

Morphology and taphonomy of an Ediacaran frond: *Charnia* from the Avalon Peninsula of Newfoundland

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Abstract: The Ediacaran frond *Charnia*, known mainly from fragmentary leaf-like fronds from around the world, is represented by completely preserved specimens with holdfasts in the Mistaken Point biota of Newfoundland. Previous reconstructions of *Charnia* from two-dimensional impressions were significantly oversimplified, resulting in three-dimensional reconstructions which highlighted a sheet-like morphology. Overlapping relationships and internal structures are rarely (if ever) preserved, and only through detailed photography together with both landmark and traditional morphometric analyses of numerous complete *Charnia* specimens can the preservational biases be removed. *Charnia* is reinterpreted here as having a series of individual overlapping primary branches attached to an internal central stalk, and with individual branches constrained by an internal, organic skeleton and/or attachments between adjacent branches. Three species, *C. masoni* Ford 1958, *C. wardi* Narbonne & Gehling 2003, and *C. antecedens* sp. nov. can be distinguished on the basis of length/width ratios and the degree of attachment of adjacent branches. Morphological, taphonomical, and ecological studies at Mistaken Point imply that *Charnia* was a sessile, epibenthic frond that fed from suspension in this deep-water volcanoclastic setting. Evolution of more rigorous connections between the primary branches allowed *Charnia* to migrate into more turbulent, shallower-water habitats by the late Ediacaran.

Charnia Ford, 1958 is a cosmopolitan Ediacaran frond first described from Charnwood Forest, England (Ford 1958, 1962, 1963, 1999; Boynton & Ford 1995), and subsequently was documented from the White Sea of Russia (Fedonkin 1985, 1992; Grazhdankin 2004), north-eastern Siberia (Fedonkin 1985), Ediacara in South Australia (Nedin & Jenkins 1998), and from the Mistaken Point Formation in Newfoundland (Fig. 1; Anderson 1978; Conway Morris 1989; Jenkins 1992; Narbonne *et al.* 2001; Clapham & Narbonne 2002; Narbonne & Gehling 2003; Clapham *et al.* 2003; Narbonne *et al.* 2005). Original descriptions of *Charnia*, interpreted from the well-preserved type specimen from Charnwood Forest, England (fig. 2; Ford 1958), highlight the relatively simple repeating pattern of both the primary branches and secondary modular elements, in addition to the overall sheet-like morphology. Ford (1958) also erected the taxon *Charniodiscus* Ford, 1958, which consisted of a disc-like organism with a rough-surfaced central boss surrounded by multiple concentric rings, and in some earlier figures showed the *Charnia* frond and the *Charniodiscus* anchoring disc as elements of the same organism or colony (Ford 1958, 1962). Later work (Ford 1963) revealed that the holotype of *Charniodiscus* was attached to a

foliate structure with fine detail that differed significantly from the holotype of *Charnia*. Jenkins & Gehling (1978) distinguished *Charnia* and *Charniodiscus* on the basis of the small-scale branching pattern in their respective fronds, a view that has been supported by virtually all subsequent workers (see review in Laflamme *et al.* 2004). In the Treatise, Glaessner (1979) defined *Charnia* as having 'Narrow petaloids with sinuous median line and sharply defined primary grooves forming acute angles with corresponding secondary grooves and branches; these are therefore in almost transverse position on the petaloids'.

Complete specimens of *Charnia* with its basal attachment bulb also preserved are exceedingly rare, with mostly fragmentary specimens described from outside Newfoundland, hindering attempts to deduce the taxonomy and biology of *Charnia*. Eastern Newfoundland is unique in producing thousands of complete fronds, including hundreds of *Charnia* specimens (Narbonne *et al.* 2001; Clapham *et al.* 2003). This paper utilizes the large number of complete specimens of *Charnia* available in the Avalon Peninsula of Newfoundland (Fig. 1) to determine the growth patterns, inter- and intraspecific variability, and evolutionary patterns of *Charnia*.

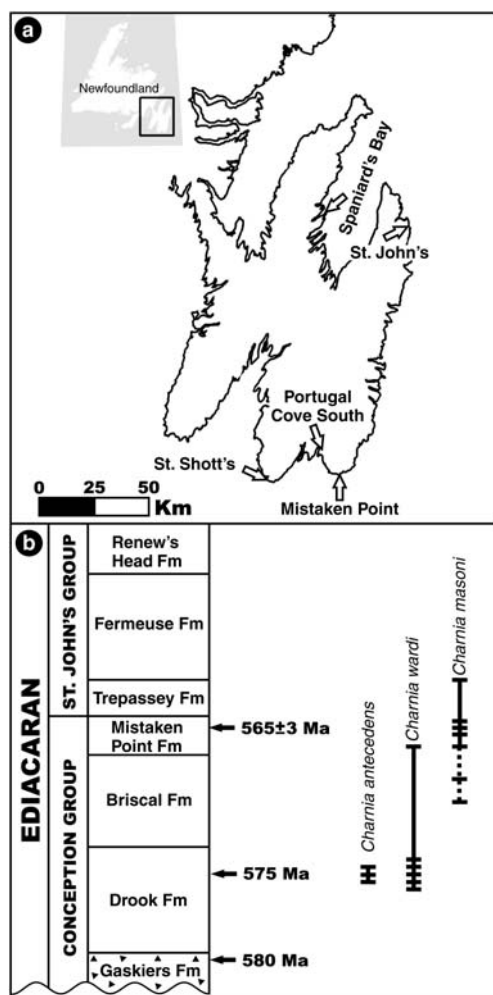


Fig. 1. Geographic and stratigraphic distribution of *Charnia* Ford, 1958. (a) Location map of Avalon Peninsula of Newfoundland Canada. (b) Composite stratigraphic section, indicating stratigraphic ranges of *C. masoni*, *C. wardi*, and *C. antecedens*. U–Pb dates from Dunning *in Benus* (1988) and Bowring *et al.* (2003).

Geographic and stratigraphic setting

The fossiliferous strata from the Avalon Zone of Newfoundland, Canada (Fig. 1a) occur in the western part of Avalonia, representing a string of microcontinental volcanic arcs that originally emplaced off the northwestern coast of Amazonia during the terminal Proterozoic (Murphy *et al.* 2002). The close proximity of the Mistaken Point assemblage to the eastern Avalonia Ediacara Biota of Charnwood Forest, England, is

supported by both biogeographic analyses and tectonic reconstructions (Waggoner 1999; Murphy *et al.* 2002). The Ediacara Biota at Mistaken Point was first reported by Anderson and Misra (1968) and Misra (1969) and subsequently documented by numerous authors. Available U–Pb dates on volcanics associated with the Mistaken Point fossil assemblage range between 575 and 565 Ma (Dunning *in Benus* 1988; Bowring *et al.* 2003), thus predating most other known Ediacara assemblages (Martin *et al.* 2000; Condon *et al.* 2005; Narbonne 2005).

Charnia ranges through much of the stratigraphic succession hosting the Avalonian assemblage, with specimens from the Drook, Briscal, Mistaken Point, and Trepassey formations, spanning upwards of 2.5 km of section of the Conception and St John's Groups and representing more than 10 million years (Fig. 1b). Sedimentological studies of the area imply that the fossil localities represent deposits in deep water axial and slope environments, well below storm wave-base (Misra 1971, 1981; Benus 1988; Narbonne *et al.* 2001; Wood *et al.* 2003; Narbonne *et al.* 2005). The Conception Group is dominated by fine- to medium-grained turbidites interspersed with thin interturbidite siltstone beds which contain the fossil horizons (Wood *et al.* 2003). Interturbidite fossil beds are numerous throughout the Avalonian strata, and are commonly blanketed by a veneer of volcanic ash, which accelerated lithification and preserved the fossil fronds in positive epirelief on the upper surfaces of fine-grained siltstone bedding planes (Narbonne 2005). The volcanic ash restricts preservation of features to those present on the upper surface of the organism, while the thickness and coarseness of the fallout ash is responsible for the varying quality and amount of epirelief of each individual specimen (Narbonne 2005). Microbial mats preserved as 'old elephant skin' wrinkles on the fossil-bearing surfaces initiated mineral encrustation of the organic material and cemented the surrounding sediment resulting in preservational 'death masks' (cf. Gehling 1999). Strata throughout the Avalon Peninsula have been subject to tectonic deformation, resulting in a significant (<40%) shortening, perpendicular to cleavage, of all fossil specimens, thus altering the shape and orientation of all structures measured from the surfaces (Seilacher 1999; Wood *et al.* 2003; Laflamme *et al.* 2004). This deformation can be corrected by applying photographic or mathematical corrections termed 'retrodeformation' (see Wood *et al.* 2003 for rationale and the formulas used in the morphological correction). All measurements presented in this paper have been retrodeformed.

Traditional interpretations of the morphology of *Charnia*

Original descriptions of *Charnia* are based on the exquisitely-preserved holotype of *C. masoni* from Charnwood Forest, England (Ford 1958). This specimen is characterized by an ovate (or lance-shaped) to strongly parallel frond which tapers abruptly at the distal tip and is composed of a series of sigmoidal to rectangular primary branches (Fig. 2). The central axis of the frond consists of a zigzag central midline resulting from the alternation of the primary branches on either side of the central axis. Branch width and length tend to increase proximally, with the smallest (and assumed youngest) branches located at the distal tip. Each primary branch is composed of several

secondary modular elements (Fig. 2), which vary in size and shape along the length of each branch. Well-preserved specimens of *Charnia* exhibit curved tertiary divisions within the secondary modular elements (Fig. 2). In *C. wardi*, these third-order divisions can be shown to represent the edges of rangeomorph elements similar to those illustrated by Narbonne (2004). Narbonne (2004, 2005) and Brasier and Antcliffe (2004) followed Jenkins (1985) in regarding *Charnia masoni* as a rangeomorph, but further study of exceptionally-preserved specimens from Charnwood Forest (Brasier & Antcliffe 2004; Brasier *et al.* 2005) and northern Russia (Grazhdankin 2004) is necessary to confirm or refute this hypothesis. The holotype slab from Charnwood Forest is broken just above the base of the frond.

