



The Vendian (Ediacaran) in the geological record: Enigmas in geology's prelude to the Cambrian explosion

G.J.H. McCall *

Western Australian Museum, Perth, Australia

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Abstract

Up to the 1950s, the Precambrian was regarded as unrewardingly unfossiliferous, records of fossils being isolated, few in number and dubious. The change came with the discovery by Reg Sprigg of body fossils in latest Proterozoic sediments in South Australia. Although there had been descriptions of isolated fossils (now recognised as Ediacaran) from rocks of this age in the nineteenth century and at the start of the twentieth century, in Newfoundland and Namibia, respectively, the Ediacara finds stimulated researches and now, at the start of the twenty-first century, diversified fossil assemblages are known, all over the world, from the period 600–543 Ma, known formerly as the Vendian and now officially as the Ediacaran. In this account, a brief description of the history of these finds is given, followed by descriptions of the most important provinces [South Australia, Leicestershire, Namibia, Russia (Podolia, the White Sea Coast, Urals and Siberia), Newfoundland (Avalon Peninsula) and Northwest Canada]: then of 27 other known occurrences of this dominantly soft-bodied and perplexing fauna (?)—it seems certain that some, at least of the fossils, are animal fossils, although some, even the greater part, could be a unique form of life, not animals or plants (“Vendobionta”). These descriptions, derived in the course of a literature search lasting over a year, are followed by discussions of important special aspects: trace fossils; geochronology and correlation; geotectonics; glaciation (the “Snowball Earth” concept applied to the Varangian/Laplandian/Marinoan glaciation, which ushered in this last subdivision of the Proterozoic); the evidence for Ediacaran and other life forms existing in the Proterozoic prior to its last, Ediacaran, chronological subdivision; the Vendozoa concept. The last section consists of short summary of conclusions. This text essentially constitutes an objective record of what has been published to 2005 on the Ediacaran System. © 2006 Elsevier B.V. All rights reserved.

Keywords: Vendian; Ediacaran; Neoproterozoic; body fossils (soft-bodied); trace fossils; glaciation

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* Present address: 44 Robert Franklin Way, South Cerney, Gloucestershire, GL7 5UD, UK. Tel.: +44 1 285 860470.

E-mail address: joemccall@tiscali.co.uk.

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“Strangely, when I exhibited my original fossil discovery of *Ediacaria flindersi*, as I named it, to the ANZAAS conference in Adelaide in August 1947, Martin was not impressed. He pronounced it fortuitous inorganic markings, as did Professor Mawson, another assiduous searcher for Precambrian fossils. Only Dr Curt Teichert came to me and said “Don’t worry Sprigg, it just might be a fossil”. The rest is now history.....” R. C. Sprigg (1991).

1. Introduction

1.1. The Vendian (Ediacaran)

The ‘Vendian’ is the Eastern European usage adopted for the latest Precambrian: the uppermost subdivision of the Neoproterozoic. The term Ediacaran has also been applied to this period, on account of the important fossil finds in South Australia, and this term in the official usage as decided at the International Geological Conference at Florence in 2004. The term Vendian is used throughout this text, but the two terms are accepted as synonymous. The time range of this period is from ~600 to 543 million years. The lower boundary is not well defined but is taken as the Varangian/Laplandian/Maranoan glaciation. The upper boundary with the Cambrian is defined by a Global Stratigraphic section in Newfoundland.

The Neoproterozoic is divided into a system of suberas, the terms Cryogenian and Tonian are used here for the divisions of the prior part of the Neoproterozoic

(below the Vendian/Ediacaran, but the alternative usage of Sinian and Riphean are avoided as far as possible, although they may be used in reference to Russian or Chinese literature. The Sinian (Harland et al., 1989) extends back from the Cambrian boundary to ~800 Ma and the Riphean actually extends from that point right across the Neoproterozoic lower boundary to ~1650 Ma.

This period assumed great importance to geologists with the discovery of soft-bodied fossils at Ediacara in the Flinders Range, South Australia, by Reg Sprigg in 1947. Individual fossils, which we now know were of the unique soft-bodied Ediacara-type had in fact been described previously—*Aspidella* by Billings in (1872) and *Rangea* by Range in 1908–1914—but it was the Ediacara find that triggered research in many parts of the world into this new and important chapter in the story of the fossils and evolution.

This account is essentially a database prepared by an exhaustive literature search over a period of 1 yr into this topic. The geographically ordered descriptive sections are followed by discussion of a number of special aspects—trace fossils, geochronology and stratigraphy, geotectonics, glaciation, possible fossil ancestors and forerunners of the Ediacara-type fossils in the earlier Proterozoic, and the Vendozoa attribution. A short final section discusses some conclusions reached by the author and wider issues: except for this, the text is a factual record of what had been published up to the year 2005.

Table 1
List of the other occurrences of the Ediacara faunas

Country, etc.	Province
NW Africa	Algeria Morocco
Australia	Amadeus Basin, Northern Territory Stirling Range, Western Australia
China	Liao Dun Peninsula, Laoning Province Eastern Heilongjiang Province Yangtse Gorge, Anhui and Hubei Provinces South Sha'anxi Province
England	Shropshire
India	Lesser Himalayas Central India
Iran	Alborz Mountains Khusk
Ireland	Wexford
Mexico	Sonora
Norway	Finnmark
Oman	Birba
Sardinia	Caligliari
South America	Argentina Brazil Uruguay
Spain	Galicia Toledo
USA	California Nevada North Carolina
Wales	Carmarthenshire

List of the provinces other than the major ones in S. Australia, England, Namibia, Russia, Canada (Newfoundland) and NW Canada.

1.2. Evidence of life in the Precambrian

Up to the middle of the twentieth century, it was taught that the Precambrian was devoid of fossils. The dictum of Lawson (1913) summed up the geological thinking:

“We look across the epi-Archaean unconformity into the ruins of an Archaic world”

Advances in knowledge since the mid-twentieth century have changed this situation. Earliest direct evidence of life in the Precambrian comes from records of microfossils in cherty rocks and stromatolites in Archaean rocks ~3500 Myr old at North Pole in the Pilbara Craton, Western Australia (Schopf, 1992). However, these remain questionable (Brasier, 2005). Stromatolites, organosedimentary structures produced by sedimentary trapping, binding and/or precipitation as the result of growth of unicellular organisms, are not uncommon in younger Archaean rocks—for example those in the Tumbiana

Formation of the Fortescue Group, Western Australia (Ho et al., 1990).

