Journal of the Geological Society, London, Vol. **164**, 2007, pp. 49–51. Printed in Great Britain.

SPECIAL

Charnia and sea pens are poles apart

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***Charnia* from the Ediacara biota is here examined in terms of its growth and development. The Ediacara biota comes from the critical period of evolution just before the Cambrian Explosion and is key to our understanding of the origin of animal life. We show that *Charnia* cannot be related to the modern cnidarian group the sea pens (Pennatulacea) with which it has for so long been compared, as generative zones cannot be homologized between these forms.**

The Precambrian Ediacara biota (Ford 1958), which immediately predates the Cambrian Explosion, is critical to understanding the origin of animal life. The classic interpretation of this biota has been that it contains the precursors of cnidarians, arthropods and annelids, and possibly also echinoderms (Glaessner 1984; Gehling 1991) and molluscs (Fedonkin & Waggoner 1997). This paradigm was challenged by arguments that these fossils belong to an extinct 'phylum,' the Vendobionta (Seilacher 1984, 1985, 1989, 1992). The problem of distinguishing between these two main positions over the last 20 years is one reason why the Ediacara biota has developed into an icon within modern palaeontology. Arguably, until an approach is presented to resolve this stalemate, the Ediacara biota will remain one of the major pieces missing from the puzzle that is the history of life (Brasier & Antcliffe 2004).

The longest ranging genus of the newly defined Ediacaran Period (Knoll *et al*. 2004) is *Charnia*. This fern-like impression has usually been classified (along with its presumed close ally *Charniodiscus*) with the similar-looking sea pens (pennatulaceans, a derived group of octocorals) (Glaessner 1984; Gehling 1991). The latter, extant colonial cnidarians (Verrill 1865; von Kölliker 1880; Kükenthal 1915; Williams 1995) have, however, no undisputed fossil record until the Jurassic (see Williams 1997, who therefore questioned their affinities to the Ediacara biota), thus implying a minimum gap in the fossil record of 350 Ma, assuming faithful representatives of their group within the Ediacaran Period. Furthermore, their direct ancestors, the alcyonaceans, have no clear record before the Silurian (Lindstrom 1978; Bengtson 1981). Here we test the relationship between modern sea pens and fossil *Charnia* that is central to the classic interpretation of the frondose Ediacara biota. Given that mode of growth is one of the most robust features that can be decoded from fossil organisms, we here explore its potential for the diagnosis of enigmatic fossil groups.

Extant sea pens (Fig. 1a) have feeding zooids on polyp leaves either side of a central stem that anchors to the sediment. Although this is reminiscent of Precambrian *Charnia* (Fig. 1b), the presence of polyp leaves is a relatively recent (possibly Tertiary) addition to sea pen morphology (Williams 1997), and most sea pens do not display this critical feature. From a study of extant sea pen ontogeny (using material from the Darwin Centre, Natural History Museum, London, UK) those forms with

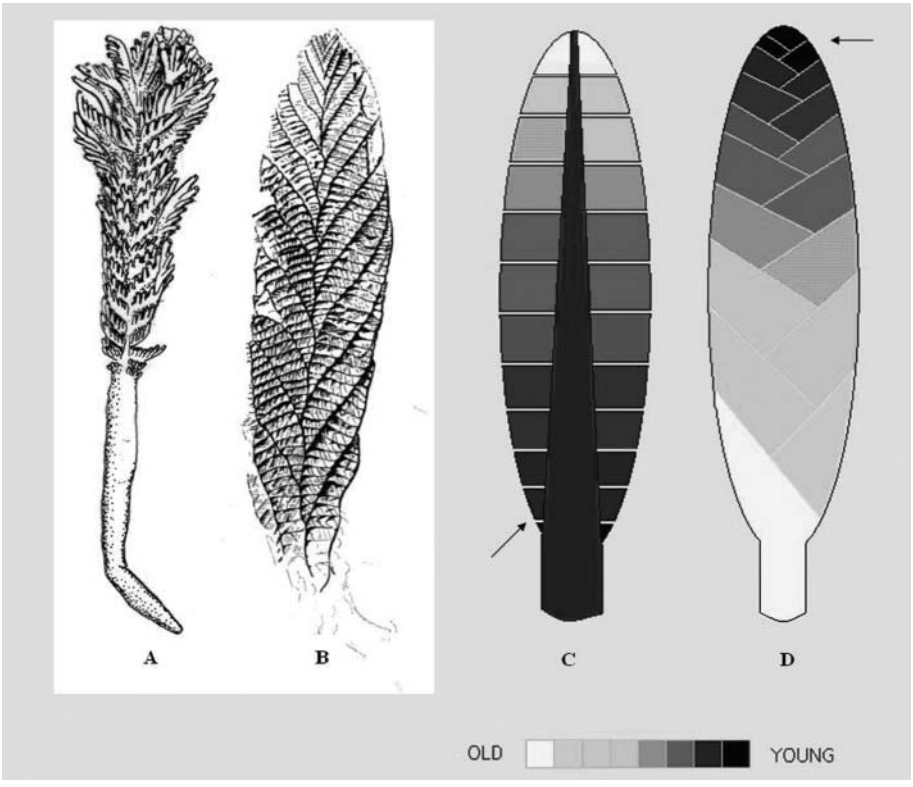


Fig. 1. New reconstructions of *Pennatula phosphorea* (**a**) from the Darwin Centre, Natural History Museum (specimen number 1888-3-1-1-6) and *Charnia masoni* holotype (**b**) from the Leicester City Museum. Specimens are 8 cm and 26 cm long, respectively. New growth schematics for the Pennatulacea (**c**) show insertion of new elements at the base and their thickening towards the apex of the frond, in contrast to Charniids (**d**), where insertion of new elements occurs at the apex of the frond.

