

## BIOTIC CHANGES IN PLATFORM COMMUNITIES ACROSS THE PRECAMBRIAN PHANEROZOIC BOUNDARY

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*Riassunto.* Il concetto della fauna di Ediacara (Tardo Proterozoico) come composta da Cnidari a corpo molle, principalmente pelagici, i quali subirono un'estinzione di massa al limite Precambriano-Cambriano, non è più sostenibile. Sembra infatti essersi verificato un graduale aumento della diversità sia nei resti che nelle tracce fossili durante il Proterozoico, aumento che ha subito una accelerazione nel Cambriano Inferiore.

La maggior parte degli organismi macroscopici del Proterozoico Superiore occupavano nicchie di acqua bassa in mari a sedimentazione terrigena. Alcuni, come *Charnia* e *Charniodiscus* erano ramificati e forse erano ancorati al fondo marino. Tuttavia altre forme ramificate, come *Pteridinium*, e le forme a sacco, come *Ernietta*, avrebbero potuto crescere e vivere entro sedimenti sabbiosi o siltosi ed essere Protozoi unicellulari ad organizzazione plasmodiale. Le forme discoidali, come *Cyclomedusa* ed *Ediacaria* erano organismi statici, che vivevano sull'interfaccia acqua-sedimento.

Ci fu un certo ricambio nei fossili vicino al limite Precambriano-Cambriano, ma c'è una crescente evidenza che molti dei fossili tipici di Ediacara ebbero discendenti nel Cambriano. Alcuni organismi sarebbero sopravvissuti spostandosi verso acque più profonde, fornendo il primo esempio di migrazione dalla costa verso ambienti più profondi.

*Abstract.* The concept of the late Proterozoic Ediacara fauna as one of soft-bodied, mainly pelagic, cnidarians which suffered a mass extinction at the Precambrian-Cambrian boundary is no longer tenable. There appears to have been a gradual increase in diversity of both body and trace fossils through the Proterozoic, accelerating in the early Cambrian.

Most late Proterozoic megascopic organisms occupied shallow water niches in clastic seas. Some, such as *Charnia* and *Charniodiscus*, were frond-like and may have been anchored on to the sea floor. However, other frond-like forms, such as *Pteridinium*, and sac-like forms, such as *Ernietta*, may have grown and lived within sandy or silty sediment and been unicellular plasmodial Protozoa. Discoid forms such as *Cyclomedusa* and *Ediacaria* were static, living at the sediment-water interface.

There was some turn-over in body and trace fossils at about the Precambrian-Cambrian boundary but there is increasing evidence that many of the typical Ediacaran body fossils have direct or close descendants in the Cambrian. Some body and trace fossils may have survived by moving into deeper water, giving the first example of an onshore-offshore migration.

### Introduction.

Precambrian platform communities were dominated by stromatolites but these were declining sharply in abundance and diversity by the late Proterozoic (Walter & Heys, 1985; Kennard & James, 1986; Walter et al., 1992). At this time, there was a marked increase in trace fossil diversity reflecting the incoming of the Metazoa (Crimes, 1992a) and it is thought that widespread grazing by these animals may have contributed to the decline in stromatolites (Walter & Heys, 1985). Their niches in carbonate platforms were, however, occupied over a short period during the early Cambrian by bioherms comprising intergrowths of archaeocyaths, calcimicrobes (*Renalcis*) and rare coralomorphs (*Cycticyathus*) (Kruse et al., 1995).

Concomitant with the decline in stromatolites, from about 600 to 540 million years ago, there was rapid development of an unusual fauna dominated disc and frond-like bodies, many of which reached sizes in excess of 10 cm. Discs were first noticed in the late Proterozoic Charnian Supergroup in the UK as early as 1840 (Boyn-ton & Ford, 1995), but the first detailed records were of three dimensionally preserved frond or sac-like bodies from the late Proterozoic Nama Group in southern Namibia (Gürich, 1929, 1933), but these discoveries went largely unnoticed until extensive material was described from an approximately equivalent horizon within the Pound Subgroup in the Ediacara hills, South Australia. These fossils, which lacked any evidence of shells, and became known as the "Ediacara fauna", were regarded as soft-bodied cnidarians, with disc-like types interpreted as jellyfish (Sprigg, 1947, 1949; Wade, 1972; Glaesner, 1984) and the frond-like forms considered as pennatulids (Glaesner, 1961). The jellyfish were widely depicted as tentacled floating forms (e.g. Wade, 1972, fig. 5-8), while the supposed pennatulids were shown with

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stems firmly anchored to the ocean floor, some like *Charniodiscus* fixed by a discoid holdfast (Glaessner, 1984; Jenkins, 1985, 1992). Similar forms have been described from late Proterozoic strata in many areas including: Charnwood Forest, England (Ford, 1958), White Sea and Siberia, Russia (Fedonkin, 1985), Podolia, Ukraine (Fedonkin, 1985), Wernecke Mountains, Canada (Narbonne & Hofmann, 1987), Newfoundland, Canada (Misra, 1969; Anderson & Conway Morris, 1982) and North Carolina (Gibson et al., 1984).

The concept of these forms as mostly soft bodied cnidarians was challenged by Seilacher (1984, p. 159) who considered many as "foliate, non locomotory quasi-autotrophs". He later included them in a separate Kingdom - the Vendobionta (Seilacher, 1992), although subsequently they were regarded as a sister group to the Eumetazoa (Buss & Seilacher, 1994). Seilacher (1984) also suggested that their apparent absence in the Phanerozoic was the result of a mass extinction at the end of the Proterozoic.

Recent research has shed new light on the habitats and mode of life of the Ediacara fauna and cast doubt on the extent to which they suffered extinction at the Proterozoic/ Phanerozoic boundary. The purpose of this paper is to review these new data and their bearing on biotic changes which were taking place in shelf communities at this time.

