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Relating Ediacaran Fronds

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Abstract.—Ediacaran fronds are key components of terminal-Proterozoic ecosystems. They represent one of the most widespread and common body forms ranging across all major Ediacaran fossil localities and time slices postdating the Gaskiers glaciation, but uncertainty over their phylogenetic affinities has led to uncertainty over issues of homology and functional morphology between and within organisms displaying this ecomorphology. Here we present the first large-scale, multigroup cladistic analysis of Ediacaran organisms, sampling 20 ingroup taxa with previously asserted affinities to the Arboreomorpha, Erniettomorpha, and Rangeomorpha. Using a newly derived morphological character matrix that incorporates multiple axes of potential phylogenetically informative data, including architectural, developmental, and structural qualities, we seek to illuminate the evolutionary history of these organisms. We find strong support for existing classification schema and devise apomorphy-based definitions for each of the three frondose clades examined here. Through a rigorous cladistic framework it is possible to discern the pattern of evolution within and between these clades, including the identification of homoplasies and functional constraints. This work both validates earlier studies of Ediacaran groups and accentuates instances in which previous assumptions of their natural history are uninformative.

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Introduction

The Ediacara biota is an assemblage of organisms from the late Ediacaran period (571–541 Ma; Pu et al. 2016) that represents the world's oldest abundant and globally distributed fossils of architecturally complex, megascopic organisms (Narbonne 2005; Fedonkin et al. 2007; Xiao and Laflamme 2009; Erwin et al. 2011). These soft-bodied organisms are typically preserved as impressions, primarily on the bottom surfaces of event beds of sandstone or volcanic ash (Narbonne 2005: Kenchington and Wilby 2014), or less commonly within event beds (Grazhdankin and Seilacher 2002; Narbonne et al. 2009, 2014; Vickers-Rich et al. 2013; Ivantsov et al. 2016), with multiple individuals revealing minute, millimeter-scale detail of their external morphology. These fossils capture a disparity of body forms and diversity of functions that belies their deceptively simplistic morphology (Erwin et al. 2011; Laflamme et al. 2013). The relatively low diversity coupled with high morphological disparity (Erwin et al. 2011) and a large number of monospecific genera (Fedonkin et al. 2007) lead to difficulties in isolating any visible hierarchy in the morphology and disagreements concerning homology statements between groupings (e.g., compare Laflamme et al. [2013] with Budd and Jensen [2015]).

The Ediacara biota immediately preceded the Cambrian "explosion" of animal diversity (Erwin and Valentine 2013) and thus occupied

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a pivotal position in the early evolution of complex life. While metazoan taxa were present, including the purported stem-group mollusk *Kimberella* (Fedonkin and Waggoner 1997), they coexisted alongside organisms whose affinities and relationships to any living phyla remain unknown and controversial (Erwin et al. 2011; Darroch et al. 2015; Droser and Gehling 2015). These uncertainties have hindered attempts to integrate these fossils into a broad-scale understanding of Neoproterozoic and Cambrian evolution (Erwin et al. 2011). Current classification methods involve controversial linkages between Ediacaran taxa based on morphological similarity of a small number of key features (Erwin et al. 2011) without any means of testing whether these characters are actually phylogenetically informative. In a significant overview of metazoan ancestry, Budd and Jensen (2015) noted this lack of rigorously defined clade-specific autapomorphies and tested synapomorphies for any previously proposed Ediacaran clades. They argued that, in the absence of autapomorphically defined clades, it is impossible to make informed assertions about homology and homoplasy in the Ediacara biota and that any understanding of these organisms is correspondingly reduced.

These difficulties can be minimized by defining Ediacaran clades through uniquely derived traits (autapomorphies), similar to other branches of fossil and extant life. Previous attempts to cladistically define the specific groups within the Ediacara biota have been met with limitations—either in terms of alpha diversity studied or temporal and geographic ranges used (Brasier and Antcliffe 2009)—or have mapped characters associated with individual Ediacaran taxa onto existing metazoan molecular phylogenies (Gold et al. 2015). Major organizational systems within and between groups of Ediacaran organisms have often been based on competing classification schemes that, at times, highlight specific a priori assumptions of how these organisms lived and grew (Pflug 1972; Narbonne 2004; Erwin et al. 2011; Brasier et al. 2012; Grazhdankin 2014). These previous groupings may be biased by features that are likely highly homoplastic (Laflamme and Narbonne 2008) and have led to interpretations of the Ediacara biota in terms of functional analogues irrespective of phylogeny (Droser and Gehling 2015).

