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## Population structure of the oldest known macroscopic communities from Mistaken Point, Newfoundland

Simon A. F. Darroch, Marc Laflamme, and Matthew E. Clapham

**Abstract.**—The presumed affinities of the Terminal Neoproterozoic Ediacara biota have been much debated. However, even in the absence of concrete evidence for phylogenetic affinity, numerical paleoecological approaches can be effectively used to make inferences about organismal biology, the nature of biotic interactions, and life history. Here, we examine the population structure of three Ediacaran rangeomorph taxa (*Fractofusus*, *Beothukis*, and *Pectinifrons*), and one non-rangeomorph taxon (*Thectardis*) across five fossil surfaces around the Avalon Peninsula, Newfoundland, through analysis of size-frequency distributions using Bayesian Information Criterion (BIC). Best-supported models resolve communities of all studied Ediacaran taxa at Mistaken Point as single cohorts with wide variance. This result is best explained in terms of a “continuous reproduction” model, whereby Ediacaran organisms reproduce aseasonally, so that multiple size modes are absent from preserved communities. Modern benthic invertebrates (both as a whole and within specific taxonomic groups) in deeper-water settings reproduce both seasonally and aseasonally; distinguishing between biological (i.e., continuous reproductive strategies) and environmental (lack of a seasonal trigger) causes for this pattern is therefore difficult. However, we hypothesize that the observed population structure could reflect the lack of a trigger for reproduction in deepwater settings (i.e., seasonal flux of organic matter), until the explosive appearance of mesozooplankton near the base of the Cambrian.

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### Introduction

Prior to the advent of macroscopic predation and system-wide ecosystem engineering at the dawn of the Cambrian explosion (Erwin et al. 2011), Ediacaran ecosystems were dominated by large, morphologically complex eukaryotes called the Ediacara biota (Narbonne 2005; Xiao and Laflamme 2009). The presumed affinities of these enigmatic organisms are uncertain (see Gehling 1991; Buss and Seilacher 1994; Narbonne 2005), although recent studies suggest that the Ediacara biota consists of a number of independent clades, including stem-animal lineages, and extinct groups of multicellular eukaryotes (Xiao and Laflamme 2009; Erwin et al. 2011; Laflamme et al. 2013). The Rangeomorpha (Jenkins 1985; Narbonne 2004) are of particular interest, as they possess alternate symmetry and (pseudo) fractal architecture that depart from extant

bilaterian bodyplans (Narbonne et al. 2009). Since the discovery of *Rangea* by Gurich (1930), the affinities of rangeomorphs have been intensely debated, with interpretations ranging from metazoans such as ctenophores (Dzik 2002) and soft corals (Jenkins 1985), to an extinct higher-order clade with no modern representatives (Pflug 1970, 1972; Seilacher 1989; Grazhdankin and Seilacher 2005; Narbonne 2004, 2005; Narbonne et al. 2009; Brasier and Antcliffe 2009; Erwin et al. 2011; Brasier et al. 2012; Laflamme et al. 2013), and stem-group metazoans or eumetazoans (Xiao and Laflamme 2009). Fractal architecture among the Rangeomorpha is expressed as modular and self-repeating organization (“frondlets” of Narbonne 2004), whereby self-similar units are assembled into larger constructions, including fronds, bushes, “fences,” and mats (Grazhdankin and Seilacher

2005; Gehling and Narbonne 2007; Bamforth et al. 2008; Flude and Narbonne 2008; Brasier et al. 2012). This architecture has been linked with an osmotrophic life strategy (Sperling et al. 2007; Laflamme et al. 2009), and is unknown among representatives of modern phyla (Narbonne 2004). Despite these difficulties in inferring taxonomic affinity, numerical paleoecological approaches can be effectively used to make inferences about organismal biology and ecology, even in the absence of concrete evidence for phylogenetic affinity (Clapham et al. 2003; Droser et al. 2006). One aspect of the Ediacara biota that has not received much attention is in-depth analysis of their population structure; given the assumption of a specific reproductive mode (i.e., sexual vs. asexual), examining the population structure of communities can provide insights into the nature of organismal growth, recruitment, mortality, and life history (Cummins et al. 1986). Paleocological study of rangeomorph population structure therefore holds the potential to yield valuable information on ancestral reproductive mode and behavior at the base of the metazoan phylogenetic tree. Here, we use data compiled by Clapham et al. (2003) for a range of rangeomorph and non-rangeomorph taxa preserved on five fossiliferous surfaces around the Avalon Peninsula, in order to investigate population structure and reproductive behavior in the oldest known macroscopic communities.

Sedimentary rocks within the Mistaken Point Ecological Reserve in Newfoundland, Canada, preserve the oldest Ediacaran communities (ca. 579–560 Ma [Narbonne et al. 2012]), with hundreds to thousands of fossils preserved in situ on the upper surfaces of large, decameter-scale bedding planes (Clapham et al. 2003). Fossil surfaces around Mistaken Point preserve communities with differences in ecological parameters such as species richness, “tiering,” and spatial structure, which led Clapham et al. (2003) to suggest that they likely represent different stages of ecological succession. Fossils are preserved as low-relief two-dimensional impressions on the upper surfaces of sandstone beds (Conception-type preservation of Narbonne 2005), from which their original three-

dimensional shape must be reconstructed. Unlike the vast majority of Phanerozoic shelly assemblages, which represent time- and space-averaged accumulations (Kowalewski et al. 1998), the soft-bodied impressions of Ediacaran fossils at Mistaken Point represent a genuine snapshot (*Konservat Lagerstätten* of Seilacher 1970) of the Ediacaran seafloor. These organisms are interpreted for the most part as benthic, non-motile, sessile osmotrophs (Narbonne 2004; Bottjer and Clapham 2006; Laflamme and Narbonne 2008), although other feeding strategies have been proposed (e.g., Seilacher 1989). Sedimentary evidence for chemoautotrophy, such as carbonates or sulfides typical of methane seep deposits (Little et al. 1998), is unknown from the Mistaken Point sections, and photoautotrophic lifestyles can be dismissed because the depositional setting is inferred to have been well below storm wave base and the photic zone (Wood et al. 2003). Filter-feeding is more difficult to discount; however, the repeated modularity of rangeomorphs suggests that feeding units were likely too small for effective filtering (Narbonne et al. 2009), although surface area to volume ratios modeled from *Fractofusus* (Gehling and Narbonne 2007) do support an absorption-based feeding strategy (Laflamme et al. 2009).

Ediacaran organisms at Mistaken Point were preserved after being smothered by volcanic ash (“Conception-style” preservation [see Narbonne 2005]). The taphonomic pathway inferred for soft-tissue preservation in these fossils is similar to the microbial “death mask” originally proposed by Gehling (1999) for localities in South Australia; the local presence of seafloor microbial mats and rapid onset of anaerobic decay likely led to early lithification of the soles of overlying ash beds, effectively casting fine-scale morphology (Narbonne 2005; Laflamme et al. 2011; Liu et al. 2011). Broad experimental support for this model was provided by Darroch et al. (2012), who demonstrated higher fidelity of soft-tissue preservation in decay experiments using microbial mats than in those without mats. In addition, because the fossil surfaces at Mistaken Point contain little evidence for postmortem transport and spatial mixing of

populations (Narbonne et al. 2001; Clapham et al. 2003), fossil assemblages are typically interpreted as census populations of in situ epifaunal organisms (Clapham et al. 2003). Although Ediacaran communities from Mistaken Point are composed exclusively of organisms lacking biomineralized shells or skeletons, the possibility that these surfaces could have experienced extensive time averaging has been suggested (Liu et al. 2011). Experimental studies suggest that any carcasses lying upon the seafloor would have decomposed within days to weeks of their initial death (Allison 1988; Brasier et al. 2010; Darroch et al. 2012), a time frame that is orders of magnitude smaller than the time-lag associated with shelly deposits (up to several hundred years [Kowalewski et al. 1998]) and on par with modern ecological studies of census populations (as discussed in Dornbos et al. 2012). Furthermore, although small (<2 cm) specimens are rare, they are not unknown (Laflamme et al. 2004, Liu et al. 2012); small-scale biological structures such as range-morph elements can be as small as a few millimeters in size (Narbonne 2004), showcasing the ability to preserve smaller individuals on bedding planes. Taphonomically and paleoecologically, therefore, the Ediacaran fossil assemblages preserved around the Avalon Peninsula represent an ideal data set for the analysis of population structure.