### Proterozoic Ediacara-type biotas.

The oldest structures bearing resemblance to discoid elements in the Ediacara fauna were described by Robertson (1962) from strata in the Northern Territory, Australia dated as between 2,400 and 1,830 Ma (Compton & Arriens, 1968). They are elliptical in shape with a central sand filled pipe and radially structured cone composed of greywacke which becomes finer grained towards the periphery. They were described as probable fossils by Robertson (1962) but reinterpreted as tectonically deformed sand volcanoes by Walter (1972). An inorganic origin is not unreasonable but the pronounced radial structures are unusual in sand volcanoes known to the authors, including the superb examples within the Carboniferous of Co. Clare (Gill & Kuenen, 1957) and cited by Walter.

The earliest reliable Ediacara-type fossils, referred to *Nimbia occlusa*, *Vendella?* and *Irridinitus?* were described from inter-tillite beds forming part of a glacial sequence in the Mackenzie Mountains, Canada and correlated with the Late Proterozoic Varanger tillites of Norway (Hofmann et al., 1990). Discoid, typically five lobed silica-rich structures occur in meandering lines and clusters on the upper surface of a glacial mixtite bed in the late Proterozoic sequence in the Garvellach Isles,

Scotland, also correlated with the Varanger tillites (Crimes et al., in preparation). They compare closely with unnamed silica rich pentamerous fossils from the Lower Cambrian of Scotland (Campbell & Paul, 1983). The main development of the Ediacara fauna, however, took place after the Varanger glaciation.

In Australia, most of the fossils occur near the top of the Proterozoic sequence within the Pound Supergroup and Jenkins (1995) has suggested that *Rangia* and *Pteridinium* occur first, with the classic Ediacara assemblage, including *Charniodiscus*, *Dickinsonia*, *Eoporpita*, *Pavancorina* and *Spriggina*, slightly later. He claims a similar occurrence in the White Sea area of Russia (Fedonkin, 1985) with *Pteridinium* and *Hiemalora* low down in the sequence and diverse species of *Dickinsonia* accompanied by *Ovatoscutum* and *Armillifera* later. Other taxa such as *Ediacaria*, *Eoporpita*, *Cyclomedusa* and *Tribrachidium*, have a longer range according to Jenkins (1995).

In Canada, the fauna is less diverse. In the Wernecke Mountains, fossils are found at two horizons which are overlain unconformably by a Lower Cambrian sequence. The faunal list includes *Charniodiscus*, *Cyclomedusa*, *Ediacaria*, *Medusinites*, *Spriggia* and *Tirasia-na* (Narbonne & Hofmann, 1987). In the Sekwi Brook area, Narbonne & Aitken (1990) record *Beltanella*, *Cyclomedusa*, *Eoporpita*, *Kullingia*, *Inkrylova*, *Pteridinium* and *Medusinites* but again the sequence is separated by an unconformity from the overlying Cambrian. In Newfoundland, the fauna is dominated by frond-like forms including *Charnia* and *Charniodiscus* and occurs near the top of the Conception Group and in the overlying St. Johns Group which is several kilometres below the local Cambrian (Jenkins, 1992).

One of the best exposed sequences is in south Namibia where the stratigraphic framework (Fig. 1) was established by Germs (1972) and refined by Saylor et al. (1995) and Grotzinger et al. (1995). The fossil occurrences are known mainly from the work of Gürich (1929, 1933), Pflug (1966, 1970a, b, 1972) and Germs (1972). *Rangia* (Pl. 1a) occurs low down in the sequence where it is accompanied by *Pteridinium* (Pl. 1b, c, d, e, f), *Ernietta* (Pl. 2a) and *Namalia*. *Pteridinium* continues through the Schwarzrand Subgroup and one of the most interesting recent discoveries (Grotzinger et al., 1995) is its occurrence near the top of the Spitskopf Member, within a few metres of a major sequence boundary with the overlying Nomtsas Formation which has yielded the Lower Cambrian index ichnofossils *Phycodes pedum* (Crimes & Germs, 1982) and *Phycodes coronatum* (Grotzinger et al., 1995). A uranium-lead date on zircons from an ash bed about 75m below the *Pteridinium* locality gave an age of 543±1 Ma. while an ash bed in the Nomtsas Formation yielded a date of 539±1 Ma. (Grot-



## PLATE 1

- Fig. a - *Rangesa*, Kliphoek Member of the Kuibis Subgroup at Kuibis Farm, Namibia. Plaster cast lodged in South African Museum, Capetown. (x 1.2).
- Fig. b - *Pteridinium*, Kliphoek Member of Kuibis Subgroup at Aar Farm, near Aus, Namibia. Field photograph (x 0.2).
- Fig. c - Close up of specimens shown in lower left of (b) but preserved as inverse impression on separate block now lying a few metres away. Note the two small examples of *Pteridinium* juxtaposed at the right apex of the largest specimen (just above coin) and possibly indicating reproduction by budding. Field photograph (x 0.5).
- Fig. d, e, f - *Pteridinium*, Kliphoek Member of the Kuibis Subgroup at Plateau Farm, near Aus, Namibia, showing the lithological similarity between the sediment inside and surrounding the fossils. Note also the full three dimensional preservation seen particularly well in the lower left side of the wall-like specimen seen in (f). Photographed on location with the specimens retained in the small museum at Plateau Farm. (dx 0.4, ex 0.5, fx 0.4).

zinger et al., 1995). This indicates that elements of the Ediacara fauna occur close to the Proterozoic-Phanerozoic boundary.

The occurrence of trace fossils in Proterozoic strata has been extensively reviewed (Crimes, 1987, 1992a, b, 1994), so only a brief summary need be given here.