The present study represents the first analysis to propose autapomorphically defined Ediacaran clades identified by modern cladistic methods. Previous work has focused on using selected features of assumed greater evolutionary significance or general similarity of form to group organisms. This leaves open the possibility for convergence or mistaken homology assertion to artificially grouped organisms, which has led to the suggestion that our knowledge of the evolutionary history of these organisms is still at an early stage (Budd and Jensen 2015). Here we seek to create a chain of common ancestry linking organisms together using a character-based system to identify shared derived features and not a priori assumptions of trait importance. For the present study we focus on taxa from three purported Ediacaran groups previously recognized on the basis of morphology (Rangeomorpha, Erniettomorpha, and Arboreomorpha; see Laflamme and Narbonne [2008] and Erwin et al. [2011]; note that Grazhdankin [2014] recognizes similar taxonomic groups under different names), which we chose for our analysis because they are widespread, abundant, and occur through a significant time range.

Methods

Our study aims to identify clade-level relationships and establish a series of strong synapomorphy-based definitions for each group. All ingroup taxa used herein have previously been assigned to one of three distinct groupings (Erwin et al. 2011): the Rangeomorpha, the Erniettomorpha, or the Arboreomorpha. We included the majority of named and described members, minimally at the genus level, that are currently accepted in each of the major groupings (Table 1). Analysis within these groups was restricted to named taxa that are well described in the literature on the basis of multiple, well-preserved specimens. Our analysis includes all frondose and non-frondose taxa within these three groups that meet these criteria, thus

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TABLE 1. Taxon list and preliminary group identification based on the literature for 21 terminal taxa examined for this study.

	Clade or group	Reference for affiliation
Outgroup		
Thaumaptilon walcotti	Cnidaria	Conway Morris 1993
Ingroup		
Charnia masoni	Rangeomorpha	Erwin et al. 2011
Beothukis mistakensis	Rangeomorpha	Erwin et al. 2011
Vinlandia antecedens	Rangeomorpha	Brasier et al. 2012
Avalofractus abaculus	Rangeomorpha	Erwin et al. 2011
Culmofrons plumosa	Rangeomorpha	Erwin et al. 2011
Trepassia wardae	Rangeomorpha	Erwin et al. 2011
Pectinifrons abyssalis	Rangeomorpha	Erwin et al. 2011
Frondophyllas grandis	Rangeomorpha	Erwin et al. 2011
Hapsidophyllas flexibilis	Rangeomorpha	Erwin et al. 2011
Fractofusus andersoni	Rangeomorpha	Erwin et al. 2011
Fractofusus misrai	Rangeomorpha	Erwin et al. 2011
Bradgatia linfordensis	Rangeomorpha	Erwin et al. 2011
Rangea schneiderhoehni	Rangeomorpha	Erwin et al. 2011
Ernietta plateauensis	Erniettomorpha	Erwin et al. 2011
Pteridinium simplex	Erniettomorpha	Erwin et al. 2011
Swartpuntia germsi	Erniettomorpha	Erwin et al. 2011
Charniodiscus spinosus	Arboreomorpha	Erwin et al. 2011
Charniodiscus procerus	Arboreomorpha	Erwin et al. 2011
Charniodiscus arboreus	Arboreomorpha	Erwin et al. 2011
Charniodiscus yorgenesis	Arboreomorpha	Ivantsov 2016

providing critical insights into expressions of homology and homoplasy in the Ediacara biota, and encompasses the temporal, geographic, and bathymetric ranges for each of the reported groups (Narbonne 2005; Boag et al. 2016). We did not synonymize the taxa based on a single criterion for character generation, as our data set encompasses multiple axes of variation, such as morphometric, growth patterning, and branching architecture, in an effort to encapsulate all the evolutionarily relevant information in these organisms.