The simple-celled prokaryotes, photosynthetic organisms, were succeeded by eukaryotes with complex protoplasmic arrangements, the cells having nuclei and organelles. There is evidence that the first eukaryote was a sort of aggregate organism, assembled from a consortium of unicellular prokaryotes (“endosymbiosis”).

The first eukaryote fossils are found in Palaeoproterozoic rocks ~2000 Myr old in the Negaunee Iron Formation, Michigan (Xiao, 2005). They have the form of coiled carbonaceous ribbons resembling *Grypania spiralis* of the Mesoproterozoic (1600–1000 Ma). Carbonaceous ribbon fossils are found in the Mesoproterozoic, in which several groups of algal fossils can be recognised, including acritarchs. Further diversification of the algal populations is evident through the Neoproterozoic (1000–540 Ma).

Table 2
Classificatory table (after Sprigg, 1947)

Class	Genus and species	Brief description
Scyphozoa	<i>Ediacara flindersi</i> Sprigg	Circular medusoid imprint, radial symmetry, surface flattened, radial and concentric features of low relief, 3 pendant processes: max. dimension 11 mm.
	<i>Beltanella gilesi</i> Sprigg	Circular medusoid, umbrella rather flat: faint groove divides umbrella zone into two regions: possibly Hydrozoa: max. dimension 110 mm.
Hydrozoa or Scyphozoa?	<i>Cyclomedusa davidi</i> Sprigg	Circular medusoid impression, concentric undulations, centre raised and distinctly nodular; radial symmetry: at least seven annular grooves: outer and median zone traversed by radial striations: max. dimension 50 mm.
	<i>Dickinsonia costata</i> Sprigg	Ovoid. Bilaterally symmetrical impression, essentially flat; median longitudinal furrow ca. 35 mm long, gives off 80–90 radiating and diverging grooves extending to outer margin, which is slightly crenulate, the notches corresponding to the surface grooves: marginal flange: length 68 mm.
	<i>Papillionate everi</i> Sprigg	The impression is rather obscure. Sprigg admits that there may be two organisms superimposed.

Table 3
Further classificatory descriptions (after Sprigg, 1949)

Class	Genus and species	Description
Hydrozoa	<i>Protodipleurosoma wardi</i>	Circular flattened bell impression with radial canals: max. dimension 59 mm. Sprigg noted the similarity to <i>Dipleurosima hemisphaerica</i> Alman (1873), a living form.
	<i>Tateana inflata</i> Sprigg	Circular medusoid, radially symmetrical with only slight radial markings, marginal notches; max. dimension 6.4 mm (i.e. very small): similarity to <i>Ediacara?</i>
	<i>Pseudorhizostomatites howchini</i> Sprigg	Convex impression with cruciform radial grooves, each branching simply once: possible further branching at their ends?: max. dimension 30 mm.
	<i>Pseudorhopilema chapmani</i> Sprigg	Convex impression with central groove giving rise to primary, secondary and possibly tertiary branching: max. dimension > 50 mm.
Problematica	<i>Medusina mawsoni</i> Sprigg	Circular medusoid, with depressed central area, convex, and surrounding annular zone raised centrally, with some radial markings. Margin circular, simple, no appendages: diameter 2.7 mm.
	<i>Madigania annulata</i> Sprigg	Like <i>Cyclomedusa</i> , but no radial markings. Many annular grooves May or may not have central papilla: diameter 170 mm. Largest Ediacaran fossil so far recorded.

The last part of the Neoproterozoic (the Vendian/Ediacaran, from ~600 to 543 Ma) was characterized by global, palaeontological and geochemical events which set the stage for all subsequent Earth history (McMenamin, 2005). Unprecedented change took place in the biosphere and the soft-bodied Ediacarans proliferated globally. Sponges were present and ancestral arthropods (?). The bulk of these fossils may have comprised a unique assemblage which has been termed “Vendozoa”, but many authorities have suggested that among these also were ancestors to Phanerozoic phyla, especially cnidarians. The first shelly fossils appeared at this time, in the form of *Cloudina* and other skeletalised forms. This last period was heralded by a glaciation of great intensity which appears to have affected low latitudes, the Varangian/

Table 4
Geographic distribution of metazoan taxa identified in Ediacaran strata (X₁ and X₂ indicate non-identity of Hydrozoa) (from Glaessner, 1984)

	S Australia	C Austria	SW Africa	S America	E Europe	Siberia	China	Britain	Sweden	Newfoundland	N W Canada	N Carolina
Coelenterata (Cnidaria)	X ₁	X			?	?				X ₂		
Hydrozoa	X	X			X	X						
Scyphozoa	X				X	X						
Conulata	X	X			?							
'Medusoids'	X	X	X		X	X		X				
Pteriniidae	X	X	X		X	X		X			X	
Rangeidae			X									
Charniidae	X	X	X		X	X		X				
Ermetiidae		X	X		X	X						
Amelida (and possibly related phyla)												
Cribricyathaea				?								
Dickinsoniidae	X				X							
Sprigginiidae	X				?							
Anabartiidae						X	X					
Sabelliditida						X	X					?
Echiura			X			X						
Other 'worms'	X	X	X		X	X						
Vendomiidae	X				X							
Parvancorinidae	X				?							
Arthropoda												
Sytematic position unknown												
<i>Redkinia</i>					X							
<i>Tribrachidium</i>	X				X							

Table 5

Composition of the Ediacaran assemblage of the Flinders Ranges, South Australia (from Jenkins, 1992)

