the base (proximal end) of the *frondose organism*, to which it may be connected by a *stem*.

Base of the unit: end of a *rangeomorph unit* closest (more proximal) to the attachment site of that *rangeomorph unit*.

Bipolar: possessing a single *growth axis* but two *apical growth tips* (Fig. 1B).

Branches: the divisions of the *frond*. *Primary* (first order) *branches* consist of *rangeomorph units*, which in turn consist of smaller *secondary/tertiary/*etc. branches, likewise consisting of *rangeomorph units* (Fig. 2A).

Concealed axis: a *stem* or zone in the plane of the *frond* that is concealed by inward furling of the *rangeomorph units* (Fig. 2G–H; see also *exposed axis*).

Deterministic growth: enlargement of a *rangeomorph unit* within finite limits of growth (see also *non-deterministic growth*).

Displayed unit: a *rangeomorph unit* in which the details of branching lie in the plane of the *frond* and thus are visible in a typical plane of preservation. *Displayed units* can either be *furled* or *unfurled* (Figs 1 and 3; see also *rotated unit*).

Distal inflation: where *inflation* of the *rangeomorph units* becomes greater away from the *base of the unit* (Fig. 1E; see also *medial inflation* and *proximal inflation*).

Element: a *branch* or *rangeomorph unit*.

Exposed axis: a *stem* in the plane of the *frond* that is not concealed by the furling of *rangeomorph units* (Fig. 2F)

Fixed: a *rangeomorph unit* that had little freedom to pivot about its own *growth axis* during life (see also *free*).

Free: a *rangeomorph unit* that had freedom to pivot about its own *growth axis* during life. Some post-mortem rotation may subsequently take place in *fixed* units.

Frond: a *rangeomorph unit* provided with one or more *apical growth tips* that can generate *primary branches* (Fig. 2B). *Fronds* may therefore be *unipolar*, *bipolar* or *multipolar*. Where *subsidiary growth tips* are present in *unipolar* forms, then these are called subsidiary fronds (Fig. 2E).

Frondose organism: an organism that possesses a *frond*. The term 'frondose' refers the whole body of the organism, including a *frond* (and any subsidiary fronds), *stem* and *basal disc* if present (Fig. 1A–D).

Furled unit: a *rangeomorph unit* that is partially folded around its *growth axis*, producing edges that lie outside the typical plane of preservation because they are rolled up against their neighbours (Figs 1H–J and 3C–H).

Glide plane of symmetry: reflectional symmetry along the *growth axis* that includes a translation of less than one full branch (but greater than zero) along the axis of reflection.

Growth axis: main axis of symmetry of a *frond*, which terminates in an *apical growth tip*. Smaller *rangeomorph units* are arranged along subsidiary growth axes.

Inflation: expansion of some *elements* of morphology during growth without the addition of new units. It provides an aspect of growth that is additional to *apical insertion* (Fig. 1C–E).

Irregular units: *branches* of a particular level of organisation (e.g. *primary*) that change or switch from *subparallel* to *radiating*, causing irregular spacing and *alignments* of *rangeomorph units* along the *growth axis* (Fig. 2D).

rangeomorph units across a range of scales, independent of hypothetical biological relationships and free from morphometrics. We return to these questions of competing terminologies in the discussion section below.

In this article, we expand upon the morphological scheme of Brasier and Antcliffe (2009), developing it into a unified taxonomic framework. We have aimed for simple technical terms that can be used across a wide range of scales (from first- to third-order rangeomorph units) and that are easy to apply in both the field and laboratory. The suggested scheme therefore makes use of simple English words wherever possible. Indeed, our project amounts to the writing of a verbal equation for growth and development. Where uncertainties arise in comparisons between taxa (e.g. of first-order branches in *Bradgatia* and *Charnia*; see Brasier and Antcliffe 2009, fig. 19), we have therefore adopted the principle of parsimony – that the simplest descriptor is sufficient. That means that the whole frondose organism is herein regarded as a single homologous structure across the eight genera analysed below. This approach allows our set of terms to be applied during comparative analyses across this taxonomic spectrum.

Our scheme is also intended to permit the classification of some (although not all) incomplete fossil specimens, provided that sufficient detail is preserved within first- and second-order branches. For the present, however, we confine this treatment to Avalonian genera whose details are well preserved down to third-order branching patterns. Such examples require that we focus upon characters that are robustly independent of tectonic strain

TABLE 1. (Continued)

Medial inflation: where *inflation* of the *rangeomorph unit* is greatest roughly half way along the *growth axis* (Table 2; see also *distal inflation* and *proximal inflation*).
Moderate inflation: where *inflation* of the *rangeomorph unit* does not change conspicuously along the *growth axis* (Fig. 2D; see also *distal inflation* and *proximal inflation*).
Multipolar: possessing more than two *apical growth tips* (Fig. 1A; see also *unipolar* and *bipolar)*.
Non-deterministic growth: enlargement of a *rangeomorph unit* without finite limits to growth (see also *deterministic growth*).
Polarity: the number of *apical growth tips* within a single *frondose organism* (Fig. 1A–E; see also *unipolar*, *bipolar* and *multipolar*).
Primary branches: the main (first order) subdivisions of the *frond*, each comprising a *rangeomorph unit* (Fig. 2A; see also *secondary* and *tertiary branches*).
Proximal inflation: where *inflation* of the *rangeomorph units* becomes greater towards the *base of the unit* (Fig. 1C; see also *distal inflation* and *medial inflation*).
Radiating branches: *branches* of a particular level of organisation (e.g. *primary*) that are aligned at increasingly steep angles to each other along the *growth axis* of a *rangeomorph unit* (Fig. 2C).
Rangeomorph unit: a unit of organisation wherein branching proceeds along a *glide plane of symmetry*, with each branch acting as an axis for lower levels of branching. At their simplest, these are self-similar structures, possessing comparable architecture at several scales of investigation (Fig. 3A–B).
Rotated unit: a *rangeomorph unit* that has rotated about its *growth axis*. It is a mechanism by which a rangeomorph unit can become undisplayed (Figs 1I and 3E,G; see also *displayed unit*).
Row: a set of *branches* arranged on one side of the *growth axis* of a *rangeomorph unit* (Fig. 2A). Rows not only comprise *primary branches*, they can also be recognised within smaller *rangeomorph units*.
Secondary branches: the main subdivisions of a *primary branch*. Also known as a second-order branch (Fig. 2A).
Stem: a stalk-like structure connecting the *frond* to a *basal disc*, where present. The stem may extend along the *growth axis*, and be either *exposed* or *concealed* (Fig. 2F).
Subparallel units: *branches* of a particular level of organisation (e.g. *primary*) that are orientated almost parallel to each other along the *growth axis* (Fig. 2B; see also *radiating units*).
Subsidiary growth tips: where a *frond* possesses a single main *polarity*, and additional growth tips are generated at subsidiary loci during later stages of growth (Fig. 2E).
Tertiary branches: the main subdivisions of a *secondary branch*. Also known as a third-order branch.
Undisplayed unit: a *rangeomorph unit* that has *rotated* about its *growth axis* so that the branching detail is no longer visible in the plane of preservation (see also *displayed* and *furled units*).
Undivided unit: a *rangeomorph unit* in which the preserved surface appears smooth, so that any details of subdivision (if they existed) cannot be seen (Figs 1J and 3H–I).
Unfurled unit: a *rangeomorph unit* that is not folded along its margins, so that the alternating pattern of rangeomorph branching may be seen within the plane of preservation (Figs 1G and 3A–B; see also *furled*, *exposed*, *concealed*). Unfurled units are commonly *free* to overlap.
Unipolar: possessing one *apical growth tip* (Fig. 1C–F).

Italics highlight those related terms that are also shown in this glossary.

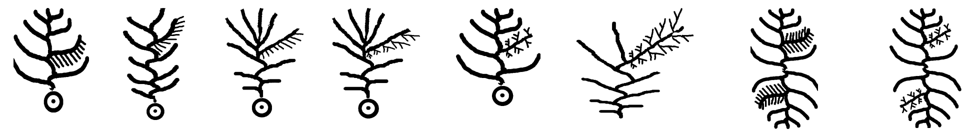
(a feature common throughout Avalonian localities; see discussion *in* Liu *et al.* 2011). Hence, our scheme makes no use of the shape-based metrics of previous systems (e.g. Laflamme *et al.* 2004, 2007; Laflamme and Narbonne 2008; see further discussion below).

The following system is therefore based on criteria concerned primarily with the internal anatomy of branching, with special reference to the figured type-specimens of genera. Fortunately, with few exceptions (e.g. *Charnia* and *Vinlandia* n. gen.), our descriptive system does not require major reorganisation of taxonomic status within or between the relatively small numbers of genera currently described. It does, however, permit us to bring the existing generic diagnoses of Avalonian taxa into much greater order, allowing them to be viewed as part of a morphological continuum and to be described objectively in relation to a shared set of character states.

THE MODEL

Our model for the rules of growth in frondose Ediacaran organisms (see Tables 1 and 2; Figs 1–3) builds upon that outlined by Brasier and Antcliffe (2004, 2009) and Antcliffe and Brasier (2007*a*, 2008). We agree with the terminology of Laflamme and Narbonne (2008) in several instances and adhere to the well-established use of primary, secondary and tertiary branches. We also concur with the concepts of branch overlap (Laflamme *et al.* 2007; Laflamme and Narbonne 2008), and degrees of branch rotation (Narbonne *et al.* 2009). But for reasons discussed later, we do not follow those authors in their revival of the terms ‘petalodium’ and ‘petaloid’ (*sensu* Pflug 1972*a*), preferring to retain the terms ‘frond’ and ‘row’, respectively. We further develop the terminology of Brasier and Antcliffe (2009) to introduce terms that are

TABLE 2. A comparison between the character states seen within eight genera of frondose rangeomorphs.



