Life after snowball: The oldest complex Ediacaran fossils

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ABSTRACT

Newly discovered fronds of the Ediacaran index fossil *Charnia* from the Drook Formation of southeastern Newfoundland are the oldest large, architecturally complex fossils known anywhere. Two species are present: *Charnia masoni*, originally described from Charnwood Forest in central England and now known worldwide, may have ranged through as much as 30 m.y. of Ediacaran time, and *C. wardi* sp. nov., a new species of *Charnia* that consists of slender fronds to nearly 2 m in length, is the longest Ediacaran fossil yet described anywhere. These fossils, which are present midway between the glacial diamictites of the Gaskiers Formation (ca. 595 Ma) and the classic Ediacaran assemblage of the Mistaken Point Formation (565 ± 3 Ma) 1500 m higher in the same section, provide our first glimpse of complex megascopic life after the meltdown of the ''snowball Earth'' glaciers.

Keywords: Ediacaran, Neoproterozoic, paleontology, snowball Earth, Avalon, Newfoundland.

INTRODUCTION

The Ediacara biota marks a critical stage in the evolution of life on Earth, the late Neoproterozoic appearance of large, soft-bodied organisms including the oldest definitive animals (Narbonne, 1998). One of the most intriguing aspects of the Neoproterozoic Era is the relationship between the severe global glaciations that characterized the middle part of this era (or ''snowball Earth''; Kirschvinck, 1992; Hoffman et al., 1998) and the subsequent early evolution of animals. Strata predating the final Neoproterozoic glaciations contain abundant cyanobacterial remains along with a few higher algae and other eukaryotes (Butterfield, 2000), but, with a few possible exceptions from slightly older and younger strata (e.g., Hofmann et al., 1990; Jensen et al., 1998), Ediacaran fossils first appear significantly above the last Neoproterozoic glacial deposits and disappear near the level of the first Cambrian-style shelly fossils. These temporal relationships have led some workers to hypothesize that the Neoproterozoic glaciations functioned as a bottleneck in eukaryote evolution and/or as an impetus for the subsequent radiation of animals (Hoffman et al., 1998; Runnegar, 2000). However, the scarcity of reliably dated Ediacaran fossil assemblages—coupled with the presence of a stratigraphic interval as thick as several kilometers between the highest Neoproterozoic tillites and the lowest definitive Ediacaran fossils in the thickest and best-studied sections—has hindered rigorous evaluation of the effects of the snowball glaciations on the early evolution of animals.

Precise U-Pb dates for the Ediacara biota range from 565 to 543 Ma (Martin et al., 2000). The oldest radiometrically dated Ediacaran assemblage anywhere is from the Avalon zone of Newfoundland (Fig. 1). Ediacaran fossils are abundant and diverse in the Mistaken Point Formation (Misra, 1969; Anderson, 1978; Anderson and Conway Morris, 1982; Seilacher, 1992; Clapham and Narbonne, 2002), which has yielded a date of 565 ± 3 Ma for a volcanic ash that covers the most fossiliferous surface near the top of the formation (Benus, 1988). The Mistaken Point assemblage contains a few cosmopolitan taxa such as *Charnia* and *Aspidella*, but most are endemic to eastern Newfoundland or are known only from Charnwood Forest in the Avalon zone of central England. No fossils have previously been reported from below the Mistaken Point Formation except for some problematic discoid structures from the upper Drook Formation (Anderson and Conway Morris, 1982; Landing et al., 1988). Our search for Ediacaran fossils lower in the succession has extended the stratigraphic record of unequivocal Ediacaran megafossils 1.5 km to the upper part of the Drook Formation. The Drook assemblage includes simple discoid and triangular fossils that will be discussed elsewhere, and two species of large fronds that form the basis of this report.