During the Riphean, trace fossils other than simple tube-like burrows (*Planolites*) were absent or exceedingly rare (Crimes, 1994). A few evolved by the time of the Varanger glaciation but a significant increase in diversity occurred contemporaneously with the evolution of the Ediacaran faunas. Diverse ichnofaunas have been described from rocks of Ediacaran age in many localities, including Australia (Glaessner, 1969; Walter et al., 1989), Namibia (Crimes & Germs, 1982; Geyer & Uchman, 1995), Canada (Crimes & Anderson, 1985; Narbonne et al., 1987; Narbonne & Hofmann, 1987; Narbonne & Aitken, 1990) and Russia (Fedonkin, 1985). These ichnofaunas are all dominated by horizontal burrows and trails, some of which are simple and pursue an irregular path (e.g. *Planolites*, *Palaeophycus*, *Torrowangea*) but others are arranged in guided meanders (e.g. *Cochlichnus*, *Helminthoida*, *Helminthopsis*, *Palaeopascichnus*, *Yelovichnus*). More complex types include minute helicoid spirals (*Harlaniella*), network structures (*Palcodictyon* - see Bekker & Kishka, 1989, pl. 1-6) and meandering collections of pellets (*Neonereites*, *Nenoxites*). Vertical burrowing is rare and the *Skolithos* from the Kuibis Subgroup (Germs, 1972) appears on re-examination to more probably represent a body fossil. There are no records of stacked or spreite burrows such as *Teichichnus*. The assemblage is, therefore, dominated by horizontal burrows or trails and is only exploiting essentially two dimensional ecospace. Some of the forms (e.g. *Nenoxites*, *Palaeopascichnus*) are, however, rather bizarre, being composed of pellets oriented perpendicular to the direction of locomotion, and have no known counterparts in the Phanerozoic.

#### The habitat and mode of life of the Ediacara-type biotas.

The early investigations of Ediacara faunas concluded that the preservation of supposed soft bodied cnidarians, such as jellyfish, required them to have been stranded on a muddy foreshore to allow the sun to dry their impressions (Sprigg, 1947). Later sedimentological studies found no evidence of exposure, although a shallow water environment was confirmed (Goldring & Curnow, 1967). Gehling (1983, 1988, 1991) has suggested that, in Australia, the fossiliferous facies represent offshore, storm wave base environments.

In Namibia, the depositional environment of the Ediacara faunas has been discussed by Germs (1983) and Saylor et al. (1995). They too failed to find any evidence

of exposure and regard the sequences as having been deposited under shallow marine conditions. Saylor et al. (1995) regard the Kliphoeck Member (Fig. 1) as deposited in a marine environment strongly influenced by tidal or deltaic currents and this is supported by our observation of large scale cross bedding in sets many metres thick and perhaps reflecting sand wave migration. The Niederhagen Member is considered a shallow water highstand deposit, while wave ripples in the Vingerbreek Member indicate deposition above fair weather wave base with only rare hummocky cross-stratification to suggest deeper, more offshore conditions (Saylor et al., 1995). Finally, the Nasep Member is interpreted as upper shoreface, probably deltaic.

Detailed sedimentological analyses of the Russian sequences in the White Sea and Siberia have yet to be published but our investigations suggest deposition in shallow water, down to about storm wave base.

In Finnmark, an Ediacara-type fauna also occurs in a shallow water subtidal marine environment (Farmer et al., 1992). Most of the Ediacaran fossils in the Wernecke Mountains, Canada come from shallow sublittoral environments, although a few may have occurred on a slope in slightly deeper water (Narbonne & Hofmann, 1987). The only other examples of deeper water deposits yielding Ediacara fossils are in the Mackenzie Mountains, Canada, where they occur in a slope setting, below wave base (Narbonne & Aitken, 1990), Newfoundland, Canada where they may have occurred in a deep sea sand fan but not at truly oceanic depths (Benus, 1988; Jenkins, 1992), and in Carolina, U.S.A. (Gibson et al., 1984).

The habitat of the Ediacara fauna was, therefore, predominantly shallow water clastic shelf seas.

It was initially envisaged that discoid elements in the Ediacara fauna like *Cyclomedusa* were planktonic medusae and frond-like forms such as *Charnia* (Pl. 2b) were considered as Pennatulacea and lived anchored to the ocean floor sediment, some by a holdfast (Sprigg, 1947, 1949; Glaessner & Wade, 1966; Wade, 1972; Glaessner, 1984). *Dickinsonia*, *Spriggina* and *Parvancorina* were all regarded as free swimming forms (Glaessner, 1984).

Critical morphological analysis led to a radically different interpretation in which the discs were considered immobile and benthic (Fedonkin, 1983; Gehling, 1991), while the fronds were regarded as having a quilted construction filled with plasmodial fluid and having no counterparts in the Phanerozoic or Recent biosphere (Seilacher, 1989, 1992). This mode of life was suggested by Seilacher (1992) not only for the frond-like forms but also for the thin, flat forms such as *Dickinsonia* and the trilobite-like *Spriggina*, a conclusion unacceptable to Runnegar (1995).