*Paleoenvironmental and Stratigraphic Setting.*— Previous studies have inferred a deepwater (toe of slope to lower slope) paleobathymetry well below storm wave base and the photic zone (Wood et al. 2003; Ichaso et al. 2007), thus restricting the fossil organisms to non-photosynthetic feeding strategies (Clapham and Narbonne 2002; Laflamme et al. 2009). The oldest Ediacaran fossils described from Mistaken Point are from the Conception Group, consisting of the Mall Bay, Gaskiers, Drook, Briscal, and Mistaken Point formations (Fig. 1). Fossils are unknown from sections below the Gaskiers tillite, characterized as a “Snowball Earth Glaciation” (sensu Hoffman et al. 1998) complete with dropstones, striated clasts, and a sharp  $-6\text{‰}$   $\delta^{13}\text{C}$  isotope excursion at the base of the Cap Carbonate (Myrow and Kaufman 1999). Overlying the Gaskiers cap carbonate are

thin  $T_{DE}$ -bedded to medium  $T_{(A)BCDE}$ -bedded turbidite deposits of the Drook Formation (Wood et al. 2003; Narbonne et al. 2005). Tops of turbidite beds are typically capped by fine-grained inter-turbidite mudstones interpreted as pelagic fallout, and sporadically overlain by coarse crystal- and lapilli-tuff volcanic ashes. Small-scale sedimentary structures, such as synsedimentary slumps, folds, faults, scours, and rip-up clasts, are occasionally found in association with the base of the turbidity sediments (Hofmann et al. 2008). The Briscal Formation consists of gray, thick- to very thick-bedded medium- to coarse-grained sandstones with rare greenish mudstones (Wood et al. 2003; Narbonne 2005). Thick-bedded turbidites ( $T_{(A)B(C)DE}$ ) in the Briscal Formation are similar in character to the thicker Drook Formation turbidites, although the very thick beds tend to be largely structureless, except for water escape structures (pillars and sheets) and small-scale erosional and load structures. Volcanic ashes are thin (a few millimeters) and sporadic, leading to fewer exposed surfaces than in the underlying Drook and overlying Mistaken Point Formations.

The Mistaken Point Formation is composed almost entirely of gray/green to reddish, medium- to thin-bedded turbiditic ( $T_{DE}$  –  $T_{(AB)CDE}$ ) sandstones. Lowermost sections are thin-bedded, fine- to very fine-grained grading upwards into fine- to medium-grained sandstones. Rare graded sandstones and debris flows are present, but are volumetrically dwarfed by the turbiditic deposits. Medium sands have been found at the base of thicker (>30 cm) beds. The turbidite beds are typically overlain by a thin (1–2 cm) mudstone interpreted as pelagic fallout (Wood et al. 2003). This thin pelagic mudstone is characterized by thin, black, “crinkly,” and discontinuous silt laminae that may represent diagenetically altered microbial mats (e.g. Wood et al. 2003; Narbonne et al. 2005). Thin (1–2 cm) beds interpreted as deepwater contourite deposits (Wood et al. 2003) are found above terminal-stage turbidite beds and, when overlain by volcanic ash, typically contain Ediacaran fossils.

The base of the St. John’s Group consists of thin- to medium-bedded gray siltstones, sand-

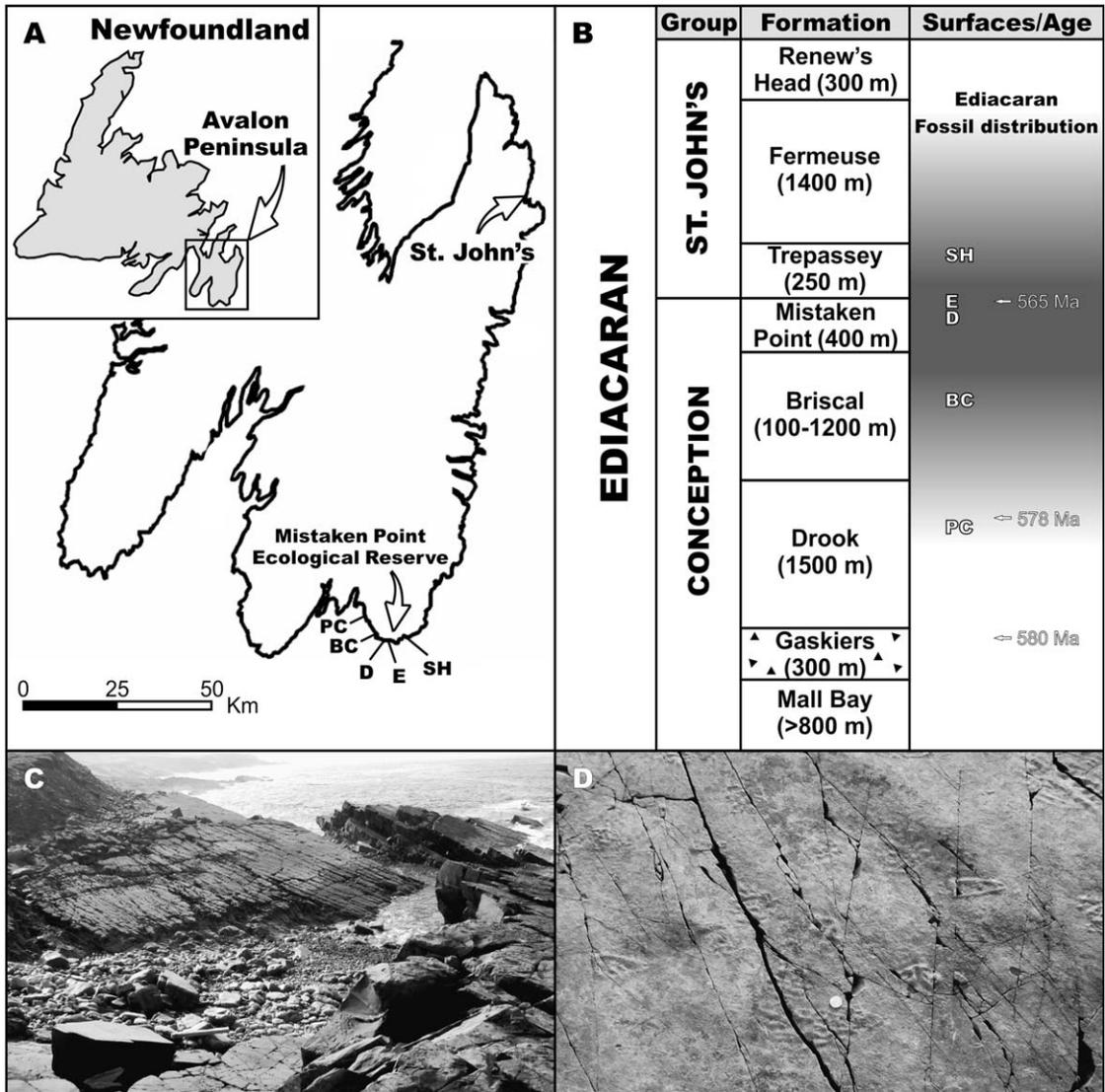


FIGURE 1. Summary locality figure and stratigraphic context for studied surfaces in the Mistaken Point Ecological Reserve. A, Locations of fossil surfaces. B, Stratigraphic column with positions of studied surfaces and radiometric dates. C, Pigeon Cove locality showing bed aspect and regional dip. D, Pigeon Cove fossil surface with Ivesheadiomorphs, *Thectardis*, and microbially induced sedimentary structures (MISS); coin for scale. Radiometric ages from Dunning in Benus (1988) and Bowring et al. (2003).

stones, and mudstones of the ~200 m thick Trepassey Formation. Beds from the Trepassey Formation are thin (rarely thicker than 10 cm) and represent  $T_{DE} - T_{(B)CDE}$  turbidite successions, with silty mudstones making up 60–80% of the formation. Large-scale soft-sediment deformation is ubiquitous throughout the section, with individual slumps reaching thicknesses of >12 m within larger slump complexes up to 60 m thick (Narbonne et al.