	Charnia	*Trepassia*	*Vinlandia*	*Beothukis*	*Avalofractus*	*Bradgatia*	*Hapsidophyllas*	*Fractofusus*
Number of poles	1	1	1	1	1	1	*2*	*2*
Number of rows	2	2	2	2	2	2	*2*	*2*
Inflation of first order proximal (p), medial (me), moderate (mo), distal (d)	p	mo	me	me	p	d	p	p
Inflation of second order proximal (p), medial (me), moderate (mo), distal (d)	mo–me	mo–me	mo–me	mo–me	mo–me	d	p	d
Displayed structure (mature) 1st order	No	No	No	No	Yes	Yes	Yes	Yes
Displayed structure (mature) 2nd order	No	No	No	Yes	Yes	Yes	No	Yes
Furled structure (mature) 1st order	Yes	Yes	Yes	Yes	No	No	Yes–No	Yes–No
Furled structure (mature) 2nd order	Yes	Yes	Yes	Yes	No	No	Yes	Yes–No
Growth axis Concealed by furling (C), Exposed as a stem (E)	C	C	C	C	E	C	E	C
Subparallel (P) or radiate (R) 1st order	P	P	P–R	P–R	P	R	P	P
Subparallel (P) or radiate (R) 2nd order	P	P–R	P–R	P–R	P	R	P	P–R
Presence of basal disc	Yes	Yes	Yes	Yes	Yes	No	No	No

novel to this work and essential to the architectural arguments developed herein. Table 1 brings these various descriptive terms together in the form of a glossary, while Table 2 allows major character states to be compared between eight rangeomorph genera.

Our unifying model can be summarised as follows. A frond is a rangeomorph unit with a growth tip that can generate primary branches. Fronds are able to grow away from a point of origin (which is often in contact with the seafloor), progressively generate new primary branches at their growth tips and 'inflate' all of the elements so formed over time. This growth may eventually cease, or it may continue indefinitely (deterministic vs. nondeterministic growth, *sensu* Brasier and Antcliffe 2009). Branches tend to exhibit forms of 'rangeomorph architecture' (*sensu* Narbonne 2004), comprising second-, third- and fourth-order self-similar units, each arranged in an alternating pattern along a growth axis. Following Brasier and Antcliffe (2009), we here propose that the differences between eight rangeomorph genera (Table 2) can be explained by variation in a limited number of architectural characteristics. Study of the best-preserved rangeomorph holotypes and paratypes shows that the morphologies of these Ediacaran organisms can be understood using the following six concepts:

Polarities

Each unit provided with a growth tip (i.e. a 'pole') is here regarded as a 'frond' (Fig. 1). In some frondose taxa, primary rangeomorph units are generated only at a single growth tip, with a single terminal pole at the apex of the frond (e.g. the genera *Avalofractus* Narbonne *et al.*, 2009; *Beothukis* Brasier and Antcliffe, 2009; *Charnia* Ford, 1958 and *Trepassia* Narbonne *et al.*, 2009). Such forms we call unipolar (Fig. 1C–F). Some taxa show a single main polarity, with subsidiary growth tips (Fig. 2E), as seen in *Bradgatia* Boynton and Ford, 1995, where large amounts of internal division can be observed in super-mature primary branches (i.e. branches that have started to generate additional branches by developing subsidiary growth tips, *sensu* Brasier and Antcliffe 2009, figs 5 and 8). Other forms show two distinct growth tips and hence are bipolar, having two poles arranged at 180 degrees (Fig. 1B; *Fractofusus* Gehling and Narbonne, 2007; *Hapsidophyllas*

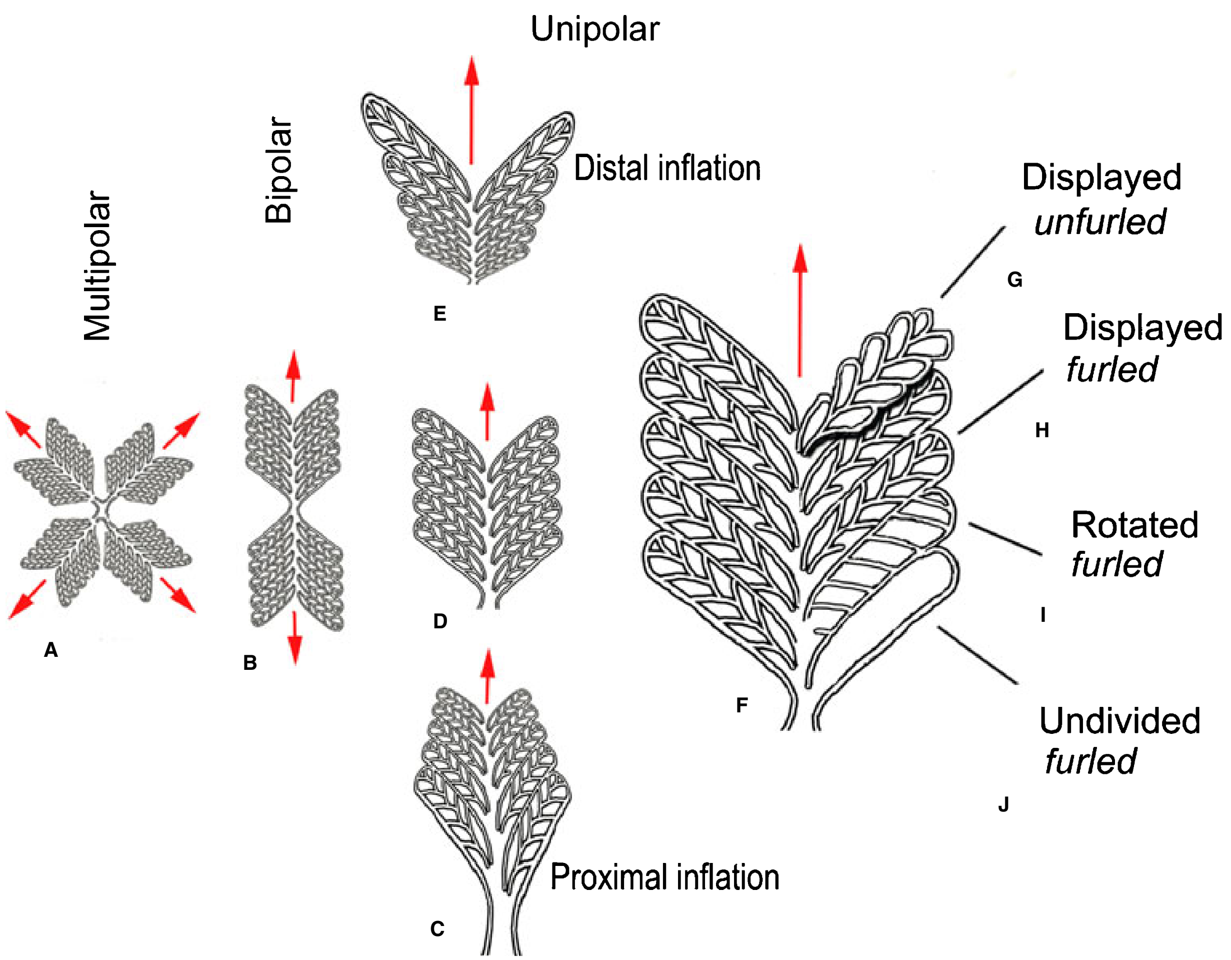


FIG. 1. Graphic illustration of rangeomorph architecture seen in Ediacaran fronds, demonstrating the concepts of polarity (A–E), inflation (C–E), furling and rangeomorph display (G–J; *sensu* Brasier and Antcliffe 2009). Arrows mark the positions of apical growth tips (which are not detailed here).

Bamforth and Narbonne, 2009). A few forms not yet encountered within Avalonia (such as *Rangea* Gürich, 1930) may have three or more growth tips and poles (e.g. Pflug 1972*a*, *b*; Grazhdankin and Seilacher 2005). We here refer to such forms as multipolar (Fig. 1A).

Rows of branches

In the manner of a fern, each frond is typically subdivided into segments called first-order (or primary) branches (see Figs 2 and 3). These in turn can be subdivided into second-order (or secondary) branches (Fig. 2A), and those into third-order (or tertiary) branches, and so on. In each frond, these branches are typically arranged in 'rows' alternately along two sides of the growth axis (Fig. 2A). Second- to third-order branches are also arranged in rows. The rows of first-order branches (*sensu* Brasier and Antcliffe 2009) are found either side of a glide plane of reflectional symmetry along the growth axis, and such an arrangement can be seen in all of the taxa discussed herein. In some cases, these alternations are regularly spaced along the main growth axis (Fig. 2B, e.g. *Charnia*), whereas in other taxa (Fig. 2D, e.g. *Beothukis*, *Trepassia*), they appear irregularly spaced. Further forms occur where three or more rows are thought to be arranged along the axis. Such taxa include *Rangea* (e.g. Jenkins 1985) and *Swartpuntia* Narbonne *et al.*, 1997, although the suggestion that this also applies to the holotype of *Charniodiscus concentricus* Ford, 1958 (Brasier and Antcliffe 2009) has yet to be confirmed across other specimens currently assigned to this genus (e.g. those described in Laflamme *et al.* 2004 or Wilby *et al.* 2011).