Due to the relative morphological simplicity (compared with the majority of metazoans) of the organisms investigated here, and their uncertain relationship to later clades, we chose not to use existing metazoan-based morphological character sets as the basis for this work. A novel data set consisting of 22 morphological characters (Supplementary Table 1, Supplementary Fig. 1) was constructed from descriptions and illustrations in the literature supplemented by our personal examination of multiple specimens, including the holotypes for all of the taxa except for the recently described *Charniodiscus yorgensis* (Ivantsov 2016).

Characters were sampled from all regions of the organisms and were specifically chosen to avoid restating previously proposed diagnostic features for a group (e.g., Laflamme and Narbonne 2008). Instead, we critically examined all structural features and decomposed them into their constituent parts. Beyond guiding our taxonomic selection, existing classification schemes had no impact on the coding of morphological features or our analysis of these features. We added new characters and character states to document all sources of variation to ensure our data set was as encompassing as possible. These include characters of the holdfast beyond its presence or absence, in particular its position relative to the sediment–water interface; see Burzynski and Narbonne (2015) for a discussion on differentiation of this feature. This combination of new characters and detailed dissection of previously suggested significant features allows us to test existing classification schemes and to evaluate the validity of existing diagnostic morphologies.

Characters were further defined to avoid oversplitting by focusing on key aspects that are functionally independent of one another. This is pivotal, because a high degree of character dependence violates a key assumption of cladistic analyses by overweighting the strength of observed relationships (O'Keefe and Wagner 2001). For example, the modularly

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repeating "rangeomorph element" (Narbonne 2004) was decomposed into four new characters that address the presence/absence of modularity, the branching nature of the element, the shape of elements that compose the petalodium, and whether those elements are self-similar and repeated at multiple scales. Each of these characters and the states within them are potential independent sources of phylogenetic information that are subsumed in the simple statement of presence/absence of a rangeomorph element (e.g., Narbonne 2004; Laflamme and Narbonne 2008). The taxa examined here show several permutations of these four characters and their states (e.g., the modular, nonbranching, tubular, and nonfractal patterns in Erniettomorphs vs. the nonmodular, branching, but nonfractal pattern seen in *Charniodiscus*) (Supplementary Table 2). Splitting the "rangeomorph element" into its constituent parts further permits the scoring of potential intermediate morphologies (i.e., a nonmodular, nontubular, branching frond with some fractal elements) that are currently unknown.

The selection of an outgroup is likely to influence our understanding of evolutionary trends within theses organisms, however there is no universally agreed upon taxon or group to serve this purpose at this time. We chose the purported cnidarian *Thaumaptilon* (Conway Morris 1993) from the Burgess Shale (Cambrian) as the outgroup for our analysis. *Thaumaptilon* is well illustrated and characterized, and shares a similar body plan to Ediacaran fronds, but is believed to represent a distinct evolutionary lineage (Antcliffe and Brasier 2007; Laflamme and Narbonne 2008). Furthermore, we also ran the analysis using an artificially generated outgroup based on an undifferentiated yet nonmodular frond without stem or holdfast. All phylogenetic investigations were done using a heuristic search algorithm with default settings in PAUP, Version 4.0 (Swafford 2003). Bootstrap support, which is resampling with replacement of the character set to investigate the strength of the signal, and Bremer decay indices, which denote the number of extra steps need to collapse a node of interest, were taken as measures of nodal support. For bootstrapping analysis, 100 replications were done with the 100,000 trees kept per replication and only nodes above 50% support retained.

Results

Heuristic search of the complete data set (Fig. 1) resulted in 12 most-parsimonious trees of length 49 with a consistency index (CI) of 0.673 (where 1.0 indicates no homoplasy of characters across the tree). Furthermore, a retention index (RI) denoting the character fit and proportion of informative states was high (0.83). From the trees, it was possible to assign autapomorphies that define each clade.