Taxa recognized herein	Likely synonyms
Coelenterata	
Phylum Cnidaria	
Class Hydrozoa	
Order Hydroida, Suborder Chondrophorina	
Family Chondrophoridae	
<i>Chondroplon Bilobatum</i> Wade, 1971	
<i>Ovatoscutum concentricum</i> Glaessner and Wade, 1966	
?Family Porpitidae	
<i>Eoporpita medusa</i> Wade, 1972a,b	
Suborder uncertain	
Family Conchopeltidae	
<i>Conomedusites lobatus</i> Glaessner and Wade, 1966	
Class Cubozoa	
?Order Carybdeida	
<i>Kimberella quadrata</i> (Glaessner and Wade, 1966)	
?Class Scyphozoa	
Family uncertain	
<i>Rugoconites enigmaticus</i> Glaessner and Wade, 1966	
<i>Wadea tenuirugosus</i> (Wade, 1972a) gen. nov.	
Sedentary medusoids or polypoids	
<i>Ediacaria flindersi</i> Sprigg, 1947	
<i>Cyclomedusa davidi</i> Sprigg, 1947	
<i>Inaria karli</i> Gehling, 1988	
<i>Medusinites asteroides</i> Sprigg, 1949	
<i>Hiemalora stellaris</i> (Fedonkin, 1980a,b,c)	
<i>Mawsonites spriggi</i> Glaessner and Wade, 1966	
<i>Mawsonites randellensis</i> Sun, 1986	
Colonial Cnidria possibly related to Pennatulacea	
<i>Charniodiscus arboreus</i> (Glaessner, 1959)	
<i>Charniodiscus longus</i> (Glaessner and Wade, 1966)	
<i>Charniodiscus oppositus</i> Jenkins and Gehling, 1978	
<i>Glaessnerina grandis</i> Glaessner and Wade, 1966	
Order Rangeomorpha	
<i>Rangea ? schneiderhoehni</i> Gürich, 1929	
Phylum Petalonamae	
Family Pteridiniidae	
<i>Pterinidium nenoxa</i> Keller, 1974	
? <i>Pterinidium simplex</i> Gurich (1933)	
<i>Phyllozoon hanseni</i> Jenkins and Gehling, 1978	
Phylum uncertain	
<i>Branchina delicata</i> Wade, 1972a,b	
<i>Nemiana simplex</i> Palij, 1976	
Coelomata	
Phylum Annelida	
Class Polychaeta	
Family Dickinsoniidae	
<i>Dickinsonia costata</i> Sprigg, 1947	
<i>Dickinsonia lissa</i> Wade, 1972a,b	
<i>Dickinsonia rex</i> nom nov. [for <i>Dickinsonia elongata</i> Glaessner and Wade, 1966 (sensu lato)]	
<i>Dickinsonia tenuis</i> Glaessner and Wade, 1966	
Family Sprigginiidae	
<i>Spriggina floundersi</i> Glaessner, 1958	
Articulate of uncertain placement	
<i>Marywadea ovata</i> (Glaessner, 1976)	
Phylum Arthropoda	

=?*Lorenzenites rarus* Glaessner and Wade, 1966=*Beltanella gilesi* Sprigg, 1947=*Cyclomedusa plana* Glaessner and Wade, 1966=*Cyclomedusa radiata* Sprigg, 1949=*Spriggia annualata* (Sprigg, 1949)=*Spriggia wadea* Sun, 1986a

Table 5 (continued)

Taxa recognized herein	Likely synonyms
Family Parvancorinidae	
<i>Parvancorina minchami</i> Glaessner, 1959	
Family Vendomiidae	
<i>Praecambrium sigillum</i> Glaessner and Wade, 1966	
?Family Trilobita	
Unnamed genus and species	
Phylum Tribrachidia nov.	
Family Tribrachidia nov.	
<i>Tribrachidium heraldicum</i> Glaessner, 1959	
Phylum Echinodermata	
Class Edrioasteroidea	
<i>Arkaruo adomi</i> Gehling, 1987	

Laplandian/Marinoan glaciation. Besides the effects of this glaciation and its retreat, the period was one characterized by the last stage of the break up of the supercontinent of Rodinia, with changes in palaeogeography and marine sedimentation patterns related to that, overprinted by the post-glacial changes. The climatic variability during this period is evidenced by fluctuations in the carbon and strontium isotope records.

2. Historical

2.1. Introduction

In the paragraphs below the history of recognition and research into the several *major* geographical developments of the Ediacara-type faunas is briefly summarised and the numerous other geographical developments are listed (see Table 1). All these ‘provinces’ are covered by descriptions in Sections 3–13: their locations are shown on a global diagram in Fig. 1, more precise locational diagrams being provided in the relevant chapters.

Table 6
Classification of fossils from the Nama Group

Group or phylum	Name
1. Group Petalonamae	<i>Rangea schneiderhoehni</i> <i>Pteridium simplex</i> <i>Ernietta plateauensis</i> <i>Nasepia altae</i> <i>Namalia villierensis</i>
2. Phylum Coelenterata (Medusoids)	<i>Cyclomedusa davidi</i>
3. Phylum Archaeocyatha (?)	<i>Cloudina hartmannae</i> <i>Cloudina riemkeae</i>
4. Problematica	

2.2. South Australia

The story of the Ediacaran fossils, believed to be soft-bodied Metazoa, commences in South Australia, the location of Ediacara in the Flinders Ranges. Megafossils had been found in the Precambrian before; Ramsay (1858), Hill and Bonney (1877) and Watts (1947, publication of much earlier work) had noted disc-like impressions in the Charnian (late Precambrian) rocks of Leicestershire, England, but thought they were inorganic (they did not apparently notice the frond-like impressions). *Aspidella terranovica* was described by E. Billings from Newfoundland in 1872 and has lately been claimed by Gehling et al. (2000) to be the earliest described Ediacara-type soft-bodied fossil. The fossil *Rangea*, another Ediacara-type soft-bodied fossil had been collected in Namibia 1908–1914 by P. Range and H. Schneiderhohn. There were also many records of Proterozoic fossils in the form of megascopic filaments, but all these appear to have been of algal affinity and not Ediacara-type fossils. No multiple fauna of Neoproterozoic ?Metazoa was known until in 1946, when Reg Sprigg, then Assistant Government Geologist in South Australia, examined old lead mines in the Ediacara Hills, a desolate low range in arid country 600 km north of Adelaide (Sprigg, 1988). A man with boundless energy and an enquiring mind, he was, despite his main interest in the potential for reopening mining there, a diligent fossil hunter and to his surprise he saw numerous casts of “jellyfishes” in an unpromising quartzite. He described them in two papers (Sprigg, 1947, 1949), including further specimens collected by Sir Douglas Mawson and his students (see Tables 2,3). He had no hesitation in describing them as Hydrozoa or Scyphozoa, although some he thought were algae. He numbered them as “among the oldest direct records of animal life in the world”, However, in his titles, he listed

