

Ediacaria booleyi: weeded from the Garden of Ediacara?

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Abstract: Sole markings from the Upper Cambrian Booley Bay Formation at Booley Bay, Co. Wexford, Ireland, previously described as the Ediacaran-type fossil *Ediacaria booleyi* appear to possess a number of morphological characteristics which are not consistent with assignment to the genus *Ediacaria*, nor any other known Ediacaran taxon. An inorganic origin for the structures has been proposed by several workers; we tentatively consider them to be at least in part organic, and are currently working to evaluate this hypothesis critically. If organic, the organisms must have had a density similar to that of the sediment in which they were emplaced, and to survive the transport process, they must have had a rigid integument. Neither of these properties appears to be consistent with an interpretation as an Ediacaran-type organism. We suggest here that the Booley Bay specimens should be removed from the genus *Ediacaria*. If *Ediacaria booleyi* is not related to known Ediacaran organisms, this would remove a key aspect of the argument against a mass extinction at the Precambrian/Cambrian boundary.

Theories about the demise of the Ediacaran biota have generally centred around concepts of physical or biomechanical shortcomings in the face of competition from newly evolving and diversifying metazoan phyla or an inability to adapt to changing environments in the Early Cambrian (e.g. Dzik 2005). Such ideas have led to the Ediacaran biota being described as a failed evolutionary experiment (e.g. Narbonne 1998). The general paucity of Ediacaran-type fossils in rocks of Early Cambrian and younger age seems to support this idea and has been considered indirect evidence for a Terminal Neoproterozoic mass extinction (Seilacher 1984). This event could have wiped out entire Precambrian ecosystems with trophic structures unlike any modern day marine food chains. However, evidence of Ediacaran-type organisms in rocks younger than latest Precambrian might indicate that this is not the case. The presence of fossils of Ediacaran aspect across the Precambrian–Cambrian boundary might instead suggest that these enigmatic organisms did not go extinct simultaneously in a mass extinction event, but perhaps were already in gradual decline: they simply dwindled out during the earliest Phanerozoic. Such an argument appears to be supported by just such an Ediacaran-type biota from Booley Bay in Co. Wexford, Ireland (Crimes *et al.* 1995) (Fig. 1). Dated to the latter part of the Late Cambrian by acritarch biostratigraphy (Moczydlowska & Crimes 1995), it has been remarked that this occurrence ‘may well be the

death knell for the idea that the Ediacara fauna was a failed evolutionary experiment’ (Palmer 1996, p. 114). The Booley Bay locality, in the Avalon Terrane of south-eastern Ireland, is unusual for not only its age, but also in the way fossils are preserved. Organisms appear to have been transported downslope into a deep marine environment by turbidity currents, impacted into the underlying mud, and there decayed, leaving casts which were then infilled by sand (Crimes *et al.* 1995) (Fig. 2). Similar preservation has not been observed in any other Ediacaran fossil locality to date. Given the significance of this site, a thorough reinvestigation of the sedimentology, palaeoenvironments and palaeontology has been in progress since March 2003. This paper presents initial results and sets out targets and aims currently being pursued.

Sedimentological setting

The first detailed work on the Lower Palaeozoic geology of the Booley Bay area was undertaken by Gardiner (1967), who established the stratigraphic succession. He assigned the pre-Ordovician rocks of the area to the Booley Bay Formation and recognized six distinctive lithofacies (Table 1).

The Booley Bay section is dominated by Facies C, but also contains elements of Facies A and E. Sole structures are common, and in particular Gardiner (1967) noted the presence of ‘bulbous

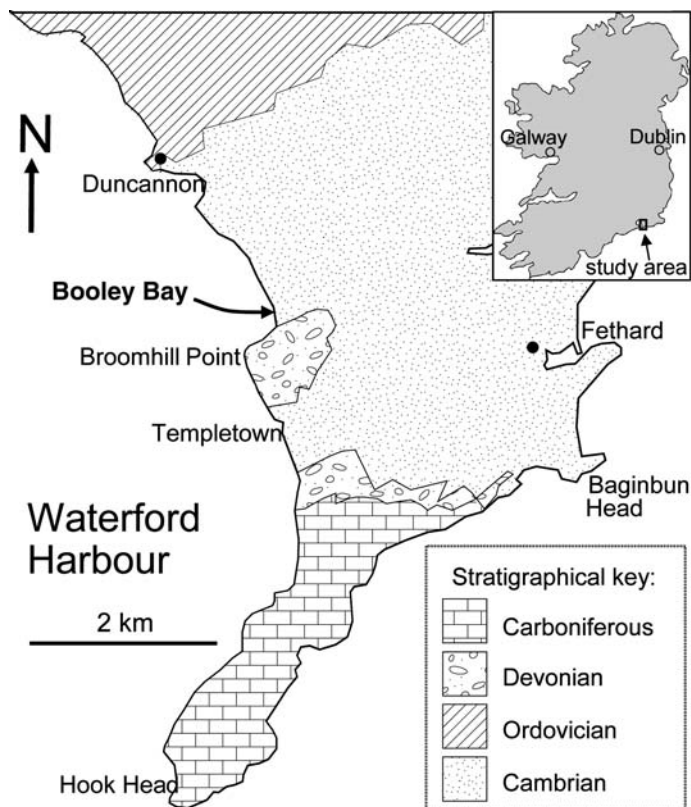


Fig. 1. Location of the study area, with regional geology.

flute moulds' and 'V-shaped flute moulds', which occurred only in Booley Bay. No body fossils were recorded from the formation. (Crimes *et al.* 1995) re-described several of these sole structures from Booley Bay as Ediacaran-type fossils. Two genera were reported, *Ediacaria* and *Nimbria*, both discoidal in shape.

The sediments in which these structures occur are thin to medium, repetitively interbedded siltstones and mudstones. Siltstone beds are generally 1–10 cm thick; mudstone beds are generally similar in thickness, but metre-scale mudstone units also occur (Facies A of Gardiner 1967). Bedding is generally tabular and laterally continuous over several tens of metres (the scale of the outcrop) and is overturned, dipping at an angle of approximately 45°, exposing the soles. The sediments were interpreted by Gardiner (1967) as distal turbidites, and all subsequent workers have closely followed this interpretation (e.g. Tietzsch-Tyler *et al.* 1994). Sole structures visible in the section include gutter casts (Fig. 3a) and flute marks (Fig. 3b), which indicate a unidirectional palaeocurrent flowing to the west. This is supported

to some extent by ripple cross-lamination (Fig. 4a). Present-day strike is approximately parallel to this direction. Hummocky-like bedding surfaces are present in some parts of the section (Fig. 4b); whilst these could be interpreted as 'hummocky cross-stratification' often associated with forming above storm wave base, there is a greater bulk of surrounding field evidence to suggest that they represent sub-critical flow in the turbidity current during emplacement. Interestingly, this flow regime is best developed in the most fossiliferous parts of the section and thus may have played a role in fossil preservation. Many beds also show evidence of liquefaction and convolution, perhaps indicating a tectonically active setting (Fig. 4c).

Structures similar to those described elsewhere (e.g. Hagadorn & Bottjer 1997; Gehling 1999) as microbially influenced sedimentary structures (for example 'wrinkle marks') are common in the section. These are currently under investigation by S. Burke and P. Orr of University College Dublin (Burke & Orr 2004, 2005), and thus will not be discussed further herein. Microbial mats have been proposed to assist in the preservation of Ediacaran