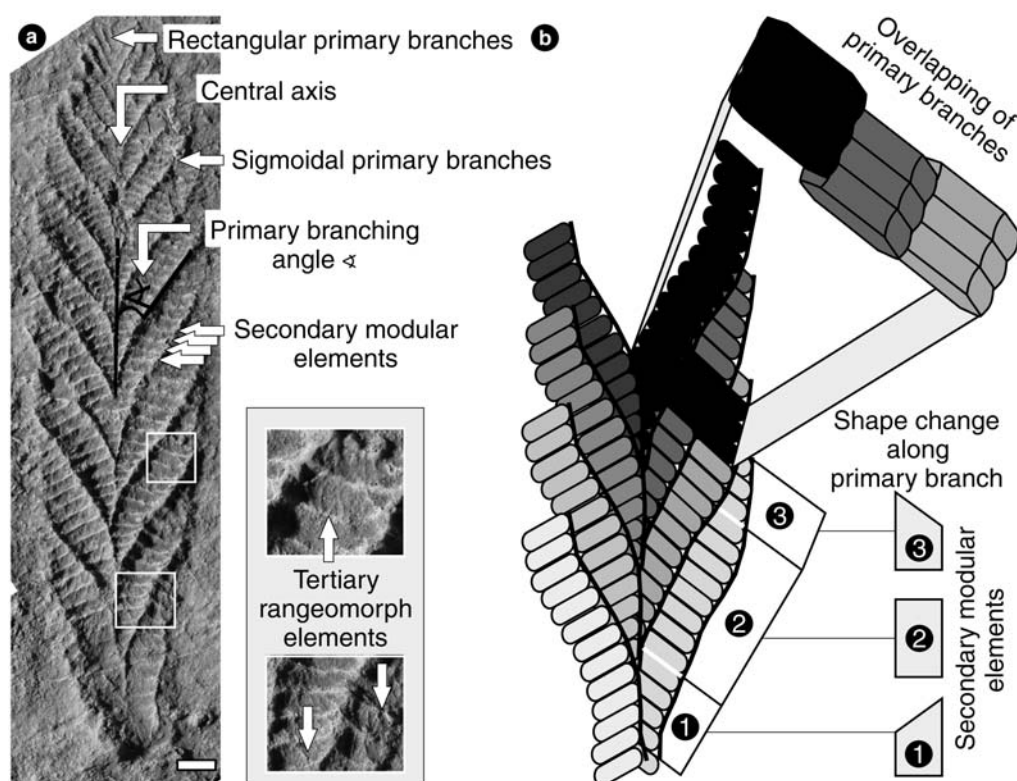


Fig. 2. *Charnia masoni*. (a) Labelled type specimen of *C. masoni* from Charnwood Forest, England, displaying the fractal, third-order microstructure present in each secondary modular element. Multiple tertiary rangeomorph elements are present within each secondary modular element. (b) Hypothetical reconstruction of *C. masoni* demonstrating the overlying relationships between adjacent primary branches. The corresponding shape of each secondary modular element is delineated by the proximity and amount of overlapping contributed by surrounding modular elements. Labels (1, 2 and 3) represent proximal, central, and distal regions of the primary branches respectively. Specimen A whitened with ammonium chloride. Scale bar 1 cm.

Landmark morphometric analysis

Previous attempts to couple traditional taxonomic work with mathematical (morphometric) descriptions were effective at Mistaken Point, and readily allowed for the segregation of characters which varied with growth versus those which represented true taxonomic differences between two morphologically similar species of *Charniodiscus* (Laflamme *et al.* 2004). However, since much of the species variation in *Charnia* is restricted to microstructural details, poorly described by distance measurements (Fig. 2), and since taphonomic characters of the volcanic ash limit the preservation of the most distal branches and secondary modular elements, the overall morphology of *Charnia* from the Avalon is difficult to investigate using traditional morphometric techniques. Recent advances in the field of landmark morphometrics has resulted in robust quantitative means of describing shapes independent of size, translation, rotation or scaling (Bookstein 1991), and may be used to quantify morphological changes in shapes. Although traditional and landmark morphometrics may not be applicable for defining the overall morphology of *Charnia*, these mathematical techniques can be applied to define the shape changes between the secondary modular elements, and possibly elucidate the origin of these shape changes.

By selecting points in two or three dimensional space that correspond to the position of a particular character on an object of interest (Lele & Richtsmeier 2001), landmarks outline or define the form in question and allow for comparisons of shape between different samples. The covariance between landmark sets can be identified and highlighted through various multivariate statistical analyses, such as principal components analysis (PCA). The goal is to isolate purely shape-driven changes between similar forms.

Morphological relationships between various components of the *Charnia* morphotype suggest a more complex external form than has been previously diagnosed for this genus. The morphological variation in the shape of the secondary modular elements, in addition to the appearance of an overlying relationship between adjacent primary branches, is ideally suited for a landmark morphometric analysis. By removing the influence of growth and size of the shape component, it is possible to compare how each secondary modular element is influenced by its neighbouring elements.

The relatively simple shape of the secondary modular elements in *Charnia masoni* can easily be defined by four unique landmarks, which provide an adequate representation of the entire secondary modular element (Fig. 3a). The restriction to traditional (Lele & Richtsmeier 2001) or Type 1

(Bookstein 1991) landmarks corresponding to biologically significant structures that represent a point in space at which three structures meet (Bookstein 1991; Lele & Richtsmeier 2001) reduce the amount of subjectivity introduced into the analysis. The chosen landmarks are structurally homologous and represent structurally similar features present on all branches analysed.

Four landmarks were placed on every complete secondary modular element from the second to the sixth primary branch of the right side of the holotype of *Charnia masoni* from Charnwood Forest. The incomplete preservation of the secondary elements on the left side of the holotype, in addition to the poor preservation of the distal branches above the sixth primary branch, restricted the analysis to the selected branches. Distal secondary modular elements (the last few secondary modular elements from region 3 in Fig. 2b) along the chosen primary branches were also excluded due to incomplete preservation. Landmarks were collected from high quality digital photographs and digitised using TPSDIGW32.EXE (by F. James Rohlf. Version 1.40; <http://life.bio.sunysb.edu/morph/>). In order to reduce human error, all landmarks were chosen and digitized by ML. Digitized landmarks were collected in a landmark coordinate matrix and converted into corresponding vectors of all possible pair-wise distances therefore restricting information to shape coordinates. Shape coordinates were transformed into Procrustes coordinates by setting the centroid location (average location of all landmarks) of each sample to the centre of a Cartesian graph (0.0), therefore removing the influence of translation on the data. Size or scale was removed by calculating the centroid size, which corresponds to the square root of the summed squared distances of each landmark from the centroid, and by rescaling the centroid size to 1.0 by dividing all landmark location by the original centroid size. Finally, rotating the rescaled forms to an optimal overlap of all landmarks by minimizing the summed squared distances between each corresponding landmark and the reference form, which is an average of all specimens, removed the influence of rotation on the data. This final step resulted in a Procrustes alignment and was performed with the 'CoorDGen6' program designed by David S. Sheets (<http://www2.canisius.edu/~sheets/morphsoft.html>).

Once the coordinate matrix has been converted into a Procrustes coordinates matrix, it is possible to analyse the relationship between landmarks and samples through standard multivariate statistics such as principal components analysis, which allows for multiple landmark configurations to be compared between multiple samples. PCA is a statistical means of comparing multivariate data by constructing principal components (or eigenvectors),

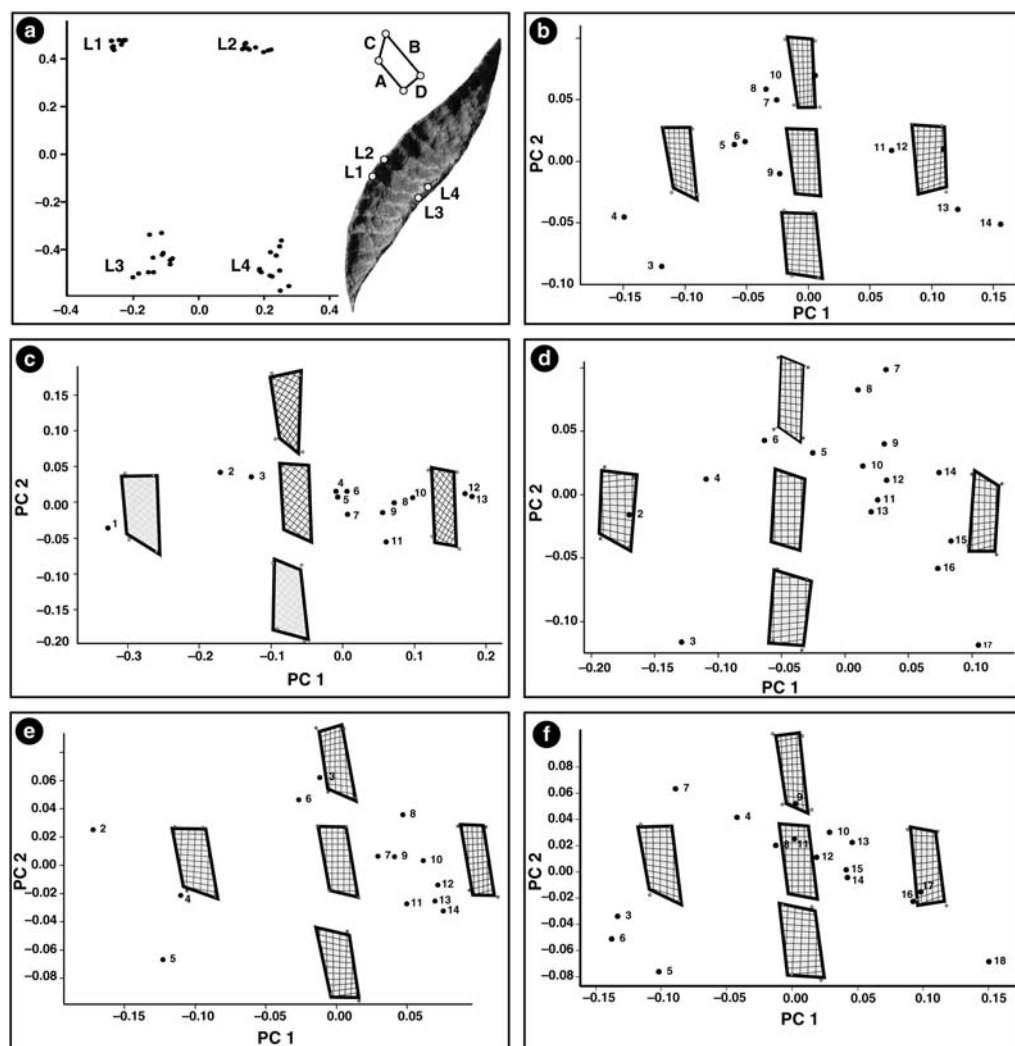


Fig. 3. Landmark morphometric analysis of the holotype of *Charnia masoni*. (a) Distribution of all four landmarks of each well-preserved secondary modular element from the second primary branch. Notice the high degree of precision surrounding landmarks 1 and 2. (b–f) Principal components analysis of the landmark analysis of the second to sixth primary branches of the holotype of *C. masoni*. Sub-rectangular to trapezoidal forms within the graphs represent the shape of the secondary modular elements without the influence of size, rotation, or translation. Notice the trend of shorter L1–L3 (a) distances in the proximal secondary elements followed by a more equidistant L1–L3 v. L2–L4 (a v. b) distances in the more central secondary modular elements, and finishing with a shorter L2–L4 (b) distance in the distal secondary modular elements. This trend continues until the secondary modular element is completely covered by an adjacent primary branch. Numbered data points from 1 (proximal to the stalk) up to 18 (distal).