GEOLOGIC SETTING

The fossils are in the Avalon zone of southeastern Newfoundland (Fig. 1), which contains a 6 km succession of Neoproterozoic strata that records the transition from deep-water basin-plain and slope deposits in the Conception and St. John's Groups to coastal and alluvial deposits of the Signal Hill Group (Williams et al., 1985; Conway Mor-

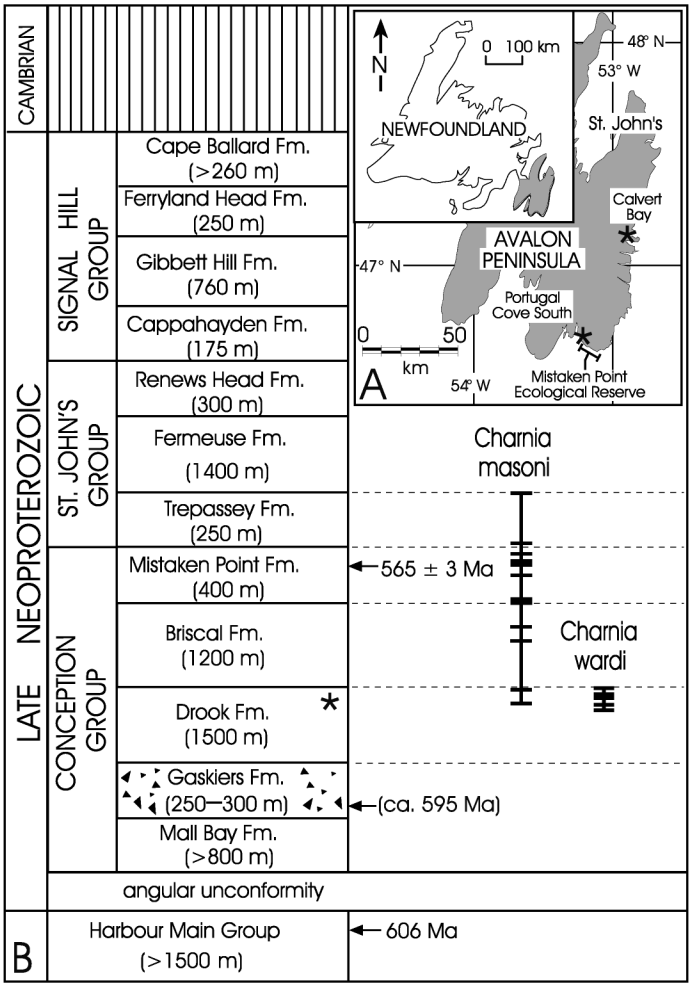

Figure 1. A: Map showing locations of upper Drook fossils (asterisks). B: Stratigraphic column showing Neoproterozoic stratigraphy of Avalon zone and stratigraphic position of new fossil discoveries in upper Drook Formation (asterisk), range and occurrences of species of *Charnia* in Newfoundland (vertical lines with bars), and available U-Pb dates.