Inflation

This refers to patterns of enlargement *between* branches of a given order along a given row (see Fig. 1). When first-order branches are compared to each other within a row, they commonly show greater enlargement towards

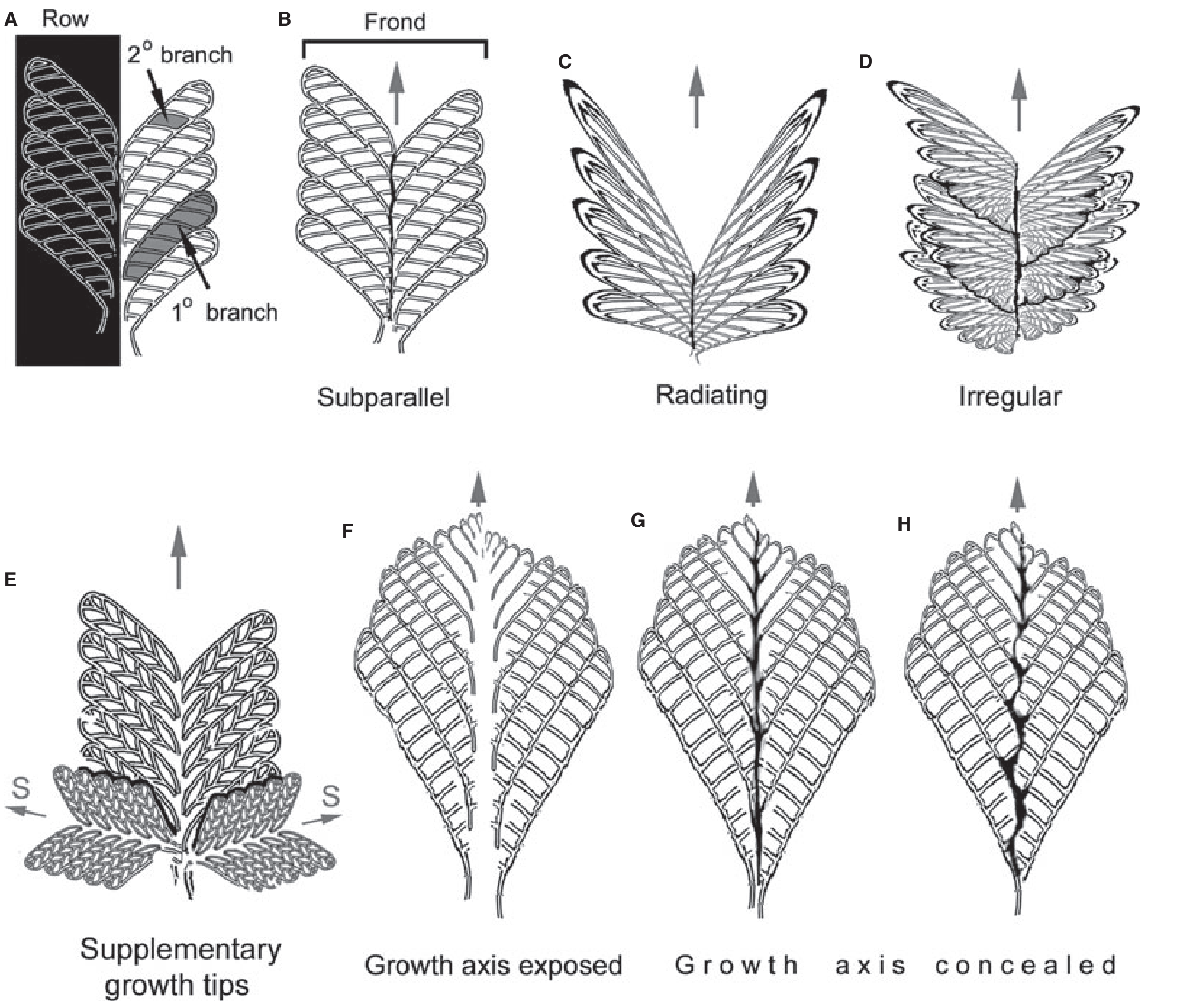


FIG. 2. A, terms for describing rangeomorph fronds, including first-order (primary) branch, second-order (secondary) branch and a single row of first-order branches. The arrows show the growth axis and point in a distal direction towards the apical growth tip of the frond. B, a single frond showing subparallel alignment of both its primary and secondary branches (cf. *Charnia*). C, frond with radiating alignments of both primary and secondary branches (cf. *Bradgatia*). D, frond with 'irregular' (i.e. subparallel to radiating) alignments of primary branches and radiating alignments of secondary branches (cf. *Vinlandia* n. gen.). E, frond showing the development of two supplementary growth tips ('S') near the proximal end (cf. *Bradgatia*). F, frond with growth axis exposed as a central stem (cf. *Charniodiscus*). G, frond with growth axis concealed by furling to form a weakly *zig-zag* to linear suture (cf. *Trepassia*). H, frond with growth axis concealed by tight furling to form a *zig-zag* suture (cf. *Charnia*).

the base of the frond. Such examples of proximal inflation (Fig. 1C) are seen, for example, in *Charnia masoni* Ford, 1958 (Fig. 4A–B) and *Fractofusus andersoni* Gehling and Narbonne, 2007 (Fig. 7C–D). In other cases, greater inflation appears to have taken place towards more distal portions of the row of first-order branches. Such distal inflation (Fig. 1E) can be seen in well-preserved examples of *Bradgatia* (Figs 6C and 8F). In yet other cases, greatest inflation is seen in the medial portions of the first-order branches, as found in well-preserved examples of *Beothukis mistakensis* Brasier and Antcliffe, 2009 (Fig. 5C). Further examples, exhibiting little or no enlargement in either direction, include mature specimens of *Trepassia wardae* Narbonne *et al.*, 2009 (Fig. 4C–D). The latter condition is here termed moderate inflation (Figs 1D and 2A–B). Varying patterns of inflation can also be found at different levels of subdivision within each frond. Thus, in *Fractofusus misrai* Gehling and Narbonne, 2007 (Fig. 7C–D), first-order branches show proximal inflation, while second-order branches show distal inflation.

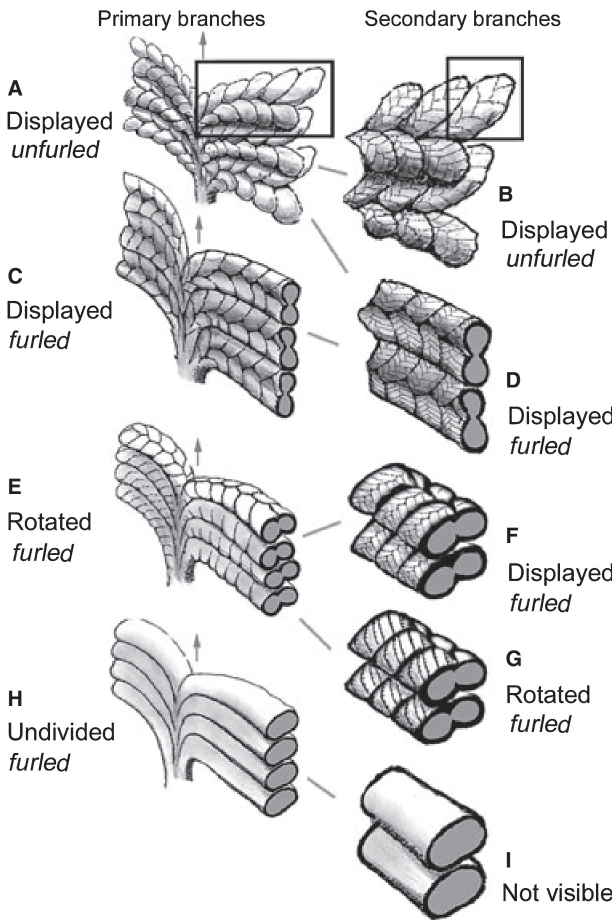


FIG. 3. Illustration of rangeomorph units that can be displayed, rotated or furled at different levels of branching. The arrows show the growth axis and point in a distal direction towards the apical growth tip. A–B, rangeomorph units displayed and unfurled within both first- and second-order branches (cf. mature *Bradgatia*). C, rangeomorph units displayed and furled within both first- and second-order branches (cf. immature *Bradgatia*). E–F, rangeomorph units rotated and furled in the first order but displayed and furled within the second order (cf. *Beothukis*). E, G, rangeomorph units rotated and furled in both first- and second-order levels (cf. *Charnia*). H–I, rangeomorph units furled but undivided at first-order level, so that second-order subdivisions cannot be seen (cf. some examples of *Charniodiscus*).

Rangeomorph display and furling

There are variations between taxa in the degree to which the rangeomorph branching architecture is clearly displayed (see Fig. 1). We here recognise four main character states that relate to 'display':

1. Displayed branches show alternating rangeomorph units on either side of the central axis of growth (Figs 1G–H and 3A–D). In many cases, the edges of these units appear to have been loose and free to overlap or rotate, in the manner of mature fern pinnules (Fig. 3B). The number of subdivisions visible within any given specimen varies not only between taxa, but also between growth stages in a single taxon and between different qualities of preservation in that taxon. Well-preserved specimens can display second-, third-, fourth- and even fifth-order sub-branches (the colloquially named 'fractal' subdivisions of Narbonne 2004) within a first-order branch.
2. Rotated branches have experienced rotation about their growth axes, so that the rangeomorph alternations have become twisted to lie beyond the surface of inspection (such that they are not displayed, except in rare three-dimensional examples of preservation; Figs 1I and 3E, G). In *Charnia* and *Trepassia*, this rotation was ubiquitous and formed an aspect of growth (e.g. Fig. 4). In others, such as *Bradgatia* (Fig. 6C–D) or *Fractofusus* (Fig. 7C–D), it could also arise from later dishevelment of displayed branches.
3. Furled branches are rangeomorph units whose edges have become furled (folded/curled up), to make smooth junctions with their neighbours (Figs 1H–J and 3C–H). This state may be present (furled) or absent (unfurled) in branches having displayed architecture, but it is especially well seen in branches that are rotated or undivided (see below). As a term, furling may also be applied to the condition of the growth axis. In some forms such as *Avalofractus*, *Hapsidophyllas* and *Charniodiscus*, a stem is clearly exposed along the central axis (Fig. 2F). Where a central stem is not visible (e.g. Fig. 2G), this concealed condition is here explained by inward furling of adjacent row margins to form a linear suture. Where this furling along the growth axis is very tight, it can result in a *zig-zag* suture along the midline (Fig. 2H), of the kind commonly seen in *Charnia* (Fig. 4B) and some specimens of *Beothukis* (Fig. 5C). As *zig-zag* sutures can change into linear sutures according to preservation, these features are not accepted here as a strong taxonomic criterion.
4. Undivided branches have edges that are typically furled, but sutures between the subunits of the branch appear smoothed over, so that rangeomorph architecture is not distinct (Figs 1J and 3H–I). This may explain the smooth and apparently featureless appearance of small and juvenile branches seen within otherwise well-preserved specimens.