which are mutually orthogonal vectors that explain the greatest amount of variance found within the data. PCA groups similar landmark arrangements (shapes) together while distancing different shape configurations from each other. Traditionally, landmark morphometrics is used to distinguish shape differences between species, but this analysis applied landmark morphometrics to shape changes

within a seemingly repeatable set of landmarks in order to distinguish shape changes within sections of a single specimen. PCA allows for the partitioning of morphological variation into components that independently describe shape variation (Strauss & Bookstein 1982; Somers 1986; James & McCulloch 1990; Cadima & Jolliffe 1996). The data reconfigured into partial Procrustes was

analysed with PCAGen6 N (<http://www2.canisius.edu/~sheets/morphsoft.html>), which performed a PCA analysis on each branch independently in order to demonstrate the variation in form of the secondary modular elements along the primary branches of *C. masoni*.

The first set of interpretations drawn from the landmark analysis is the degree of variance within each individual landmark. As seen in Figure 3a, the spread of landmarks 3 and 4 is much greater than the spread surrounding landmarks 1 and 2. Since landmark identification of these points is similar, this variation implies deformation of the terminations of the secondary lobes and, therefore, a translation of the landmarks out of their 'normal' positions. If this hypothesis is correct, the relatively tight landmark arrangement for landmarks 1 and 2 may suggest that the only true shape variation of the secondary modular elements can be explained with a translation of only two landmarks, and with most of the translation restricted to the 'Y' axis (Fig. 3a). This hypothesis is further substantiated by the repeatable and predictable shape changes of the secondary lobes along the primary branches. As demonstrated in Figures 3b–f, the proximal modular elements (region 1 in Fig. 2b) along all five primary branches are characterized by smaller L1–L3 landmark distances (distance A in Fig. 3a), while the central secondary lobes (region 2 in Fig. 2b) are more uniform in L1–L3 v. L2–L4 distances (distances A and B in 3a), whereas the terminal secondary lobes (region 3 in Fig. 2b) have a distinctively smaller L2–L4 landmark distance (distance B in 3a). This is in stark contrast to the L1–L2 (distance C in 3a) or L3–L4 (distance D in 3a) distances, which are uniform in shape distances throughout the entire length of the primary branches. This suggests that there is a semi-rectangular shape for each secondary lobe, and that the trapezoidal or rhombic shape classically associated with the secondary lobes of *Charnia* is a taphonomic response to overlying from adjacent primary branches. The translation and predictability of the landmarks represent an artificial termination of the secondary lobes due to imbrication or onlapping from adjacent primary branches. This hypothesis suggests that the true termination of the secondary lobe is located beneath the overlying adjacent primary branch, and that this onlapping relationship accounts for the shape of the secondary lobes in *Charnia*.

Taphonomy of Newfoundland *Charnia*

The *Charnia* forms from Mistaken Point and the surrounding Avalonian localities are morphologically diverse, but as most specimens are

taphomorphs of the well-known species of *Charnia masoni* (Fig. 4) or *Charnia wardi* (Fig. 5), the true taxonomic diversity is likely quite limited. The shapes of the specimens vary greatly as an expression of taphonomy on the classical *C. masoni* morphoshape. Due to local differences in ash thickness and tectonic deformation of the beds containing the fossils, the morphological expression of the classical *C. masoni* morphoshape greatly varies between localities. The soft-bodied nature of *Charnia* and the apparent flexibility of the primary and secondary branches contributed to the morphological disparity between specimens.

The selective nature of the preserving ash restricts preservation of features present on the upper surface of the organism at the interface between the underlying sediment and the overlying fallout ash (Narbonne 2005). Even small amounts of ash that reached the substrate prior to felling of the organism resulted in poor preservation of morphological traits, a process that was largely responsible for the decrease in resolution distally from the holdfast to the tip of the frond (Seilacher 1992; Wood *et al.* 2003; Laflamme *et al.* 2004). The thickness and coarseness of the fallout ash responsible for the preservation of all Ediacaran fossils at Mistaken Point also dictates the overall external morphology and epirelief of each individual specimen (Narbonne *et al.* 2001). Stalks and finer microstructural details that are well preserved in specimens of *C. wardi* are invariably associated with a thin, fine fallout ash (Fig. 5a–f), and are typically absent or difficult to see in specimens preserved beneath thicker, medium- to coarse-grained volcanic tuffs (Fig. 5g–h). However, the cylindrical, three-dimensional morphology of *C. wardi* is best seen in thick coarse ash (Fig. 5g–h) since thinner, finer fallout ash was more prone to compaction than the coarser-grained tuffs (Narbonne & Gehling 2003).

It is evident that taphonomy played a major role in controlling the preservational form of *Charnia* specimens from Newfoundland and presumably elsewhere. Three distinct morphological forms are readily recognized even when taphonomic variation is taken into account. The nature of these species, one of which is new, and their relationships to previously described taxa are discussed at the end of this paper (see Systematic palaeontology).

Taphomorphology of *Charnia*

Taphonomic processes responsible for the preservation of soft-bodied Ediacara Biota govern the final morphology of the fossils found (Jenkins 1985; Gehling 1991; Narbonne *et al.* 1997; Narbonne 2005; Grazhdankin & Seilacher 2005).

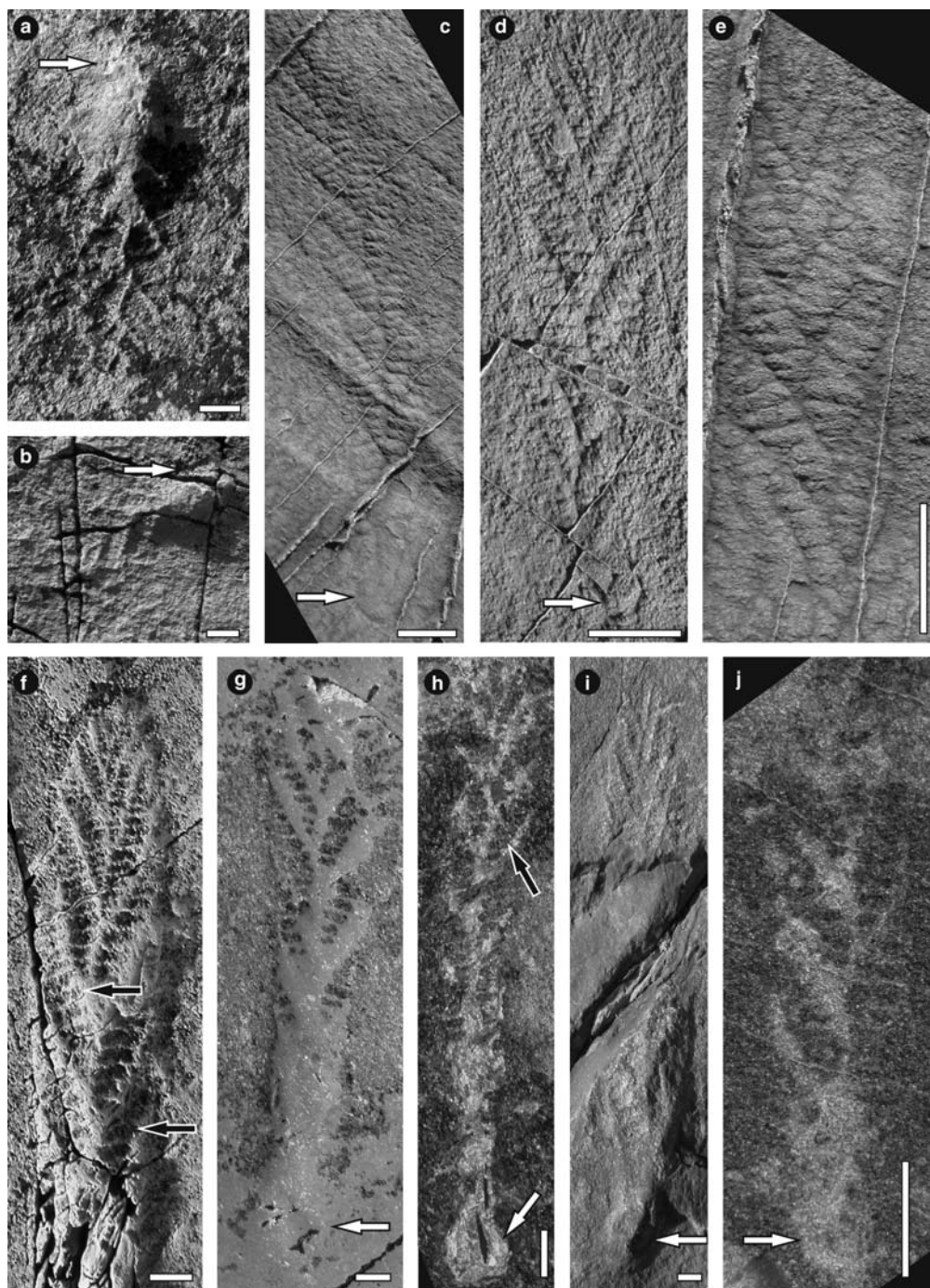


Fig. 4. *Charnia masoni* preserved in positive epirelief on the upper bedding plane surfaces. (a–b) Juvenile specimens of *C. masoni* displaying basal attachment disc from the ‘E’ surface of the Mistaken Point Formation (Landing *et al.* 1988). (c–e) Latex moulds whitened with ammonium chloride of *C. masoni* from Sword Point of the Mistaken Point Formation. (c) and (d) displaying basal attachment disc. (f) *C. masoni* from a loose block believed to be from Long Beach of the Mistaken Point Formation. Specimen whitened with ammonium chloride. (g–i) *C. masoni* from Long Beach of the Mistaken Point Formation, displaying basal attachment discs. (j) *C. masoni* from Lower Mistaken Point from the Mistaken Point Formation. White arrows indicating basal anchoring discs, black arrows indicating possible tertiary divisions. All scale bars 1 cm.