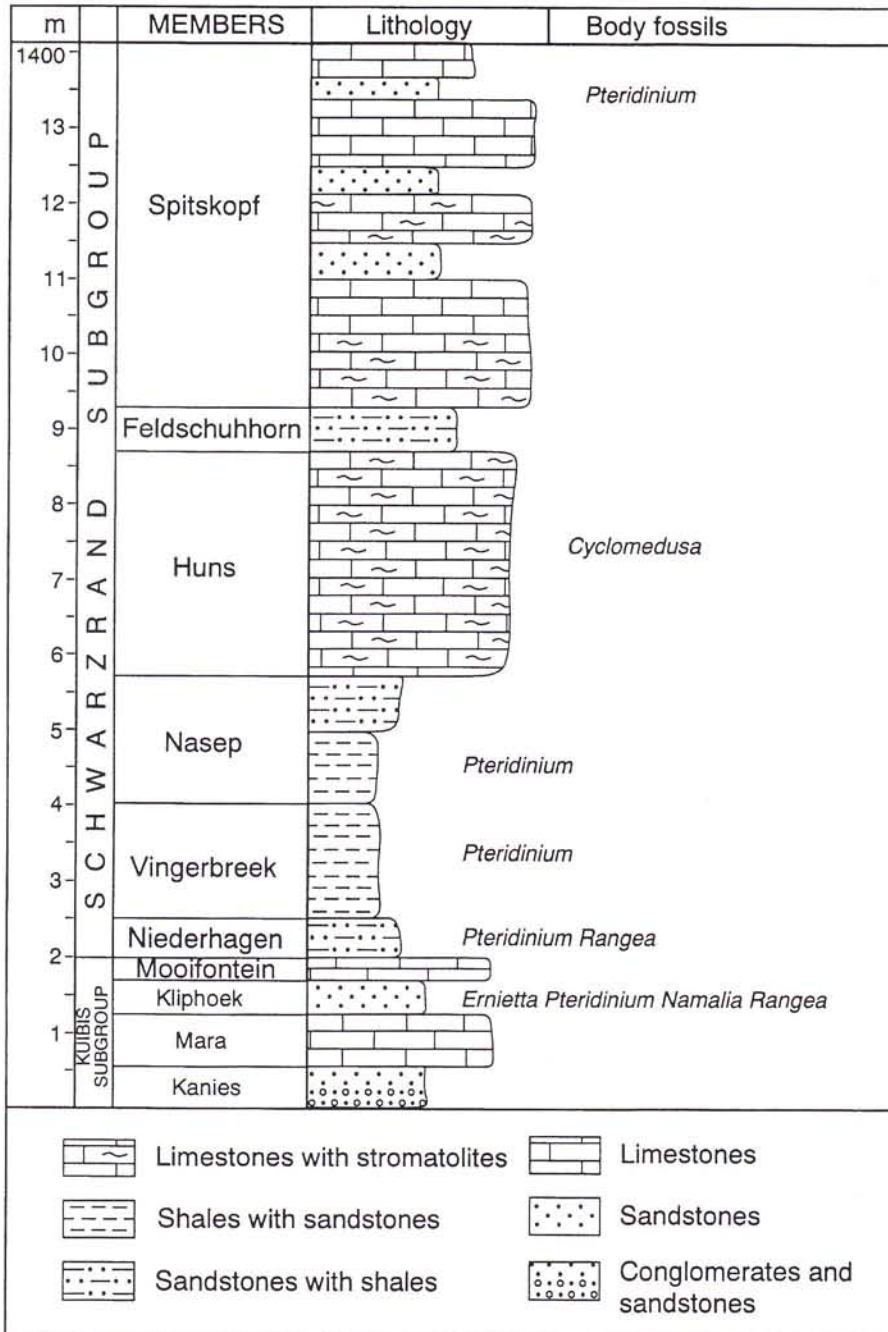


Fig. 1 - Schematized stratigraphic section of part of the Nama Group in South Namibia showing main fossil horizons. Data from Germs (1972), Saylor et al. (1995) and Grotzinger et al. (1995).

The disc and frond-like forms show no evidence of a mouth, anus or digestive system and may have lived chemotrophically (Seilacher, 1984, 1989; Crimes et al., 1995; Crimes & Fedonkin, in preparation). Preservation in high relief of some of the disc-like forms such as *Cyclomedusa* and *Ediacaria* suggests they were rigid and composed of some strong material, like chitin (Retalack, 1994; Crimes et al., 1995), a conclusion also reached on independent toponomic evidence (Norris, 1989; Allison & Briggs, 1991).

Until recently, such preservation was unknown after the Precambrian (Seilacher, 1984). However, Upper Cambrian strata in Eire have yielded disc-like fossils of Ediacaran type which were transported and dumped by

a turbidity current, thus demonstrating that they too were not soft-bodied but rigid (Crimes et al., 1995).

Three dimensional preservation of the vane or frond-like forms, such as *Pteridinium* or *Rangea* and sac-like forms, such as *Ernietta* is, however, all the more remarkable because our observations, mainly in Australia, Namibia, Russia and the Ukraine, show that they occur in a wide variety of facies, from low energy siltstones to high energy coarse grained sandstones. They are commonly twisted, buckled and overfolded, pointing to a tough but rubbery consistency, rather than a rigid form (cf. Jenkins, 1992). Explanations for their three dimensional preservation include: (i) early mineral precipitation within the matrix (Jenkins, 1992), (ii) low

rates of microbial decomposition (Runnegar, 1992), (iii) absence of scavengers and limited bioturbation (Conway Morris, 1993) and (iv) the supposed existence of cyanobacterial mats, thus enabling bacterially induced mineral crusts to form "death masks" (Gehling, 1991). Our investigations suggest an alternative explanation which will now be discussed, particularly with reference to the Namibian material.

*Ernietta* and *Pteridinium* are most abundant in Southern Namibia where they occur within the Kliphoeck Member of the Kuibis Subgroup on Aar and Plateau Farms (Richter, 1955; Pflug, 1966, 1970a, b, 1972; Germs, 1972). We have also found abundant *Ernietta* at the same horizon on Wegkruip Farm, near Bethanie, and *Pteridinium* has been recorded from the overlying Niederhagen, Vingerbreek and Nasep Members of the Schwarzrand Subgroup (Germs, 1972), as well as in much younger strata, near the top of the Spitskopf Member, close to the inferred Precambrian - Cambrian boundary (Grotzinger et al., 1995). *Rangaea* is less common and has only been recorded from the Kliphoeck Member of the Kuibis Subgroup and the Niederhagen Member of the Schwarzrand Subgroup (Germs, 1972).