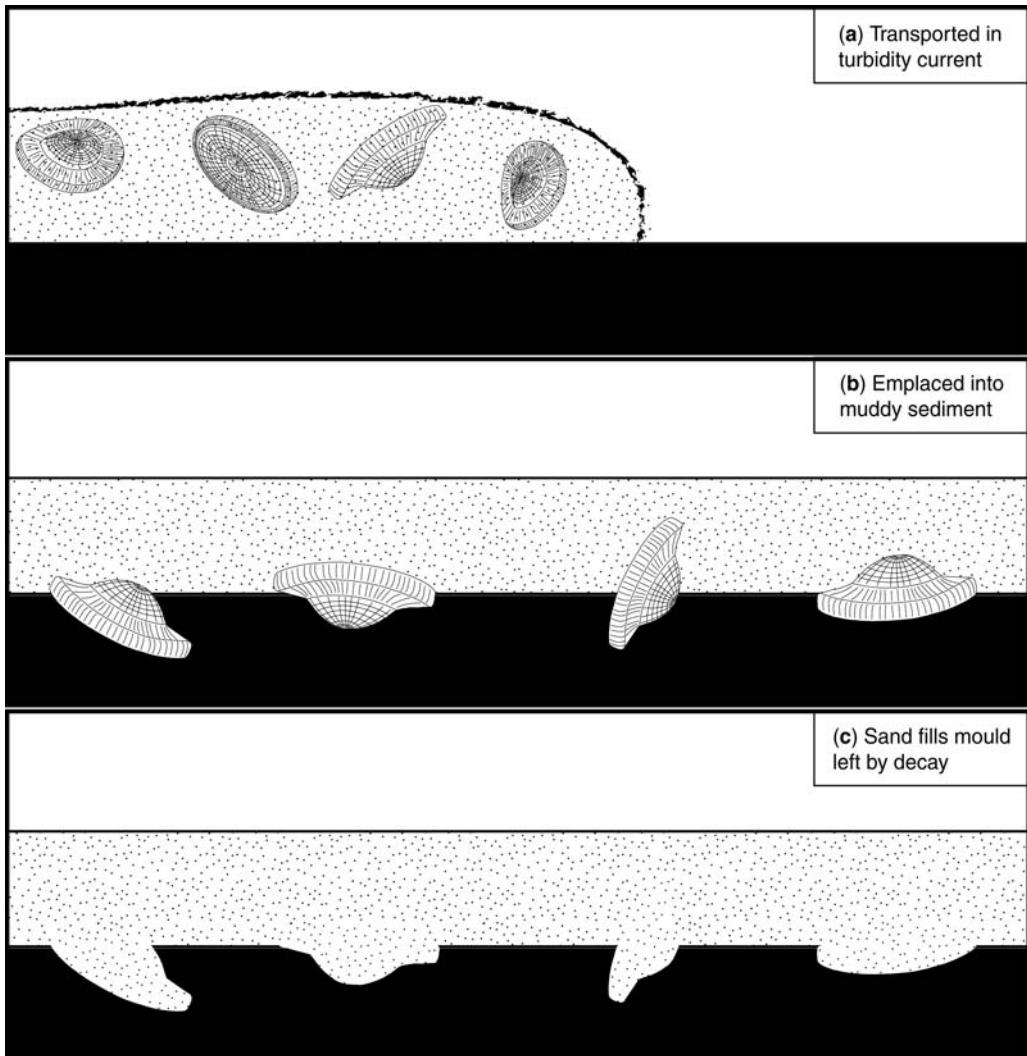


Fig. 2. Taphonomic model for *E. booleyi* proposed by Crimes *et al.* (1995).

fossils (Gehling 1999) and so their presence at Booley Bay might have facilitated Ediacaran-style preservation to occur. However, microbial binding of soft sediment may also have helped form and retain some of the clear sedimentary structures present in the section.

Ediacaria booleyi

Specimens of the discoidal Ediacaran fossil *Ediacaria* were first reported from the Booley Bay Formation at Booley Bay, SE Ireland by (Crimes *et al.* 1995); these were assigned to a new species, *E. booleyi*. As diagnosed, the new species differed quite considerably from the type species,

E. flindersi. Aside from superficial variations in external ornamentation, the specimens of *E. booleyi* were preserved as three-dimensional positive hyporelief casts on the bases of siltstone beds overlying dark mudstone layers. This led (Crimes *et al.* 1995) to propose that it must have been in possession of a rigid exoskeleton to allow appreciable sediment penetration. This presented an intriguing reconstruction and interpretation for the specimens. Perhaps here in the Late Cambrian were the last vestiges of a once widespread biota forced to live in deeper water due to competition from newly evolved metazoans exploiting shallow shelf environments. Marginalization and competitive pressure may also have been responsible for these

Table 1. *Facies elements of the Booley Bay Formation, as described by Gardiner (1967)*

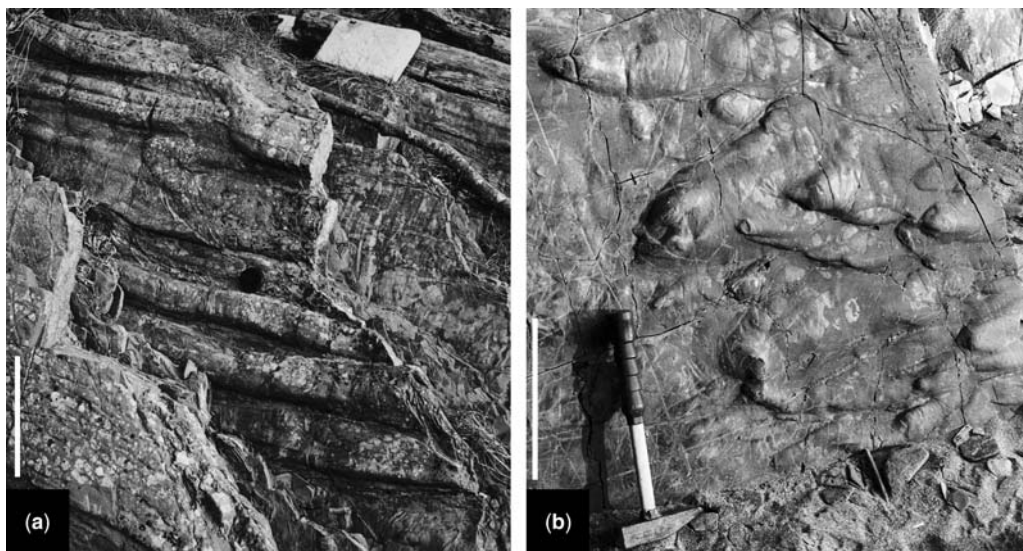
	Description
Facies A	Black shales
Facies B	Banded shales
Facies C	Siltstone-shale cycles with widespread sole structures
Facies D	Sandstone-shale cycles
Facies E	Siltstone-shale cycles with sparse sole structures
Facies F	Conglomerates

organisms constructing some form of rigid test, a characteristic rare in the Ediacaran period.

Two hundred and ten specimens on twelve different surfaces have now been examined as part of this study; isolated specimens on these surfaces have not been measured due in most cases to their inaccessible location high on steeply dipping beds. Two additional surfaces are separated from the main outcrop and may represent repetition of other stratigraphic levels: specimens on these have not been measured due to inaccessibility. It should be noted that most of these specimens were probably not observed by Crimes *et al.* (1995), who reported 27 measurable and several partial specimens on seven surfaces. We must also note that due to the fractured nature of the outcrop, collection of specimens risks severe damage: all specimens

described herein were examined (and remain) in their natural exposure.

The basic morphology of *E. booleyi* was originally reconstructed (Crimes *et al.* 1995) to be circular in overall plan, although a full circle has never yet been seen in outcrop (see below). Even specimens preserved sub-parallel with the bedding surface are preserved as a semicircle, which may cast doubt on the notion that these structures were originally totally discoidal in outline. A range of direction and angle of protrusion (these terms are clarified in Fig. 5) from the bed sole is observed in all forms. The angle of protrusion varies from 0° to about 55°, but both mean and modal values are approximately 20°. A χ^2 -test on the direction of protrusion of all 210 measured specimens (using 30° divisions), with a null hypothesis of random orientation, can be rejected at a significance level of $p < 0.01$. The vector mean of the direction of protrusion is 347.9°. This is broadly similar to palaeocurrent direction, perhaps indicating that this had a strong influence on orientation. Similar tests on the most populous surface, which has 89 measured specimens, also reject the null hypothesis of random orientation at $p < 0.01$, and produce a vector mean direction of protrusion of 345.0°. This is similar enough to the results for all measured specimens to confirm that the overall values are not an artefact of averaging over twelve different surfaces (Fig. 6). Statistical analysis and interpretation of this data is continuing. One well-exposed bedding surface in Booley Bay demonstrates clearly that in some instances these structures are