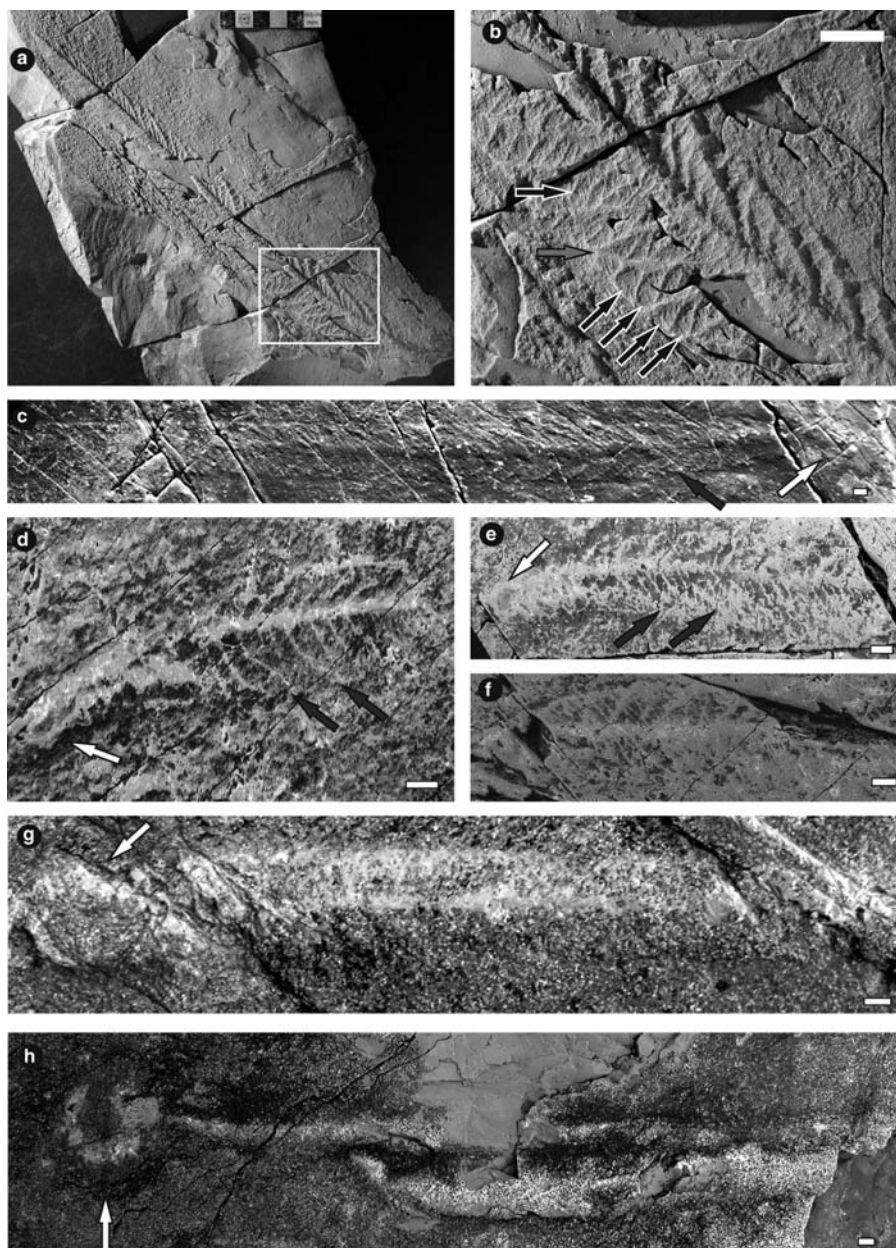


Fig. 5. *Charnia wardi* preserved in positive epirelief on the upper bedding plane surfaces. (a) Type specimen of *C. wardi* from the Drook Formation displaying the prominent central ridge and repeatable *Charnia* branching pattern. (b) enlarged view of the area indicated in A displaying the rangeomorph elements (grey arrows) restricted to one per secondary modular element and also demonstrating the rare longer and acutely angled primary branches (termed bundles; white arrows). (c) *C. wardi* from the Drook Formation. (d–f) *C. wardi* from the Mistaken Point Formation. Specimens at this horizon are significantly smaller than those from older formations. d–e displaying basal anchoring disc (white arrows). (g–h) Poorly preserved specimens of *C. wardi* from the Drook Formation, preserved under thick, coarser grained volcanic tuffs and with large basal anchoring disc (white arrow, only visible in upper frond). (h) Two specimens of *C. wardi* in close proximity to one another. White arrows indicate basal anchoring discs, black arrows indicate tertiary divisions, and grey arrows indicate branch bundling. All scale bars 1 cm.

Understanding the effects of these processes allows more accurate interpretation of the original morphology of the fossil. As the Ediacara Biota was smothered beneath volcanic ash (Conception-style preservation of Narbonne 2005) or cast beneath beds of sandstone with the chemical assistance of microbial mats (Flinders- or Fermeuse-style preservation of Narbonne 2005), the overall morphology of the preserved organisms has been restricted to near two dimensional impressions that remained after fossilization. Morphological reconstruction of three-dimensional forms from impressions has always been difficult when interpreting Ediacaran fossils (Narbonne *et al.* 1997; Gehling *et al.* 2000; Grazhdankin & Seilacher 2002; Dzik 2002), and has commonly resulted in oversimplification of the real external morphology. Overlapping relationships and internal structures are rarely preserved, resulting in three-dimensional reconstructions highlighting sheet-like morphologies. Internal features, such as strengthening structures (non-mineralized organic skeletons), may be difficult to interpret from well-preserved specimens displaying only the external form (Narbonne 2004). This seems particularly true of *Charnia*, which originally may have been nearly cylindrical and in which all the elements have been superimposed onto a two dimensional sheet. The following section will explore the 'taphomorphology', or the altered morphology remaining after preservation, of *Charnia* in order to reconstruct the original three-dimensional configuration.

Several specimens of *Charnia* from Mistaken Point and Spaniard's Bay display significant variation in the angle of primary branching (Table 1), a predictable shape-change of the secondary modular elements within each primary branch (Fig. 3), and a variable central zigzagging midline (compare specimens from Figs 4–6). These traits suggest that *Charnia* represents a series of independent, overlapping, primary branches, which result in the taphonomic expression of a complete, unsegregated sheet.

Each individual primary branch is overlapped by a second branch located on the opposite side of the midline, resulting in the covering of proximal secondary modular elements (region 1 in Fig. 2b) and therefore smaller L1–L3 landmark distances (distance A in Fig. 3a) for these secondary lobes. As each primary branch alternates and overlaps along the midline, the taphonomic response is a zigzagging central furrow. Furthermore, each primary branch is also overlapped by an adjacent primary branch as the distal tip is tucked in underneath the overlying branch (region 3 in Fig. 2b), resulting in smaller L2–L4 landmark distances (distance B in Fig. 3a) for these secondary modular elements. This hypothesis suggests that the outer rim/margin present in *Charnia* most

likely represents the natural termination of the distal tip of a branch, as it is tucked in underneath the overlying branch (region 3 in Fig. 2b), and does not represent a true distal boundary. In contrast, the secondary modular elements located along the middle of each primary branch (region 2 in Fig. 2b) are characterized by a more rectangular shape, which consists of somewhat equidistant L1–L3/ L2–L4 landmark distances, resulting from the limited amount of overlapping from adjacent primary branches. The secondary modular elements in region 2 (of Fig. 2b) may best represent the true shape of each individual secondary modular element due to the limited amount of overlap from adjacent primary branches. The distal primary branches located near the tip of the frond (rectangular primary branches, Fig. 2a) are significantly more rectangular in shape and lack the characteristic sigmoidal shape (sigmoidal primary branches, Fig. 2a), resulting from the limited amount of overlap with adjoining primary branches.

The overall alternating branching pattern, which has come to represent *Charnia*, varies little, despite the numerous specimens present at Mistaken Point (Fig. 4). In *C. masoni*, the proximal secondary lobes (region 1 in Fig. 2b) are acutely angled as a direct response to the acute angle of the primary branches. After the initial acute branching, the primary branches continue to curve until a maximal branching angle is reached (between 19°–37°, Table 1). At this point the secondary modular elements are located at right angles to the base of the primary branches (region 2 in Fig. 2b). At the distal tip of each primary branch, the secondary modular element branching angle becomes acute as the primary branch dips underneath the distal tips of the overriding branch (region 3 in Fig. 2b). In *C. masoni*, these branches are strictly parallel and errors in overlapping are virtually non-existent, requiring that each primary branch be attached to an internal central stalk at the proximal branching site and also anchored at the distal tip by an internal outer margin (Narbonne 2004, Fig. 3d) or that each primary branch was joined to adjoining primary branches by flexible soft tissue.

The secondary modular elements vary between a pill-shaped to a more rectangular- or straight-sided shaped secondary modular element. This variation in the shape of the secondary modular elements is directly linked to the soft-bodied nature of *Charnia*. If secondary elements were compressed laterally either during death or preservation, the original box-shaped secondary elements could have been modified into a pill-shaped element. This variation in shape cannot represent a taxonomic variation because both types of modular elements are preserved on the same specimen, and commonly on the same primary branch.