Table 7

The system of classification suggested for Ediacara-type organisms by Fedonkin in Sokolov and Iwanovski, 1985 (1990 translation)

Symmetry group	Form	Subdivision	Vendian examples	Remarks
Radialia	Symmetry axis of infinitely high order	Undifferentiated forms	<i>Beltanelliformis</i> <i>Nemiana</i> <i>Paliella</i> <i>Tirasiana</i>	B and N are the most primitive forms, comparative symmetry rare in Recent Cnidarians.
		Forms with concentric differentiation of the body 1) Oligocyclic 2) Polycyclic 3) Constant number of concentric rings	1) <i>Cyclomedusa</i> 2) <i>Eoporpita</i> 3) <i>Ediacaria</i>	<i>Cyclomedusa</i> , a very diverse and common genus in Vendian: classification needs improving. <i>Ediacaria</i> is the largest Vendian medusoid.
	Symmetry axis of uncertain order		<i>Armillifera</i> <i>Bonata</i> <i>Elasenia</i> <i>Evmiakisia</i> <i>Hiemalora</i> <i>Stauridinia</i> <i>Elasenia</i>	These may combine radial and concentric body plan.
	Radial symmetry of a stable order	1) Three-fold symmetry 2) Four-fold symmetry 3) Six-fold symmetry	1) <i>Albumares Tribraichidium</i> 2) <i>Cono-medusites</i> 3) <i>Pomoria</i>	Doubts whether <i>Tibraichidium</i> is an organism of Coelenterate level. <i>Pomoria</i> , a small Vendian medusoid is unique in this respect
Bilatera	Bilateral Symmetry	Unsegmented	<i>Platypholina</i> <i>Vladimissa</i>	
		Segmented 1) Polymerous 2) Sabellitids 3) Oligomorous	1) <i>Dickinsonia</i> <i>Palaeoplatoda</i> 2) <i>Sabellitides</i> <i>Paleolina</i> <i>Saarina</i> <i>Caluptrina</i> 3) <i>Praecambridium</i> <i>Vendia</i> <i>Vendomia</i> <i>Pseudovendia</i> <i>Onega</i>	

them as Early Cambrian, this attribution being later corrected.

In 1957, Hal Mincham and Ben Flounders visited the site (Glaessner, 1984) and made a large collection of fossils which they presented to the South Australian Museum. From photos taken by them, Glaessner, although he had initially poured cold water on Sprigg's finds (Sprigg, 1991), came to realise that here were fossils never seen before (see Table 4). In 1958, an expedition was mounted, led by Dr Brian Daily of the Museum. The fossils collected filled two small trucks and a trailer. The locality was then proclaimed a State Reserve. Another expedition was mounted by the Museum and Martin Glaessner, representing the University of South Australia Geology Department. Over years of systematic collection more than 1500 fossils

were collected. Other fossiliferous localities were later identified in the same Pound Quartzite, which is the highest stratigraphic unit in the Adelaide System—so named by Mawson (1938) who measured the section and noted worm tracks. The name was taken from Wilpena Pound, an elliptical synclinal feature 40–60 km to the south of the Ediacara site.

In all the fossiliferous localities, the fossils are confined to a section up to 112 m thick (Wade, 1970). The Pound Quartzite has a white member above a dominantly reddish member, the upper member being named the Rawnsley Quartzite, and the silty fossiliferous unit within it was later, in a stratigraphic revision, termed the Ediacara Member (Jenkins, 1981). The total thickness of the Pound Quartzite varies because of erosion at its top, below the Uratanna Formation, and original conditions of

Table 8

Geographic distribution globally of fossil remains of Ediacara-type soft-bodied organisms [after Sokolov and Iwanovski, 1985 (1990 translation)]

	1	2	3	4	5	6	7	8	9
<i>Nemiana simplex</i> Palij		x	x	x					
<i>Beltanelliformis brunsa</i> Menner	x	x							
<i>Bronicella Podolica</i> Sokolov			x						
<i>Sekwia excentrica</i> Hofmann								x	
<i>Nimbia oclusa</i> Fedonkin									
<i>N. dniesteri</i> Fedonkin		x	x						
<i>Tirasiana disciformis</i> Palij		x							
<i>T. coniformis</i> Palij		x							
<i>Cyclomedusa davidi</i> Sprigg		x	x	x			x		
<i>C. radiata</i> Sprigg		x	x	x					
<i>C. plana</i> Glaessner et Wade		x	x	x					
<i>C. gigantea</i>					x				
<i>C. serebrina</i> Palij				x					
<i>C. minuta</i> Fedonkin	x								
<i>C. delicata</i> Fedonkin	x								
<i>Ediacaria flindersi</i> Sprigg		x	x	x	x			x	
<i>Beltanella gilesi</i> Sprigg					x				
<i>Medusinites asteroides</i> (Sprigg)	x	x	x	x				x	
<i>Medusinites patellaris</i> Sokolov			x						
<i>Planomedusites grandis</i> Sokolov			x						
<i>Kullingia concentrica</i> Føyn et Glaessner				p				x	
<i>Kaisalia mensae</i> Fedonkin		x							
<i>Ovatoscutum concentricum</i> Glaessner et Wade		x		x	x				
<i>Chondroplon bilobarum</i> Wade		x			x				
<i>Eoporpita medua</i> Wade		x	x	x					
<i>Mawsonites spriggi</i> Glaessner et Wade				x					
<i>Protodipleurosoma wardsi</i> Sprigg					x				
<i>P. rugulosum</i> Fedonkin		x	x						
<i>Hallidaya brueri</i> Wade								x	
<i>Lorensinites rarus</i> Glaessner et Wade					x				
<i>Pseudorhizostomites howchini</i> Sprigg		x	x	x					
<i>Rugoconites enigmaticus</i> Glaessner et Wade					x				
<i>R. tenuirugosus</i> Wade					x				
<i>Hiemalora stellaris</i> Fedonkin		x	x	x					
<i>Pomoria corolliformis</i> Fedonkin		x							
<i>Bonata septata</i> Fedonkin		x							
<i>Armillifera parva</i> Fedonkin		x							
<i>Evmiaksia aksinovi</i> Fedonkin		x							
<i>Irridinites multiradiatus</i> Fedonkin			x						
<i>Veprina undosa</i> Fedonkin		x							
<i>Elasenia aseevae</i> Fedonkin			x						
<i>Tribrachidium heraldicum</i> Glaessner		x	x	x					
<i>Scinnera brooksi</i> Wade								x	
<i>Albumares brunsa</i> Fedonkin	x								
<i>Anfesta stankovskii</i> Fedonkin		x							
<i>Staurinidia crucicula</i> Fedonkin		x							
<i>Conomedusites lobacus</i> Glaessner et Wade		x	x	x					
<i>Persimedesites chahgazensis</i> Hahn et Pflug								x	
<i>Ichnusina cocozzi</i> Debrene et Naud									x
<i>Glaessnerina longa</i> (Glaessner et Wade)				p	x			p	
<i>G. grandis</i> (Glaessner et Wade)									x
<i>Arborea arborea</i> (Glaessner)					x				