2001, 2005), suggesting that the Trepassey Formation was deposited on an unstable slope (Wood et al. 2003).

*Analysis of Population Structure from Size-Frequency Histograms.*—Size-frequency distributions are a well-established technique in marine biology for investigating population structure in marine benthos. Organisms with seasonal reproduction and recruitment typically show distinct modes in size frequency,

which correspond to individual age classes (Billet and Hanson 1982; Fujita and Ohta 1990). Repeated sampling of these populations at multiple time intervals can provide insights into ecology, environmental stability, and growth rates (Fujita and Ohta 1990; Babcock 1991). These analyses have traditionally been done on scleractinian corals (Bak and Meesters 1998, 1999), bivalved mollusks (Lightfoot et al. 1979; Comtet and Desbruyères 1998), and echinoderm meadow-type communities composed of holothurians (Billet and Hanson 1982; Rowe 1971, 1972), ophiuroids (Fujita and Ohta 1989, 1990; Packer et al. 1994), and echinoids (Forcucci 1994). More recently, similar statistical techniques (such as mixing models) have been applied to fossil data sets to help establish sexual dimorphism and multiple instars in fossil arthropods (Chapman and Hunt 2001), and population structure in Cambrian eocrinoids (Zamora et al. 2013).

### Methods

We used data compiled by Clapham et al. (2003) from the Pigeon Cove (PC), Bristy Cove (BC), Mistaken Point D and E, and Shingle Head (SH) surfaces exposed around the Avalon Peninsula (see Fig. 1). Three rangeomorph taxa (*Fractofusus* Gehling and Narbonne 2007, *Beothukis* Brasier and Antcliffe 2009 [Narbonne et al. 2009], and *Pectinifrons* Bamforth et al. 2008), and one non-rangeomorph taxon (*Thectardis* Clapham et al. 2004) were selected for analysis. Analyses were restricted to taxa with sufficient sample sizes (>40), and to those attributes that could be characterized largely in two dimensions, e.g., height and width for upright fronds, or length and width for interpreted flat recliners such as *Fractofusus* (see Gehling and Narbonne 2007; Laflamme and Narbonne 2008) (Fig. 2). This minimum sample size was chosen to reflect the smallest samples used by Chapman and Hunt (2001). The different life habits (e.g., upright vs. reclining) among the studied taxa mean that measures such as “length” and “width” may correspond to different attributes. We use “length” to describe the longest linear dimension of the entire preserved fossil as preserved on the bedding plane; this

corresponds to true length in flat recliners such as *Fractofusus*, but to height above the substrate in upright fronds like *Beothukis* or upright conical organisms like *Thectardis*. Similarly, “width” (maximum measurement orthogonal to “length”) corresponds to the true width of upright and reclining taxa such as *Beothukis*, *Thectardis*, and *Fractofusus*, but corresponds to height in a fence-like organism like *Pectinifrons*. The orientations of these measurements are given in Figure 2. We omitted taxa with more pronounced three-dimensional structure (e.g., *Bradgatia*) because fossils in these sections are typically flattened, excluding at least one entire dimension from view (Flude and Narbonne 2008).

*Thectardis*, *Pectinifrons*, and *Beothukis* are demonstrably monospecific (Clapham et al. 2004; Bamforth et al. 2008; Brasier and Antcliffe 2009; Narbonne et al. 2009) and are therefore ideal subjects for analysis. Subsequent field and taxonomic studies of *Charnia* by Laflamme et al. (2007), Brasier and Antcliffe (2009), and Narbonne et al. (2009) resulted in corrections to Clapham et al.’s (2003) original database. The net result was the attribution of the vast majority of specimens of “*Charnia*” from the Bristy Cove and Mistaken Point D and E surfaces to new genera, most notably *Beothukis*. Although two species of *Fractofusus* have been identified, they are easily differentiated by overall shape and are effectively temporally restricted in the Mistaken Point Ecological Reserve: oval-shaped *F. andersoni* is restricted to the BC and LMP surfaces, whereas the spindle-shaped *F. misrai* is restricted to the D, E, and G surfaces of the upper Mistaken Point Formation (Gehling and Narbonne 2007). Sample sizes from the LMP and G surfaces were relatively small (<40), and so are not treated here. Recently, Liu et al. (2011, 2012) suggested that several of the more enigmatic fossils preserved on the Mistaken Point surfaces (specifically the Ivesheadiomorphs) actually represent taphomorphs of other taxa whose morphology has been decayed and obscured by the growth of microbial mats over carcasses, rendering their identification difficult. To avoid this potential problem, we omitted Ivesheadiomorphs from analyses.

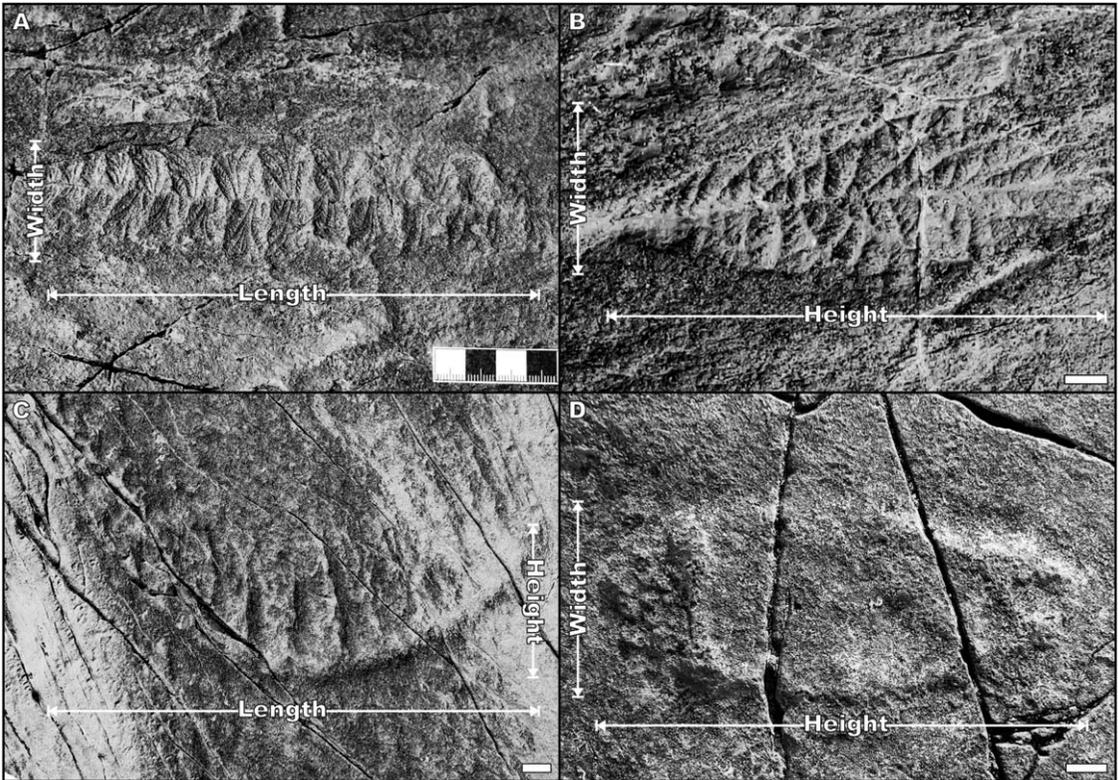


FIGURE 2. Bed-surface photographs of studied taxa, showing preservational style and measured physiological traits. A, *Fractofusus misrai* (E surface). B, *Beothukis* (E surface). C, *Pectinifrons* (D surface). D, *Thectardis* (PC surface). Scale bars, 1 cm or 1-cm increments.