Table 1. Distance measurements, number of primary and secondary branches, and the primary branching angle of *Charnia* from Mistaken Point Newfoundland. All measurements have been retrodeformed to adjust for tectonic shortening

Specimen	Morphotype	# Primary	# Secondary	Length (cm)	Width (cm)	L/W ratio	Angle range	Mean
<i>Charnia masoni</i>								
Sword Point 1	Ovate	11	14	13.1	4.0	3.2	20–32	26
Sword Point 2	Ovate	9	13	15.1	5.8	2.6	25–40	29
Sword Point 3	Ovate	9	11	10.6	4.2	2.5	27–35	30
Sword Point 4	Ovate	13	13	23.9	6.6	3.6	17–29	21
Sword Point 5	Ovate	13	14	25.7	5.2	4.9	18–32	24
Sword Point 6	Ovate	11	12	11.9	3.3	3.6	26–42	31
Sword Point 7	Ovate	11	13	18.9	3.9	4.9	17–42	30
Sword Point 8	Ovate	11	13	14.4	3.0	4.8	22–43	31
Sword Point 9	Ovate	9	11	7.3	2.5	2.9	26–40	30
Sword Point 10	Ovate	11	14	21.1	4.6	4.6	20–33	26
	Average	11	13	16.2	4.3	3.8	22–37	28
Lower Mistaken Point 1	Parallel	8	8	6.0	1.2	5.2	23–29	25
Long Beach 1	Parallel	7	11	14.6	3.5	4.2	23–33	27
Long Beach 2	Parallel	8	9	13.0	2.3	5.6	16–35	26
Long Beach 3	Parallel	11	10	16.9	3.8	4.4	13–29	24
	Average	9	10	12.6	2.7	4.8	19–31	26
<i>Charnia wardi</i>								
							Reg/Bdl	Reg/Bdl
Lower Mistaken Point 2	Short	28	10	23.9 +	4.6	N/A*	42–64/26–36	53/29
Lower Mistaken Point 3	Short	23	8	11.0 +	2.8	N/A*	49–86/22–37	65/31
Lower Mistaken Point 4	Short	28	11	20.9 +	5.3	N/A*	43–74/21–35	58/26
Lower Mistaken Point 5	Short	19	9	17.3 +	5.7	N/A*	45–88/29–39	62/33
Lower Mistaken Point 6	Short	28	12	12.9 +	3.4	N/A*	42–58/23–30	48/27
	Average	25	10	N/A*	4.3	N/A*	44–74/24–35	57/29
ROM 54349	long	>60	12	61.6 +	4.4	N/A*	39–64/21–31	49/26
ROM 38628	long	>30	12?	30.2 +	3.0	N/A*	35–63/16–32	46/24
Drook 1	long	N/A*	N/A*	49.7	2.7	18.4	N/A*	N/A*
Drook 2	long	N/A*	N/A*	36.6	2.3	15.9	N/A*	N/A*
Drook 3	long	N/A*	N/A*	48.3	3.8	12.7	N/A*	N/A*
Drook 4	long	N/A*	N/A*	42.2	3.2	13.2	N/A*	N/A*
Drook 5	long	N/A*	N/A*	37.9	3.9	9.7	N/A*	N/A*
Drook 6	long	N/A*	N/A*	45.2	2.8	16.1	N/A*	N/A*
Drook 7	long	N/A*	N/A*	77.9	2.8	27.8	N/A*	N/A*
Drook 8	long	N/A*	N/A*	77.4	2.9	26.7	N/A*	N/A*
Drook 9	long	N/A*	N/A*	65.7	5.2	12.6	N/A*	N/A*
	Average	N/A*	N/A*	53.4	3.4	17.0	N/A*	N/A*
<i>Charnia antecedens</i>								
ROM 54348		8	N/A*	19.6	4.1	4.8	13–36	19
Drook 10		9	10	25.5	5.1	5.0	15–31	23
	Average	8.5	10	22.5	4.6	4.9	13–33	21

N/A*, elements of the frond that were poorly-preserved and could not be counted/measured.

Reg/Bdl, the differences in branching angles between regular and bundled branches.

+, minimal distance measurements from incomplete specimens.

The width of the frond and the number of secondary modular elements in *Charnia masoni* from Mistaken Point varies considerably between specimens, resulting in specimens that vary from the traditional ovate shape (Fig. 4a–e, i–j) to those that appear more parallel-sided (Fig. 4f–h). Specimens with a more parallel-sided appearance typically exhibit a larger frond length v. width ratio (Fig. 4f–h; Table 1) and fewer secondary modular elements per primary branch when compared with the ovate form (Table 1). Furthermore, the parallel sided morphs of *C. masoni* do not exhibit the under-lying of the distal tip of the primary branch typically visible in the ovate forms of *C. masoni* and the average angle at which the primary branches diverge from the central stalk is more acute (Table 1). A final character of interest is the apparent sharp edge, almost resembling an outer rim, which constrains the distal tips of the primary branches in the parallel-sided form, but which is absent from the well-preserved ovate form.

Taphonomy is most likely responsible for the parallel-sided and ovate morphs, although the morphological shape variation between the two morphotypes is possibly ontogenetic or based on branching angles (Fig. 7b–c). The sharp termination of the distal region of each primary branch in the parallel sided morph of *C. masoni*, in addition to the absence of the overlapping of the distal secondary modular elements (region 3 in Fig. 2b) and the apparent shape and size variation of these same distal elements is suggestive that the distal secondary lobes were not preserved (Fig. 7c). For proper preservation of Ediacara Biota at Mistaken Point, the organism must have been trapped between the muddy substrate and the overlying veneer of volcanic ash. It is probable that, as *Charnia* was felled and then covered by fallout ash, the distal tips of the primary branches were curved upwards and therefore were jutting outside of the veneer of ash required for proper preservation (Fig. 7c). This resulted in a sharp outer margin in the parallel-sided morph of *Charnia*, and may explain both the size and shape variations in the distal modular elements. The taphonomic margin produced by trapping volcanic ash between the distal tips of the primary branches and the underlying muddy substrate distorts the familiar ovate shape of *Charnia*, and should not be used as a taxonomic means of distinguishing between species of *Charnia*. Therefore, it is important to stress that the frond widths presented in this paper represent minimum distances, especially when comparing the parallel-sided taphomorphs to other specimens from around the world.

The type specimen of *C. masoni* from Charnwood Forest is broken just above its base, but several specimens of *Charnia masoni* from Mistaken

Point exhibit holdfast discs (Fig. 4a–d, g–j). The presence of a holdfast disc is consistent with the view that *Charnia* was an erect frond similar in function to other stalked Ediacaran organisms.

As with *C. masoni*, *C. wardi* is composed of several primary branches, which are overlapped by adjacent primary branches at the proximal anchoring site, and are tucked under adjacent branches at the distal tip, resulting in the appearance of a complete, unsegregated sheet. Primary branches are typically rectangular or sigmoidal throughout their length, although certain rare branches are more acutely angled than their surrounding primary branches, producing ‘bundling’ of the branches (Fig. 5b; Table 1). Branch bundling results in a greater exposure of the secondary modular elements that make up the displaced branch, although it also results in an increased amount of overlap with adjacent branches, therefore reducing the exposure/preservation of the overridden branches. This taphonomic character explains irregularities in the outer margin of the frond, which represent the distal termination of each individual branch, and not a true physical character. Unlike *Charniodiscus*, which has a definitive outer rim or margin of soft tissue, the outer margin of *Charnia* is irregular as the distal tip of each independent branch is tucked under adjacent branches.

The oldest specimens of *C. wardi* from the Drook Formation (Figs 1, 5a–c, g–h) are up to an order of magnitude longer (longest specimens up to 185 cm) than the youngest specimens of the basal Mistaken Point Formation. (between 11 and 23.9 cm, averaging 17.2 cm; Table 1), however none of the specimens from the basal Mistaken Point Formation are complete (Fig. 5d–f). Both the Drook and the Lower Mistaken Point specimens exhibit similar frond widths (averaging 43 mm and 34 mm respectively; Table 1), and share the characteristic branch bundling, central midline, primary branch shape, and secondary modular elements.

C. wardi is thought to be composed of a series of alternating primary branches which cross-over on either side of the central stalk, thus sometimes obscuring the preservation of the stalk. In areas where the preservation of the primary branches crossing over the stalk is best, the branch overlapping results in a zigzagging central midline characteristic of *Charnia*. The most parsimonious explanation for the varying morphology of the central stalk is that the support structure which serves as a basal anchoring site for each primary branch lies internally. In cases where the primary branches are well preserved and cross over the centre of the frond, the midline is obscured or missing, whereas in examples where central midline is well defined, the primary branches are

poorly preserved. It is believed that the presence of a straight, central stalk results from composite moulding of the internal stalk onto the surface expression of the primary branches, and explains how the primary branches cross over the central stalk in some specimens (Narbonne & Gehling 2003).

Due to the coarseness of the volcanic tuff that blanketed specimens from the Drook (Fig. 1), the original 3D morphology was better preserved when compared to the easily compressible, fine-grained volcanic ash which is typical of the remainder of the Mistaken Point assemblage. The high relief (sometimes up to 10 mm) of the specimens from the Drook Formation, suggests that the original 3D morphology of *C. wardi* was more cylindrical than sheet-like in shape.

The type specimen of *Charnia wardi* consists exclusively of the distal tip of the frond, but many other specimens preserve disc-like holdfasts on their proximal end. Although most specimens (e.g. Fig. 5c) preserve basal holdfasts, which appear smaller than would be expected for an Ediacaran frond of this size (Peterson *et al.* 2003), additional specimens of *C. wardi* exhibit larger discs (Fig. 5h–i). It seems likely that the apparent scarcity of holdfast discs and the small size of many of the ones that are preserved reflects the fact that the *Charnia* holdfast was largely buried in the substrate, and would have resulted in the poor expression of the basal anchoring disc (Narbonne & Gehling 2003) whereas the majority of the *Charniodiscus* holdfasts at Mistaken Point rested on the substrate (Seilacher 1992, 1999; Laflamme *et al.* 2004).