Table 8 (continued)

	1	2	3	4	5	6	7	8	9
<i>Charniodiscus concentricus</i> Ford			p					x	
<i>C. planus</i> Sokolov				x					
<i>C. oppositus</i> Jenkins et Gehling		x	x		x				
<i>C. longus</i> Glaessner et Wade						x			
<i>Phyllozoon hanseni</i> Jenkins et Gehling						x			
<i>Charnia masoni</i> Ford		x		x			x	x	x
<i>Pteridinium simplex</i> (Gürich)							x		
<i>Pteridinium nenoxa</i> Keller		x	x	x		x			x
<i>Rangea schneiderhoehni</i> Gürich							x		
<i>Nasepia altae</i> Germs							x		
<i>Baicalina sensilis</i> Sokolov									x
<i>Arumberia banksi</i> Glaessner et Walter									x
<i>Namalia villiersiensis</i> Germs							x		
<i>Ernietta plateaensis</i> Pflug							x		
<i>Inkrylovia lata</i> Fedonkin		x							x
<i>Archangelia valdaica</i> Fedonkin		x							
<i>Podolimirus mirus</i> Fedonkin					x				
<i>Valdania plumosa</i> Fedonkin						x			
<i>Ramellina pennata</i> Fedonkin					x				
<i>Vaveliksia velikanovi</i> Fedonkin						x			
<i>Zolotytsia biserialis</i> Fedonkin						x			
<i>Vaizitsinia sophia</i> Sokolov et Fedonkin						x			
<i>Lomosovis malus</i> Fedonkin						x			
<i>Dickinsonia costata</i> Sprigg		x	x	x		x			
<i>D. elongata</i> Glaessner et Wade						x			
<i>D. tenuis</i> Glaessner et Wade						x	x		
<i>D. lissa</i> Wade						x		x	
<i>D. brachina</i> Wade									x
<i>Platypholinia pholiata</i> Fedonkin						x			
<i>Vladimissa missarzhevskii</i> Fedonkin						x			
<i>Palaeoplatoda segmentata</i> Fedonkin						x			
<i>Praecambridium sigillum</i> Glaessner et Wade								x	
<i>Parvancorina minchami</i> Glaessner						x		x	
<i>Velancorina martina</i> Pflug								x	
<i>Vendomia menneri</i> Keller						x			
<i>Vendia sokolovi</i> Keller									x
<i>Pseudovendia charnwoodensis</i> Boynton et Ford									x
<i>Onega stepanovi</i> Fedonkin						x			
<i>Spriggina floundersi</i> Glaessner								x	
<i>S. borealis</i> Fedonkin						x			
<i>Marywadea ovata</i> Glaessner								x	
<i>Protechiurus edmondi</i> Glaessner								x	
<i>Bomakellia kelleri</i> Fedonkin						x			
<i>Mialsemia semichatovi</i> Fedonkin								x	

1=Lety (Summer) Coast, 2=Zimny (Winter) Coast, 3=Dniester Basin, Podolia, Ukraine, 4=Khorbusuonka River Basin, Olenek Uplift, Siberia, 5=Flinders Ranges, South Australia, 6=Namibia, 7=Charnwood Forest, England, 8=Newfoundland, 9=other locations, ×=present, p=forms tentatively assigned to this species.

sedimentation: it may reach 3000 m, but is usually near 1000 m. The fossiliferous strata are just above the base of the Rawnsley Quartzite, which is 300 m thick at the find locality. Initially (up to 1959), the occurrence was believed to be of Early Cambrian (Tommotian) age. The

stratigraphic sequence as depicted by Glaessner (1984) is shown in Fig. 2. The fossiliferous occurrence asterisked in the older Moorillah Formation in this figure (c. 2000 m below the Ediacara Member) represents the finds of *Bunyerichmus dalgarnoi*, initially believed to be a trace fossil but later believed to be a subumbrella print of a medusa, about 24 cm in diameter.

The Ediacara fauna of South Australia has been the subject of a large volume of research publications since 1959, led initially by Martin Glaessner and Mary Wade; and later carried out by Jenkins (see Table 5), Gehling and others. This research will be covered later in Section 3.

2.3. Leicestershire, England

The Neoproterozoic fossils of the Charnwood Forest provide some of the earliest records of Ediacara fossils, for Ramsay in 1858, Hill and Bonney in 1877 as well as Watts in 1947 described disc-like impressions (Ramsay thought they were organic, the others dismissed them as inorganic concretions) and these were surely the disc parts of *Charniodiscus*. The modern recognition of body fossils stemmed from the discovery of plant-like impressions by a schoolboy, Roger Mason, and scientific description by Ford in 1958. Two separate fossils were erected by Ford (1958); *Charnia masoni* sp. nov. and *Charniodiscus concentricus* sp. nov. However, the fact that in a single example the disc of the latter is attached to the fronds of *Charnia* indicated that they are parts of the same organism. Medusoids have also been described. Ford (1980) assigned the Charnian fauna to the “Vendian Period” of Precambrian time. Nearby in Warwickshire, the Hartshill Formation is almost certainly at least in part correlative with the Charnian, but it has yielded only trace fossils (Brasier et al., 1978, Brasier, 1979; Brasier and Hewitt, 1979).

The Charnwood Forest occurrences are further described in Section 4.