We find strong support for the Rangeomorpha, Arboreomorpha, and Erniettomorpha clades, whose membership mimics those proposed by Erwin et al. (2011), and a sister relationship between Rangeomorpha and Erniettomorpha. Arboreomorpha can be defined by their secondary branches, which are spherical or hemispherical in shape, with no lower subdivisions present. They also display differentiation along the coronal plane (i.e., the plane that subdivides the petalodium into a back/front or dorsal/ventral) and the lack of a modular petalodium, though this is also present in *Thaumaptilon*. The Rangeomorpha–Erniettomorpha clade is defined by having a petalodium composed of modular elements that do not show any differentiation in the coronal plane. Rangeomorpha, the most diverse and disparate of the three clades investigated, is defined by having a petalodium composed of branching, modular elements that display self-similar (fractal) morphology. Our analyses suggest that the ancestral condition was a single-sided petalodium, though the majority of taxa displaying this condition may be biasing this. Erniettomorphs are defined as having petalodia composed of undifferentiated, nonrepeating tubular modular elements that are uniform in width. The unique "bag-shaped" morphology of *Ernietta* is derived from the fusion of the two petaloids at their edge as marked by a major suture (Ivantsov et al. 2016), and we scored this as such, even though the petaloids do not form the single, flat plane seen in most other fronds.

The consensus tree presents a semiresolved topology that broadly supports previous

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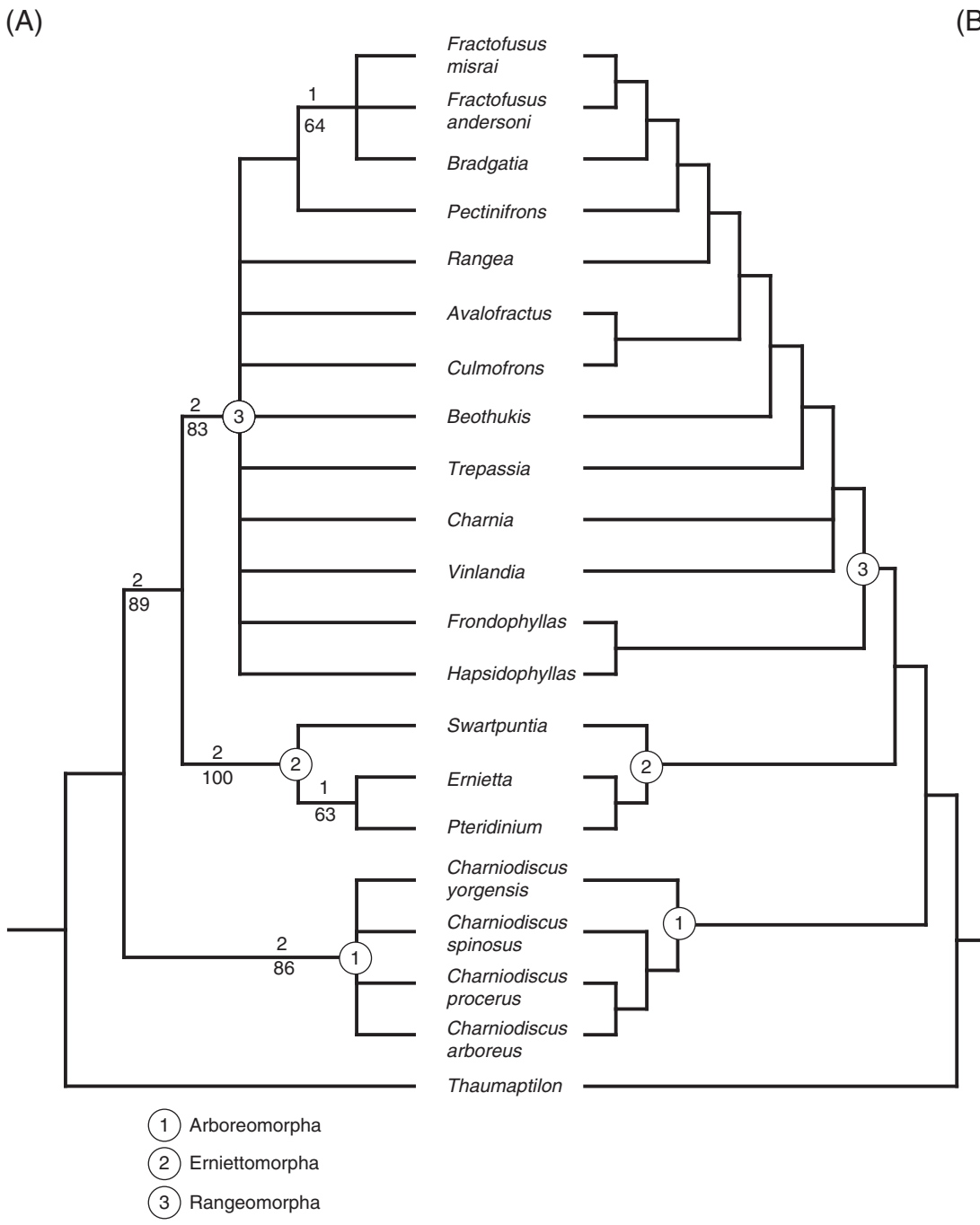