These four character states can be found together within the impressions of a few remarkable specimens, as seen, for instance, in the complex impression of the paratype for *Beothukis mistakensis* (OUMNH ÁT.411/p; see Brasier and Antcliffe 2009, p. 380, fig. 18) and in several examples of that taxon from Spaniard's Bay (Narbonne *et al.* 2009). These examples all demonstrate how second-order rangeomorph units can be furled along their axes. Likewise, tight rotation and furling of higher order units can be seen in exceptional material of *Charnia masoni* preserved in three-dimensional casts from Russia (e.g. PIN 3993-7018; see Grazhdankin 2004, p. 207, fig. 2B). Variation in the degree of rangeomorph display results in fronds that possess a similar gross morphology, but quite distinct details of architecture (e.g. Fig. 3). For example, rangeomorph structure can be displayed within both the first- and second-order branches of some taxa and may be visible in smaller sub-branches as well (Fig. 3A–D; e.g. *Avalofractus*). In other forms such as *Beothukis*, rangeomorph elements are typically rotated and undisplayed in the first-order branches (Fig. 3E), but clearly displayed in the second-order branches (Fig. 3F). In some taxa, the furling of branch margins can be highly variable (Table 2, 'Yes-No'). Further taxa, such as *Charnia*, exhibit rangeomorph elements that have been rotated at all stages visible for inspection (Fig. 3E, G), and are thus undisplayed throughout.

Alignment of branches

Within a frond, the branches usually show a specific pattern of axial alignment (see Fig. 2). Two main kinds of alignment may be distinguished:

1. Subparallel branches, with branch axes aligned in a broadly parallel series along the length of the branch or frond (Fig. 2B; e.g. *Charnia*).
2. Radiating branches, with branch axes arranged at differing angles along the length of the branch or frond (Fig. 2C; e.g. *Bradgatia*).

In several taxa, these alignments may change gradually, or switch rapidly, from subparallel to radiating within a single specimen, to form a pattern here called 'irregular' (Fig. 2D; e.g. *Vinlandia* n. gen and *Beothukis*). In *Trepassia wardae* (Fig. 4C), the first-order branches are mainly subparallel, but the second-order branches vary from subparallel to radiating (see Table 1). While such radiating alignments could conceivably arise from the freedom of certain rangeomorph units to pivot about their axes, they clearly form part of the growth habit in several taxa.

Presence of a basal disc

Several taxa have a frond connected to a basal disc either via a distinct stem (e.g. *Beothukis*, *Avalofractus*) or without a distinct stem (*Charnia*, *Vinlandia* n. gen.). The basal disc, where present, may have been used for attachment of the organism to the substrate. No evidence for such a basal disc has yet been confirmed in *Bradgatia*, *Fractofusus* or *Hapsidophyllas*.

By considering these features, the body plans of rangeomorph taxa can be characterised with reference to twelve main character states, as shown for the eight specimens described in Table 2.

MERITS OF THE NEW DESCRIPTIVE SYSTEM

This system has been tested in the field and laboratory over several years, and we are confident that it provides an improvement upon previous taxonomic diagnoses, many of which are based upon shape metrics (length to width ratios) or on concepts relating to gross morphological shape (e.g. Laflamme *et al.* 2007) – characters that could be regarded as insufficiently robust for generic diagnoses. Substantial (and not accurately quantified) tectonic strain at many Avalonian sites makes this point particularly relevant (see discussion *in* Liu *et al.* 2011). There is also a common difficulty in compiling shape metrics from incomplete but otherwise well-preserved specimens, where only part of the internal architecture can be well discerned. Our new approach attempts to overcome these difficulties by basing taxonomy upon patterns of internal branching, rather than upon statements of overall shape. Consequently, we recommend the use of branching patterns as a means of disentangling the taxonomy of rangeomorph fronds at generic level. This is in contrast to features such as the numbers of branches at first- and second-order level, which are here regarded as more useful for distinguishing species. Shape metrics may likewise be useful for characterising Ediacaran rangeomorphs at species level, but we feel that too little is yet known about ontogenic variation within these frondose taxa (e.g. Brasier and Antcliffe 2004), or of variation in relation to ecological conditions, to accept shape metrics as a safe diagnostic criterion. We raise the concern that some forms have varied their length to width ratios in non-isometric ways during growth, as, for example, in relation to ambient seafloor conditions.

This scheme now provides a coherent framework of the kind needed for future studies into rangeomorph growth, evolutionary relationships and ecology. In the systematic section at the end of this article, we demonstrate the utility of the proposed terms by providing emended diagnoses for each of the eight rangeomorph genera discussed and figured herein.

DISCUSSION

Along with other authors (e.g. Flude and Narbonne 2008; Laflamme and Narbonne 2008; Narbonne *et al.* 2009), we respect the efforts of Hans Pflug (1971, 1972*a*, *b*) in mapping out the details of what is now termed rangeomorph architecture (Narbonne 2004). Unlike those authors, however, we do not recommend redeployment of Pflug's largely forgotten terminology for the description of Avalonian fossils, for the following reasons. Pflug (1972*a*, *b*) was working on much younger (*c*. 549–543 Ma) and rather more complex Ediacaran material from Namibia, specifically, *Rangea*, *Ernietta* and *Pteridinium* (see Fedonkin *et al.* 2007, pp. 69–87). Unfortunately, his work is written in a language so personal and so model-driven that it admits of no easy employment here. Our understanding of his work is that he envisaged a suite of new conceptual terms. 'Corpus' was used to refer to the whole body of the fossil (often provided with a stem but without a basal disc). 'Petaloid' was used for leaf-shaped elements of somewhat uncertain homology with our structures, perhaps 'rows'. Bunches of six petaloids were collectively referred to as a 'flabellum'. 'Feather structure' was then used to refer to smaller subdivisions within these branches, of the kind we here call rangeomorph units (each constructed from a feather shaped 'petalon', a 'shaft' and a 'root'; Pflug 1972*a*, *b*, fig. 2). 'Petalodium' was seemingly employed to describe the pair of rows of primary branches found on either side of a 'petaloid groove', but paradoxically, according to our reading of his models, these two-rowed petalodia did not necessarily arise directly from a single growth axis (see Pflug 1972*a*, *b*, fig. 3). In other words, Pflug's terminology does not appear to be synonymous with the terms used by Narbonne *et al.* (2009). Nor can it be applied with ease to Pflug's Namibian material (see, for example, Grazhdankin and Seilacher 2005, who use the term 'vane' for structures we here call 'rows'). Added to this is the problem that Pflug (1972*a*, *b*) assigned the following terms to different subdivisions within the rangeomorph body, in ascending order of size: 'petalon' (Greek, plural 'petala'), 'petaloid' (English, pl. 'petaloids'), flabellum' (Latin, pl. 'flabella') 'petalodium' (Latin, pl. 'petalodia') and corpus (Latin, pl. 'corpi'). His scheme therefore requires a complete understanding of the life cycle and growth of any given rangeomorph taxon, and of its homologies with other taxa. It also requires us to be sure we are looking at a whole organism, not just parts of it. Unfortunately, it seems safer to admit our ignorance here (as highlighted by Brasier and Antcliffe 2004) and to employ a less convoluted, and more permissive, terminology.

We therefore advocate the use of the clear and simple terms outlined in Tables 1–2 and Figures 1–3. These terms can be applied to all portions, or subdivisions, of rangeomorph architecture, even by a novice. Thus, a 'branch', a 'row' or a 'growth axis' can be named regardless of the level of subdivision to which it belongs. Authors such as Ford (1958), Glaessner (1984) and Jenkins (1992), as well as the authors in Fedonkin *et al.* (2007), have likewise used the English term 'frond' for the leaf-like body of the organism. It is true that 'frond' has sometimes been used to refer to the whole 'frondose organism', including any stem or basal disc, whereas we use 'frond' to specifically refer to a rangeomorph unit provided with one or more apical growth tips that can generate primary branches. We avoid the term 'frondlet' for subdivisions of a frond (e.g. Narbonne 2004) because of its uncertain application across the various genera and its ready confusion with 'frond'. We prefer instead to use Narbonne's more utilitarian term of 'rangeomorph unit' (or its synonym, 'rangeomorph element'), because it can be used at all scales. We avoid Pflug's term 'petalodium' (1972; *pace* Laflamme and Narbonne 2008; Narbonne *et al.* 2009), not only because it is easily confused with 'petaloid' and 'petalon', but because it is controversial. We do not agree that Pflug's usage was intended to be synonymous with the whole leaf-like body. Finally, we would remark that the terms 'petalon', 'petaloid, 'petalodium', 'flabellum' and 'corpus' have not proved practical for Ediacaran teaching, field work or research.

CONCLUSION

The terminology introduced herein is intended to provide a secure basis for the diagnosis of rangeomorph fossils, allowing enigmatic specimens to be recognised and classified within a coherent framework. It also recognises the morphological variation seen in these organisms and allows for the accommodation of future discoveries of rangeomorph morphotypes, hopefully without the need for further terminology. The taxa as diagnosed herein (see below for diagnoses) may represent 'way-points' along a phylogenetic continuum. We have attempted to provide a clear definition of the genotypic concept for Ediacaran fronds, so as to divide this morphological continuum into discrete entities. Cladistic analysis of these trends is still preliminary (note, for example, the unrooted tree presented in Brasier and Antcliffe 2009), in part because it is still very difficult to polarise characters in our data matrix by means of ancestor–descendant relationships. Most important here will be the filling out of the morphospace of Ediacaran organisms (see Antcliffe and Brasier 2007*b*), through the discovery of additional forms with character combinations that are currently undocumented. Our aim is that this proposed framework should help to provide a template for the description and analysis of growth and evolution, in new and existing rangeomorph taxa.

The picture of rangeomorph architecture is becoming ever more coherent and complete, thanks to the efforts of several independent teams working around the world, all of them contributing significantly to the overall body of evidence (e.g. Grazhdankin 2004; Laflamme *et al.* 2004;

Narbonne 2004; Gehling and Narbonne 2007; Hofmann *et al.* 2008; Brasier and Antcliffe 2009; Narbonne *et al.* 2009). We believe that debates regarding the nature of these organisms now require a consistent working terminology that focuses upon the architecture of branching anatomy, such as the one proposed herein. Once such a consensus is achieved, it is hoped that exciting questions relating to evolutionary context, ontogenetic dynamics and ecological models should come to the fore.