2.4. Namibia

Precambrian “Metazoa” were collected from the Nama Group in Namibia (South West Africa) by P. Range and H. Schneiderhohn from 1908 to 1914, and these were described by Gurich (1930, 1933). Publications by Richter (1955), Pflug (1966, 1970a,b, 1972a,b, 1973) and Germs (1972a,b,c, 1973a,b, 1974) followed. Gurich named *Rangea schneiderhoehni*, *R.? brevior*, *Pteridinium simplex* and *Orthogonium paralelum*. He believed that the first two genera of frond-like organisms were probably Ctenophora and the

latter probably a sponge. Somewhat later, *Paramecium africanum* was found in the Nasep Quartzite Member higher in the succession, not in the Kuibis Formation where the original discoveries had been made. Another supposed body fossil from the same horizon was thought to be an Archaecyathid but was later identified by Glaessner (1963) as a trace fossil, *Archaeichni haughtoni*. Pflug (1966) described and named *Ernietta plateauensis*, which he thought had attributes between Annelids and Arthropods. Pflug (1970a,b) also described *Rangea* and *Pteridinium* in great detail, demonstrating their complexity. Germs (1968) found a new fossil, *Namalia villiersiensis* and another, *Nasepia altae*, in the Nasep Quartzite Member of the Schwarzkranz Formation. Shelly fossils were also discovered in the Schwarzkalk Limestone Member of the Kuibis Formation and Huns Limestone Member of the Schwartrand Formation, and were named *Cloudina hartmannae* and *Cloudina riemkeae* (Germs, 1972b) (see Table 6). Trace fossils were found in many different lithological units and stromatolites in the limestone Members mentioned above as well as the Spitzkopf Limestone Member of the Schwartrand Formation. Germs (1972b) compiled a memoir-type bulletin, which besides describing the fossils of Ediacara-type found by the author, covered Problematica, microfossils, trace fossils and stromatolites.

The fossiliferous beds occur in the lower part of the Nama Group. The three divisions, Kuibis, Schwartrand and Fish River Subgroups (Germs, 1972b) have more recently been subdivided into a number formations and end members (Kroner et al., 1980; Tankard et al., 1982). The Nama Group consists of a sequence of alternating clastics, mainly orthoquartzites and limestones. Faunal assemblages of Ediacara-type also occur in both, mainly in clastic sediments, but the richest such fauna comes from the lowermost Subgroup, the Kuibis Subgroup, at several localities. They come mainly from orthoquartzites and the composite, sessile, leaf or bag shaped organisms dominate, although the presence of trace fossils (*Planolites*, *Skolithos*) indicates that the fauna was not entirely sessile.

There have been many later publications on the Namibian biota and these are covered together with the stratigraphic framework and detailed descriptions of Germs (1972b) in Section 5.

2.5. Russia (White Sea, Urals, Siberia, Ukraine-Podolia)

The rocks of the Vendian Period were separated from the Riphean in the East European Platform in the mid-



Fig. 1. Global distribution of sites where Ediacara-type fossils have been reported.

20th Century (Sokolov, 1952, 1973; Sokolov and Fedonkin, 1985). From the point of view of analogy with the Ediacaran faunal assemblage, the discovery of equivalent assemblages was really initiated in the 1970s in northern Russia, in the White Sea Region, firstly about 60 km west and later about 100 km north of the city of Archangelsk (Glaessner, 1984). However, single finds of anomalous fossils had been reported in boreholes in northern Russia and also from outcrops along the Dniester River in Podolia, in the western Ukrainian Shield, some 300 km north of the Black Sea. The assemblages in these two regions, although widely separated on the East European Platform are very similar, and these two regions, the Winter Coast of the White Sea and Podolia remain to this day among the most important collecting areas of Vendian fossils and trace fossils. At the time when Glaessner was writing, 10 general and 10 species were shared in common between the Ediacara collections and those of the East European Platform: M. A. Fedonkin, at that time, believed that he had collections of 60–80 different species of body fossils as well as many trace fossils. Collections of Ediacara fossils were extended to Siberia in the early 1980s, in the Olenek Uplift, the Angara River region and the River Maya Area near the Sea of Okhotsk in Eastern Siberia. The Vendian fauna of the East European Platform, particularly that of the White Sea coast, is the most like the Ediacaran type fauna from South Australia of any of the many global occurrences now known, and this similarity has, wisely or unwisely, given cause to jiggling about the pieces of the megacontinental mass of Rodinia, so as to bring them closer together.

The results of researches in all these regions of Russia and the Ukraine are covered in Section 6.

2.6. *Canada, Newfoundland*

A rich fauna was found at Mistaken Point, in the Avalon Peninsula, south of St. Johns (Anderson and Misra, 1968; Misra, 1969). Since then many more late Precambrian fossil localities have been recognised. The Mistaken Point Formation occurs at the top of the Conception Group and is described as being composed of grey to pale red sandstone and purple shale, with some tuffs, and is profusely fossiliferous with a variety of frond-like and disc-like impressions (Williams and King, 1975). Fossils occur on bedding plane surfaces, commonly showing asymmetrical ripple marks, in thin horizons (<1 cm thick) beneath tuff horizons. They are concentrated towards the top of the Formation and occur in five or more horizons. The Conception Group occurrences have been considered to resemble those of the Charnian, in England, both in setting and nature of the fauna. There is, however, a glacial tillite in the lower part of the Conception Group (Fig. 65), something missing in the Charnwood Forest. The dating of the Conception Group was then uncertain: Anderson (1972) covers this discussion. There is general agreement that the Group is Vendian and the tillite represents the Varangian (Laplandian) Glaciation. Hardness and cleavage prevented removal of specimens and Anderson and Misra (1968) reported that they had to work in situ in the field or by making casts and peels.