The sediment filled three dimensional nature of *Ernietta* and *Pteridinium* has led to suggestions that they may have lived on the ocean floor, partially filled with sediment during life but with a proportion of their bodies protruding above the sediment/water interface (Seilacher, 1992, fig. 1). Unless they were all open cylinders parallel to the flow, any bottom tracted sediment would stack up around them and there would be a lithological difference between the sediment inside and outside their bodies, to reflect the variation in hydrodynamic conditions. However, the fill is normally remarkably similar to or identical with the surrounding sediment (Pl. 1d, e, f. Pl. 2c, d, e) (see also Wade, 1968, p. 256). Also, we found five examples at Aar and Plateau Farms in which parallel lamination appears to intersect the body wall and show no deflection or change in thickness (Pl. 2e) and, in two cases, the laminae appear to continue undeflected within the body of the organism. Another sectioned specimen of *Pteridinium* (Pl. 2f) appears to show not only parallel lamination, but perhaps also faint cross lamination passing through the upward continuation of the body wall. Also, examples of *Ernietta* from Wegkruip Farm appear to be sacs closed at both ends and some specimens of *Pteridinium* from Aar Farm may show two terminations, although other material indicates a more complex structure, with several vanes meeting along an axis (e.g. Jenkins, 1992, p. 149). These observations suggest that *Pteridinium* and *Ernietta* may not only have lived totally immersed in the sediment (see Buss and Seilacher, 1994, fig. 4) but have actually grown wholly within it. Jenkins et al. (1981, fig. 5c)

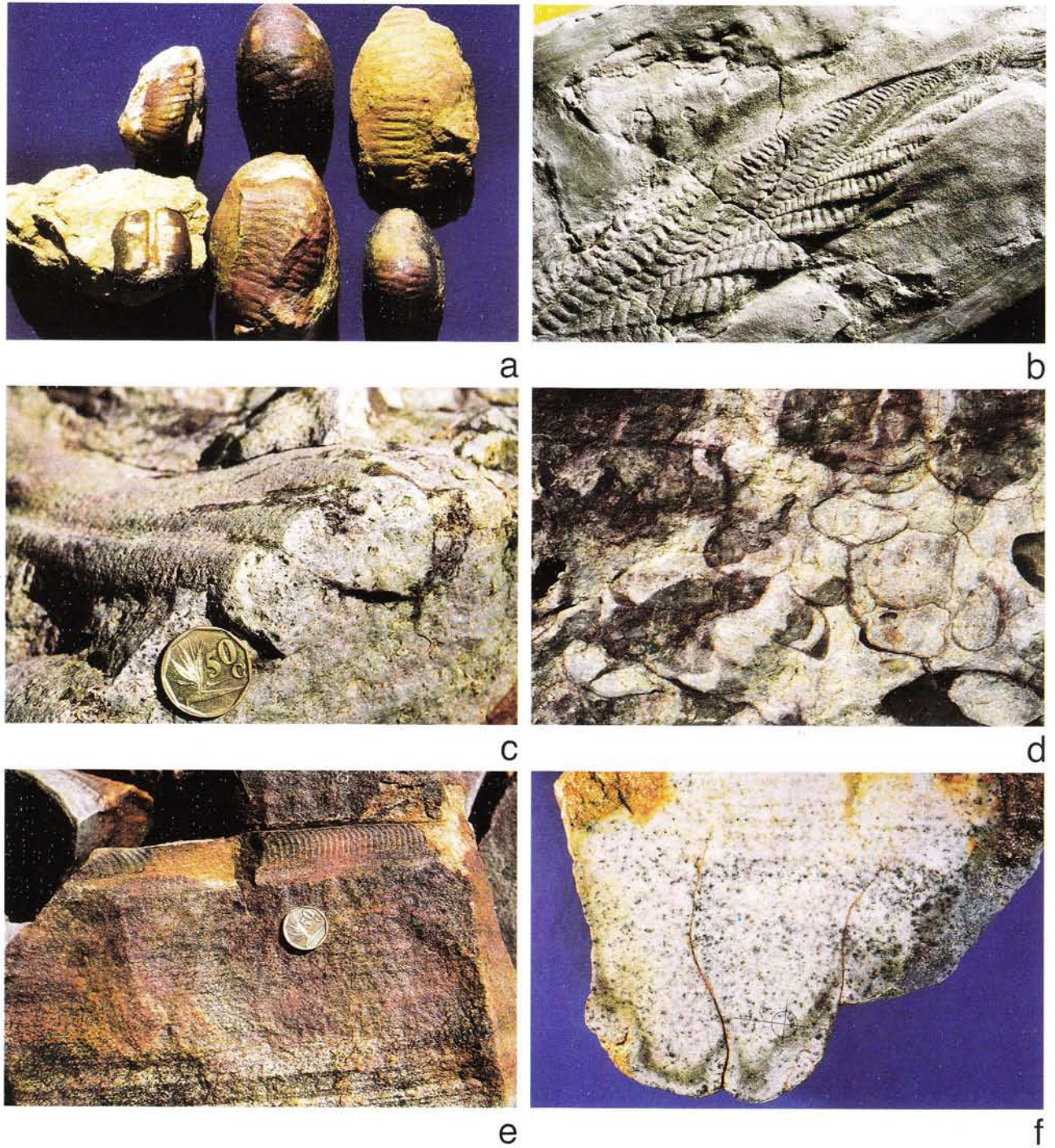
illustrate an example of *Ernietta* from the Kuibis Subgroup with a graded fill and suggest it was filled intermittently and buried by a turbidity current. However, this was a collected, isolate specimen and it is not known if the grading was present in the surrounding sediment, in which case this example too could have grown *in situ*. Interestingly, other examples figured by Jenkins et al. (1981, fig. 5a, b) appear to be closed at both ends, thereby making progressive filling difficult. It seems that these genera may have instead grown by a process of sediment pervasion, in which their walls develop as a body of protoplasm that migrates through the pore spaces between the sand grains which would then serve to support the organism. In the case of *Pteridinium*, some examples may have developed as twin, closed cylinders (Pl. 2c) but other, perhaps less complete specimens, may have been open above (Pl. 2f).

Some specimens of *Pteridinium* and, more particularly *Ernietta* show "external" ornament replicated through several laminae (cf. Jenkins et al., 1981, fig. 5a), suggesting the organisms were multi-foliate, with an onion-like form and may have grown as a series of sequential chambers.