Unlike the typical, repeatable branching pattern that typifies *C. masoni* and *C. wardi*, several specimens from the Drook Formation of Mistaken Point (Fig. 6) and the Mistaken Point Formation from the Bonavista Peninsula (O'Brien & King 2004) of Newfoundland, and possibly from the Rawnsley Quartzite, Flinders Ranges, South Australia (Nedin & Jenkins 1998), display a disorganized branching pattern sufficiently distinct from *C. masoni* to warrant the definition of a new species of *Charnia*. *Charnia antedecens* n. sp. is characterized by severe shape variation within the primary branches, interpreted to be a result of disproportioned overlapping from adjacent branches, which had the effect of producing a disorganized rather than the highly repetitive shape that is typical of other *Charnia* species (Fig. 6, see grey arrows). This disproportioned overlapping of the primary branches may have resulted from poor (or nonexistent) anchoring of the distal tips of the primary branches with the internal marginal rim or with the central stalk. The rectangular distal termination of the primary branches (Fig. 6a–c) is a direct and predictable result of the *Charnia* branching pattern

once untucked from the overlying primary branch (region 3 in Fig. 2b). The taphonomic sigmoidal shape of a primary branch of *Charnia* is lost once the distal tip is exposed from beneath the overriding branch. The acutely angled secondary modular elements of *C. antedecens* are similar to the most proximal secondary modular elements (region 1 of Fig. 2b) of *C. masoni*, and may be a result of the very acute primary branching angles, which are on average more acutely angled than in *C. masoni* (Table 1). Unlike *C. masoni*, primary branches in *C. antedecens* retain the initial branching angle and only rarely change orientation at the distal tip. Through both quantitative and qualitative analysis of several complete specimens of *Charnia* from Mistaken Point and Spaniard's Bay Newfoundland, it is possible to decouple the influence of taphonomy from the morphological shape remaining after fossilization, and use differences in morphological responses to taphonomy in order to elucidate new species.

Life habits of *Charnia*

Infaunal v. epifaunal

Charnia was originally interpreted as a sessile benthic, epifaunal organism with an elevated frond that extended upward into the water column (Ford 1958), a view that has been supported by virtually all subsequent workers (e.g. Jenkins & Gehling 1978; Glaessner 1979; Fedonkin 1992; Jenkins 1992; Runnegar & Fedonkin 1992). Recently, the apparent absence of a basal holdfast in many specimens outside of Avalonia (and the presence of peculiar truncated laminae in the sediment encasing a three-dimensional cast of *Charnia masoni* from the White Sea) led Grazhdankin (2004) and Grazhdankin & Seilacher (2005) to suggest an infaunal lifestyle for White Sea and Newfoundland *Charnia*, similar to the lifestyle they envision for *Pteridinium* and *Rangea* (Grazhdankin & Seilacher 2002, 2005). In contrast with the White Sea, no infaunal organisms or burrows have been found in the Conception Group. The White Sea specimens described by Grazhdankin (2004) have not been studied, but all evidence from the Avalonian specimens of *Charnia* supports the traditional view that they represent sessile fronds that were elevated above the sea floor. Support is as follows:

(1) Preservation beneath ash—As with all other fossils and taxa in the Conception Group, Avalonian specimens of *Charnia* are preserved exclusively at the interface between the underlying mudstone and the overlying volcanic ash-fall tuff. Quality of preservation commonly decreases with distance from the holdfast, implying that minute

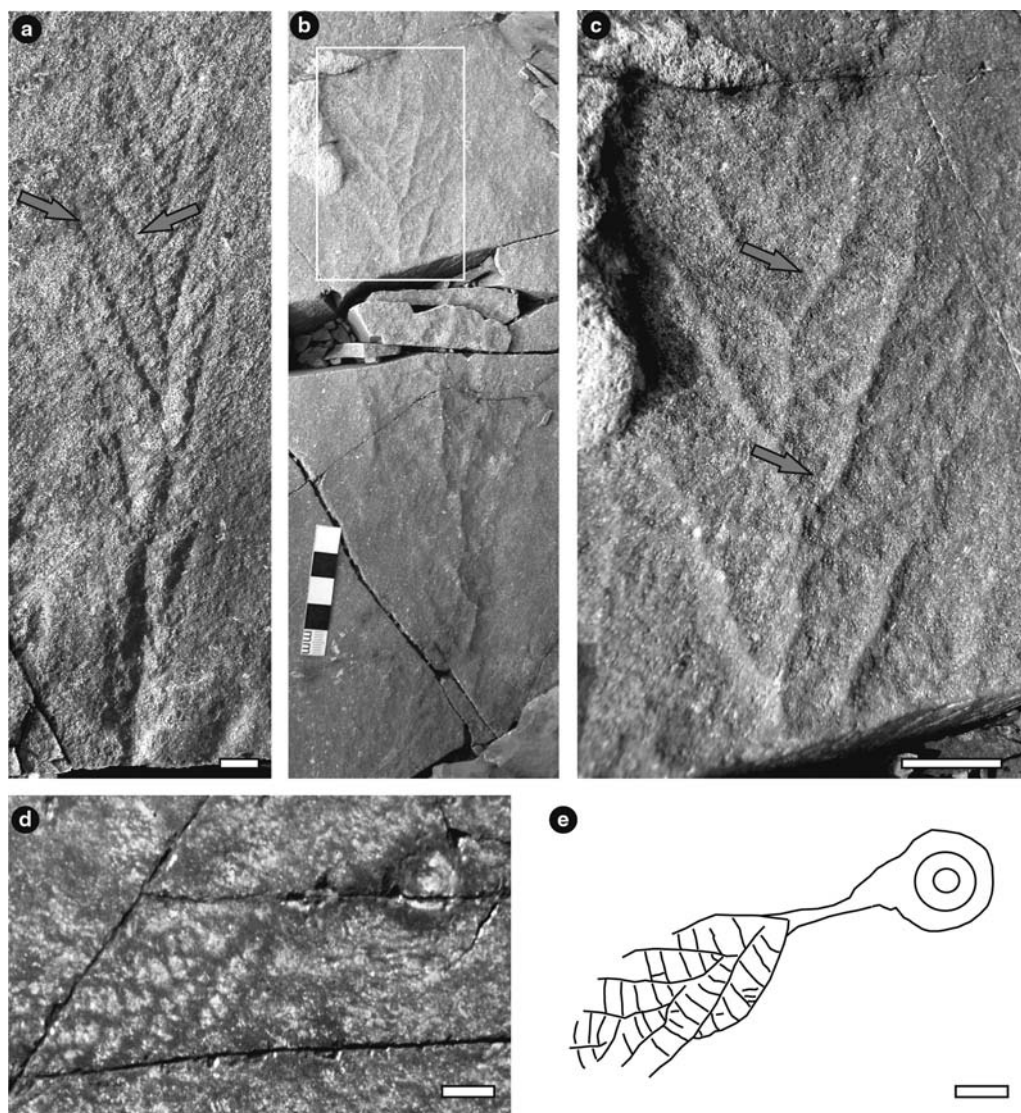


Fig. 6. *Charnia antecedens* n. sp. from the Drook Formation. (a–c) and *Charnia* sp. displaying prominent stem and holdfast from the Briscal Formation (d–e). (a) Holotype of *C. antecedens* n. sp. ROM 54348. Arrows indicate defects in the traditional *Charnia* branching pattern resulting from overlap with adjacent primary branches. (b) *C. antecedens* n. sp. with close-up in (c). Notice that the branches overlap the central axis, forming a zigzagging pattern. Arrows indicate defects in the traditional *Charnia* branching pattern resulting from overlap with adjacent primary branches. (d) Frond with well defined stem and composed of *Charnia*-like primary and secondary branching patterns indistinguishable from *C. masoni*. Prominent stem may represent poorly preserved or lost basal primary branches. (e) Line drawing of D. All scale bars 1 cm.

quantities of ash were increasingly likely to be present beneath the frond distally from the holdfast (see above). These taphonomic aspects are consistent with preservation as an 'Ediacaran Pompeii' beneath volcanic ash falls (Seilacher 1992;

Narbonne 2005), but are difficult to envision for an infaunal organism or colony. Specimens preserved in their entirety were either already dead on the sea floor or were recumbent and covered immediately by the ash, whereas more

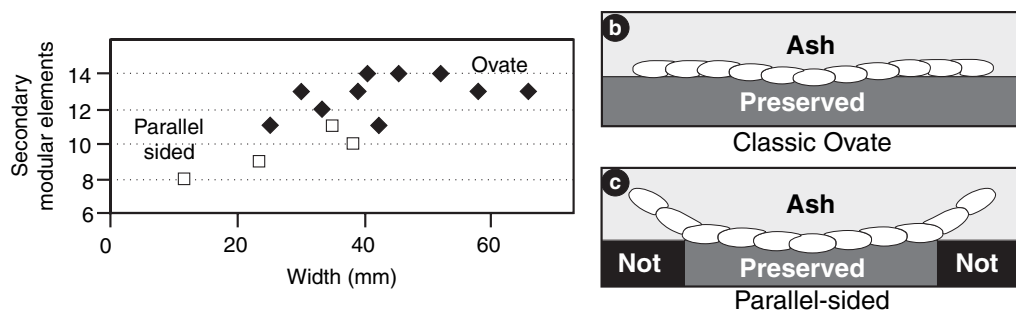


Fig. 7. (a) Traditional morphometric analysis of *Charnia masoni* from the Mistaken Point Formation. White filled squares represent the parallel-sided morph of *C. masoni*, whereas the black diamonds represent the ovate morph. Growth trend lines are similar and the increased number of secondary modular elements with width represent a taphonomic response due to preferential ash preservation. (b–c) Interpretive figure displaying (b) complete preservation of ovate frond and (c) incomplete preservation of distal tips of primary branches resulting in the preservation of a parallel-sided frond shape.

upright specimens are now represented only by the abundant discs, some of which exhibit partial stem impressions (Wood *et al.* 2003).

(2) Fossil orientations—All frondose taxa on every fossiliferous bedding plane in the Portugal Cove South-Mistaken Point area show strong unimodal current orientations that reflect contour-parallel or rarely down-slope currents (Seilacher 1999; Wood *et al.* 2003). Orientations of specimens of *Charnia* on each surface are indistinguishable from those of the other frondose taxa on the same bedding surface, with a strong preferred orientation down current with basal holdfasts serving as anchors. These current orientations would be expected if *Charnia* was an elevated frond like *Charniodiscus*, but would be difficult to explain if *Charnia* was infaunal.