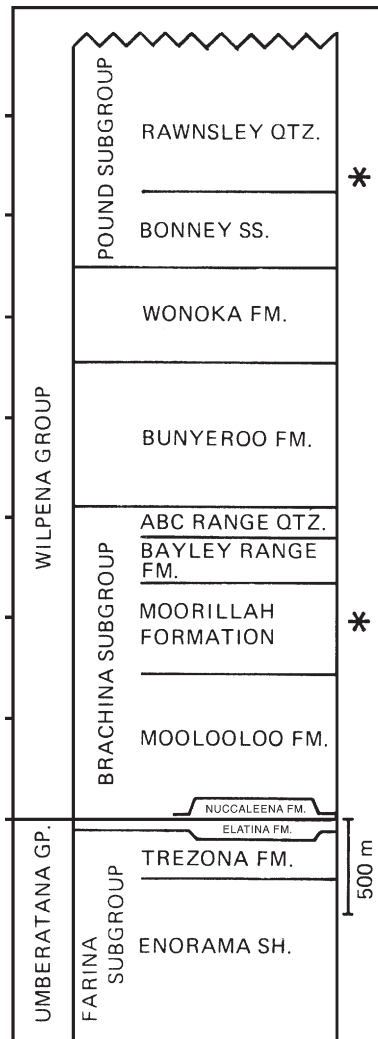


Fig. 2. The stratigraphic section at Ediacara (from Glaessner, 1984. Reprinted with permission of Cambridge University Press).

The researches on the Newfoundland occurrences are covered in more detail in Section 7.

2.7. Northwest Canada (North West Territories, Yukon, British Columbia)

Hofmann (1981) discovered an Ediacara-type fauna, the first discovery in the Canadian Cordillera, in the Mackenzie Mountains of northwest Canada and Narbonne and Aitken (1990) and Narbonne et al. (1995) later made extensive collections and described these occurrences in detail. Narbonne and Hofmann (1987) described extensive collections from the Wernecke Mountains in the Yukon. The Yukon finds were in a shallow-water environment, like the Ediacara finds in the type area, but the later Sekwi

Brook, Mackenzie Mountains, North West Territories finds (Narbonne and Aitken, 1990) were in sediments of a deeper slope facies, of turbiditic character.

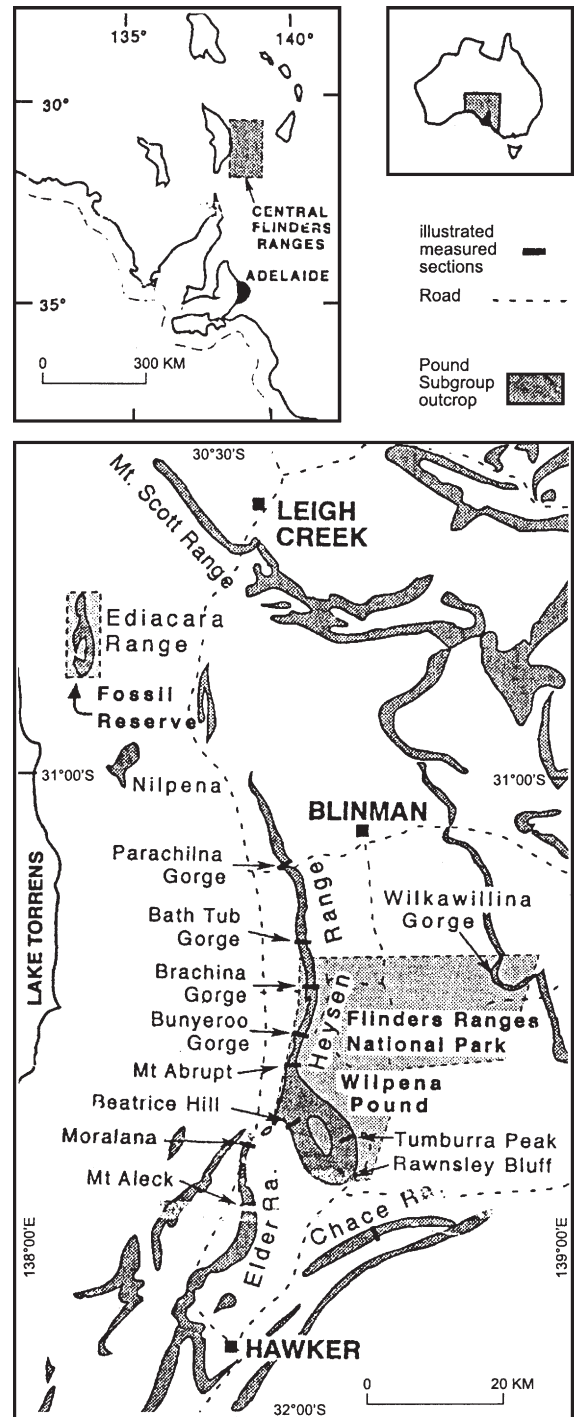


Fig. 3. Locality diagram of collection sites and Pound Subgroup outcrops (stippled) in the Flinders Ranges, South Australia (after Gehling and Rigby, 1986).

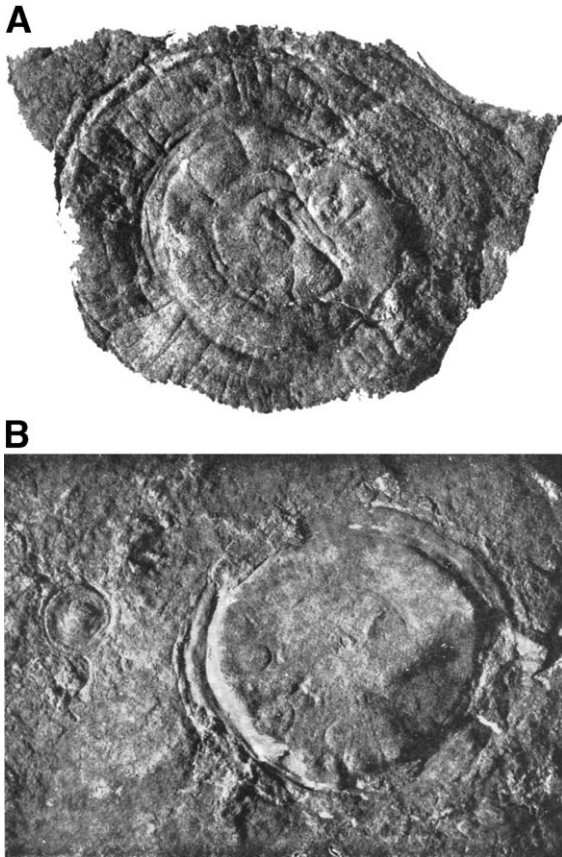


Fig. 4. (A) *Ediacaria flindersi* Sprigg ($\times 5/8$); (B) *Beltanella gilesi* Sprigg ($\times 2/3$) (from Sprigg, 1947).