Length, width, and height measurements for individual specimens (see Fig. 2), as well as fossil orientation, were recorded in the field; measurements were subsequently retrodeformed by mathematically removing tectonic bed-parallel shortening (technique and rationale as explained in Clapham et al. 2003 and Wood et al. 2003; although see Liu et al. 2011; all data recorded in Supplementary Information). The bed-parallel component of tectonic shortening was treated as pure shear and estimated by restoring elliptical frond hold-fasts to their presumed circular shape. A single average shortening factor was applied uniformly across the bedding plane to retrodeform fossils to their original shape. Variations in the amount of shortening within a single bedding plane will introduce errors into the retrodeformed dimensions but those errors will be random around the mean and will not bias the results on average.

Finally, for statistical approaches to reliably reproduce population structure, it is critical to use metrics that provide a reliable proxy for age (e.g., Sumrall 2010). We therefore investigated growth patterns in our studied groups through investigation of allometric growth in length, width, and height measurements (see also Laflamme et al. 2004).

*Data Treatment and Analysis.*—Logarithmic transformation of size data typically produces a more accurate representation of population structure, and better reflects age distributions than non-transformed data (Bak and Meesters 1999; Meesters et al. 2001). We therefore used the natural log of length, width, and height measurements, and analyzed the data by using a statistical method for likelihood-based model selection (Bayesian Information Criterion, “BIC”) using the package MCLUST in R (Fraley and Raftery 2007; R Development Core Team 2010). This approach was designed to identify the most likely number of size modes

with the measurement data, corresponding to the number of age classes represented in the population. Whereas some model-based approaches will favor more complex solutions (see Chapman and Hunt 2001), BIC adds a penalty to the likelihood estimate, which allows comparison of best-fit estimates with different numbers of estimated parameters (Fraley and Raftery 2007). Univariate BIC analyses were first run on single (i.e., length or height) measurements assuming equal variance; without this constraint the most favored solutions can be biologically unrealistic (G. Hunt personal communication 2012). Univariate analyses can also potentially be misled if growth in the measured dimension is allometric (such that growth rates increase or decrease later in development). We therefore also performed multivariate BIC analyses on data sets where a sufficient number of individuals (>40) possessed complete measurements in two dimensions (e.g., both length and width). In multivariate analyses we considered four Gaussian mixture models treated by MCLUST that assume elliptical distribution; the parameterization of covariance matrices within these models are discussed by Fraley and Raftery (2007), and make different assumptions on shape, volume, and orientation.

## Results

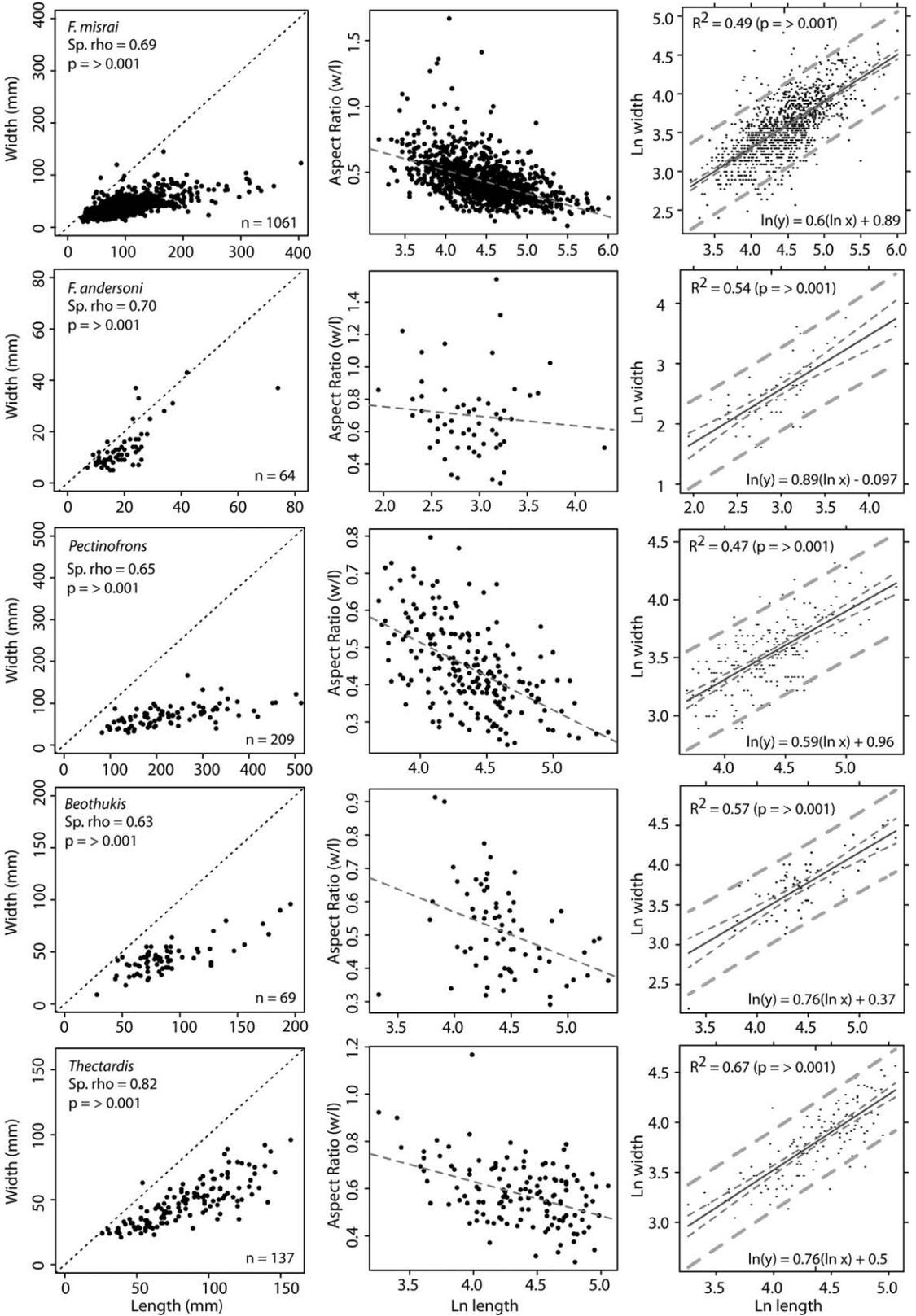
*Growth Models and Allometry.*—Although the relationship between size and age can be complex in marine invertebrate groups and can be affected by environmental factors (Hughes 1984; Hughes and Jackson 1985), we consider the fossil assemblages studied here to be of small enough spatial extent (see Table 1) for the communities to be functionally environmentally homogenous. Among all

studied taxa, plotting lengths and widths reveals approximately linear relationships (although are mostly heteroscedastic; Fig. 3) and shows relatively strong linear dependence on logged axes ( $R^2$  values  $\sim 0.4$ – $0.7$ ). However, plotting length against aspect ratio (width/length) reveals that individuals typically become more elongate with overall size increase, and so growth is mildly allometric. These patterns were consistent for all taxa across all studied surfaces (although data are much more scattered in some taxa, e.g., *F. andersoni*). We therefore infer for these taxa that the height of individuals (length in reclining organisms such as *Fractofusus*; see Fig. 2A) increased relatively rapidly throughout growth, whereas width (corresponding to height in *Pectinifrons*; Fig. 2B) increased relatively slowly. Width measurements were therefore excluded from univariate analyses, while multivariate analyses considered both height (or length—see above), and width.