GENERIC DIAGNOSES

Remarks. Below, we provide emended generic diagnoses for some of the best-preserved Avalonian frondose taxa, using the new terminology proposed herein. We have omitted, for the time being, those taxa whose details cannot yet be confirmed at third or lower orders of branching (e.g. *Frondophyllas* Bamforth and Narbonne, 2009; *Pectinifrons* Bamforth *et al.*, 2008; *Parviscopa* Hofmann *et al.*, 2008; *Primocandelabrum* Hofmann *et al.*, 2008; *Culmofrons* Laflamme *et al.*, 2012). Nor do we consider *Charniodiscus* here, owing to uncertainties that remain about the nature of the holotype in relation to other specimens from Avalonia and Australia (cf. Laflamme *et al.* 2004; Brasier and Antcliffe 2009; Wilby *et al.* 2011). Internal patterns of frond architecture are taken from observations of exceptionally well-preserved and mature specimens, either on bedding planes directly or from casts and digital images. Table 1 provides a summary of the diagnostic criteria for selected genera, with illustrations (Figs 4–8), and more formal descriptions, presented in the same order as in the text.

Charnia Ford, 1958

Frond unipolar, comprising two rows of primary branches arranged alternately along a tightly furled central axis, forming a *zig-zag* suture (Figs 4A–B and 8D). First-order branches typically show proximal inflation, whereas second-order branches show moderate-to-medial inflation. All first to third-order branches are aligned in markedly subparallel series, with furled margins, having rangeomorph elements that are rotated and undisplayed. A basal disc is sometimes preserved.

Trepassia Narbonne, Laflamme, Greentree and Trusler, 2009

Frond unipolar, comprising two rows of irregularly spaced primary branches arranged along a furled central axis, commonly forming a linear suture (Figs 4C–D and 8H). Inflation of first-order branches is moderate with no clear direction, while that of second-order branches is mainly medial. Alignments of first-order branches are subparallel. Those of second- and third-order branches within a single specimen are more irregular and range gradually or switch abruptly from subparallel to distinctly radiate. Mature first- to third-order branches have furled margins, with rangeomorph elements that are rotated and undisplayed. A basal disc is sometimes preserved.

Vinlandia gen. nov. Brasier, Antcliffe and Liu

Frond unipolar, comprising two rows of irregularly spaced primary branches, arranged alternately along a furled central axis, forming a linear to *zig-zag* suture (Figs 5A–B, 8C and 9). Inflation of first- and second-order branches is moderate to medial. First- and second-order branches are arranged in radiating to subparallel series. All first- to third-order branches have furled margins, with rangeomorph elements that are rotated and undisplayed. A basal disc is rarely preserved.

Beothukis Brasier and Antcliffe, 2009

Frond unipolar, comprising two rows of primary branches arranged in irregularly spaced alternations along a furled central axis, forming a linear suture (Figs 5C–D and 8B). Inflation of first- and second-order branches is moderate to medial. Mature first- and second-order branches typically have furled margins, with alignments that are arranged in radiating to subparallel series. Rangeomorph elements of the first-order branches are usually undisplayed, whereas those of second-order branches are clearly displayed. A basal disc and stem is sometimes preserved.

Comment. As primary branches were seemingly free to move, and not fixed to each other except at their bases, presentation of the fronds can be highly variable, as noted in the paratype (Brasier and Antcliffe 2009, fig. 18).

Avalofractus Narbonne, Laflamme, Greentree and Trusler, 2009

Frond unipolar, comprising two rows of first-order branches arranged in subparallel series that alternate either side of a stem exposed along the central axis (Figs 6A–B and 8A). Inflation of first-order branches is proximal, while that of second-order branches appears moderate to medial. Mature first- to third-order branches are displayed and not furled or rotated. A basal disc is sometimes preserved.

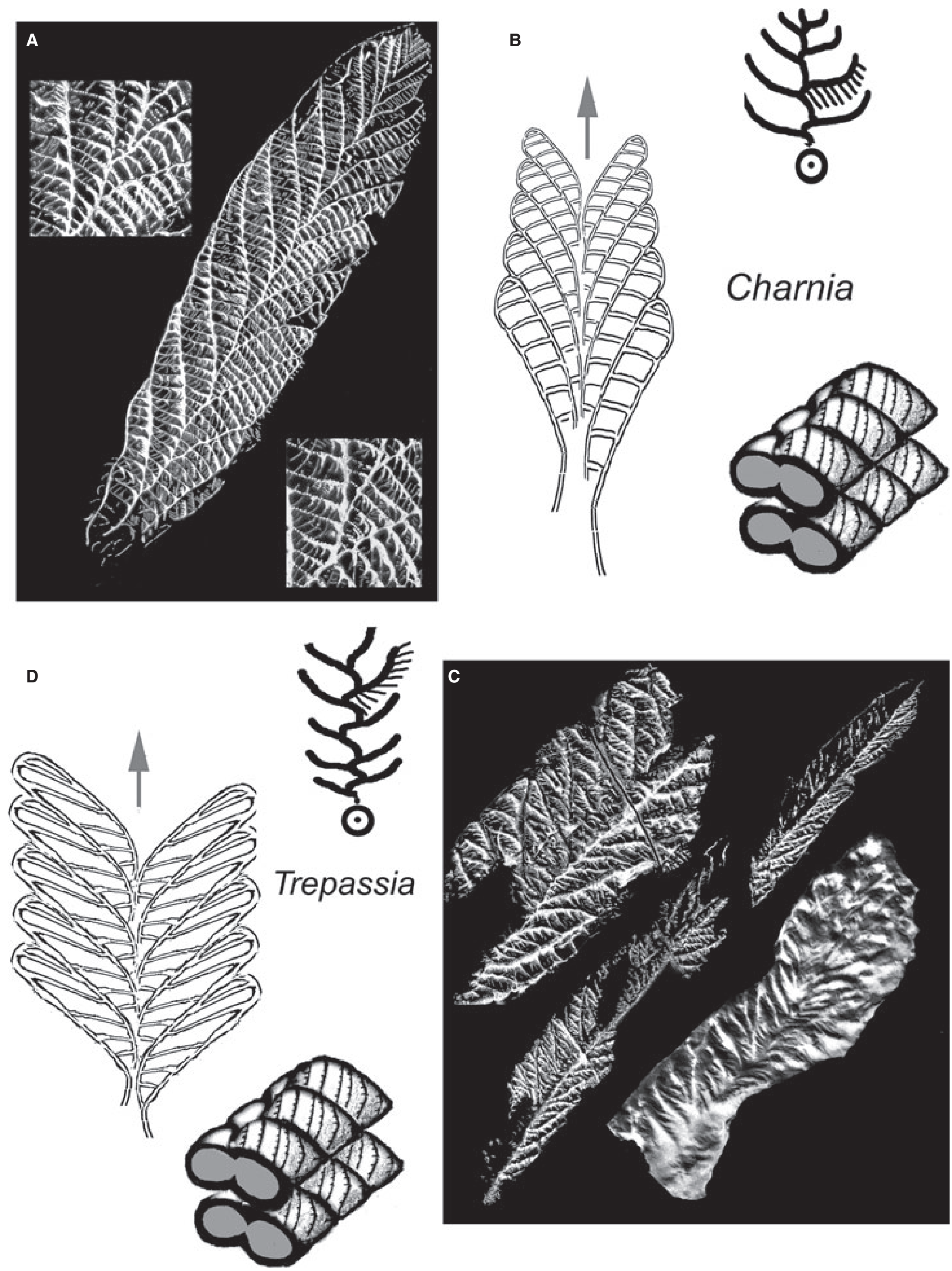


FIG. 4. A, camera lucida of the holotype of *Charnia masoni* (LEICT G279) with enlargements of main sketch showing detail. B, schematic sketches of *Charnia*. C, above and middle shows camera lucida drawings of the holotype of *Trepassia wardae* (ROM38628); at lower right is shown a digital image of juvenile OUMNH ÁT.467/p from Spaniards Bay (locality of Narbonne, 2004). D, schematics of *Trepassia* showing architecture. Parts A and C in Figures 4–7 are based on camera lucida drawings that are not retrodeformed.