**Fig. 3.** Sole structures in the Booley Bay Formation: (a) Gutter casts; (b) Flute casts. Both scale bars 250 mm.

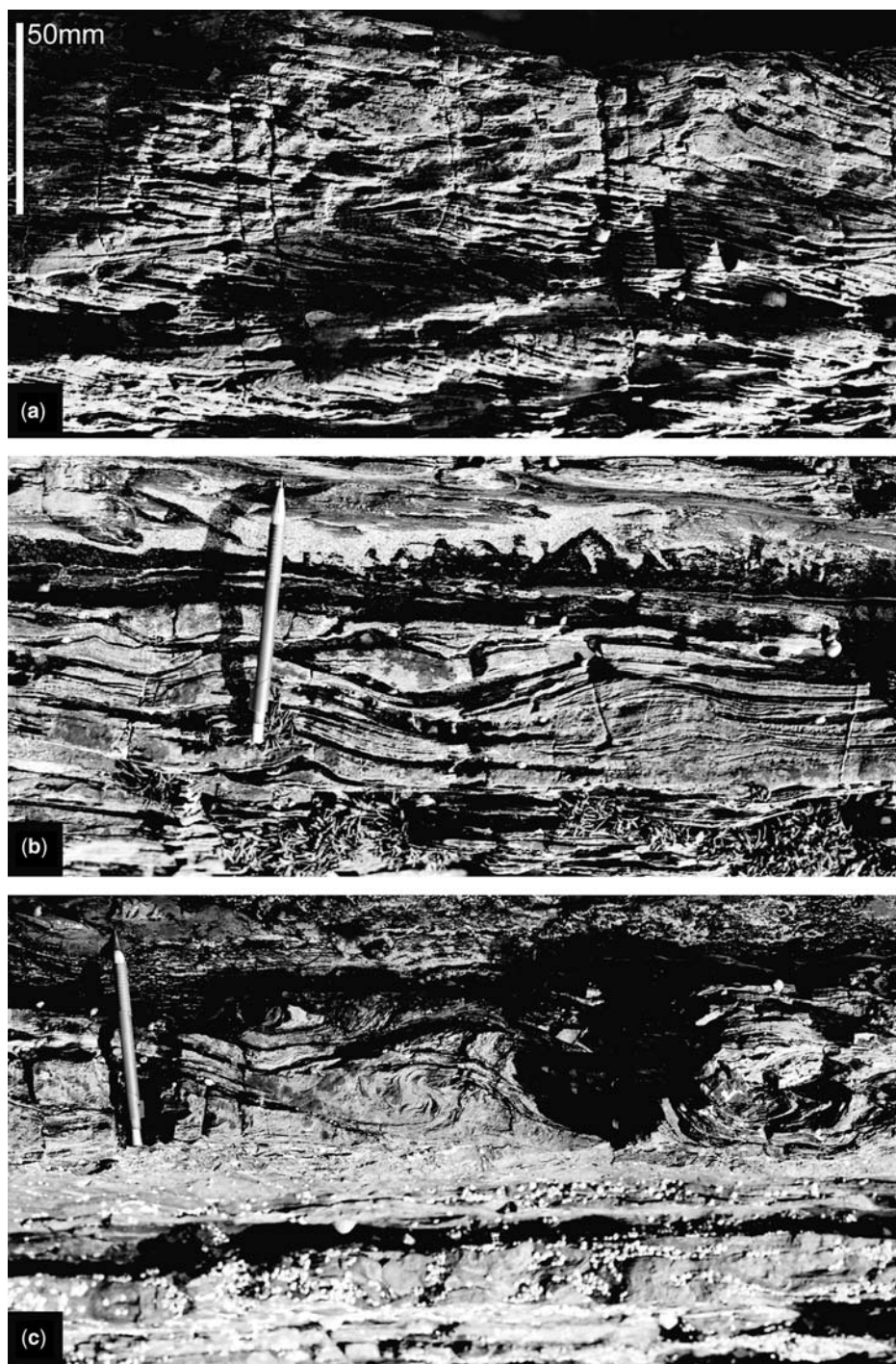


Fig. 4. Sedimentary lamination in the Booley Bay Formation: (a) Cross-lamination; (b) Hummocky-like lamination; (c) Convolute lamination. Pencil in b and c is 15 cm long. All 3 photographs have been inverted to show features in the correct stratigraphic orientation.

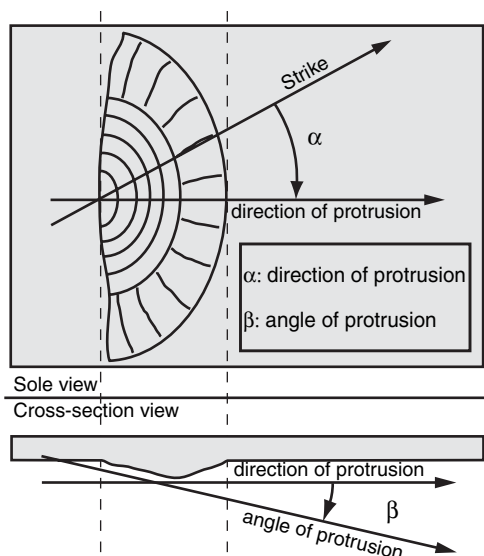


Fig. 5. Definition of terms used in the text.

grouped into palaeocurrent parallel zones or bands (Fig. 7).

In terms of size (Fig. 6), the structures range from 5–200 mm in radius. The mean radius of the measured specimens was 42 mm, with a modal value of 25 mm. Several different morphological variations are seen, which may cast doubt on the idea that the specimens referred to *E. booleyi* all belong to the same genus or species, even if these structures are biogenic. However, taphonomic preservational variation may play as large a part as original morphological disparity in distinguishing these forms. Several representative specimens are described below to illustrate these variations.

As stated above, despite initial interpretations of *E. booleyi* as being the imprints of originally disc-shaped organisms, not much more than half of each disc is ever observed in outcrop. The outer surfaces on the exposed side can be covered by a very fine concentric ornament. Depending on the original composition of the test this ornament may represent growth lamellae. Several specimens display this quite well, including the 'ventral side' holotype of Crimes *et al.* (1995, plate 6C), which has only very slight relief from the bed sole. A second specimen (Fig. 8) has a concentric ornament consisting of ridges of 1 mm in thickness, spacing and relief. It also has a raised annular band (with radius approximately half the total radius) about 1 cm thick, with crudely radial elongate depressions of thickness and relief both approximately 1 mm, spaced irregularly at about 2–3 mm intervals. One possible explanation for this form is that it may represent a 'swing mark' or 'scratch circle' (Jensen *et al.* 2002). However, in other specimens (Fig. 9),

it can be seen that the concentric ornament is not truly circular, but rather ovoid in outline. This presents obvious problems for it to have been generated by rotation of a rigid body, fixed at a central point, over the surface of the sediment, as is the case with swing marks. Elongation from tectonic strain cannot, however, be definitively ruled out at this stage. Analogue modelling is currently being undertaken by us to critically evaluate this hypothesis.

Some specimens display a combination of concentric and radial ornament, the radial aspect of which is quite variably developed. It has been suggested that forms displaying stronger concentric lamination in the centre, with radial ornament developed towards the outer edges of the discs (Fig. 10) may represent the dorsal side of specimens (Crimes *et al.* 1995, plate 3). The specimen in Figure 10a clearly shows both radial and concentric ornament, the relief of which is less than 1 mm. Spacing of the ornament is irregular, and in the case of the concentric ridges, which are less than 1 mm thick, the spacing is clearly greater parallel to, rather than perpendicular to, strike (horizontal in the photographs). Other specimens show a contradictory spacing pattern, perhaps indicating that this is an original character, rather than due to, for example, later deformation, although deformation of a soft-body is also a possibility.

Other forms display a much stronger and pervasively developed radial ornament. The specimen in Figure 11 displays quite a coarse radial ornament, which extends in an irregular fashion across the entire surface of the half disc. This appears to superimpose an underlying fainter, but conspicuous and regular, concentric ornamentation. The specimen in Figure 12 has a total radius of approximately 5 cm, with a central disc of radius approximately 1.5 cm. This central disc exhibits a faint concentric ornament of minuscule relief. An irregular, approximately radial ornament extends from the margin of the central disc to the outer margin. This is reminiscent of specimens from the Holy Cross Mountains in Poland originally described as *Medusites*, reclassified as a new genus and species *Brzechowia brzechowiensis*, and eventually redescribed as *Velumbrella czarnockii* (Stasinska 1960). Conway Morris (1993) compared these fossils with the rotascids and *Eldonia*, and all of these were included in Class Discophylla by Friend (1995). However, even in the best similar specimen from Booley Bay, only about half of the disc is preserved (poorly), and the ornament is not as regular as the structure of *Velumbrella*.

Many of the specimens examined in this study possessed essentially an inner zone dominated by a concentric ornament of fine rings, which is seen to pass abruptly into an outer area, which is flared or crudely radial (Fig. 13). This outer flared zone,

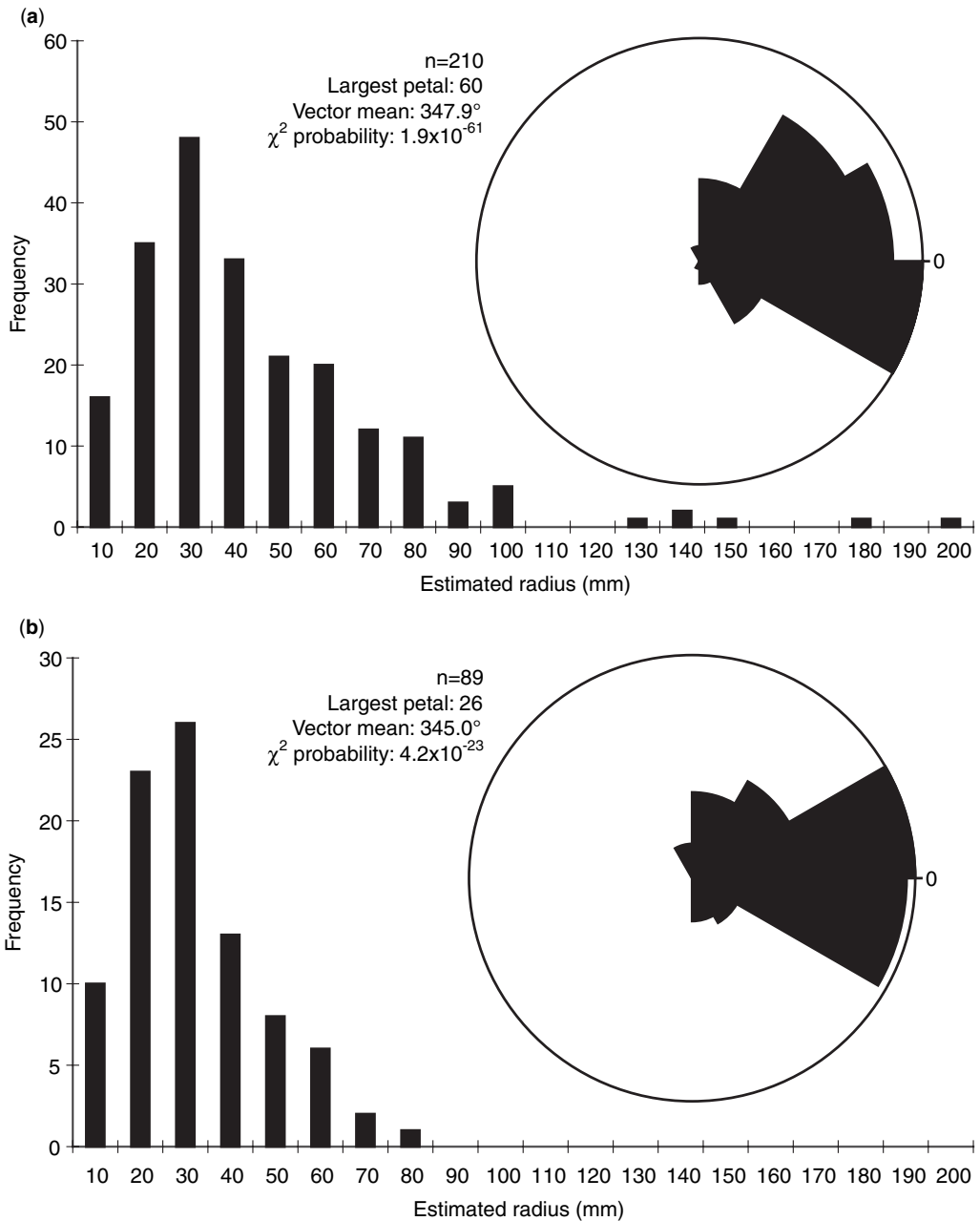


Fig. 6. Size (bar graph) and orientation (rose diagram) data for (a) all measured specimens; (b) the most populous surface. Statistical text on the figure refers to the rose diagrams.