*Size-Frequency Distributions.*—Size-frequency histograms typically reveal positive (right) skewed unimodal distributions with large variance (Fig. 4); the majority of taxa show relatively few individuals in the smallest size classes, followed by a peak in the lower end of the distribution, and decreasing numbers in larger size classes. The minimum sizes of individual taxa are equivalent across different fossil surfaces: minimum lengths of *F. misrai* are 33 mm and 24 mm (D and E surfaces respectively); minimum length of *F. andersoni* (BC surface) is 7 mm; minimum height of *Beothukis* (E surface) is 28 mm; minimum height of *Thectardis* is 26 mm (PC surface); and the minimum lengths of *Pectinifrons* are 82 mm and 40 mm (D and SH surfaces respectively). Barring the paucity of very small individuals, most distributions appear log-

TABLE 1. Fossil surfaces with area surveyed, size of smallest preserved (biological) features, number of fossils surveyed, and total species richness (SR). Surfaces are listed in order of inferred ecological succession (Clapham et al. 2003). Data from Clapham et al. (2003).

Surface	Area (m <sup>2</sup> )	Smallest feature (mm)	No. of fossils	SR
Shingle Head (SH)	47.0	3	370	6
Mistaken Point D (D)	63.4	1.8	1488	8
Bristy Cove (BC)	0.71	0.3	106	4
Mistaken Point E (E)	104.75	0.5	4188	12
Pigeon Cove (PC)	16.7	2	239	3



normal. The one notable exception is *Thectardis*, for which the distribution has relatively neutral skew, is less peaked, and appears normal. To test for log-normal vs. normal distributions among size-frequency data, we performed Shapiro-Wilk tests on both unlogged and logged length measurements (Table 2); *Beothukis* (E surface), *Pectinifrons* (SH surface), *F. andersoni* (BC surface), and *F. misrai* (D surface) all show statistical log-normal distribution (i.e., return  $p > 0.05$  when data are logged), and *F. misrai* (E surface) and *Pectinifrons* (D surface) approach log-normality ( $p = 0.02-0.03$ ). *Thectardis*, by contrast, is statistically normally distributed (i.e.,  $p > 0.05$  with unlogged data).

Univariate BIC analyses indicate that virtually all populations are best described as a single group (assuming either equal or unequal variance), and transitions from one to two groups produce marked decreases in BIC (Table 3, Fig. 4). The exception is (again) *Thectardis*, for which models assuming equal variance prefer one group, whereas those allowing unequal variance prefer two. Density functions for both solutions have been superimposed on (logged) size-frequency distributions for illustration.

In multivariate analyses, MCLUST produces best-fitting solutions for models that assume ellipsoidal, diagonal, and spherical distributions (Fraley and Raftery 2007). Of these, the four most biologically realistic are those that assume ellipsoidal distributions, as they allow for unequal variance in the two axes. These four models differ in their parameterizations, in constraining shape, volume, and orientation; these are denoted “E” (constrained equal) and “V” (unconstrained) so that each model can be assigned a three-letter code that corresponds to its specific parameters: EEE (equal variance), EEV (equal volume and shape), VEV (equal shape), and VVV (unconstrained) (see Fraley and Raftery 1999, 2003, 2007). The results of multivariate BIC

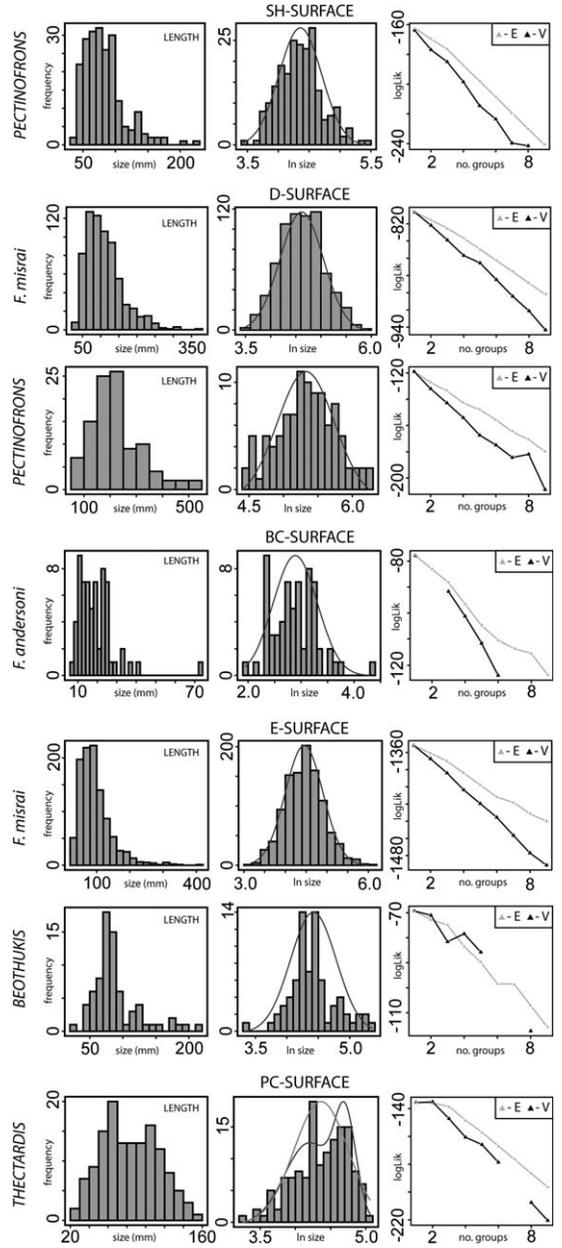


FIGURE 4. Composite figure showing size-frequency distributions, logged size frequency, and the results of BIC (univariate data). Density functions from BIC have been superimposed on logged size data for illustrative purposes. E and V in BIC plots correspond to models assuming equal and unequal variance, respectively.

FIGURE 3. Left panels: Length and width measurements for studied Ediacaran taxa, with 1:1 lines dashed. Middle panels: Length vs. aspect ratio (width/length); trend lines are ordinary least squares regressions. Right panels: Logged (ln) measurement data with linear regressions (allometry); 95% confidence intervals (dark gray) and prediction intervals (light gray) are also plotted. Coefficients of determination ( $R^2$ ) and regression slopes are reported in panels as standard equations.

TABLE 2. Results of Shapiro-Wilk tests for all taxa, on all studied surfaces. Note that length measurements for all taxa are statistically log-normally distributed (or approach log normal distribution, e.g., *F. misrai* on the E surface, and *Pectinifrons* on the SH surface), with the exception of *Thectardis*, which is normally distributed.