The three dimensional preservation of the frond-like *Rangaea* (Pl. 1a) from nearby Kuibis Farm suggests that it too may have grown within the sediment but its rarity, and our failure to find any specimens *in situ*, preclude firm conclusions and a reclining or sediment-sticking habit is possible (cf. Seilacher, 1992).

It is difficult to comprehend how complex multicellular organisms could grow through the sediment without causing any disturbance of fine parallel lamination. The possibility that *Pteridinium*, *Ernietta* and probably *Rangaea* were unicellular plasmodial organisms should therefore be considered. Zhuravlev (1993) has suggested that many of the Ediacaran organisms, including the frond-like *Charnia*, may be unicellular and he draws comparisons with the present day Xenophyophores, which are Protozoa and have a rigid agglutinated skeleton, with a texture indistinguishable from the sediment. The body plan of some of these organisms is closely comparable to some Ediacaran forms and growth by migration of naked protoplasm through pore spaces in the sediment seems feasible. This would also explain how some, at least, were closed sacs or cylinders.

One specimen of *Pteridinium* at Aar Farm (Pl. 1c) has two similar but smaller examples adjacent to its apex in an arrangement that might imply asexual reproduction by fission, with the production of buds (see also Pflug, 1970a). This method of reproduction is common in the Protozoa and would explain the crowding of specimens seen at some localities (Pl. 1b). However, the global distribution of *Ernietta* and, more particularly, *Pteridinium*, in late Precambrian sequences must imply



## PLATE 2

- Fig. a - Specimens of *Ernietta* illustrating three dimensional preservation and sac-like nature, from the Kliphoeck Member of Kuibis Subgroup at Wegkruip Farm, near Bethanie, Namibia. Specimens to be lodged with the Namibian Geological Survey, Windhoek, Namibia. (x 0.5).
- Fig. b - *Charnia masoni*, Ust-Pinega Formation Winter Coast, White Sea, Russia. Specimen lodged with Palaeontological Institute, Moscow. (x 0.4).
- Fig. c - Sectional view of *Pteridinium* on joint surface from the Kliphoeck Member of Kuibis Subgroup at Aar Farm, near Aus, Namibia to show the fossil preserved as two parallel cylinders, with fill lithologically identical to surrounding sediment. Field photograph (x 0.7).
- Fig. d - Sectional view of many *Ernietta* on a joint plane to show similarity in sediment inside and outside the specimens. Kliphoeck Member of Kuibis Subgroup at Aar farm, near Aus, Namibia. Field photograph (x 0.6).
- Fig. e - Sectional view of side of *Pteridinium* on joint planes toward the top of the photograph, showing undisturbed parallel lamination within and below the body wall. Kliphoeck Member of Kuibis Subgroup at Aar Fann, near Aus, Namibia. Field photograph (x 0.4).
- Fig. f - Polished section of one end of a small specimen of *Pteridinium* from Kliphoeck Member of Kuibis Subgroup at Aar Farm, near Aus, Namibia showing specimen walls, represented by vertical cracks, passing up through possible faint cross lamination and parallel lamination. Note similarity in sediment within and outside fossil on right side. Specimen to be lodged with Namibian Geological Survey, Windhoek, Namibia. (x 0.9).

some effective means of distribution which might involve encystment or sexual reproduction with the production of pelagic larvae.

The variable orientation of some specimens of *Ernietta* with respect to the bedding might suggest that they were exhumed and transported. If they were sand filled and rubbery this would be possible and might explain the deformation of some examples. However, the similarity seen between the sediment inside and outside numerous specimens (e.g. Pl. 2d) renders this unlikely in all but a few cases. Runnegar (1992, p. 76) notes that in Namibia many of the specimens are embedded in sandstones as twisted or folded, randomly oriented casts and moulds and he concludes that they were obviously engulfed by a moving mass of sand prior to burial away from the place where they lived. This account presumably refers to *Pteridinium* and possibly *Ernietta*. Such movement is inconsistent with the observation of undisturbed sedimentary structures passing through some of the organisms and with the noted similarity between the sediment inside and outside their bodies. Also, *Pteridinium* displays variable orientation and deformation at several localities in Australia and Russia (Fedonkin, 1981), so large scale mass movement is unlikely to have been responsible for all these occurrences. However, if the organisms formed an integral part of the sediment and had flexible body walls, any localised soft sediment movement during diagenesis would deform them and could have resulted in some of the incongruous shapes observed. Minor, local, sediment movement appears more likely to explain the deformation in most examples than long distance transportation. The random orientation seen in some *Pteridinium* and *Ernietta* may simply reflect variable life orientation. The cases where long *Pteridinium* do show a degree of preferred orientation, with their bases parallel to bedding, may indicate a preferred life position.

Nevertheless, these forms commonly occur in high energy deposits, where a degree of reworking of the sediment is to be expected and some specimens, particularly of the smaller *Ernietta*, may well have been redeposited.

The distribution of Ediacara-type organisms on the late Proterozoic ocean floor is therefore illustrated, particularly in relation to the Namibian occurrences, in Fig. 2. Some frond-like forms such as *Pteridinium* and *Ernietta* may have grown wholly or largely in the sediment (1-4), other fronds such as *Rangia* (5) may have existed on the ocean floor or perhaps also in the sediment, while better developed fronds with holdfast discs, such as *Charniodiscus*, may have been anchored into the sediment, with the frond allowed to wave in the ocean currents. A few of the sediment filled forms such as *Ernietta* and, less commonly, *Pteridinium* might, however,

be exhumed (7, 8) by erosion and redeposited. Discoid forms such as *Ediacaria* and *Cyclomedusa* (10) may have remained static, living by chemical diffusion. Local carbonate banks may also have supported stromatolites (9).

The immobility of most preserved Ediacaran body fossils is confirmed by an almost total absence of trace fossils in the same beds, although they do occur within other facies in the sequences.