FIGURE 1. Phylogeny of Ediacaran fronds using *Thaumaptilon* as the outgroup to polarize the data. (A) Bootstrap consensus tree numbers by the node represent the Bremer support (above the branch) and bootstrap support (below the branch) for each node. (B) Strict consensus tree.

subdivisions within the Rangeomorpha, identifying a clear separation between single-sided and tightly constrained (undisplayed per Brasier et al. 2012) "charnids" (*Vinlandia*, *Charnia*) and the double-sided primary- and secondary-branching (displayed and unfurled per Brasier et al. 2012) "rangids" (*Rangea*, *Fractofusus*, *Bradgatia*). *Beothukis*, *Culmofrons*, and *Trepassia*

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are found notably outside the "charnid" subgrouping, forming possible transitional steps uniting the "charnids" with the "rangids." Our whole-fossil analysis of *Beothukis* and *Culmofrons* does not support the recent suggestion that the two taxa may be synonymous at the genus level (Liu et al. 2016). Within the Erniettomorpha, *Ernietta* and *Pteridinium* form a sister relationship to the exclusion of *Swartpuntia*, though this may be due to the latter having a more classical "frond" appearance, including the presence of a stem and stalk. There is little resolution within the Arboreomorpha, which reflects the general similarity of all species in this clade and suggests that the alpha taxonomy of this clade requires more granular traits, such as segment count and frond shape (Laflamme et al. 2004), that are not appropriate for beta taxonomic-level analyses such as this.

Discussion

Focusing on a subset of Ediacaran taxa with a similar gross body plan ("fronds") but significant structural and architectural variation avoids the issue of character inflation without adding resolution. Incorporating all 10 proposed groups from Erwin et al. (2011) would have required a character set that was unscorable across much of the taxon set. While missing data are not necessarily a hindrance to phylogenetic analyses (Wiens and Morrill 2011), it is the nature of how those missing data are distributed that would be of concern (Wiens 2003). If the data are randomly distributed (i.e., if most columns are partially scored by taxon across the matrix), more characters (even if only partially scored) aid in phylogenetic resolution. However, this is not the case if the data are clustered into nonoverlapping partitions (i.e., most columns are empty; Wiens 2003) as found in an Ediacara biota–wide analysis. As such, the *amount* of missing data is not as troubling as the *distribution* of the missing data.

Another possible challenge for this taxon set is whether there is enough discernible morphology to create the valid characters and states necessary to establish a well-supported evolutionary tree. While large data sets are not a prerequisite (Simões et al. 2016), lower quantities of data limit resolution power (Bremer et al. 1999). Our results show that there are enough distinct morphological data among Ediacaran fronds to generate a viable phylogenetic signal, even given our limited understanding of multiple aspects of the biology and physiology of these organisms.