Taxon	Unlogged		Logged	
	W	p-value	W	p-value
SH surface				
<i>Pectinifrons</i>	0.8968	< 0.001	0.9966	0.027
D surface				
<i>Pectinifrons</i>	0.9447	< 0.001	0.9966	0.15
<i>F. misrai</i>	0.9146	< 0.001	0.9909	0.79
BC surface				
<i>F. andersoni</i>	0.9414	< 0.001	0.9834	0.56
E surface				
<i>Beothukis</i>	0.8651	< 0.001	0.9966	0.062
<i>F. misrai</i>	0.8639	< 0.001	0.9966	0.02
PC surface				
<i>Thectardis</i>	0.9817	0.063	0.9685	<0.001

analyses considering these four models reinforce those of univariate analyses; the highest BIC values among all models for all taxa indicate one group (Table 3, Fig. 5).

When density functions output from BIC analyses are plotted for individual fossil surfaces, size distributions for species occurring on multiple surfaces overlap (Table 4, Fig. 6). *Pectinifrons* (SH and D surfaces) shows a relatively small degree of overlap, whereas *F. misrai* (D and E surfaces) shows nearly complete overlap (although distributions of both taxa are statistically distinguishable using Kolmogorov-Smirnov tests:  $R = 0.16$ ,  $p < 0.001$ , and  $R = 0.81$ ,  $p < 0.001$  for *F. misrai* and *Pectinifrons* respectively).

### Discussion

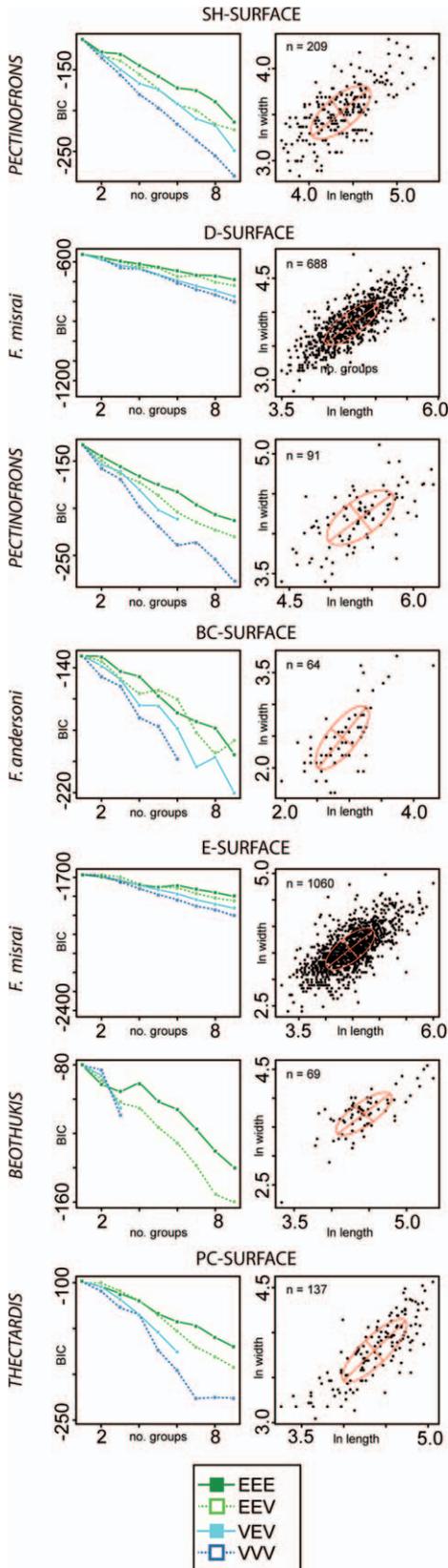
*Population Structure in Mistaken Point Communities.*—Our results indicate that, for the vast majority, analysis of population structure using BIC resolves communities of all studied Ediacaran taxa around Mistaken Point as single groups (i.e., unimodal distributions). Although univariate analysis of *Thectardis* from the Pigeon Cove surface produces some evidence for two groups (i.e., bimodal distribution), this result is equivocal (involving a minimal increase in BIC) and requires the assumption of unequal variance. These results are reinforced by multivariate analyses, which also produce highest BIC values for one-group solutions. Significantly, reanalysis of *Thectardis* using multivariate (length plus width) data resolves a single group with highest BIC.

We suggest that these data can be explained by one or a combination of the following hypotheses: (1) the *all for one* model, in which all studied populations represent single age classes opportunistically colonizing new substrate; (2) the *slow and steady* model, in which the Ediacaran organisms preserved around the Avalon Peninsula possessed slow growth rates relative to rates of reproduction and/or recruitment; and (3) the *continuous reproduction* model, where organisms reproduce aseasonally (= continuously), so that size modes are absent.

In terms of the *all for one* model, populations of individuals with extremely similar sizes (for example, holothurians [Billet and Hanson 1982; Rowe 1971, 1972]) typically indicate a

TABLE 3. Most likely (highest BIC) number of groups for all studied surfaces, for both univariate (length or height), and multivariate (length or height plus width) data. Bed surfaces are listed in order of inferred ecological succession (Clapham et al. 2003).

Taxon	No. of groups (univariate)		No. of groups (multivariate)	
		<i>n</i>		<i>n</i>
SH surface				
<i>Pectinifrons</i>	1	213	1	209
D surface				
<i>Pectinifrons</i>	1	102	1	91
<i>F. misrai</i>	1	688	1	688
BC surface				
<i>F. andersoni</i>	1	64	1	64
E surface				
<i>Beothukis</i>	1	74	1	69
<i>F. misrai</i>	1	1060	1	1060
PC surface				
<i>Thectardis</i>	1	137	1	137



single highly synchronous reproductive event and are characteristic of unstable and ephemeral sedimentary environments. However, the large size variance recorded across all taxa suggests that it is unlikely that the studied populations represent single age classes and/or recruitment events. On the Mistaken Point E surface in particular, *Fractofusus misrai* has a minimum length of 2.4 cm and a maximum length of 40.4 cm. This trend is shared across all taxa on all studied surfaces—the difference between minimum and maximum lengths and widths is typically an order of magnitude. The observed variation in size could potentially have been caused by spatial differences in environmental factors (see Meesters et al. 2001), but given the relatively small spatial areas surveyed for these data (Table 1), environmental factors were likely homogeneous. Furthermore, small and large individuals are not spatially confined to different parts of the exposed fossil surface (personal observations). In addition, the vast majority of fossiliferous surfaces preserved around the Avalon Peninsula are underlain by varying thicknesses of hemipelagite, which likely represents background sedimentation in the absence of turbidites (Wood et al. 2003). This observation would then preclude a scenario whereby the preserved Ediacaran organisms represent opportunistic “blooms” exploiting new substrate, and more likely represent climax communities with differences in taxonomic composition and relative abundance reflecting local conditions of current energy, nutrient availability, and dissolved oxygen (see also Grazhdankin 2004; Wilby et al. 2011; Gehling and Droser 2013). Lastly, when individual density functions from (univariate) BIC analyses are plotted for all fossiliferous

FIGURE 5. Multivariate BIC plots (left) and classifications (right) plotted onto logged length and width data. Ellipses superimposed on classification plots correspond to covariances of the components (see Fraley and Raftery 2007). The four models are given three letter codes (either E for constrained or V for unconstrained) that correspond to model parameterizations in shape, volume, and orientation, respectively. Details of model assumptions are given in Fraley and Raftery (2007). Note that BIC resolves single-group solutions for all studied taxa.

TABLE 4. Statistical parameters (mean, variance, and covariance) for density functions derived from BIC analysis for all taxa (logged measurements). Note that parameters for *Thectardis* are given for the 1-group solution.