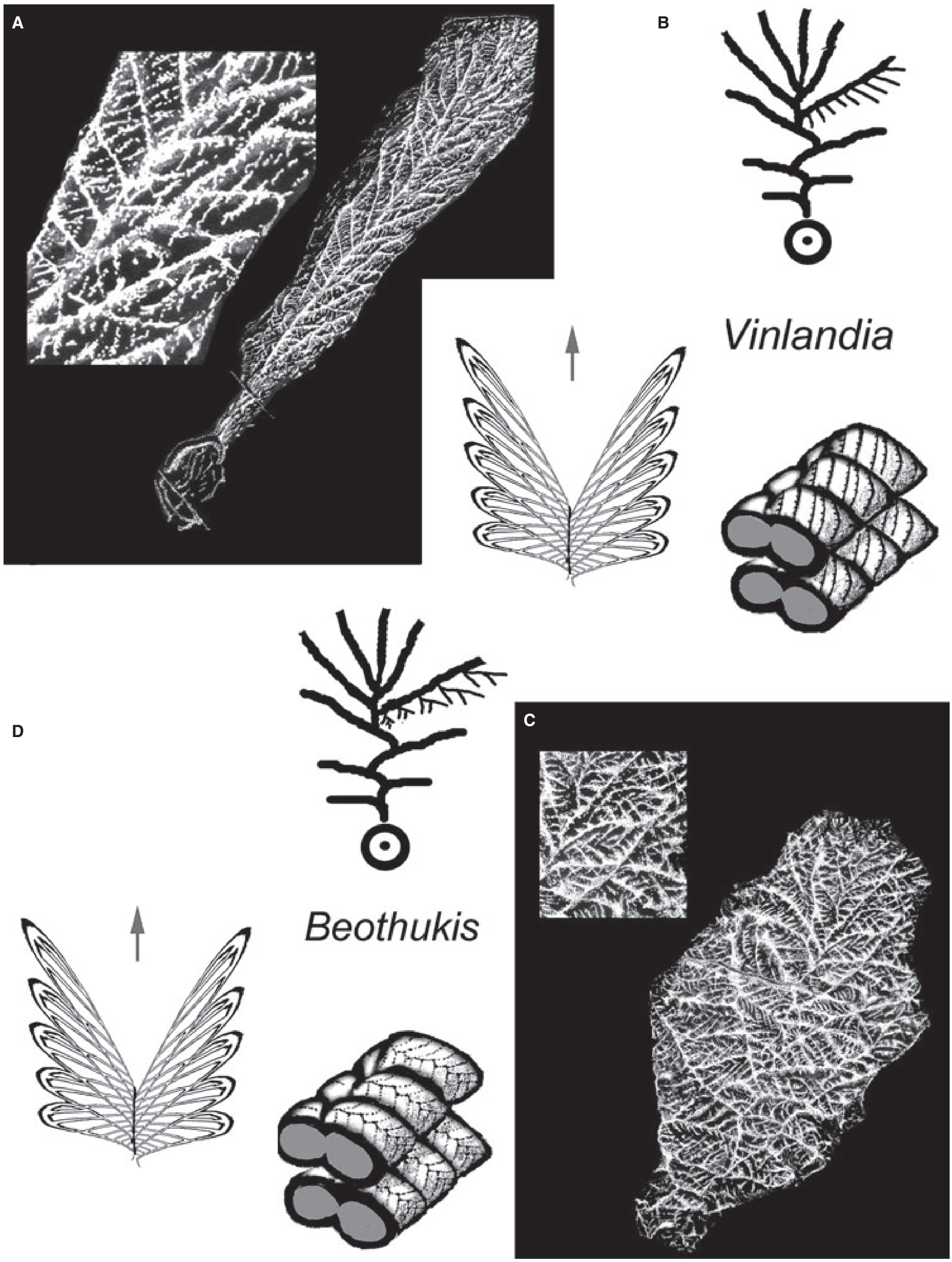


FIG. 5. A, camera lucida of the new designate plesiotype of *Vinlandia antecedens* gen. nov. (OUMNH ÁT.409/p.) with enlargement of main sketch showing detail. B, schematics of *Vinlandia* showing architecture. C, camera lucida of the holotype of *Beothukis mistakensis* (OUMNH ÁT.410/p) with enlargement of main sketch showing detail. D, schematics of *Beothukis* showing architecture.

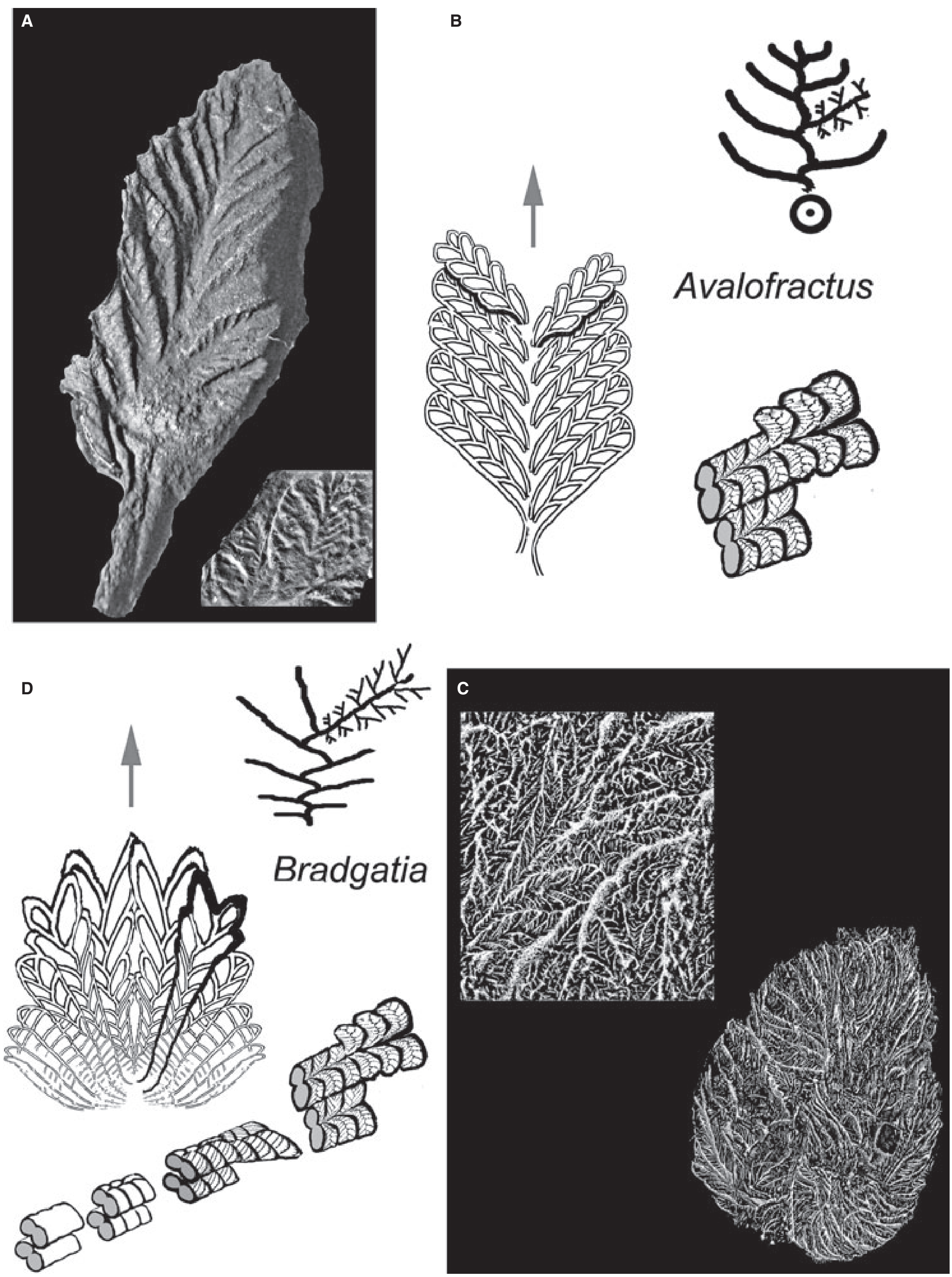


FIG. 6. A, digital image of the paratype of *Avalofractus abaculus* (NFM F-754) with inset image showing details of a cast OUMNH ÁT.465/p. B, schematics of *Avalofractus* showing architecture. C, camera lucida of the holotype of *Bradgatia linfordensis* (LEICT G26) with enlargement of second specimen showing detail. D, Schematics of *Bradgatia* showing architecture.

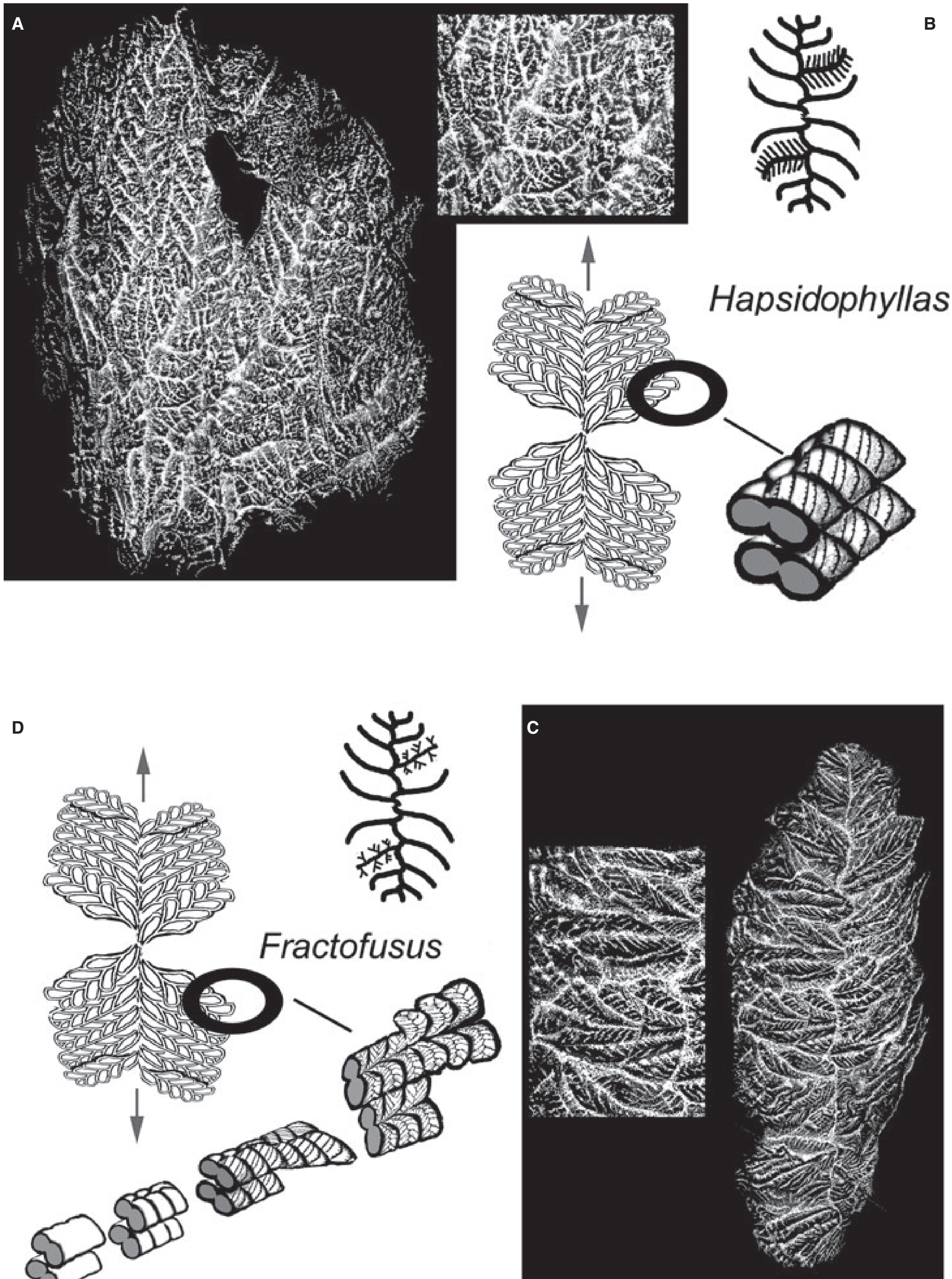


FIG. 7. A, camera lucida drawing of a specimen of *Hapsidophyllas flexibilis* (*in situ* on the Mistaken Point F Surface), with enlargement of main sketch showing details. B, schematics of *Hapsidophyllas* showing architecture. C, camera lucida of *Fractofusus misrai* (OUMNH ÁT.407/p) with enlargement of main sketch showing details. D, schematics of *Fractofusus* showing architecture.