Fronds such as *Charnia*, *Charniodiscus*, and *Rangea* are abundant in Ediacaran assemblages worldwide and provide some of the most iconic images of the Ediacara biota. Early workers viewed the frondose morphology as representing a major division in Ediacaran taxonomy (Glaessner 1979), but this has fallen out of favor as subsequent studies have increasingly concluded that Ediacaran fronds are polyphyletic (Laflamme and Narbonne 2008; Erwin et al. 2011; Grazhdankin 2014). Our cladistic analysis confirms that Ediacaran fronds occur in multiple Ediacaran clades, two of which (Erniettomorpha and Rangeomorpha) also contain non-frondose taxa. This supports the view that fronds are an ecomorph *Bauplan* (i.e., taxa that are similar in morphology due to similar niche usage but may not be closely related phylogenetically; see Williams 1972) found among unrelated Ediacaran groups (Laflamme and Narbonne 2008). Our whole-organism analysis finds strong support for the three groupings (Arboreomorpha, Erniettomorpha, and Rangeomorpha) suggested by previous work based on major structural differences in the components of the petalodium (Laflamme and Narbonne 2008; Erwin et al. 2011). Our study also provides a set of synapomorphies to define each clade (Fig. 1, Table 2), building a framework to address issues of homology raised by Budd and Jensen (2015).

The artificially generated outgroup allowed us to test the robustness of our primary analysis topology (Fig. 2). This run (120 most-parsimonious trees of length 49, CI 0.667, RI 0.83) confirms the distinct nature of the three clades, though we find a different interrelationship between them. There is a shift in the positioning of the Arboreomorpha into a sister relationship with Rangeomorpha, uniting the two predominantly upright frondose clades. This topology further suggests that modularity is homoplastic among frondose organisms. While these results are intriguing, we do not

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TABLE 2. Synapomorphies listed in terms of character (state) for the three major clades using both *Thaumaptilon* (A) and artificially generated outgroup (B) analyses. We note that the difference between unambiguous and ambiguous synapomorphies is dependent on the resolution of the node preceding that of interest. As selection of outgroup alters the sister-clade relationships (see Figs. 1 and 2), using only the unambiguous-synapomorphy list is an overly conservative estimate of the number of apomorphies per clade.

	Clade	Unambiguous synapomorphy	Ambiguous synapormorphy
A	Arboreomorpha	8 (3), 11 (3),	22 (2)
	Erniettomorpha	3 (1), 5 (0), 13 (2), 14 (0),	2 (0), 4 (1)
	Rangeomorpha	8 (2), 15 (0), 18 (0)	2 (1), 4 (2), 13 (1)
B	Arboreomorpha	9 (1), 19 (1)	1 (0), 4 (0), 8 (3), 22 (2)
	Erniettomorpha	11 (0)	3 (1), 4 (1)
	Rangeomorpha	11 (1), 15 (0), 18 (0)	2 (1), 4 (2), 8 (2)

place significant weight on the resulting trees, beyond the confirmation of the distinctness of the three clades, due to the hypothetical nature of this outgroup.

The precise and testable criteria used in constructing the evolutionary history of each clade allows for detailed examination of major growth and evolutionary patterning across these clades. One potential area of interest concerns growth process—either through insertion or inflationary models (Brasier et al. 2012). Growth by insertion implies that new branches are added throughout life, at either or both poles, to increase the size of the organism. This is contrasted with inflationary growth, in which organisms attain their adult complement of sections/branches early in ontogeny and subsequent growth involves enlargement of existing sections/branches. We find preliminary support for an ancestral inflationary type of growth, which could have significantly influenced multiple aspects of the organism's biology and has been suspected to be a major discriminating factor in Ediacaran phylogenetics (Antcliffe and Brasier 2007; Brasier et al. 2012). Differences in growth strategy are also suspected to influence maximum size due to the need to ensure a large surface area to volume ratio for effective osmotrophic feeding (Laflamme et al. 2009). Both strategies (inflation vs. insertion) at either or both poles have been reported in Erniettomorpha and Rangeomorpha (Grazdankin and Seilacher 2002; Antcliffe and Brasier 2007; Gehling and Narbonne 2007; Laflamme et al. 2009, 2012; Narbonne et al. 2009; Ivantsov et al. 2016), with additive growth seen in the oldest-known Rangeomorpha *Trepassia*. It is of interest that the terminal addition pattern is seen in charnids (Antcliffe and Brasier 2007) and the erniettomorph *Pteridinium*. This pattern is similar to that reported in several bilaterian groups as well as the enigmatic Ediacaran fossil *Dickinsonia* and has been suggested to link them to basal Bilateria (Gold et al. 2015). The identification that this feature is homoplastic and evolved at least three times across Ediacaran groups urges caution in using growth strategies as a major classification criterion in this area of the tree of life. Within the Arboreomorpha we do not see variation in growth strategy, as all known taxa grew by branch inflation (Laflamme et al. 2004), with the number of branches a potential species-level diagnostic feature.