polyp leaves show a growth polarity that is basal, with leaf insertion at the base of the rachis (see Fig. 1a). We compare this with the holotype (Fig. 2) and related specimens of *Charnia* from 565–550 Ma rocks from England and Newfoundland. The best preserved *Charnia* show the largest branches at the base of the frond, becoming smaller towards the tip, a feature that can also be seen in related forms such as *Bradgatia* and *Charniodiscus*, which have been observed by many workers to share a fundamentally similar construction (Seilacher 1989; Brasier & Antcliffe 2004; Narbonne 2004).

These new data show that growth patterns in modern sea pens and Precambrian *Charnia* differ in fundamental ways. The crucial point, as illustrated by Figure 1, is that new segments are added at the base of the frond in sea pens, but at the apex in *Charnia*. The growth mode of sea pens is thus one of segments added at the base of the frond, which move up the creature in a conveyor-belt fashion as segments are added below (Fig. 1c). The reverse polarity, with segments added at the apex, is true in *Charnia* (Fig. 1d). Thus our highly weighted feature, the generative zone, cannot be homologized between *Charnia* and sea pens. We take this to imply that it is most unlikely that *Charnia* was a sea pen. This new method of analysing growth indicates that the frondose Ediacara biota was unique (Seilacher 1989) and not the direct Precambrian representative of modern groups (Glaessner 1984).

This is not the end of the matter because putative analogues for *Charnia* and *Charniodiscus* continue to be postulated. For example, *Stromatoveris* (Fig. 3; Shu *et al*. 2006), a suggested ctenophore from the early Cambrian of Chenjiang, has recently been placed alongside the Precambrian 'Charniomorpha'. However, true charniomorph fronds from the UK, Canada and Australia (Brasier & Antcliffe 2004; Narbonne 2004) show the following diagnostic features, absent in *Stromatoveris* (compare Figs 1b and 2): a glide plane of symmetry; similar upper and lower surfaces; a holdfast. In contrast, *Stromatoveris* shows the following features, absent in true 'Charniomorpha': a central space; a central axis; distinct upper and lower surfaces; interbranch connections. If affinities between modern and enigmatic fossil groups are to be put forward and sustained, then we recommend that developmental homologies between them be demonstrated. We argue above that the hypothesis of pennatulacean affinities can no longer be maintained for this reason. A similar caution should now be applied to all other mooted affinities for the Ediacara biota, including the recent *Stromatoveris* claim.

Thanks go to M. Evans (Leicester City Museum), S. Halsey (Darwin Centre, Natural History Museum), M. Harrison (Bradgate Park Trust) and



Fig. 2. *Charnia masoni*(holotype) from the Leicester City Museum; specimen is 26 cm long. *Pennatula phosphorea* from the Darwin Centre, Natural History Museum (specimen number 1888-3-1-1-6); specimen is 8 cm long.

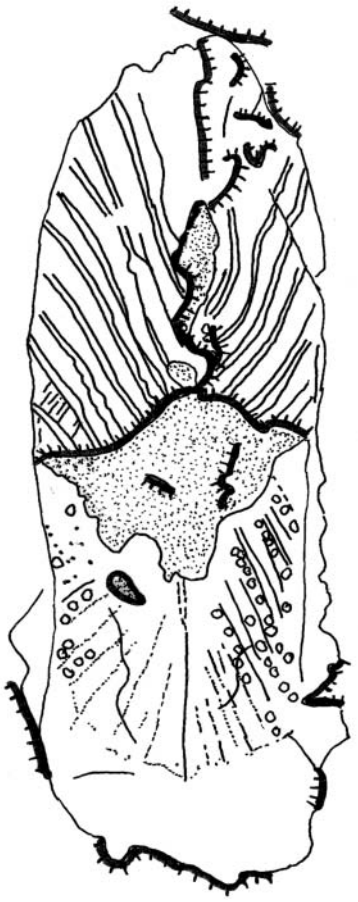


Fig. 3. A reconstruction of *Stromatoveris*, modified from Shu *et al*. (2006), illustrating features discussed in the text, in contrast to features seen in 'charniomorph' specimens.

O. Green (Department of Earth Sciences, University of Oxford). We are grateful for the very helpful feedback on the manuscript provided by D. McIlroy (Memorial University, Newfoundland) and G. C. Williams.

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Received 6 June 2006; revised typescript accepted 10 October 2006.
Scientific editing by Duncan McIlroy