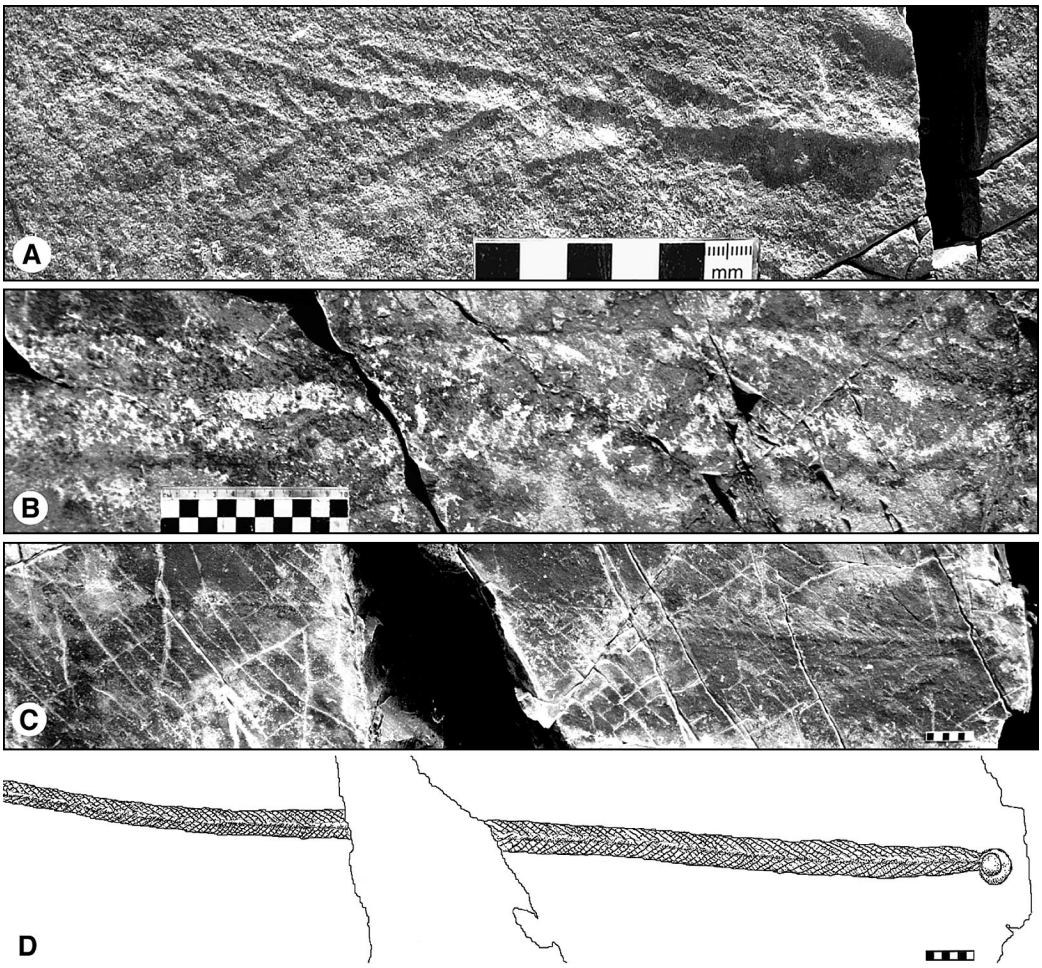

Figure 2. Field photographs of *Charnia* from upper Drook Formation near Portugal Cove South. All specimens are preserved in positive epirelief beneath volcanic ashes. Divisions on scale bars are in centimeters. A: *Charnia masoni*, ROM 54348. B: Detail of proximal part of largest specimen of *C. wardi* showing first- and second-order branch pattern. C: Proximal part of complete, 1.6-m-long frond of *C. wardi* with holdfast (far right) and good preservation of branches. ROM 54349. D: Line drawing of C illustrating details of holdfast and branch morphology.

ris, 1989; Myrow, 1995). This sedimentary succession is punctuated by the glaciogenic rocks of the Gaskiers Formation (Eyles and Eyles, 1989; Myrow and Kaufmann, 1999), which represent the highest evidence of Neoproterozoic glacial activity in the section. Strata of the Conception, St. John's, and Signal Hill Groups are unconformably overlain by Lower Cambrian and younger strata.

The greatest abundance of specimens is in coastal outcrops 3 km south of the village of Portugal Cove South (Fig. 1), where fossils are in strata continuous into the type section of the Drook Formation. Geologic mapping (Williams and King, 1979) and consistency of Conception Group stratigraphy over the Avalon Peninsula (Williams et al., 1985) confirm that new fossil occurrences are within the uppermost 300 m of the Drook Formation, ~1500 m below the classic Ediacaran fossils at Mistaken Point higher in the same section. Their location on outcrops within the Mistaken Point Ecological Reserve precludes collection, but replicas of specimens from Portugal Cove South are in the Royal Ontario Museum, Toronto (ROM).

The Drook fossils are ~1.5 km above the glaciomarine diamictites of the Gaskiers Formation (Fig. 1B). A maximum age is provided by a U-Pb date of 606 Ma (+3.7/−2.9 m.y.) in Harbour Main strata several kilometers below the Gaskiers Formation (Krogh et al., 1988). Long-standing lithostratigraphic correlation of the Avalonian successions of Boston Bay and Newfoundland is now supported by strikingly similar U-Pb dates both below and above tillites in the respective successions and by the presence of the Ediacaran fossil *Aspidella* above the tillites in both areas (Thomson and Bowring, 2000, their Fig. 7); the base of the Squantum Member diamictite of the Roxbury Formation, generally regarded as the correlative of the Gaskiers Formation in the Boston basin, is dated as 595.5 ± 2 Ma (Thomson and Bowring, 2000). Ongoing studies of volcanic ash beds throughout the succession may provide more precise radiometric data, but the position of the new Ediacaran fronds >1.5 km stratigraphically below the oldest dated Ediacaran fossils known anywhere (565 ± 3 Ma, Benus, 1988) implies a considerable range extension for the Ediacara biota.