Comment. All known specimens of *Avalofractus* are small (<100 mm) and potentially immature (early ontogenetic state), raising the possibility that this taxon may represent the unfurled or partial (fragmentary) remains of a juvenile form belonging to another rangeomorph taxon.

Bradgatia Boynton and Ford, 1995

Frond unipolar, with subsidiary growth tips present in mature specimens, at the distal ends of large first-order branches (Figs 6C–D and 8F). First- to second-order branches tend to be distally inflated. First-order branches comprise two rows of second-order branches with the freedom to overlap and rotate. First-order branches arranged in radiating series, alternating along a furled central axis. Towards their bases (and often in juvenile stages), first- to second-order branches typically furled and sometimes rotated, but rangeomorph elements become progressively displayed and unfurled in the direction of growth (Fig. 6D). A basal disc is not confirmed.

Comment. In Brasier and Antcliffe (2004, fig. 8), *Bradgatia* was envisaged as a colony of *Charnia*-like fronds. In this article, as in Brasier and Antcliffe (2009, fig. 19), we favour the more parsimonious hypothesis that the whole frondose organism of *Bradgatia* is homologous to the frond of *Charnia*.

Hapsidophyllas Bamforth and Narbonne, 2009

Frond bipolar, comprising two rows of primary branches emanating alternately from a central axis, which may be displayed (Figs 7A–B and 8G). Inflation of first-order branches is proximal, and inflation of second-order branches is also proximal. First-order branches show subparallel alignments of units with displayed structure, with both furled and freely overlapping margins. Second-order branches are often poorly preserved, but are seemingly rotated and furled, and possess subparallel alignments. A basal disc is not seen.

Comment. These frondose organisms can appear (falsely) to be multipolar, owing to freely overlapping margins of their first-order branches. Juvenile morphologies are poorly known.

Fractofusus Gehling and Narbonne, 2007

Frond bipolar, comprising two rows of primary branches arranged in irregularly spaced alternations along a furled central axis, forming a *zig-zag* suture (Figs 7C–D and 8E). Inflation of first-order branches is proximal, while inflation of second-order branches tends to be distal. First-order branches show subparallel alignments of units, with displayed structure, often infolded or rotated in juvenile stages. These units are broadly perpendicular to the main central axis, along which they can be either furled or overlapping. Axes of second-order branches are subparallel to radiating, often freely displayed and overlapping towards their margins. A basal disc is not seen.

The system of nomenclature presented above is based upon the growth and structural architecture of rangeomorph organisms. That being so, it is evident that some previously described specimens, and species, do not comply with the generic definitions proposed herein for their respective taxa. We therefore present below a revised synonymy list and diagnosis for the taxon *Charnia antecedens* Laflamme *et al.* 2007, assigning it as the type species of *Vinlandia* gen. nov. We also provide an updated taxonomy of *Charnia masoni* to resolve several taxonomic irregularities regarding that genus. For reasons of strict formality, we repeat the generic diagnoses of *Vinlandia* and *Charnia* in the section below.

SYSTEMATIC PALAEONTOLOGY

Genus VINLANDIA gen. nov.

Derivation of name. Named after the old Norse name for Newfoundland, Vinland.

Diagnosis. Frond unipolar, comprising two rows of irregularly spaced primary branches, arranged alternately along a furled central axis, forming a linear suture. Inflation of first- and second-order branches is moderate to medial. First- and second-order branches are arranged in radiating to subparallel series. All first- to third-order branches have furled margins, with rangeomorph elements that are rotated and undisplayed. A basal disc is rarely preserved.

Type species: Vinlandia antecedens Laflamme, Narbonne, Greentree and Anderson, 2007, Newfoundland, Canada.

Vinlandia antecedens (Laflamme, Narbonne, Greentree and Anderson, 2007)
Figures 5A, 8C, 9

?1998 ‘*Charnia masoni*’; Nedin and Jenkins, p. 315, fig. 1.
?2003 ‘*Charnia masoni*’; Narbonne and Gehling, p. 28, fig. 2a.
.2004 ‘Bush-like form, possibly comparable with *Bradgatia* but showing *Charnia*-like attributes’ O’Brien and King, p. 210, pl. 5A.
v.2007 *Charnia antecedens* sp. nov. Laflamme, Narbonne, Greentree and Anderson, p. 249, fig. 6.

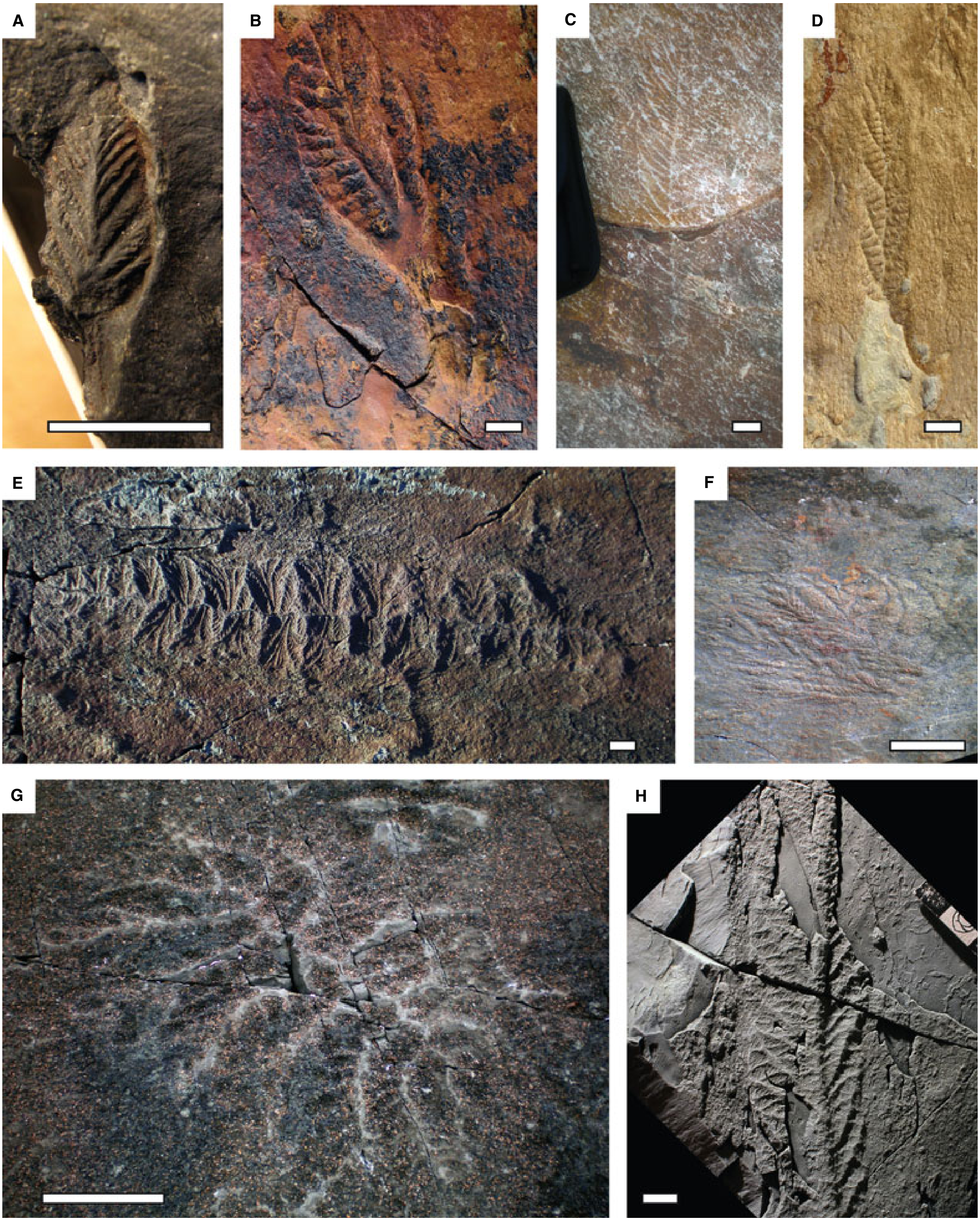


FIG. 8. Rangeomorph Ediacaran taxa from the Avalon region of Newfoundland for which emended diagnoses are provided in the text. A, *Avalofractus abaculus*, Upper Island Cove. B, *Beothukis sp*. Bonavista Peninsula. C, *Vinlandia antecedens* gen. nov., Bonavista Peninsula. D, *Charnia masoni*, Bonavista Peninsula. E, *Fractofusus misrai*, Mistaken Point. F, *Bradgatia sp*., Little Catalina. G, *Hapsidophyllas flexibilis*, Watern Cove. H, *Trepassia wardae* holotype ROM38628. Scale bars represent 10 mm (A–E, H), 50 mm (F) and 100 mm (G).

.2008 *Charnia antecedens*; Hofmann, O'Brien and King, pp. 17, 19, figs 13.7–13.8, 15.2–15.5?
v.2009 *Charnia antecedens*; Brasier and Antcliffe, p. 378, fig. 16.

Diagnosis. As per genus.

Holotype. ROM 54348 (Fig. 9A); redesignated from *Charnia antecedens* holotype, from the Drook Formation, Conception Group, Mistaken Point Ecological Reserve, Newfoundland.