Within the Rangeomorpha the presence of additive growth is seen in two separate groups (Fig. 1B), the derived "charnids" (*Trepassia*, *Charnia*) and the multifoliate rangid *Pectinifrons* (Bamforth et al. 2008; Narbonne et al. 2009). This suggests convergence of growth patterns between charnids and *Pectinifrons*, as *Pectinifrons* is nested within a clade with multiple members displaying inflationary growth. While it may at first seem unlikely that a major shift in growth strategy occurred multiple times within a clade, we know that the evolution of growth by insertion has occurred several times within eukaryotes (Gold et al. 2015). Furthermore, the exact nature of how inflation occurs seems to differ between charnids and *Pectinifrons*, implying that the developmental pathways may differ between the two. *Pectinifrons* employs insertion for the addition of struts along the pedicle, which is then followed by branch inflation for subsequent growth of primary branches (Bamforth et al. 2008). In contrast, charnids appear to grow either exclusively by primary

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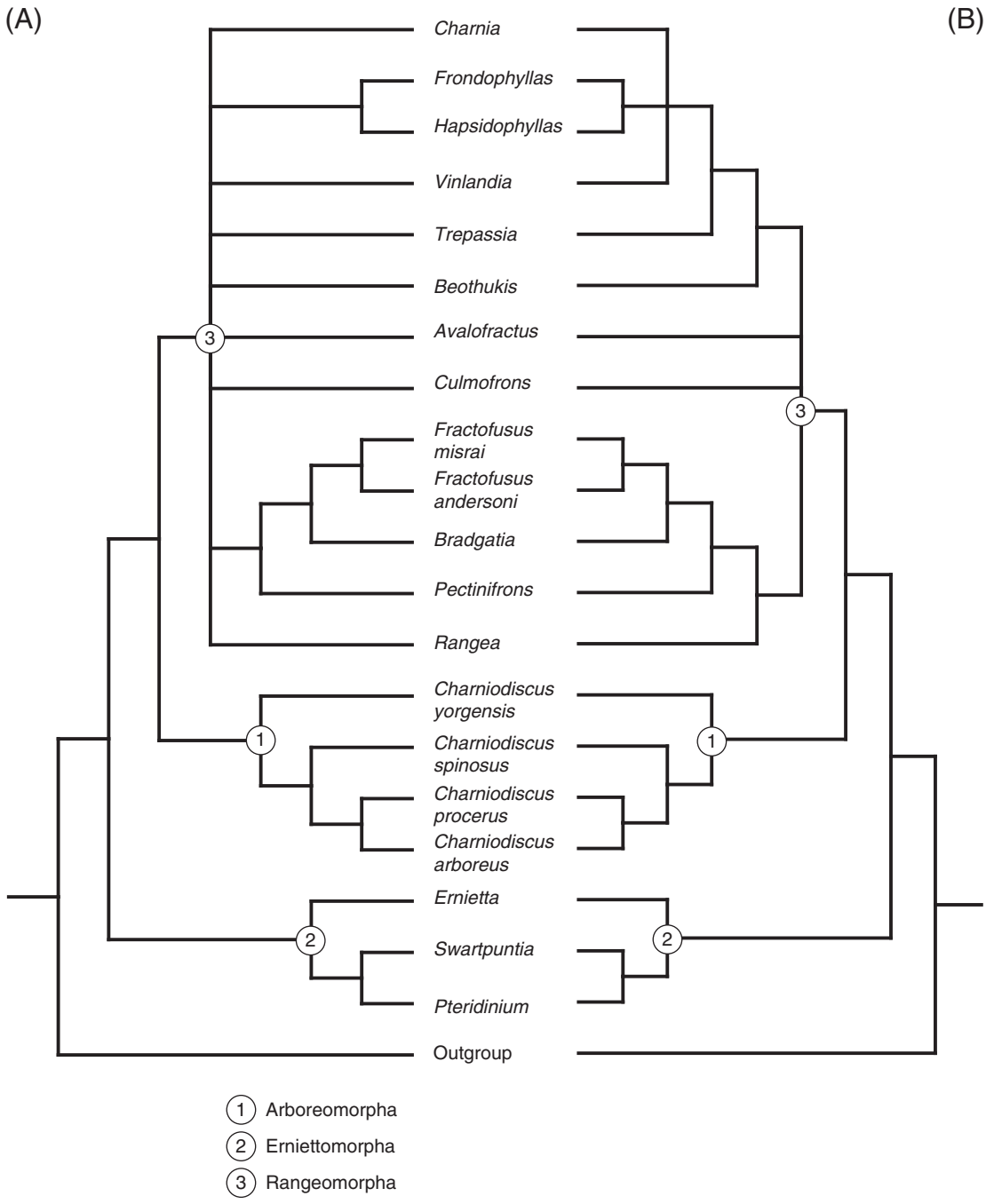