Bed	<i>Fractofusus</i>			<i>Pectinifrons</i>			<i>Beothukis</i>			<i>Thectardis</i>		
	Mean	Var	Cov	Mean	Var	Cov	Mean	Var	Cov	Mean	Var	Cov
SH	–	–	–	4.36	0.12	0.17	–	–	–	–	–	–
D	4.61	0.19	0.20	5.33	0.17	0.18	–	–	–	–	–	–
BC	2.89	0.17	0.25	–	–	–	–	–	–	–	–	–
E	4.45	0.21	0.22	–	–	–	4.42	0.13	0.17	–	–	–
PC	–	–	–	–	–	–	–	–	–	4.36	0.15	0.18

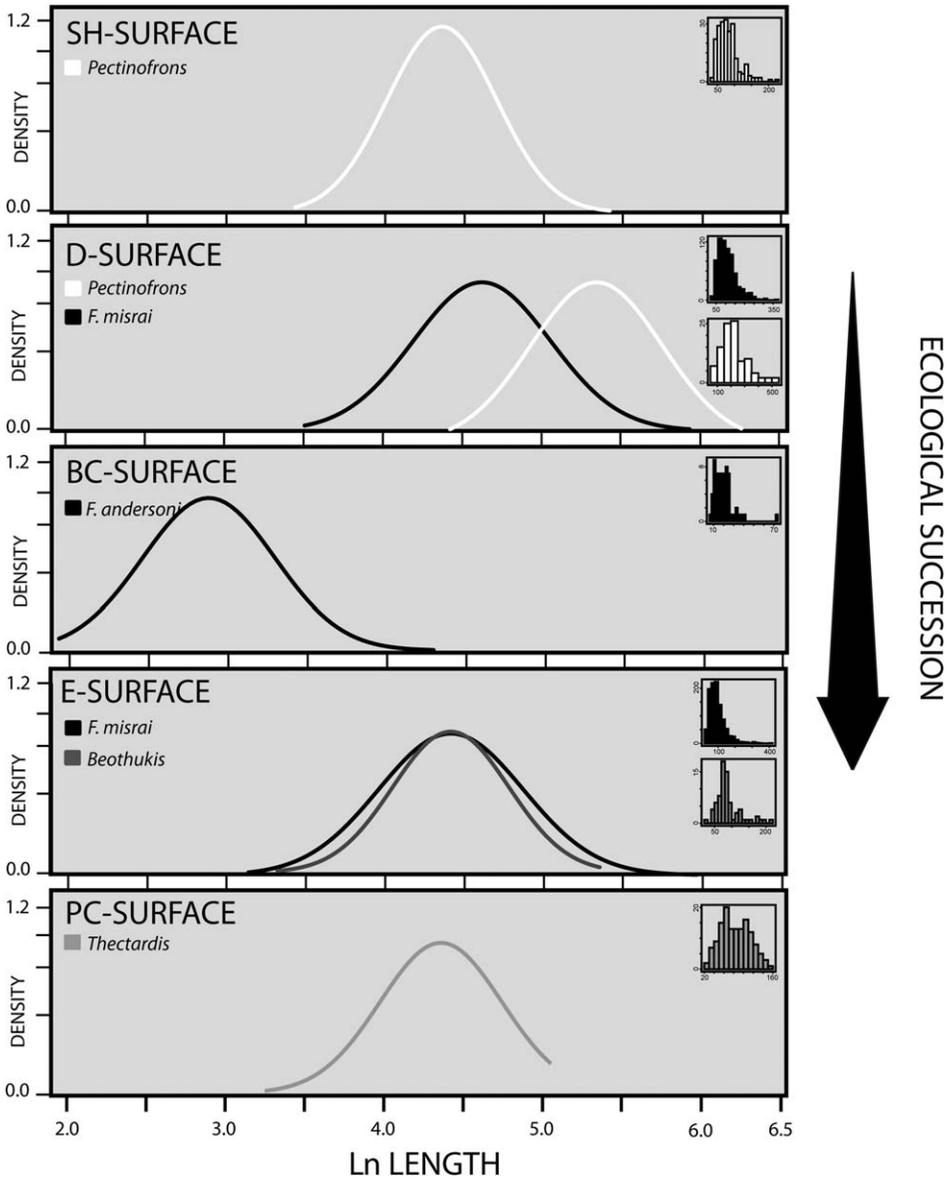


FIGURE 6. Density functions output by BIC for all taxa plotted for different beds in proposed ecological and successional sequence.

surfaces, taxa preserved on multiple surfaces (and therefore seemingly at different stages of ecological succession [see Clapham et al. 2003]) exhibit similar means, modes, and variances. Illustrating this, populations of *Fractofusus misrai* (see Table 3, Fig. 6) on the D and E surfaces form a standing size mode when these two surfaces are superimposed, thus constituting strong evidence against interpretation of these populations as single age classes.

Under the *slow and steady* model, rangeomorphs would be interpreted as reproducing seasonally but growing relatively slowly, resulting in size-frequency distributions that appear more or less continuous and lack multiple size modes. Many invertebrate groups in the deep sea exhibit slower growth rates than related taxa in shallow water (for example, bivalves [Turekian et al. 1975], octocorals [Cordes et al. 2001], and vestimentiferan tubeworms [Berquist et al. 2000]). Most of these, however, also exhibit commensurately slow rates of seasonal reproduction such that distinct size and age classes are still preserved in populations (Turekian et al. 1975). In general, gametogenesis is an energetically intensive process, and rapid/frequent production of gametes is unusual in deeper-water, nutrient-limited environments (although there is little direct evidence to suggest that the paleoenvironmental settings around Mistaken Point were necessarily nutrient-limited—the Ediacaran deep ocean may have held relatively large amounts of DOC, and nutrients may also have been delivered along contour currents [see Sperling et al. 2007, 2011]). As a result, although we cannot rule out the “*slow and steady*” hypothesis, we consider it unlikely.

In terms of the *continuous reproduction* model, a scenario involving aseasonal or continuous reproduction across all studied Mistaken Point taxa is plausible in light of the fact that, in modern deepwater settings, continuous reproduction has been reported across multiple phyla (Rokop 1974; Gage and Tyler 1991; Tyler and Young 1992). Seasonally synchronous reproductive cycles, seasonal peaks in reproductive intensity, and seasonal recruitment are also widespread among in-

vertebrate taxa, but are mostly reported from continental margin settings at depths above 3000 m (Gooday 2002). The observed size-frequency distributions are strongly suggestive of year-round recruitment, with smallest size classes in, e.g., *F. misrai* represented by a peak at ~75 mm length. Rokop (1974) reported similar population structure in trawled samples of the ophiuroid *Ophiacantha normani* from the San Diego trough.

Although the exact reasons behind why different invertebrate groups adopt seasonal or aseasonal reproductive strategies are still unclear, we suggest that the aseasonal reproductive strategies inferred from our rangeomorph data reflects non-analogue ocean structure and the nature of organic matter export to the seafloor in the Ediacaran. In shallow water, seasonal reproduction and gametogenesis are stimulated by changes in water temperature, whereas deepwater settings are largely homogenous with respect to most seasonal variables (Menzies 1965). Among groups that do exhibit seasonal reproduction in the deep ocean (including echinoderms, mollusks, and crustaceans [see Young 2003 for a review]), the “trigger” that stimulates gamete production is largely driven by a seasonal flux of organic matter to the seafloor (Tyler 1988; Tyler et al. 1990; Witte 1996; Morales-Nin and Panfili 2005). Evidence for seasonality in middle Cambrian eocrinoid populations from relatively deepwater facies suggests that this flux was established soon after the Precambrian/Cambrian boundary (Zamora et al. 2013). Therefore, the fact that Ediacaran rangeomorph communities possess population structures typical of continuous and aseasonal reproduction may in turn suggest that the seasonal trigger for gamete production and release in deepwater settings was not established until after the Precambrian/Cambrian boundary. In support of this hypothesis, Butterfield (2009, 2011) infers a radical change in the character and volume of plankton over this transition; the evolution of predatory mesozooplankton would have consolidated slow-sinking picoplankton into larger particulate matter, which would moreover have been inaccessible to osmotrophic organisms such as rangeomorphs (Butterfield 2009;

Laflamme et al. 2013). Further evidence for this change comes from microfossils (Peterson and Butterfield 2005) and geochemical proxies (Logan et al. 1995).