Plesiotype. OUMNH ÁT.409/p; new designated plesiotype (Figs 5A and 9B–D) from the Mistaken Point Formation, near to the town of Catalina, Bonavista Peninsula, Newfoundland.

Discussion. Since the reallocation of *Charnia wardi* (Narbonne and Gehling, 2003) to the type species of *Trepassia wardae* (Narbonne *et al.*, 2009), it has become apparent that the even more distinct *Charnia antecedens* ought no longer to remain within *Charnia*. O'Brien and King (2004, p. 210) have already commented on the clear intermediary nature of this form as 'possibly comparable with *Bradgatia* but showing *Charnia*-like attributes'. We agree with this and therefore place *C. antecedens* within *Vinlandia* gen. nov. This then allows us to characterise the morphological sequence from *Beothukis mistakensis* through *Vinlandia antecedens*, to *Trepassia wardae* and thence to *Charnia masoni*, with much greater clarity (see Table 2 for the anatomical states of each taxon). In this way, each genus now represents a fundamental constructional type within a morphological continuum. *Vinlandia* has rotated rangeomorph elements throughout and can thereby be distinguished from *Beothukis*, which typically has fully displayed rangeomorph elements in mature second-order (but not first- or third-order) branches. Both taxa show radiating first- and second-order elements. *Vinlandia* is distinguished from *Trepassia* and *Charnia* in having a marked tendency towards radiating rather than subparallel first- and second-order branches. In contrast, *Trepassia* has moderately radiating second-order branches, while *Charnia* has subparallel second-order branches. Species differences within each of these genera may be established on the basis of numbers of branches and shape metrics.

Genus CHARNIA Ford, 1958

Emended diagnosis. Frond unipolar, comprising two rows of primary branches arranged alternately along a tightly furled central axis, forming a *zig-zag* suture. First-order branches typically show proximal inflation, whereas second-order branches show moderate-to-medial inflation. All first- to third-order branches are aligned in markedly subparallel series, with furled margins, having rangeomorph elements that are rotated and undisplayed. A basal disc is sometimes preserved.

Type species. *Charnia masoni* Ford, 1958, Charnwood Forest, England.

Charnia masoni Ford, 1958
Figures 4A, 8D

v* 1958 *Charnia masoni* Ford, p. 212, pl. 13, fig. 1.
? 1959 *Charnia* sp. Glaessner, p. 1472, text-fig. 1b.
? 1959 *Rangea*? sp. Glaessner, *in* Glaessner and Daily, p. 397, pl. 46, fig. 2.
1961 *Charnia* sp. Glaessner, p. 75, text-fig.
1962 *Charnia* sp. Glaessner, p. 484–485, pl. 1, fig. 4.
1966 *Rangea grandis* Glaessner and Wade, p. 616, pl. 100, fig. 5.
1973 *Glaessnerina grandis*; Germs, p. 5, fig. 1D.
1981 *Charnia masoni*; Fedonkin, p. 66, pl. 3, figs, 5, 6; pl. 29, fig. 1.
1985 *Charnia masoni*; Fedonkin, p. 99, pl. 12, fig. 4; pl. 13, figs 2–4.
v* 1995 *Charnia grandis*; Boynton and Ford, p. 168, fig. 1.
.1996 *Glaessnerina grandis*; Jenkins, p. 35, fig. 4.1.
?1998 *Charnia masoni*; Nedin and Jenkins, p. 315, fig. 1.
.1999 *Charnia grandis*; Ford, p. 231, fig. 3.
.2001 *Charnia masoni*; Narbonne, Dalrymple and Gehling, p. 32, pl. 1C.
v.2003 *Charnia wardi* Narbonne and Gehling, p. 28 (*partim*), fig. 2b,c.
.2004 *Charnia* Grazhdankin, p. 207, fig. 2.
.2005 *Charnia masoni*; Narbonne, Dalrymple, Laflamme, Gehling and Boyce, p. 28, pl. 1I.
.2007 *Charnia masoni*; Laflamme, Narbonne, Greentree and Anderson, p. 243, fig. 4a–j.
.2008 *Charnia masoni*; Hofmann, O'Brien and King, p. 17 (*partim*), fig. 13.1.
.2008 *Charnia grandis*; Hofmann, O'Brien and King, p. 18, fig. 14.
.2008 *Charnia masoni*; Grazhdankin, Balthasar, Nagovitsin and Kochnev, p. 804, fig. 2A.
.2009 *Charnia masoni*; Bamforth and Narbonne, p. 907, fig. 7.5.
.2011 *Charnia masoni*; Wilby, Carney and Howe, pp. 656–657 (*partim*), figs 2A, 3A.

Diagnosis. As per genus.

Discussion. The emended diagnoses provided in this article provide an opportunity to revisit the taxonomic concept of *Charnia masoni*. We no longer see a need to distinguish *C. grandis* from *C. masoni* on the basis that the fronds are large or possess more than a particular number of primary

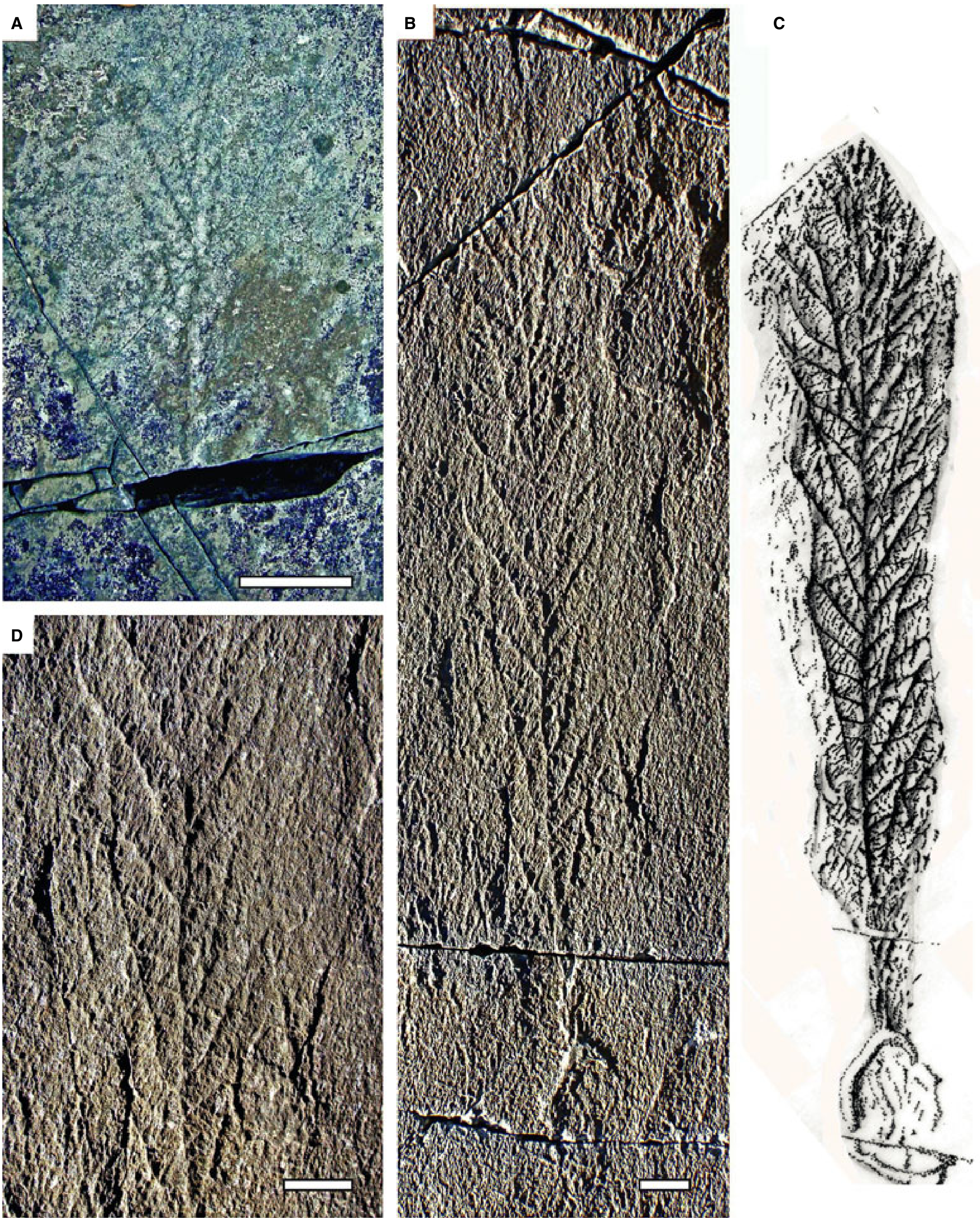


FIG. 9. A, holotype of *Vinlandia antecedens* gen. nov. ROM54348. B, newly designated plesiotype of *V. antecedens* OUMNH ÁT.409/p. Specimen remains *in situ* at locality 9 of Hofmann *et al.* 2008 (their fig. 13.8). C, drawing of the specimen in part B. D, enlargement of image in part B showing details of branching. Scale bars represent 50 mm (in A) and 10 mm (in B and C).

branches. As we have documented elsewhere (Antcliffe and Brasier 2007*a*, 2008; Brasier and Antcliffe 2009), *Charnia* is a genus that grows by the apical insertion of new primary branches and by their proximal inflation, within which the concept of *C. grandis* clearly fits. We see, however, no evidence for distinctive juveniles of *C. grandis*, which is therefore regarded as a large growth variant of the smaller *C. masoni* (cf. Brasier and Antcliffe 2009).

The distinct nature of the holotype of *Trepassia wardae* (see Narbonne *et al.* 2009; ROM38628) is agreed upon by us. However, we here suggest the reassignment of a specimen once placed within *C. wardi* (see Narbonne and Gehling 2003, ROM54349; later removed to *Trepassia wardae* by Narbonne *et al.* 2009) to *Charnia masoni*. Inspection of this specimen at the Royal Ontario Museum has not confirmed the presence of internal features here regarded as diagnostic for *Trepassia wardae* (see above).

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