FIGURE 2. Phylogeny of Ediacaran fronds using artifically generated outgroup to polarize the data. (A) Strict consensus tree. (B) Majority rules consensus tree.

addition (*Trepassia*) or by terminal primary addition with inflation of previously added primaries (*Charnia*) (Narbonne et al. 2009). The insertion growth strategy seen in *Pectinifrons* and charnids may be paedomorphic, as other rangids are suspected to undergo branch addition to "adult" complement very early in ontogeny, with the inflationary growth model becoming dominant later in their life cycles (Gehling and Narbonne 2007).

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The linking of Erniettomorpha and Rangeomorpha as sister clades is notable, though caution is advised due to the lack of resolution of this group using the artificially generated outgroup (Fig. 2). The proposed synapomorphies for this group include the lack of differentiation in the coronal plane and the modular construction of their petalodia (or in the case of some Erniettomorpha, the entire organism). Should the phylogeny prove valid, this may signal a common developmental system or be convergent, related to how they obtained nutrients through osmotrophy (Laflamme et al. 2009). While it is tempting to accept this clade at face value and suggest that the lowest level of rangeomorph branching (which can resemble a tube) is homologous to the large tube of an erniettomorph, several factors suggest to us that modularity may be homoplastic. First is the nature of the modular elements. Within Erniettomorpha, the modules are uniform and tubular and possess no lower level of differentiation, which sharply contrasts with the repeated branching of the major elements in Rangeomorpha (Laflamme and Narbonne 2008), which may have evolved to increase surface area as volume expands. Based on the results of this study, modular construction (Narbonne 2004) appears to be a common morphological adaptation among Ediacaran clades to increase body size (see the discussion in Hoyal Cuthill and Conway Morris 2014), with little homology in its developmental origins. The repeated evolution of modularization may be a function of the limited genetic tool kit available to these organisms (Narbonne 2005; Hoyal Cuthill and Conway Morris 2014).

Conclusions

Our cladistic analysis provides a clear and rigorously defined set of synapomorphies to establish monophyletic clades of Ediacaran organisms. We find strongly supported Rangeomorpha, Erniettomorpha, and Arboreomorpha that correspond to previously proposed groupings, lending strength to existing morphogrouping schemes. We also find that growth strategies seem to have been somewhat plastic within these clades, as insertionary growth appears to have evolved multiple times within the fronds. Finally, while our analysis produces a sister-group relationship between the Rangeomorpha and the Erniettomorpha, the convergence on a modular body construction is not unique to these taxa and appears to have been widespread across the Ediacara biota. This framework can be extended to incorporate other members of the Ediacara biota such as the Dickinsoniomorpha and Triradialomorpha, and thus bring Ediacaran fossils into the age of cladistics.

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