often only very subtly developed, displays no semblance of systematic skeletal or biological organisation and it is difficult to reconcile with it being part of an outer rigid test. As common as this feature is, it was never fully incorporated in the original reconstruction by Crimes *et al.* (1995). It may represent an outer zone of soft tissue, however again this is

extremely difficult to establish. An alternative is that it may well represent drag marks of the discs drawing down onto the sediment along the leading edge. This is a possibility for the small specimen figured in Figure 13b; here the outer radial zone is seen to inflect at an angle of approximately 110–120° to the plane of the half disc. The

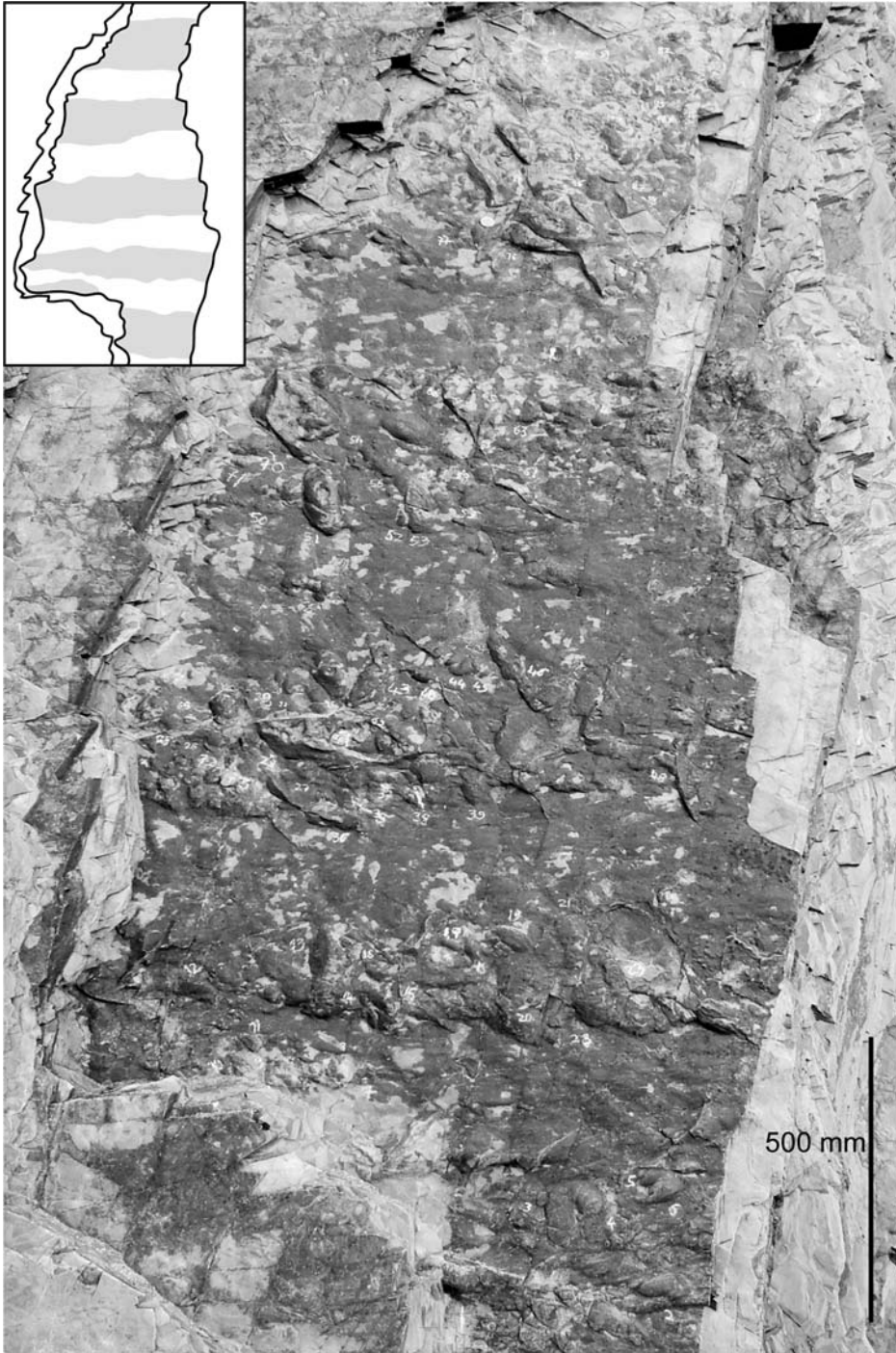


Fig. 7. Fossils in palaeocurrent parallel bands (shaded on inset) on bed sole.

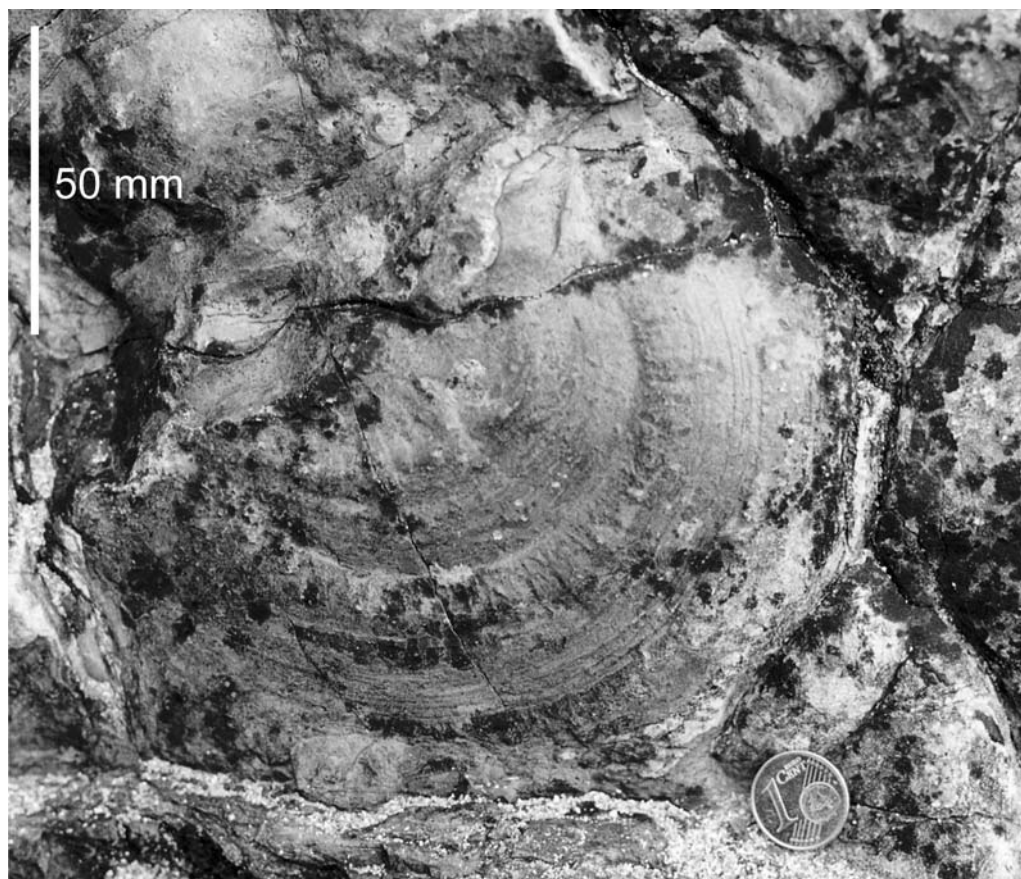


Fig. 8. Specimen exhibiting well-defined concentric structures.

specimen illustrated in Figure 13a also displays a set of curved lineations restricted to the upper portion of the visible disc, which are concentrically stacked and preserved in strong hyporelief. If considered part of the original organism then they may represent tentaculate processes along the periphery. However, they pass rapidly into a flared periphery lower down, and have not been observed in any other specimen examined to date. A more plausible explanation is that they represent systematic excavation of sorts, perhaps post mortem grazing by an unknown organism.

Other problematic structures

Smaller circular sole markings described by Crimes *et al.* (1995) as *Nimbia occlusa* Fedonkin 1980 occur on many beds at Booley Bay but are particularly common on three surfaces. These structures are circular to oval rings of diameter 2–8 mm, often with a central peak, occurring in positive hyporelief (Fig. 14). Whole and partial rings both

commonly occur. Originally interpreted by (Crimes *et al.* 1995) as the impressions of ringed discs, these have subsequently been reinterpreted as swing marks by Jensen *et al.* (2002).