### Was there a mass extinction at the end of the Precambrian?

Seilacher (1984) suggested that an apparent absence of Ediacara-type body fossils in the Phanerozoic indicated a mass extinction at the end of the Precambrian. There is, however, increasing evidence that such fossils, or their direct descendants, continue at least well into the Cambrian.

Conway Morris (1993) has recorded Ediacaran-like fossils from the Middle Cambrian Burgess Shale in British Columbia, Canada and the Lower Cambrian Parker Slate of Vermont, U.S.A. He regards *Emmonsaspis* as a frond-like fossil, possibly related to *Pteridinium*, while *Thaumaptilon* was considered to be similar to frond-like Ediacaran fossils such as *Charniodiscus*, *Khatyspytia* and *Vaizitsnia*. *Emmonsaspis* occurs in sediment finer grained than most *Pteridinium* and rather than growing in the sediment it may have been benthic with the frond extending above the sediment-water interface. Halstead Tarlo (1967) regards *Xenusion* from the Lower Cambrian of Sweden as related to *Charnia* or *Rangia* while McMennamin (1986) compares it with *Charniodiscus*. However, a new more complete specimen strongly suggests it is a lobopod (Dzik & Krumbiegel, 1989).

Recently, Crimes et al. (1995) have described large discoidal forms similar to *Ediacaria* from the Upper Cambrian of Eire. Smaller discs, referable to *Cyclomedusa*, occur in the Lower Cambrian of Finnmark, Norway (Crimes & McIlroy, in preparation). Indeed, there are many reports in the literature of discoid fossils, commonly regarded as medusoids, in Lower Palaeozoic strata and many bear comparison with *Cyclomedusa* or *Ediacaria*, both of which anyway show marked morphological variability. Examples include "medusoid impressions" from Late Cambrian strata in Newfoundland (Nautiyal, 1973) and New Brunswick (Pickerill, 1982. Tanoli & Pickerill, 1989). The latter material has, however, been compared with the Middle Cambrian *Velumbrella* from Poland by Conway Morris (1993), who suggests a possible relationship with echinoderms.

*Heliomedusa*, *Stellostomites* and *Yunnanomedusa* from the Early Cambrian at Chengjiang, Yunnan, China, were interpreted by Sun & Hou (1987) as medusoids but *Heliomedusa* has been reinterpreted as a brachiopod





Fig. 2 - Distribution of organisms on the late Proterozoic sea floor. All organisms depicted occur in South Namibia, apart from *Charmiodiscus*.

(Jin & Wang, 1992) while *Stellostomites* and *Yunnanomedusa* may be junior synonyms of *Eldonia* (Chen et al., 1995). A relationship between *Eldonia* and discs such as *Cyclomedusa*, is possible though perhaps unlikely.

The forms which seem most commonly to span the Proterozoic - Phanerozoic boundary are the discs with numerous fine but sharp concentric ridges, widely regarded as chondrophorines and assigned to one of several genera, some of which may be synonymous. Examples from the late Proterozoic of Russia include *Kaisalia* and *Kullingia* (see Fedonkin, 1985, pl. 1-6 and 6-6). The latter genus was originally described from the late Proterozoic of Sweden and Australia (see Foyt & Glaessner, 1979, fig. 8a, b). More recently, excellent examples have been recorded from the basal Cambrian Unit 2 of the Chapel Island Formation on Newfoundland, Canada (Narbonne et al., 1991). Similar forms have been described from the Lower Cambrian of Chengjiang, China as *Rotadiscus* (Sun & Hou, 1987, pl. 3) but these are considered by Conway Morris (1993, p. 597) to be related to *Velumbrella*. Forms resembling *Kullingia* but smaller and with additional radial ornament, have been described from the Lower Cambrian of Spain as *Scenella* and also referred to the chondrophorines (Yochelson & Gil Cid, 1984) but, according to Conway Morris (personal communication, 1996), it has a hard shell and cannot therefore have been a chondrophorine. There is also little to separate the Proterozoic *Kullingia* and *Kaisalia* from *Silurovelella* from the Silurian of New York, U.S.A. (Fisher, 1957), *Plectodiscus* from the Devonian Hunsrück Slate, Germany (Yochelson et al., 1983) and the Carboniferous of Malaysia (Stanley & Yancey, 1986), or even from *Palaeophacmaea* from the Lower Cretaceous of Japan (Stanley & Kanie, 1985).

There are also many other discoidal structures preserved in strong relief on sandstone or siltstone soles and described as trace fossils. The simplest are flat to button shaped circular to subcircular structures and recorded widely from the late Proterozoic as *Namiana* and *Beltanelliformis*. The literature was reviewed by Narbonne & Hofmann (1987) who considered *Namiana* a junior synonym of *Beltanelliformis*. Remarkably similar structures have, however, been described from Cambrian and younger strata as *Bergaueria* (see Pemberton et al., 1988). They occur in the Lower Cambrian in Alberta and Newfoundland, Canada (Arai & McGugan, 1968), California, U.S.A. (Alpert, 1973), North Spain (Crimes et al., 1977), Central Spain (Schmitz, 1971) and India (Raina et al., 1983); the Middle Cambrian in Wyoming, U.S.A. (Boyd, 1974) and Arizona, U.S.A. (McKee, 1945); and the Upper Cambrian in Argentina (Aceñolaza, 1978) and Poland (Radwanski & Roniewicz, 1963). Narbonne & Hofmann (1987) noted the similarity between *Beltanelliformis* and *Bergaueria* but suggested that

the former represented the impression of a soft bodied organism, while the latter was a hemispherical burrow fill. Both commonly show concentric ornament. In section, however, it may be impossible to maintain any consistent differentiation, so that, for example, *Beltanelliformis* from the late Proterozoic of Canada illustrated by Narbonne & Hofmann (1987, pl. 75, fig. 2, 4) seems remarkably similar to an example of *Bergaueria* from the Silurian figured by Pickerill (1989, fig. 3c). Some structures referred to *Beltanelliformis* appear as complete spheres but, these apart, it is difficult to maintain the separation from *Bergaueria*.