(3) Tiering—Mistaken Point communities show a pronounced tiering of fossils on each bedding surface which is strikingly similar to that observed in communities of filter-feeding animals throughout the Phanerozoic (Clapham & Narbonne 2002). Specimens of *Charnia* occur in all three tiers, but adult specimens are especially common in the middle and upper tiers with the longest specimens dominating the uppermost tier (Clapham & Narbonne 2002). This style of tiering is typical of epifaunal suspension-feeding organisms (Ausich & Bottjer 1982, 2001); tiering of infauna did not begin until the middle or late Palaeozoic and is in any case dissimilar to that shown by *Charnia* and other Mistaken Point taxa (Droser & Bottjer 1993).

Feeding

Several different feeding strategies have been suggested for members of the Ediacara Biota,

including photo- or chemoautotrophy (McMenamin 1986), absorbing dissolved nutrients directly from seawater (Seilacher 1989), and suspension feeding (Jenkins & Gehling 1978; Clapham & Narbonne 2002; Laflamme *et al.* 2004). Phototrophic feeding strategies can be dismissed for the Mistaken Point Ediacara Biota since the accumulation of kilometres of metre-thick turbidites, the complete absence of any shallow-water sedimentary features such as storm beds, Hummocky Cross-Stratification and Swaley Cross-Stratification (HCS-SCS), or exposure features such as desiccation cracks, all suggest that these organisms were living in deep-water ecosystems well below the euphotic zone and storm wave base (Wood *et al.* 2003). Chemoautotrophy is also a tenuous proposition due to the rarity of sulphides or carbonates typical of hydrogen sulphide or methane seeps (Little *et al.* 1998). The tiering structure described from the Mistaken Point communities (Clapham & Narbonne 2002) differs from that exhibited by marine phototrophic communities (which grow preferentially towards the surface and, therefore, are largely unconstrained by height above the sea bottom; Foster 1975) and from chemosynthetic communities (which have less need for modern style tiering), and is strikingly similar to that of epifaunal suspension-feeding organisms (Clapham & Narbonne 2002). The distinction between absorbing dissolved nutrients directly from seawater and suspension filter feeding is difficult to distinguish since both models explain the strong tiering component of the Mistaken Point assemblages (Clapham & Narbonne 2002) and the proportion of regular, irregular and aggragated lateral distributions (Clapham *et al.* 2003).

If the frond leaf is correctly interpreted as a nutrient-gathering structure, the presence of an inferred internal stalk in lieu of a simple stem in

Charnia masoni, *C. wardi*, and *C. antecedens* would have allowed these organisms to feed along the entire length of the frond and resulted in the frondose branching elements being attached directly to the basal anchoring structure (Clapham & Narbonne 2002). *C. wardi* demonstrates clear evidence of an internal central stalk (Fig. 5a–f), and further support for the idea that *C. masoni* also contained an internal stalk comes from a single specimen of *Charnia* sp. from the Briscall Formation which displays both the classic *C. masoni* alternating branching structure and a stem attached to a basal anchoring disc (Fig. 6d–e). Ediacaran fronds typically exhibit a central stalk from which the primary branching units diverge (Jenkins & Gehling 1978; Glaessner 1979; Narbonne *et al.* 1997; Narbonne & Gehling 2003; Laflamme *et al.* 2004), which provided a means of supporting the frond upright in addition to a rigid branching point for further subdivision of the frond. This central stalk is commonly an extension of the stem, which joins the frond to the basal anchoring structure.

Affinities of *Charnia*

Charnia was originally interpreted as a macrophytic alga (Ford 1958), but this was immediately disputed, and this genus was subsequently regarded as a pennatulacean Cnidarian (Glaessner 1979, 1984) a lichen (Retallack 1994), a stem group of the Fungi (Peterson *et al.* 2003), a representative of an extinct high-order taxonomic group of class (Jenkins 1985) or kingdom (Seilacher 1992; McMenamin 1998) level, or any one of a variety of other explanations. As shown above, sedimentological studies implying a deep-water axial/slope environment well below storm wave base for the Mistaken Point assemblage and a community organization similar to that of Phanerozoic and modern filter-feeding animals rules out any affinities for *Charnia* that rely on photosynthesis for feeding (such as plants, algae, or lichen) and implies that an animal origin is most likely. Narbonne (2004, 2005) and Brasier & Antcliffe (2004) followed Jenkins (1985) in regarding *Charnia* as a representative of the rangeomorphs, and extinct phylum-level group of basal animals that characterized early Ediacaran communities (Narbonne 2004).

In the only treatment of the Ediacara Biota in the *Treatise of Invertebrate Paleontology* to date, Glaessner unified *Charnia*, *Charniodiscus* and *Glaessnerina* under the family Charniidae (Glaessner 1979, based on the overall frond-like morphology of all three members (Glaessner 1979). Inclusion of *Glaessnerina* in the Charniidae is clearly justified; indeed, *Glaessnerina* may well

be a junior synonym of *Charnia* (Runnegar & Fedonkin 1992; see Systematic palaeontology). The tiering structure of early Ediacaran communities (Clapham & Narbonne 2002; Laflamme *et al.* 2004) is highly suggestive that the frondose morphology represents a biological response in order to maximize food gathering, and not an evolutionary character that warrants all frondose Ediacarans to be placed within a separate and distinct clade (see also Narbonne *et al.* 1997). The tertiary rangeomorph microstructure present within *Charnia* differs significantly from the branching pattern present within *Charniodiscus*, consisting of several primary branches joined together by a single sheet, in which each branch is subdivided into several perpendicular secondary elements composed of parallel tertiary branches (Jenkins & Gehling 1978; Jenkins 1996; Laflamme *et al.* 2004). Therefore, Jenkins (1985) is followed here in excluding *Charniodiscus* from the Charniidae.

Conclusions

The abundance and taphonomic diversity of fronds from the Avalon Peninsula of Newfoundland has allowed reinterpretation of the classic Ediacaran frond *Charnia*. Numerous specimens from Avalon show that the frond was tethered to the seafloor with a spherical or bulbous holdfast, which was buried in the substrate. Descriptive, quantitative, landmark and traditional morphometric analyses imply that *C. masoni* exhibited a series of overlapping primary branches that taphonomically controlled the morphological expression of secondary-order modular elements. Individual branches appear to have been closely fixed in position, implying that *C. masoni* had either an internal organic skeleton or organic attachments between branches. *C. antecedens* n. sp. is broadly similar in morphology, but exhibits primary branches that were commonly dislodged or ripped-out of sequence, suggestive of a weaker connection with adjacent branches than is evident in *C. masoni*. *C. wardi* is interpreted as a cylindrical, rod-like frond with an internal central stalk, and branches whose attachment with each other was intermediate between the very loose organization of *C. antecedens* and the more rigorous organization of *C. masoni*.

Disorganized forms of *Charnia* (*C. wardi* and *C. antecedens*) dominate the oldest assemblages of *Charnia* in the Drook Formation (575 Ma) but are vastly overshadowed by more organized forms (*C. masoni*) in the Mistaken Point Formation (565 Ma) and Charnwood Forest, and have not been reported from younger occurrences of *Charnia* from the White Sea or Siberia (<555 Ma; Knoll *et al.* 1995; Martin *et al.* 2000; Grazhdankin

2004), which consist entirely of *C. masoni*. The ecological consequence of an increased rigidity in *Charnia* was the eventual capability to colonize shallower waters affected by wave turbulence and periodic energetic storm events. Our systematic, taphonomic and stratigraphic occurrence of *Charnia* reveals a more ecologically and evolutionally dynamic taxon than was previously recognized, and highlights the difficulties associated with interpreting a three-dimensional form from two-dimensional impressions.

Systematic palaeontology

Genus *CHARNIA* Ford, 1958

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

Diagnosis (new): Parallel-sided to ovate, distally and proximally tapering frond composed of multiple, sigmoidal to rectangular primary branches alternating along a central stalk, overlapping adjacent primary branches and typically crossing over the central midline forming a zigzagging central axis. Primary branches composed of multiple secondary modular elements arranged acutely to almost perpendicularly to the primary branches. Proximal tapering of frond lacks a distinct stem. Surface expression of basal disc commonly small or missing.

Comparisons: *Charnia masoni* is similar in many respects to *Glaessnerina grandis* Glaessner & Wade, 1966. The two forms are segregated on the basis of the large angle of the secondary modular elements, which are oblique in *Glaessnerina* and may represent a taphonomic response to a soft-bodied morphology. Runnegar & Fedonkin (1992) considered *Glaessnerina* a junior synonym of *Charnia*, but Jenkins (1996) considered *Glaessnerina* a valid genus based on the apparent arrangement of the primary branches, which he considered to be a sequence of overlapping leaves. The evidence provided both in this study and independently by Jenkins (1996) and Nedin & Jenkins (1998) of the overlapping sequence of primary branches in *Charnia* further supports the synonymy of *Charnia* and *Glaessnerina* proposed by Runnegar & Fedonkin (1992).

Several of the morphological characters that were used previously to segregate *Charnia* from *Charniodiscus* have now been identified in both genera, and thus are no longer valid. The basal anchoring structure is present in both genera, albeit a larger fraction of the disc is preserved in *Charniodiscus* while a significant portion of the

disc appears to have been buried in *Charnia*. The concentric rings or raised central boss within the basal holdfast in *Charniodiscus* is absent from all studied *Charnia*. The characteristic stalk from which diverged the primary branches in *Charniodiscus* is present as an internal structure in *Charnia wardi* and inferred to be present internally within *C. masoni* and *C. antecessens*.

With the loss of several key characteristics distinguishing *Charnia* and *Charniodiscus*, the few remaining differences become pivotal in segregating both genera. The foremost differentiating character resides within the alternating branching pattern, which overlaps the central stalk, and results in a zigzag central mid line in *Charnia*. Detailed analysis of the nature of the tertiary divisions further help define the differences between *Charnia* and *Charniodiscus*: *Charnia* is characterized by highly repetitive, curved divisions that are inferred to represent rangeomorph microstructure, whereas *Charniodiscus* is composed of several primary branches from which diverge perpendicular secondary branches highlighted by tertiary branching divisions (Jenkins & Gehling 1978; Jenkins 1996; Laflamme *et al.* 2004). Finally, as demonstrated above (see 'Morphometric Analysis'), the sigmoidal taphomorphology of each primary branch due to the overlying relationship of the primary branches in *Charnia* is strikingly dissimilar to the alternating branches of *Charniodiscus*.