Another distinctive kind of structure, which occurs in positive hyporelief in the sequence, apparently in direct association with fabrics of microbial origin, is a series of sub-parallel ridges radiating from a slope. These appear similar to structures from the Arumbera Sandstone of Central Australia described by Glaessner & Walter (1975) as the Ediacaran-type fossil '*Arumberia banksi*', which has subsequently been reported from the Urals (Bekker 1980, 1990), China (Wang *et al.* 1984), France, Newfoundland and the Channel Islands (Bland 1984), the White Sea region of Russia (Grazhdankin 2004), and Britain (Bland 1984; McIlroy *et al.* 2005). Brasier (1979), however, suggested that these were inorganic structures, and McIlroy & Walter (1997), noting similarities between forms assigned to '*Arumberia*' and flute marks generated experimentally by Allen

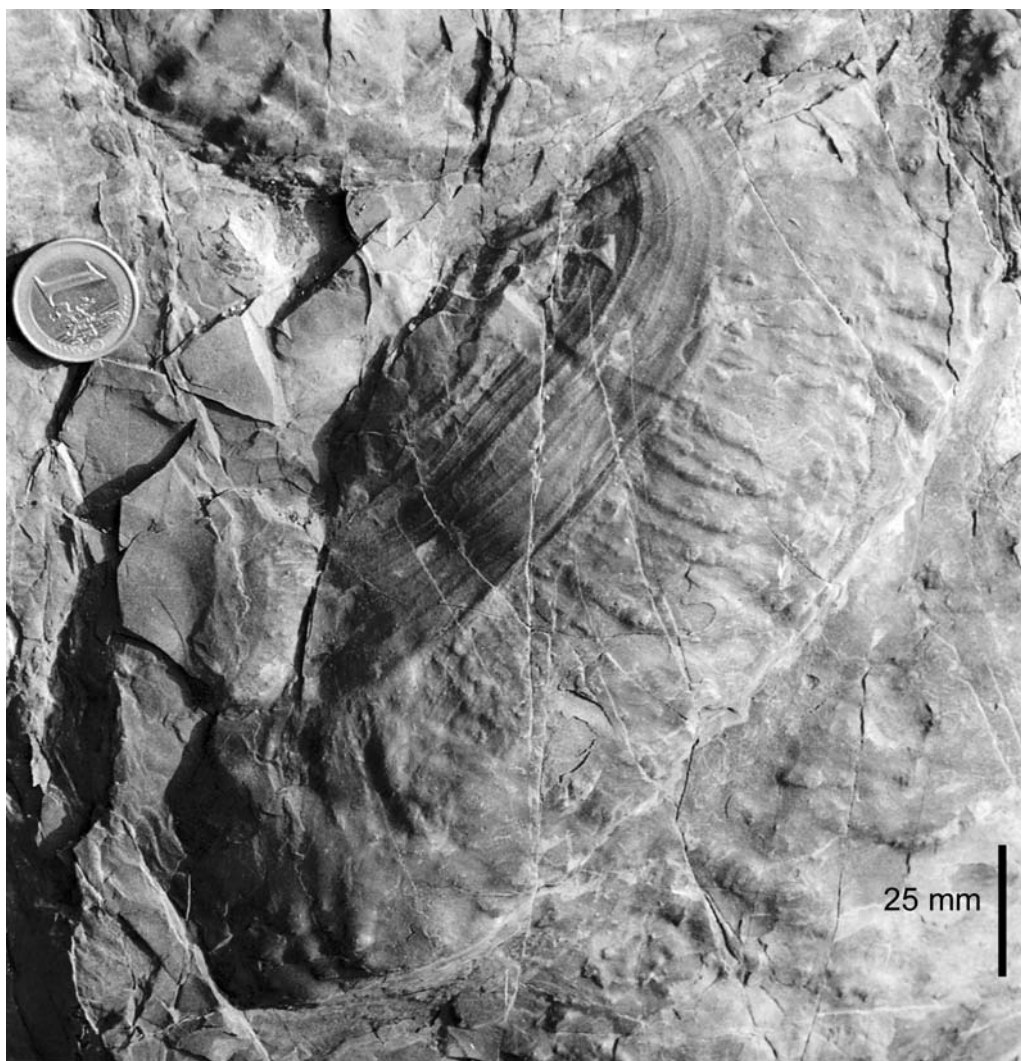


Fig. 9. Specimen with pronounced ovoid rings.

(1984), concluded that '*Arumberia*' was a microbially-influenced sedimentary structure. This has generally been accepted by other workers (e.g. Hagadorn & Bottjer 1997; Waggoner 1999; Grazhdankin 2004). Two different specimens are figured here. The first (Fig. 15a), from the Booley Bay Formation at Templetown, consists of a bulbous form approximately 10 cm in diameter in positive hyporelief, which is covered by subparallel unbranched ridges of thickness 1 mm separated by thin grooves in a regular pattern. The ridges do not extend beyond the slope; however a fainter network of curved lines is observed to extend away from the specimen. The relationship of the ridges and grooves to the palaeocurrent is unknown, as

the specimen occurs on a faulted block, and there are no other current indicators visible on the bed. The second specimen (Fig. 15b) is from Dollar Bay (immediately south of Booley Bay). An elongate (c. 20 cm) thick ridge, which is covered by a thin layer of underlying sediment, has subparallel ridges and grooves several centimetres in length extending from the slope in a linear pattern. In this specimen, the ridges and grooves are approximately parallel to palaeocurrent. The specimens resemble examples figured from Britain (Bland 1984), Australia (Glaessner & Walter 1975), and the Urals (Bekker 1980, 1990).

A further structure described in an unpublished MSc thesis (J. Vohnhof 1997) from the section at

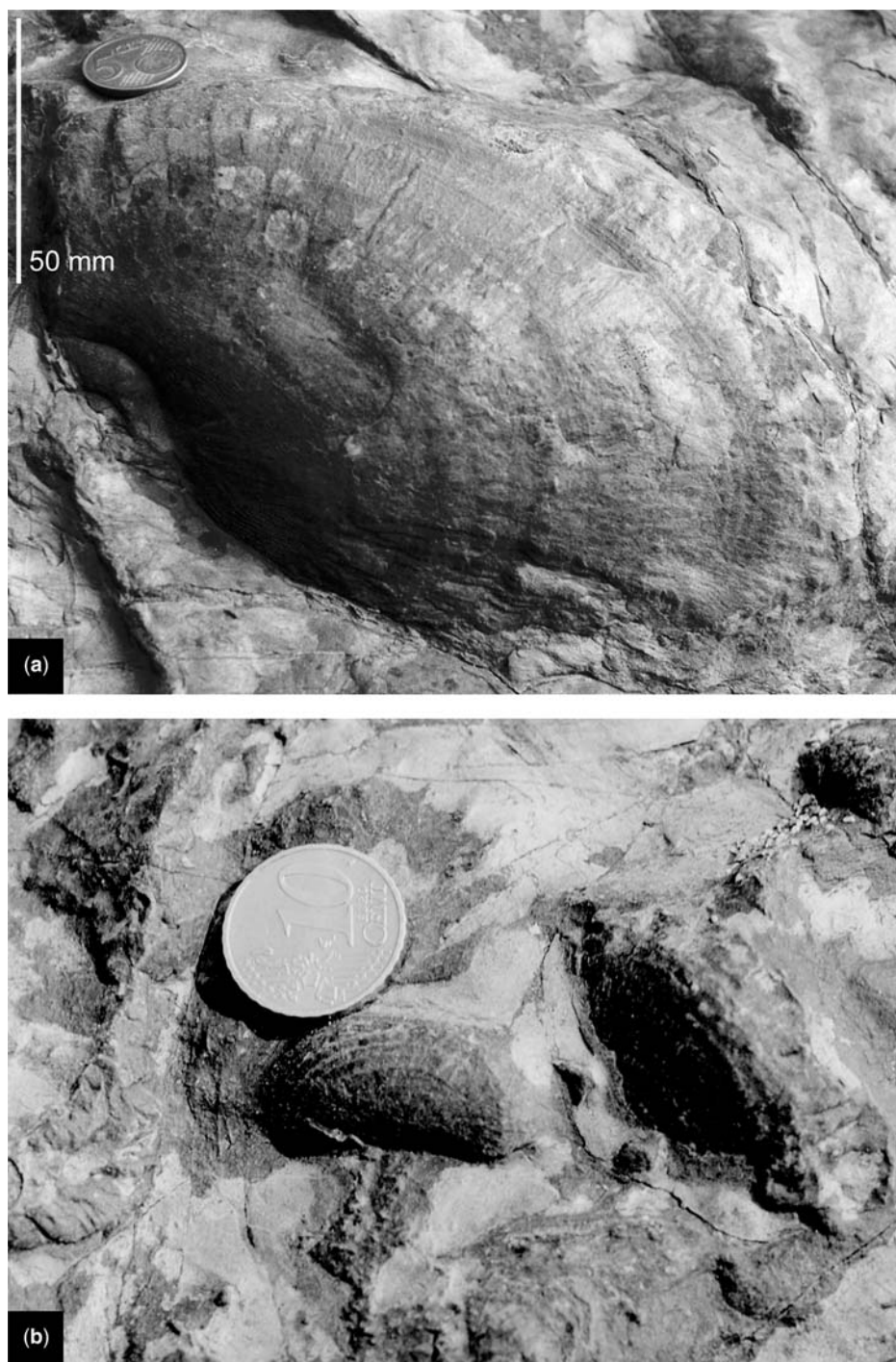


Fig. 10. Specimens of (a) large and (b) small size showing both radial and concentric ornament. Note the similarity in form despite the size difference. Coin in (b) has diameter 20 mm.