*Reproduction in Ediacaran Organisms.*—Interpreting the circumstances leading to specific population structures demands certain assumptions about the actual methods of reproduction (i.e., sexual vs. asexual). Ediacaran reproduction has not been heavily discussed in the literature, largely because physiological evidence for reproductive structures has not been preserved in the fossils themselves. No Ediacaran larvae have ever been recovered to support claims that some taxa represent stem- or crown-group metazoans (see, e.g., arguments supporting arthropod affinities for *Parvancorina* and *Spriggina* [Lin et al. 2006]). Moreover, arguments for Ediacaran taxa representing separate life stages of the same organism (e.g., Brasier and Antcliffe 2004) are limited and as yet unsubstantiated.

Nevertheless there are disparate lines of evidence that have been used to hint at the existence, in many Ediacaran taxa (especially within the rangeomorph assemblages that dominate at Mistaken Point), of a free-swimming or planktonic life stage early in development.

First, biogeographic analyses of Ediacaran assemblages reveal that similar (if not identical) Ediacaran genera often co-occur on paleocontinents separated by deep oceanic basins (i.e., display low levels of endemism [Laflamme et al. 2013]). Although previous studies have suggested that the Mistaken Point assemblages contain a high proportion of endemic taxa, more recent discoveries indicate many of these organisms may have been more widely distributed than previously thought (e.g., Narbonne et al. 2009; Wilby et al. 2011). Throughout the Ediacaran, rangeomorph taxa are found as far apart as Laurentia, South Australia, Southern Africa, Avalonia, and the White Sea area of Russia; there is little tectonic or paleomagnetic evidence to suggest that any of these terranes were juxtaposed during the Ediacaran (Waggoner 2003). Waggoner (1999, 2003) noted that the tectonic terranes of Australia, Baltica, and northern Laurentia share several complex

(albeit mostly non-rangeomorph) Ediacaran forms that are distinctive at the genus or species rank, a biogeographical pattern that is inconsistent with paleogeographical reconstructions. Without the existence of a free-swimming or planktonic method of dispersal, it is hard to envisage how specific taxa could have achieved these worldwide distributions. Second, Clapham et al. (2003) demonstrated that spatial patterning in the Mistaken Point assemblages is extremely similar to that of modern-day assemblages, suggesting that the constituent organisms had similar methods of dispersal and settling, and some may have possessed teleplanic larvae. Third, claims of asexual “budding” in rangeomorph taxa are equivocal. Narbonne et al. (2009) suggested that the modular construction typical of rangeomorphs could allow for a vegetative (asexual) reproductive strategy for fronds such as *Avalofractus*; however, recent discoveries of juvenile rangeomorph fronds (Liu et al. 2012), which are morphologically identical to adult forms and distinct from individual rangeomorph modules, suggest that vegetative reproductive strategies are perhaps unlikely for many Ediacara biota.

Although none of these observations in isolation provide definitive evidence for a mobile life stage, taken together they support a scenario wherein many Ediacaran taxa were free-swimming or planktonic early in development before settling on the sediment substrate. In the absence of evidence for asexual budding, this would suggest sexual reproduction by means of gametogenesis. Additional support for this hypothesis comes from the inference of sexual reproduction in the Ediacaran taxon *Funisia* (interpreted as a stem-group cnidarian or poriferan [Droser and Gehling 2008]). In this view, the paucity of individuals in smallest size classes (see Fig. 4) may correspond to the typical size of post-larvae immediately after settlement; however, the relative sizes of these individuals (~20–50 mm) would make them unusually large when compared to those of extant invertebrate groups.

These discussions suggest that (1) some, if not all, Ediacaran taxa may have reproduced sexually; (2) of these, many may have had a

free-swimming or planktonic life stage early in development; and (3) reproduction, at least in deeper-water settings, may have been continuous. Although the data presented here do not specifically address (1) and (2), we believe that the biogeographic (Waggoner 1999, 2003) and spatial (Clapham et al. 2003) observations recorded by other workers are sufficient for tentative support for these statements. The population structure and biogeography of rangeomorph taxa in particular suggest continuous reproduction; the different size-frequency distributions found for *Thectardis* (normal, as opposed to log-normal) may lend validity to the proposed affinity of this taxon as a sponge (Sperling et al. 2011), which are capable of reproducing both asexually (via budding) and sexually (Witte 1996). In terms of (3), among modern groups continuous reproduction in deep water environments can be either synchronous or asynchronous. Asynchronous reproduction is achieved when individuals have distinct gametogenic cycles that are out of phase, so only a proportion of individuals breed at any one time. In synchronous reproduction, adults remain reproductively active throughout the year, such that only a few gametes are released at any one spawning (Rokop 1974, 1977). Although continuous reproduction would seem to generate low probabilities of fertilization, it is a reproductive strategy that has survived into the modern day in extant phyla, enhanced by the gregarious lifestyles employed by many modern invertebrate groups (Tyler and Young 1992).

The wide dispersal of many Ediacaran taxa, including rangeomorphs, suggests a larval stage capable of spending extended periods in the plankton, and as such, capable of feeding (planktotrophic). This interpretation meshes well with inferences by Strathmann (1985, 1993), who suggested that the possession of feeding larvae is an ancestral trait in marine invertebrates, possibly stretching back to the origin of the metazoa. Set against this, it is not inconceivable that many deepwater Ediacaran taxa may have been able to achieve extremely wide distribution with relatively short dispersal distances (i.e., with lecithotrophic larvae); modern deep-sea taxa can have

extremely large ranges, and ocean currents, seamounts, and other topography do not present serious barriers to dispersal (e.g., McClain and Mincks Hardy 2010). This interpretation would fit better with that of Petersen (2005), who provided molecular evidence to suggest that lecithotrophy (rather than planktotrophy) is the ancestral state among modern metazoan groups. With a better understanding of how (if at all) the Rangeomorpha are related to extant phyla, we suggest that population data such as these may become a powerful tool in resolving development and dispersal strategies at the base of the metazoan tree.

### Conclusions

Analysis of population structure using BIC demonstrates that communities of four different Ediacaran taxa (three rangeomorphs and one possible sponge) are best described as single distributions, which nevertheless have wide variance. Size-frequency distributions show that populations are dominated by smaller individuals, which form a standing size mode in beds that have been interpreted as representing different stages in ecological succession; taxonomic differences between surfaces may therefore instead reflect local conditions of current energy, nutrient availability, and dissolved oxygen. These data are strongly suggestive of continuous (year-round) reproduction, assuming that the studied organisms reproduced sexually. Modern benthic invertebrates in deeper-water settings have been shown to reproduce both seasonally and aseasonally, so distinguishing between biological (reproductive strategies) and environmental (lack of a seasonal trigger) causes is not possible at this point. We suggest a potential explanation for the observed population structure in terms of seasonal flux of organic matter from surface waters; this flux stimulates seasonal reproduction in modern deep-sea benthos, but may not have been established until the Cambrian. A prediction of this hypothesis might therefore be that counterpart communities in shallow-water settings (where seasonal changes in temperature might be expected to trigger synchronous gamete production and release) should exhibit

multiple size modes, indicating seasonal reproduction and recruitment.

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