Discoid structures resembling *Bergaueria*, but with numerous unbranched radial ridges surrounding a central axial cylinder, are designated as *Astropolichnus* and occur commonly in the Early Cambrian (e.g. Crimes et al., 1977; Pillola et al., 1994). Similar probably synonymous, structures occur in the Early Cambrian of Chengjiang and were designated as *Yunnanomedusa* (Sun & Hou, 1987) and also at the same horizon in Poland where they were referred to "*Peytoia*" (Masiak & Zylinska, 1994). Similar structures have also been recorded as *Aspidella* by Vodanjud (1989) from the Khatyspyt Formation of the Olenik uplift, Siberia regarded as late Proterozoic by Knoll et al., (1995). An example from the late Proterozoic of Newfoundland recorded as *Aspidella terranovica*, Walcott 1899 by Hofmann (1971, pl. 5-2) with the comment that it may not belong to this "species" has much in common with *Astropolichnus* consisting as it does of a nearly flat depression and radial ridges and grooves which pass out from the depression to the periphery (Hofmann, 1971, p. 15). There is clearly need for a thorough re-examination of all these circular structures, but it seems that some forms continued with little change from the Proterozoic into the Phanerozoic.

Indeed, it appears that many elements of the Ediacara fauna continue well beyond the Proterozoic and even forms such as *Spriggina* and *Vendia* are now considered as forerunners of the trilobites (Runnegar, 1982; Conway Morris, 1985; Jenkins, 1992). A soft bodied trilobite has also been described from the late Proterozoic in South Australia (Jenkins, 1992). Some unusual forms such as *Dickinsonia*, *Bomakellia* and *Tribrachidium* have not yet been recorded in the Phanerozoic nor have the sediment pervading forms of *Pterinidium* and *Ernieetta*, which may have suffered from the advent of deep burrowing at about the base of the Cambrian. There clearly was some faunal turn-over at the Proterozoic/Phanerozoic boundary but there does not seem to have been a mass extinction.

A similar conclusion can be reached from the trace fossil evidence. There is a gradual increase in trace fossil diversity which accelerates into the Phanerozoic

(Crimes, 1992a) so that all the main trace fossil lineages were established by the end of the Early Cambrian, including complex burrow systems (e.g. *Chondrites*, *Phycodes*, *Treptichnus*), spreite burrows (e.g. *Diplocraterion*, *Treichichnus*) and trilobite traces (*Cruziana*, *Diplichnites*, *Rusophycus*). Many of these forms continue through much or all of the Phanerozoic. There is, however, an absence in the Cambrian of the short ranging bizarre forms which characterise the late Proterozoic (e.g. *Harlaniella*, *Nenoxites*, *Palaeopascichnus*). The trace fossils and body fossils suggest that a period of "early evolutionary failure" has been replaced by the "dawn of evolutionary success" at about the base of the Cambrian (Crimes, 1994). However, continuation of many ichnogenera across the boundary (Crimes, 1992a) precludes any mass extinction.

#### Changes in the habitat of the Ediacara survivors.

The delicate discoid fossils, such as *Kullingia*, referred to the chondrophorines seem to have normally occupied a shallow water niche in both the late Proterozoic and Phanerozoic (e.g. Yochelson & Gil Cid, 1984; Stanley & Kanie, 1985; Narbonne et al., 1991). The same seems to have been true of the discoid structures, such as *Beltanelloides*, *Bergaueria* and *Astropolichnus*. However, the more complex discoid types such as *Ediacaria* seem to have left their shallow water niches of the Proterozoic to inhabit the deep sea by the Late Cambrian (Crimes et al., 1995). Also, whereas most frond-like forms existed in shallow water in the Proterozoic, their records from the Lower and Middle Cambrian come from a deeper water slope environment (Conway Morris, 1993).

Rather more is known about the habitats of the trace fossils. Tightly meandering burrows (e.g. *Helminthoida*), spirals (e.g. *Protospiralichnus*) and network structures (e.g. *Paleodictyon*) are present in late Proterozoic and early Cambrian shallow water sediments but subsequently migrated into the deep ocean (Crimes & Anderson, 1985; Crimes et al., 1992; Crimes & Fedonkin, 1994).

It appears that not only the trace fossils but also the body fossils show an onshore-offshore migration at about the base of the Cambrian, probably to escape the intense competition and dispersal pressures which must have by then built up in the shelf communities.

#### Conclusions.

The main conclusions that can be drawn from this study are:

1. Megascopic body and trace fossils increased markedly in abundance and diversity through the late

Proterozoic, mostly occupying shallow water niches in clastic seas. There was minimal penetration into deeper waters and true oceanic depths were probably not colonised.

2. The late Proterozoic shelf communities included static benthic organisms (e.g. *Cyclomedusa*, *Ediacaria*), frond-like forms anchored to the sea-floor (e.g. *Charniodiscus*) and other frond or vane-like forms (e.g. *Pteridinium*) and sac like forms (e.g. *Ernietta*) which grew wholly within the sediment by a process of permeation and may be related to unicellular Protozoa. Pelagic organisms were much less abundant than was first thought.

3. Trace fossils are rare in most beds with Ediacara fossils. They are most notably absent in those beds where the body fossils lived within the sediment. In other facies, the ichnofauna is dominated by horizontal burrows and trails exploiting two dimensional ecospace.

4. There was a turn-over in body and trace fossils at about the Proterozoic-Phanerozoic boundary but most forms which became extinct were rather bizarre, including body fossils such as *Bomakellia* and *Tribrachidium* and trace fossils such as *Nenoxites* and *Palaeopascichnus*.

5. There is increasing evidence that many or most Ediacaran body and trace fossils have direct or close descendants in the Cambrian and even younger strata. There does not seem to have been a mass extinction at the close of the Proterozoic.

6. Some of the Ediacara survivors may, however, have escaped the intense competition of shallow water niches by a process of onshore-offshore migration.

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