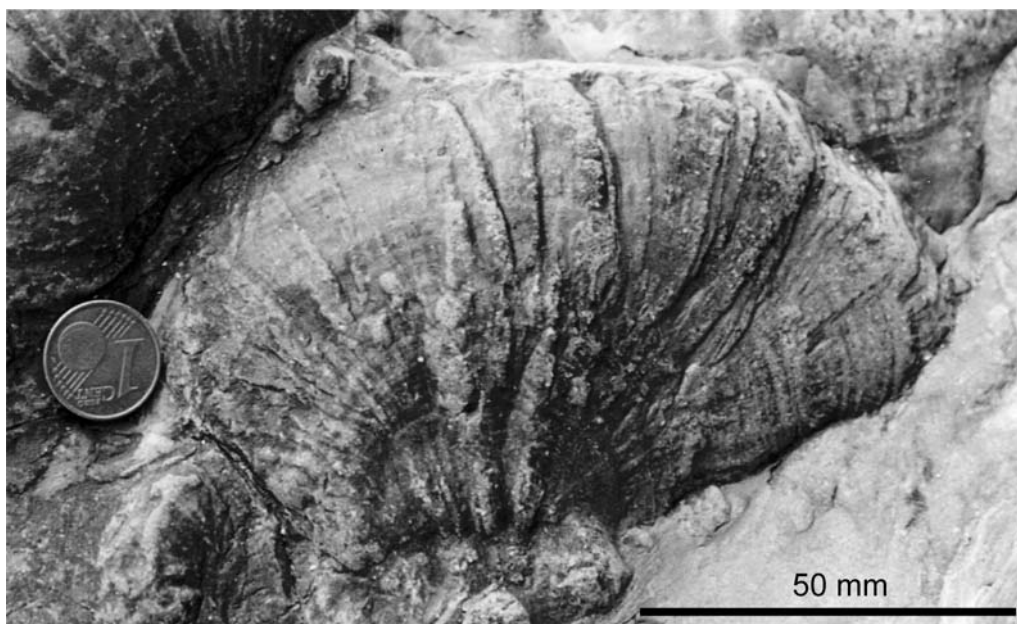


Fig. 11. Specimen showing irregular, approximately radial features and sharp regular concentric rings.

Booley Bay is a subcircular ridge in positive hyporelief, about 1 cm in diameter. The circle is not complete however, having a 2–3 mm gap on one side; the ridge on one side of this gap

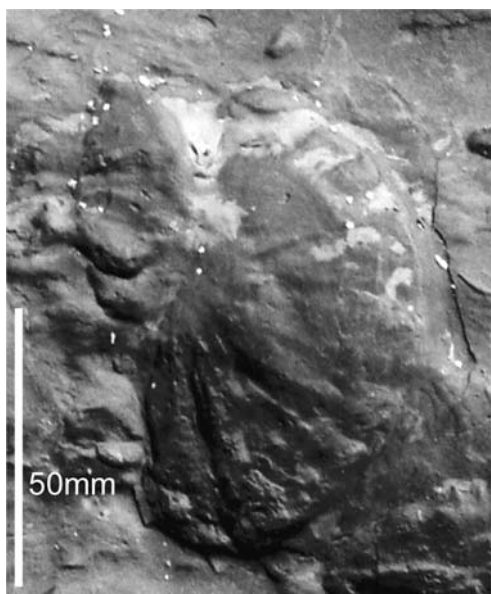


Fig. 12. Specimen with a small, flat central disc and radial marks extending to the periphery on a sloped outer area.

is orientated away from that on the other side, suggesting the beginnings of an anticlockwise-outwards spiral. The specimen in question, however, has unfortunately gone missing subsequent to collection.

Another set of problematic structures occurs in positive hyporelief on at least three beds in Booley Bay (Fig. 16a). These are elongate tubes up to 5 cm in diameter, approximately palaeocurrent parallel, striated along the outside, parallel to the sides of the structures. At first glance these resemble gutter casts, but this explanation is not tenable, as on closer examination several of the structures reverse direction (Fig. 16b). No definite interpretation can thus be suggested at this time, but a sedimentological origin appears most likely. The structures are intimately associated with a stratigraphically underlying laminated black material with a patchy surface, the laminations of which appear to be deformed to accommodate the structures. This is also of unknown origin.

The age of the Booley Bay Formation

The dating of the Booley Bay succession to the late part of the Late Cambrian is based solely on acritarch biostratigraphy undertaken by Moczydlowska & Crimes (1995). Previous palynological investigations suggested that the formation ranged in age

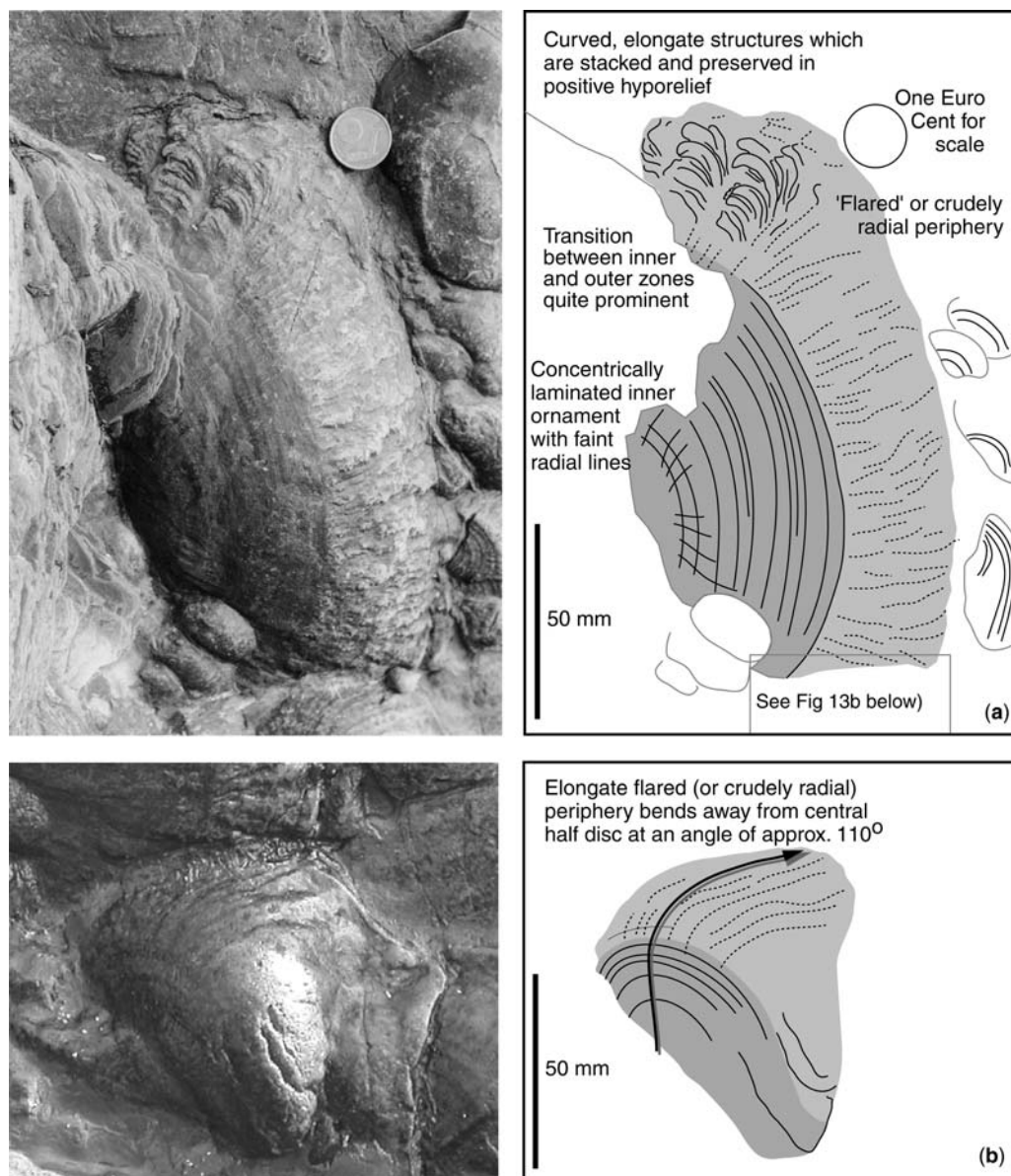


Fig. 13. Specimens showing a distinctive, crudely radial or flared periphery.

from Early Cambrian to Arenig (Gardiner & Vanguetaine 1971) or Middle Cambrian (Smith 1981). Four sample localities were collected by Moczydlowska & Crimes (1995), from which 17 acritarch species were recovered. Of these only two species, *Stellechinatum uncinatum* and *Cristallinium randomense*, have sufficiently short stratigraphic ranges to be useful for biostratigraphic

purposes and are thought to be Late Cambrian to Tremadoc in age. Attempts to better constrain the age range of the Booley Bay succession are currently underway. In the absence of volcanic ash horizons yielding zircons for radiometric dating, acritarch biostratigraphy remains the best hope of increasing the chronostratigraphic resolution of the sequence.