Species *Charnia masoni* Ford, 1958

Figure 4a–j

Diagnosis (new): Parallel-sided to ovate *Charnia* with broad, semicircular distal termination, zigzagging central axis and sigmoidal primary branches. Length to width ratio less than 5:1 (typically between 2:1 and 3:1). Primary branches highly acute (typically less than 30° from midline).

Description: *Charnia masoni* is characterized by a distally tapering, ovate frond with a broad, semicircular to arrow-shaped distal termination. The type specimen from Charnwood Forest is 188 mm long and 46 mm wide, consisting of 18 primary branches on either side and composed of a maximum of 22 (average 18) secondary modular elements per branch. Specimens from Mistaken Point are typically slightly smaller (Table 1), averaging 160 mm long by 41 mm wide, with fewer primary branches (max 13) and secondary modular elements (max 14). The primary branching angle (as defined by the angle between the central midline and the base of the primary branch; see Fig. 2a) is strongly acute and ranges on average between 19° and 37° (mean of 26°–28°, Table 1).

Primary branches are composed of multiple, rhombic secondary modular elements, which form acute to right angles with the base of the primary branches, and result in an almost transverse position along the entire length of the primary branches. The primary branches are strongly angled at both proximal branching site and the distal tips (which curve to run almost parallel to the central midline), resulting in a sigmoidal shape. In specimens with primary branches characterized by relatively more obtuse branching angles (greater than 30° from the central midline), the branching angle remains relatively constant throughout the entire length of the primary branch and results in rectangular primary branches when compared to the acutely angled sigmoidal branches. A distinct, zigzagging central midline is characteristic of *Charnia*. Unlike the typical sigmoidal shape of the basal primary branches (sigmoidal primary branches, Fig. 2a), the distal primary branches located near the tip of the frond are rectangular and composed of significantly smaller and rectangular rather than rhombic secondary modular elements (rectangular primary branches, Fig. 2a). The proximal secondary modular elements on each primary branch are characterized by smaller L1–L3 landmark distances (distance A in Fig. 3a) while the distal elements are defined by smaller L2–L4 landmark distances (distance B in Fig. 3a). Therefore, along a primary branch, the shape of the secondary modular elements varies from a trapezoid in the proximal region (region 1 in Fig. 2b) to a rectangle in the central region (region 2 in Fig. 2b) and finally returning to a trapezoid (albeit a mirror image to the proximal elements) as the distal region (region 3 in Fig. 2b) is overridden by another primary branch (see regional shape changes along primary branches in Fig. 2b). Primary branches extend proximally to the base of the frond into a small, typically poorly preserved or absent basal anchoring disc (Fig. 4a–d, g–j), resulting in the complete absence of a stem.

Occurrence and stratigraphic range: Oldest representatives from the Mistaken Point and Trepassey formations of Newfoundland. Additional specimens from Charnwood Forest in England and the White Sea as well as northeastern Siberia in Russia. Available U–Pb dates and chemostratigraphic correlations imply an age range 565 to <549 Ma for *Charnia masoni*.

Species *Charnia wardi* Narbonne & Gehling, 2003

Figure 5a–h

Diagnosis: (modified from Narbonne & Gehling 2003.) Very long, parallel-sided *Charnia* that

distally narrows to an acute tip, with straight central ridge or furrow. Complete specimens typically with >10:1 length v. width ratios. Primary branching angle typically greater than 45° (average range between 44° – 74°), with occasional acutely angled branch bundles (average range between 24° – 35°).

Description: *Charnia wardi* is a strongly elongate and tapering frond, which narrows to an acutely angled, arrowhead-shaped distal tip. A prominent central stalk (15–45 mm wide, mean 29 mm) forms a medial ridge from which and over which diverge several parallel-sided primary branches. Primary branches alternate on each side and overlap across the medial stalk, resulting in a zigzag branching pattern that locally obscures the central stalk. Most primary branches are either sigmoidal or rectangular throughout their length but taper to a point along their distal edge, and are composed of multiple (between 9 and 12) rectangular to rhombic secondary modular elements. Primary branching angle is typically greater than 45° (Table 1) from the central midline, although rare primary branches are angled more acutely (between 24° and 35° from the midline) and result in longer primary branches that cover and overlap adjacent primary branches (herein termed ‘bundles’). Displaced bundles show a rangeomorph structure (cf. Narbonne 2004) of complexly and fractally branching modules that form the edges of the curved third-order divisions (Fig. 5a–b). A taphonomically distinct outer rim represents the distal termination of each individual primary branch.

Comparison: *Charnia wardi* is unique in the genus *Charnia* in possessing a >10:1 length to width ratio and in attaining lengths of well over a meter. In juvenile or incomplete specimens, the presence of rare branch bundling in addition to the strongly linear shape and composite moulding of the central stalk allows for the differentiation of *C. wardi* from all other charnids. *Paracharnia dengyingensis* Sun 1986, known only from a single poorly preserved specimen from the Yangtze Gorge, China, exhibits similar length to width ratios, however, the significantly wider central stalk, which represents greater than half of the overall width, and the unusual secondary stalks which are found on each individual frondlet or petaloid leaf readily distinguish *P. dengyingensis* from *C. wardi*.

Occurrence and stratigraphic range: *Charnia wardi* is known only from the Conception Group of the Avalon Peninsula. It was first described from the upper beds of the Drook Formation (Narbonne & Gehling 2003), and the present study extends the distribution of *C. wardi* into the basal beds of the

Mistaken Point Formation to include specimens described (but not figured) as '*Charnia* species B' by Clapham *et al.* (2003).

Species Charnia antecessens sp. nov.

Figure 6

? '*Charnia masoni*... (P36574)' Nedin & Jenkins, 1998, p. 315, Fig. 1

'*Charnia masoni*, ROM 54348' Narbonne & Gehling, 2003, p. 28, Fig. 2a

'*Charnia* Ford, 1958 (circled and indicated by letter C)' Clapham *et al.*, 2004, p. 1033, Fig. 2

? 'Bush-like form, possibly comparable with *Bradgatia* but showing *Charnia*-like attributes' O'Brien & King, 2004, p. 210, Pl. 5A.

Diagnosis: *Charnia* with rectangular primary branches with inconsistent width throughout their length, acutely angled secondary modular elements throughout entire length of primary branch, and 'V' shaped proximal region.

Material: Holotype (ROM 54348; Fig. 6a) from the upper part of the Drook Formation of the Conception Group of Newfoundland. Two additional specimens from the upper Drook Formation were photographed and latexed in the field.

Description: *Charnia antecessens* consists of an ovate to elliptical frond in which the primary branches are not consistent in shape throughout their length and exhibit significant tapering of the frond at the proximal anchoring region. The frond is composed of 8–10 acutely angled (average 21°) primary branches that remain relatively constant in branching angle throughout the entire length of the branch. Primary branches rectangular to trapezoidal in shape instead of the traditional sigmoidal shape of *C. masoni* branches. Distal terminations of the primary branches are rectangular rather than tapered. Primary branches consisting of approximately 10–12 secondary modular elements acutely angled with the primary branches and lying almost perpendicular to the central axis, unlike the typically right-angled branching of *C. masoni*. Anterior region strongly tapered to form a 'V' shaped proximal region. Basal anchoring disc absent or small and poorly preserved.

Comparisons: The overall morphology of *C. antecessens* is most similar to *C. masoni*. The increased amounts of imbrication of the primary branches when compared to *C. masoni*, in addition to the acute branching angle of the secondary modular elements and the 'V' shaped proximal region are all suggestive of a distinct and diagnosable difference between both species. *C. antecessens* is known mostly from early Ediacaran assemblages

whereas *C. masoni* is known mostly from younger Ediacaran assemblages, implying that the differences between these taxa are unlikely to reflect taphonomy.

Derivation of name: *antecessens*, due to the implied ancestral origin of this species.

Occurrence: Three specimens are known from the Drook Formation of the Conception Group of Newfoundland. Additional specimens of *Charnia antecessens* are known from the correlative Mistaken Point Formation from the Bonavista Peninsula (Avalon zone, Newfoundland; O'Brien & King 2004). A single specimen similar to *C. antecessens* was also described and figured as *C. masoni* from the Rawnsley Quartzite, Flinders Ranges, South Australia (Nedin & Jenkins 1998), but our examination of the additional specimens listed in their paper revealed a heterogeneous collection of discs, discs with stems and fronds that are difficult to relate to *Charnia* at the present time.

Identification Key

Charniidae:

- A) Strongly linear *Charnia* with >10:1 length:width ratio. Prominent straight central stalk present and rare branch bundling

***Charnia wardi*:** Very long and tapering *Charnia* that distally narrows to the tip, with straight central ridge or furrow. Complete specimens typically with >10:1 length v. width ratios. Primary branching angle typically greater than 45° (average range between 44°–74°), with occasional acutely angled branch bundles (average range between 24°–35°).

- A) Ovate to cylindrical *Charnia* with <10:1 length:width ratio. Midline zigzagging and central stalk missing. Go to B
- B) *Charnia* with irregular primary branching. Primary branches rectangular and inconsistently branching. Significant increases in overlap from adjacent branches resulting in jumbled branch arrangement. Significant tapering of the proximal region of frond, resulting in 'V-shaped' proximal region.

***Charnia antecessens*:** *Charnia* with rectangular primary branches with inconsistent width shape throughout their length and acutely angled secondary modular elements throughout entire length of primary branch.

- B) *Charnia* with regular and consistent branching. Primary branches sigmoidal and parallel along entire length. Go to C
- C) Smaller *Charnia* (less than 200 mm in length) with fewer than 20 primary branches

***Charnia masoni*:** Cylindrical to ovate *Charnia* with broad, semicircular distal termination, zig-zagging central ridge, and sigmoidal primary branches. Length: width ratio less than 5:1 (typically between 2:1 and 3:1). Primary branches highly acute (typically less than 30° from midline).

C) Significantly larger *Charnia* (greater than 500 mm in length) with greater than 20 primary branches

Charnia grandis

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