FRONDOSE FOSSILS

Fronds occur at 10 stratigraphic levels throughout the uppermost 300 m of the Drook Formation near Portugal Cove South and one level at Calvert (Fig. 1). The fossils are preserved on the shaly tops of turbidite beds under volcanic ashes, a preservational style typical of the Mistaken Point assemblage (Seilacher, 1992; Narbonne, 1998). All fronds on any given bedding plane are strongly current aligned, implying that the fronds were tethered to the sea bottom and were in a prone position when they were covered by volcanic ash.

The Drook fronds (Figs. 2 and 3) are morphologically similar to *Charnia* in being parallel-sided fronds that taper to a swelling or small discoidal holdfast at their proximal end. All well-preserved Drook fronds also exhibit the two orders of branching microstructure diagnostic of *Charnia*—the primary order consists of nested, sigmoidal branches arranged in an alternate pattern about a midline; these are divided serially into rectangular second-order chambers. With the exception of *Glaessnerina*, which was subsequently referred to as *Charnia* (Runnegar, 1992), no other Ediacaran taxon has been described that consistently shows this shape or microstructure. Some specimens from the Drook Formation and throughout higher formations in the Avalon Peninsula (Fig. 1) show sporadic, fine, interfering ridges within the second-order chambers, but this feature appears to be taphonomic, reflecting preservation of the fusiform bodies as raised features on bed

Figure 3. Holotype of *Charnia wardi* from upper bedding surface in Drook Formation at Calvert. Specimen was whitened with ammonium chloride. Divisions on scale bar are in centimeters. ROM 38628.

tops rather than as the sole structures that are the typical preservation of *Charnia* elsewhere. Two distinct species can be recognized among the Drook specimens of *Charnia*.

Examples of the type species, *Charnia masoni* Ford, 1958, occur on four bedding planes near Portugal Cove South. Specimens of *C. masoni* in the Drook Formation (Fig. 2A) range from 45 to 300 mm in length and from 9 to 80 mm in width; their length is typically 3–5 times as long as their width. Microstructure consists of primary branches 5–12 mm wide that are divided serially into rectangular secondary divisions 3–5 mm long. These observations and values are well within the range of variation of *Charnia masoni*.

A new species of *Charnia* (Figs. 2B–2D, 3) is present at six stratigraphic levels in the upper Drook Formation near Portugal Cove South and at one level in Calvert. These fronds are the longest Ediacaran fossils known anywhere; specimens range to 1.85 m. The two orders of branching structure diagnostic of *Charnia* are clearly visible, but the extremely long and slender shape of these specimens characterizes a new species, *Charnia wardi*, which is formally defined in Appendix 1. *Charnia wardi* is thus far known only from the Drook Formation of southeastern Newfoundland and is the oldest complex Ediacaran fossil yet described anywhere.

Charnia masoni was first described from Charnwood Forest in central England (Ford, 1958) and subsequently was reported from the Mistaken Point Formation in Newfoundland (Anderson, 1978), the White Sea and Siberia in Russia (Fedonkin, 1990), and the Ediacara Member in Australia (Nedin and Jenkins, 1998). It is one of the most distinctive and cosmopolitan Ediacaran taxa and has become an index fossil for this biota. In the Avalon succession of Newfoundland, *Charnia masoni* ranges through nearly 2000 m of strata to near the top of the Trepassey Formation (Fig. 1B). This great stratigraphic thickness implies a long time range, a view supported by chemostratigraphic correlations and available radiometric dates (Kaufman et al., 1997; Martin et al., 2000), which suggest that *Charnia masoni* persisted for ~30 m.y. of Neoproterozoic time, the longest stratigraphic range known for any Ediacaran taxon.

Charnia was originally interpreted as a macrophytic alga (Ford, 1958), but morphologic features and the common occurrence of in situ *Charnia* in deep-water settings (Glaessner, 1984; Jenkins, 1985; Clapham and Narbonne, 2002) are not consistent with this interpretation. Numerous interpretations of the affinities of the Ediacara biota have been proposed, but most workers have regarded *Charnia* as a pennatulacean Cnidarian (Glaessner, 1984; Jenkins, 1985) or as a representative of an extinct high-order taxonomic group (Seilacher, 1992).