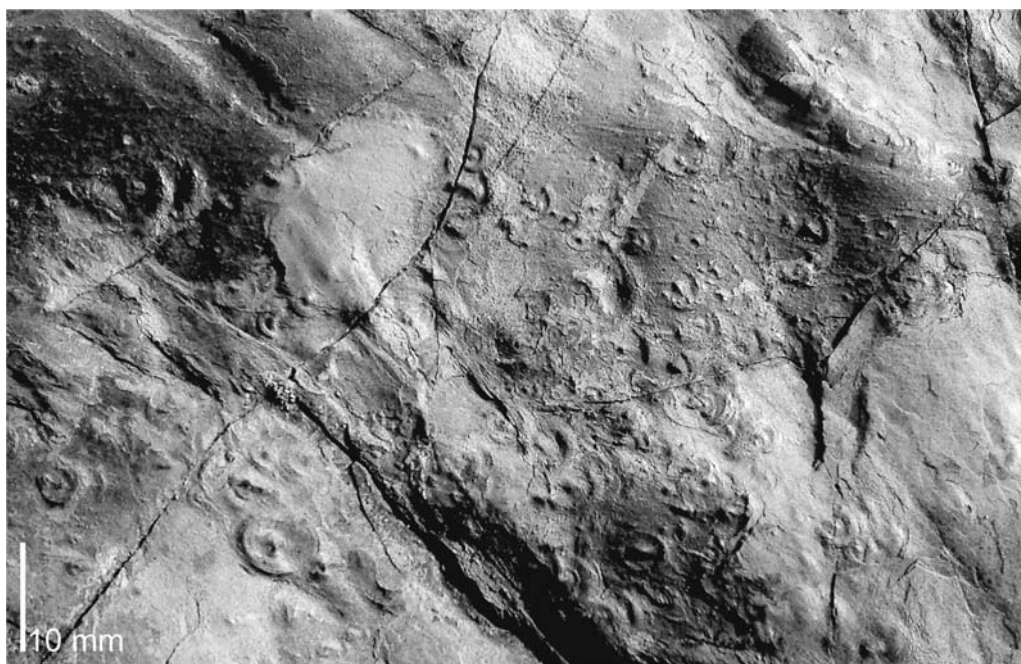


Fig. 14. Swing marks previously assigned to the Ediacaran genus *Nimbia*.

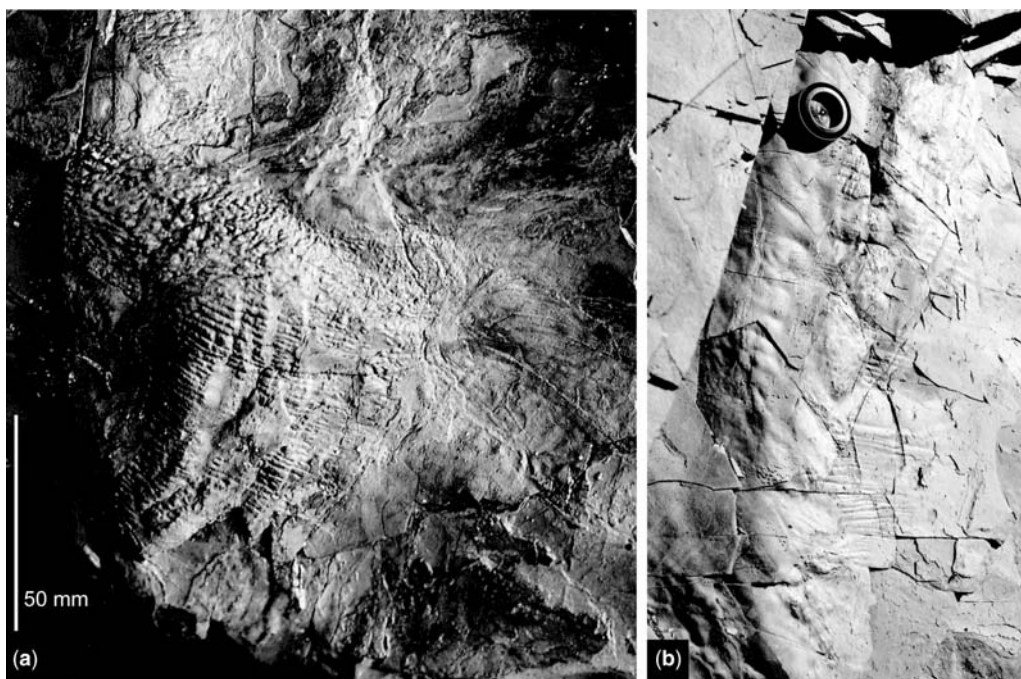


Fig. 15. Specimens of the microbially influenced sedimentary structure 'Arumberia' from the Booley Bay Formation at (a) Templetown (scale bar 50 mm) and (b) Dollar Bay (film canister lid has diameter 35 mm).

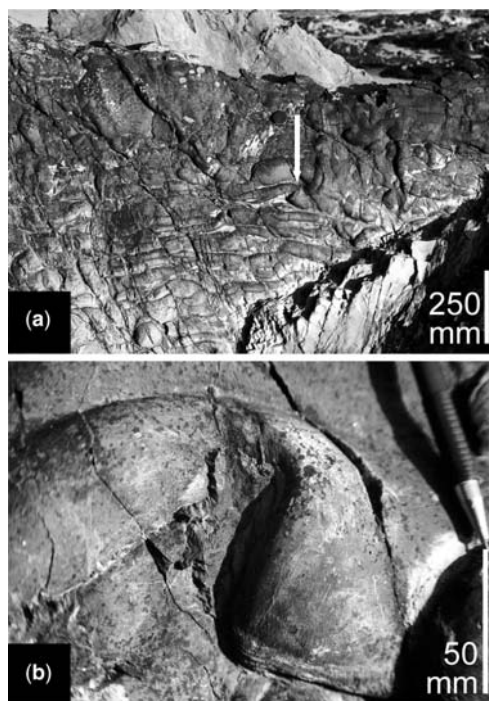


Fig. 16. Unidentified structures from Booley Bay: (a) Whole bedding surface; (b) Close-up of arrowed structure in (a).

Discussion

Interpretation of the Booley Bay specimens is of considerable importance to the development of models concerning the ultimate demise of the Ediacaran group as a whole. At present, there are five possible interpretations for their origin and affinity: these are listed below.

They are a species of the genus Ediacaria

Specimens of the genus *Ediacaria* have been reported from many locations worldwide, including Russia (Fedonkin 1990; Serezhnikova 2005), India (De 2003), Canada (Narbonne & Hofmann 1987; Narbonne 1994), and Australia (Sprigg 1947; Glaessner & Wade 1966; Wade 1972; Jenkins 1992, 1996), and it is regarded as a cosmopolitan taxon. The genus was initially described by Sprigg (1947), with one species, *Ediacaria flindersi*, from a small number of specimens from the Ediacara Hills, Flinders Ranges of South Australia. More extensive collections and detailed study by Glaessner & Wade (1966) and Wade (1972) assigned many new specimens to this genus, and also led to the removal of several specimens to new taxa. The genus was rediagnosed to account

for these changes, and was described as showing a central disc and an outer ring, without any marginal flange. The central disc, which varies from two-thirds to three-quarters of the total radius, was noted to often be slightly elevated above the outer ring, but the disc was otherwise flat. Surface features were limited to concentric grooves and a sharp annular furrow (not necessarily parallel to the outer margin) on the disc, and radial furrows on the ring. The genus was also discussed by Jenkins (1992, 1996), who considered that the type specimen was damaged in such a way as to preclude full assessment of its true relationships (R. J. F. Jenkins, pers. comm., 2005). A principal question in this regard was whether the specimen may have had a stalk, and hence represents holdfast.

In a study of discoidal fossils from the Fermeuse Formation of Newfoundland, Gehling *et al.* (2000) listed *Ediacaria*, along with most other flat discoidal Ediacaran-type fossils, as synonyms of *Aspidella terranova*, and interpreted *Aspidella* as a holdfast of a larger frond-like organism. Pending further investigation of the gradation of form noted, it is suggested that their synonymy list not be formally applied as it reduces the information conveyed by the names of the fossils (see MacGabhann 2007): although Gehling *et al.* (2000) suggested assignment of specimens to one of the preservational variants noted to counter this problem, this has not been applied in practice (e.g. Hofmann & Mountjoy 2001; Pyle *et al.* 2004; Droser *et al.* 2006). In this study, we regard the genus *Ediacaria* as a form genus, diagnosed as per Wade (1972).

Crimes *et al.* (1995) diagnosed *E. booleyi* as a large, circular disc with the dorsal side divided into three concentric zones (a flat central zone, steeply sloping middle zone, and gently sloping outer flange), with additional concentric lines and numerous thin radial features, which become more prominent towards the periphery. The ventral side was described as having alternate areas of coarse and fine concentric markings, and numerous fine radial lines. Although some of the specimens described here may seem to approach the basic morphology of *Ediacaria* (i.e. an inner disc with concentric structures and outer ring with radial lines), the three-dimensional aspect of most of the Irish specimens is not seen in the type material of *Ediacaria*. Neither do the flat Irish specimens conform to that of the type; the concentric rings are far more prominent and the radial aspect of the Irish specimens is far more crude and irregular, compared to the straight, thin, regular grooves seen on some specimens of *E. flindersi*. The assignment of the Irish specimens to the genus *Ediacaria* is therefore considered highly problematic. We suggest that the Booley Bay specimens should not be assigned to this genus.

They are of Ediacaran-type, but not in the genus Ediacaria

Very few Ediacaran-type discoidal fossils (*Medusinites* and *Nemiana* for example) are found in fossil form with a significant three-dimensional aspect to their morphology preserved. Of those that are currently known, none resemble *E. booleyi*.

One of the more compelling arguments presented by Crimes *et al.* (1995) for an Ediacaran-type fossil interpretation of *E. booleyi* is the apparent lack of a convincing mouth or anus in any of the specimens. The lack of any such structures, which have not been reported in any Ediacaran-type fossil, has led to one interpretation that the organisms, at least in some cases, relied on simple diffusion of nutrients and/or oxygen across the body wall (Seilacher 1989, 1992). This has obvious limitations in the ability for the surface area of an organism to feed and support a growing internal volume and may explain why many true Ediacaran-type organisms remained quite flat and thin, often adopting a quilted constructional morphology (e.g. Seilacher 1989, 1992). The three-dimensional relief of the fossils (e.g. Figs 9–10) does not seem to be designed to maximize surface area relative to total body volume and would present a problem for a simple nutrient and/or oxygen absorbing lifestyle. This is especially important considering the largest specimen measured in the field had an estimated total diameter of nearly 40 cm; such sizes are reached by thin Ediacaran organisms including *Ediacaria* and *Dickinsonia*, but not by any forms with a strong three-dimensional aspect. The Irish specimens cannot, therefore, be interpreted in terms of the Vendobionta hypothesis of Seilacher (1992), and the lack of preserved mouth, anus or respiratory structures cannot be used as a guide to their affinities.

Alternative interpretations of Ediacaran fossils regard them as stem or crown group representatives of extant phyla (e.g. Gehling 1991) in which features such as mouths are simply not preserved. If this is the case, the occurrence of structures similar to Ediacaran-type fossils in the Cambrian may be important in terms of preservational circumstances rather than biology (Jensen *et al.* 1998), as it is of course beyond doubt that non-mineralized organisms existed in the Cambrian.

We also note that the original transport and depositional model for *E. booleyi* (as proposed by Crimes *et al.* 1995) appears to be hydrodynamically unstable, as the direction of projection of the organism out of the sediment after impactation is up-current, and would maximize its hydrodynamic resistance (Fig. 17a). An interesting outcome from this observation is that it may provide an

explanation for the flared periphery to many of the specimens. The force of the current flowing against the upwardly projected rear portion of the disc and its resultant drag would force the structure to rotate slightly in the sediment. This could possibly account for the drag like marks forming the flared radial periphery to many of the specimens on the downstream side (Fig. 17b). If the structure was not securely fastened to the bottom and the current continued to flow against it, it would presumably continue to rotate before flipping free. Even to penetrate the sediment to the degree originally suggested, the density of the organism must have been at least the same as the density of the sediment into which it was emplaced. This point was alluded to by Palmer (1996). The only way to increase the density of an organism to that of the surrounding sediment is to provide it with mineralized skeletal structures. Initial analogue flume experiments that we conducted using density compensated silicon rubber replicas of the

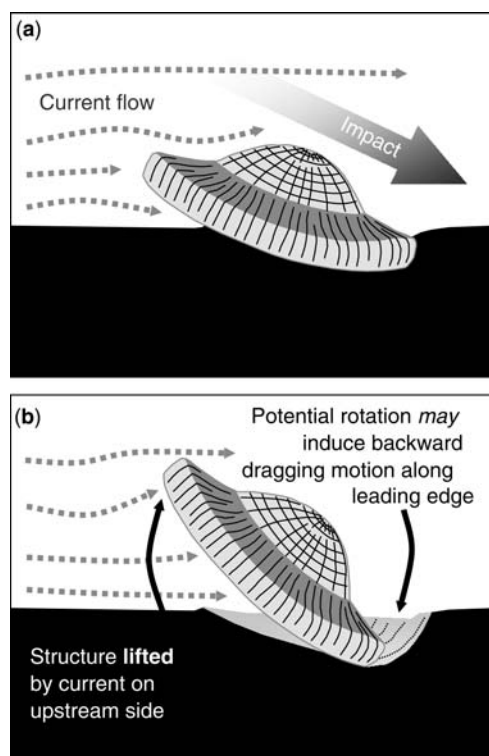


Fig. 17. Reconstruction of *E. booleyi* (modified from Crimes *et al.* 1995): (a) post-impact and (b) entrainment in the seafloor. Note how continued current action acting against the rear of the structure (projecting upstream) would eventually lift it up and possibly out of its impact position.

Crimes *et al.* (1995) reconstruction for *E. booleyi* appear to support this hypothesis. These are ongoing, and the results will be published elsewhere. In addition, the proposed taphonomic model requires the organism to have a tough integument to survive transport, coupled with some rigidity to allow appreciable sediment penetration. This component of rigidity in particular is inconsistent with an interpretation of these structures as Ediacaran-type fossils.

If an Ediacaran affinity is to be rejected for *E. booleyi* then only two plausible biogenic interpretations can be proposed for the structures.

They are body fossils, but not of true Ediacaran affinity

A radially symmetric body plan may suggest a cnidarian affinity. The density of living medusoids (e.g. Scyphozoa medusae, or jellyfish) is close to that of seawater (1.03 g cm^{-3}). This and their nektic habit present problems for them becoming entrained in turbidity currents. This likely also applies to other Cambrian discoidal fossils, such as the medusiform stem-group echinoderms of the Class Discophylla (Friend 1995), although there is some suggestion that discophyllans may have been benthic. An alternative is that the organism was a benthic polyp such as a solitary coral or anemone. Still, however, the problems of density and construction of an outer rigid test, enclosing the entire organism, arise. There are no modern analogues to compare with; however the Psammocorallia as defined by Seilacher (Seilacher 1992; Seilacher & Goldring 1996) do provide one possibility. These 'sand corals' are thought to have lined the inside of their enteron with sediment grains, which acted as ballast. It is possible that *E. booleyi* contained sand within its body, which could account for much of the density deficit. The concept may be useful in trying to begin to understand the taphonomy of the *E. booleyi* specimens, but as Crimes *et al.* (1995) point out, the Irish specimens bear little relation to the morphology outline in published accounts of Psammocorallia.

Many of these problems could be dismissed if the possibility is considered that the organisms were benthic, and autochthonous or preserved *in situ*. Attractive as this idea is, it does not easily explain the occurrence of the structures in regularly spaced palaeocurrent parallel bands (Fig. 7), nor how benthic organisms could be preserved on erosional turbidite soles. An interpretation of the structures as benthic organisms would require a reinterpretation of the sedimentology of the strata (long overdue), which we are currently undertaking.

They are biogenic sedimentary structures

An alternative explanation is that the structures are, in fact, trace fossils. This could explain why a full circle or disc is never observed in any of the specimens. The structures may have been made by an organism, which grazed upon the seafloor in an arcuate fashion. Also, at least one specimen (Fig. 14a) displays strong evidence for systematic excavation. Two important considerations arise when invoking a trace fossil explanation for the structures. Firstly, a range of sizes can clearly be demonstrated for similar structures (e.g. Fig. 10). Secondly, and more importantly, the structures are all approximately aligned, with the semicircular outlines directed downstream of the prevailing current direction. They are also in some instances grouped into distinct bands, which traverse bedding surfaces broadly in the direction of the palaeocurrent. This strongly suggests that the structures may have indeed been moved and aligned by current action. Alternatively, as discussed above, a swing mark origin could be invoked for several of the structures. This has yet to be fully tested.

They are simply abiogenic sedimentary structures

The variety in form, and lack of complete discoidal imprints may be considered as arguments against an organic origin, as may the lack of a sharp boundary to the structures in several cases and association with flute casts and 'Arumberia'-like structures. However, variability in form may be explained by taphonomic or original biological differences (indeed there is no reason to assume that the assemblage is necessarily monospecific or monogeneric), and the lack of complete specimens, as discussed above, may be explained by current orientation. Finally, for several specimens it is simply not the case that a sharp edge is absent: the specimen illustrated in Figure 11, for example, shows a very sharp edge truncating the ornamentation where the structure protrudes from the bed sole. Further, most of the specimens which do not show a sharp edge are those with the crudely radial structures potentially formed by current-induced rotation of the specimens, as discussed above. This would tend to obliterate sharp edges.

In any case, it is hard to understand how such consistently complex radial and concentric structures could be produced purely from a simple turbidity current, but this option cannot be ruled out at this stage.

Conclusion

Whilst we do not discount the possibility of a wholly inorganic origin for the structures described as *E. booleyi*, they are here tentatively considered at least in part biogenic. This is due to a combination of factors:

1. The range of sizes (the radius of specimens varies from c. 0.5 cm to c. 20 cm) exhibited by the different forms, while retaining reasonable constancy of structure.
2. The variance in angle of protrusion and relief (from flat to c. 3 cm) in forms which are otherwise morphologically similar.
3. The long axes of forms which are ovoid in outline are randomly oriented on the bedding surface.
4. The sharp boundary between the inner concentric-ornamented disc and the outer zone of radial structures.

We do not think that these structures should be assigned to the genus *Ediacaria*, and their apparently high density and rigid integument are inconsistent with their interpretation as Ediacaran-type fossils. Confirmation of this hypothesis would add considerable weight to proposals that the Ediacaran biota became extinct in a mass extinction at the end of the Ediacaran Period.

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