CONCLUSIONS

The oldest reliably dated Ediacaran fossils known anywhere are from the Mistaken Point Formation (565 ± 3 Ma) of eastern Newfoundland. Our discovery of specimens of the Ediacaran index fossil *Charnia* in strata of the Drook Formation extends the known range of the Ediacara biota >1.5 km below this level. The Drook specimens of *Charnia* range to nearly 2 m in length and exhibit consistent morphology among specimens; the fossils show clear differentiation into a holdfast and a frond and two orders of serial subdivision into regular branches and chambers. They probably represent the oldest large, morphologically complex fossils known anywhere.

The size and complexity of the Drook fronds imply that, despite their age, the origin of the Ediacara biota and other animals must considerably predate even this early occurrence. This has significant implications for evolutionary scenarios that link Neoproterozoic glaciations and the early evolution of animals. If the Gaskiers tillite represents a Marinoan glaciation (sensu Kennedy et al., 1998), then, assuming an age of 595 Ma for the beginning of the Gaskiers glaciation (Thomson and Bowring, 2000) and a likely duration of ~10 m.y. for the Marinoan glaciation (Hoffman et al., 1998), these fossils may postdate the end of the Marinoan glaciation by as little as 10 m.y. This implies either that evolution proceeded at a rapid rate, perhaps as fast as the early Tertiary radiation of mammals, or that *Charnia* and perhaps other clades of Ediacaran organisms evolved before the terminal Neoproterozoic glaciation and passed unscathed through the evolutionary bottleneck of the snowball Earth. Alternatively, the low stratigraphic position of the Drook fronds above the Gaskiers tillite, coupled with the distinctive and apparently unique cap carbonate that overlies this tillite (Myrow and Kaufman, 1999), may provide further evidence for chemostratigraphic (Kaufman et al., 1997), geochronologic (Brasier et al., 2000; Barfod et al., 2002), and micropaleontological (Knoll, 2000) suggestions of a regional North Atlantic glaciation that postdated the global Marinoan glaciation of the snowball Earth and that may have significantly influenced the early evolution of animals.

APPENDIX 1. SYSTEMATIC PALEONTOLOGY

Genus—*Charnia* Ford, 1958.
Type species—*Charnia masoni* Ford, 1958.
Charnia wardi sp. nov.

Type Specimen and Locality. ROM 38628 (Figs. 2B–2D, 3) is from coastal outcrops of the Drook Formation at Calvert, Newfoundland (Fig. 1). This specimen was discovered by M.M. Anderson and was figured, without stratigraphic or locality data, in a compendium of Ediacaran fossils as a ''pennatulacean'' (Fig. 4 of Anderson, 1978).

Diagnosis. This very long, slender *Charnia*, has linear parallel margins and a length/width ratio of >10.

Description. Nine well-preserved specimens (Figs. 2B–2D, 3), along with numerous poorly preserved ''straps'' showing the same shape and dimensions but mostly or completely lacking the distinctive microstructure, are present. The relief of the frond above the mudstone surface ranges from 1 to 8 mm and is directly proportional to the thickness of the overlying ash; however, the thickest ashes in the Drook Formation tend to be the coarsest, so microstructure is poorly preserved or absent on most high-relief specimens. A complete gradation exists between high-relief specimens under thick crystal tuffs that typically show a median groove and flattened specimens under thin ashes that typically show a median ridge. Fronds are parallel sided with sharp, linear outer margins; they are 35–70 mm wide and to 185 cm long, and have a length/width ratio >10. Fronds taper distally to a point (Fig. 3) and taper proximally to a 2–7-cm-diameter circular holdfast (Figs. 2C and 2D) that may represent the top of a larger structure buried in the substrate. Two orders of microstructure are present on the fronds. The primary order consists of nested, sigmoidal branches 6–12 mm wide arranged in an alternate pattern about a midline; these are divided serially into rectangular second-order chambers 3–6 mm wide.

Etymology. The species name honors the Ward family of Portugal Cove South—Katherine, Eugene, Bradley, and Krista—who have greatly assisted our work on the Mistaken Point fossils and have been tireless guardians of their town's fossil heritage.

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