Hofmann et al. (1985) had described earlier a further find elsewhere in the Cordillera, in the Mount Robson Provincial Park, British Columbia, in a carbonate platform setting containing also shallow-water shales and siltstones. Hofmann et al. (1990) described a fauna from intertillite beds, lower in the Windermere Supergroup than any of the other discoveries: this unique discovery is of impressions of slightly less obvious biogenicity than the other occurrences in Western Canada, but similarity of the discs with those in the other occurrences impressed these authors as to their biogenicity.

The descriptions of the Western Canada occurrences are exceedingly well presented and this region must be considered now as a major site of the Ediacara-type fauna. These occurrences are more fully described in Section 8.

2.8. Other occurrences

The principal geographical developments of Ediacaran/Vendian sediments and faunas are introduced

above. During the last 30 yrs, a number of new developments have been described, and some already fossiliferous sequences which were already mentioned in the literature have been added to the global record of Ediacaran assemblages. These developments are listed here in Table 1, fuller mention being given later in the text.

3. South Australia

3.1. Introduction

The geological setting of the Ediacara finds (Fig. 3) is briefly introduced in Section 2. Sprigg (1947, 1949) published two descriptions of the fossils, very well presented with drawings and photographs of high quality. In the first he described the find briefly as beneath the Cambrian Archaeocyathinae limestones in the Flinders Ranges, the fossils occurring as imprints on the surface of flaggy quartzites. Five genera and species

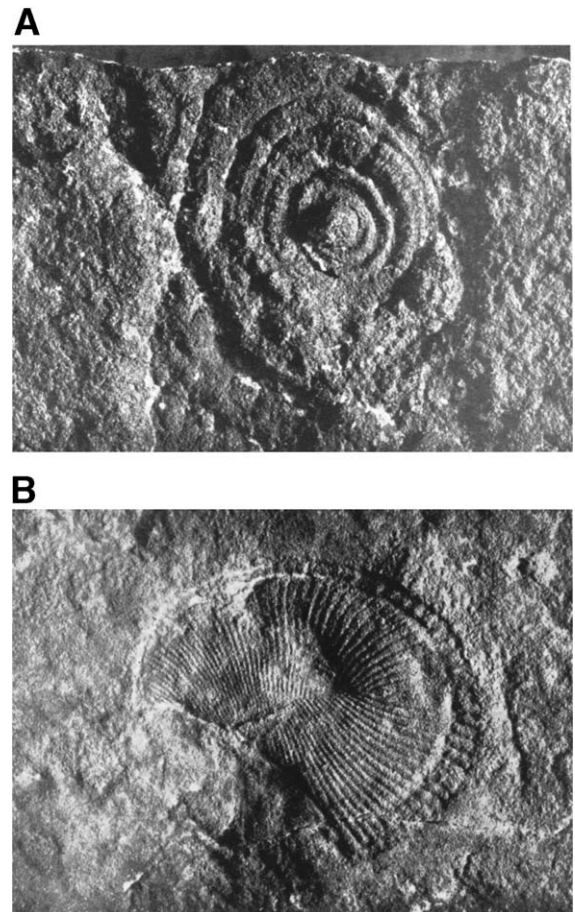


Fig. 5. (A) *Cyclomedusa davidi* Sprigg ($\times 5/3$); (B) *Dickinsonia costata* Sprigg ($\times 1$) (from Sprigg, 1947).

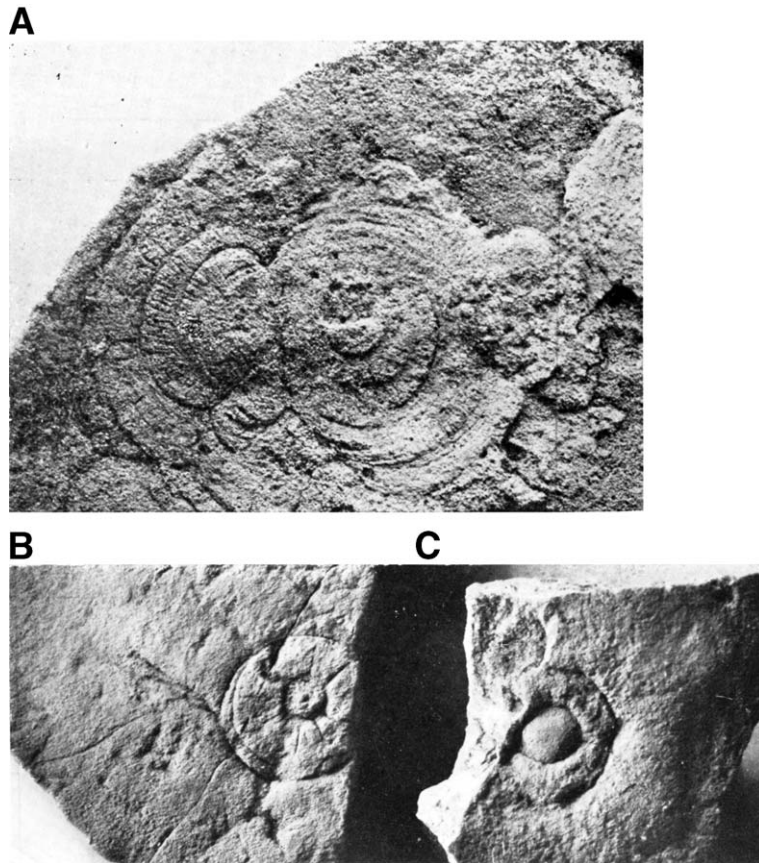


Fig. 6. (A) *Cyclomedusa davidi* Sprigg showing two lateral buds replicating adult form; (B) *Medusina asteroides* Sprigg, holotype; (C) *Medusina mawsoni* Sprigg, holotype (from Sprigg, 1949).

were described which were considered to be almost certainly pelagic Coelenterata, several being referred to the Class Scyphozoa and one or more species being possibly more correctly referred to the Hydromedusae. The more problematic fossils might be pneumatophores or “swimming bells”. All appeared to lack hard parts. He noted that fossil jellyfish as casts and imprints were



Fig. 7. *Madigania annulata* Sprigg, holotype (from Sprigg, 1949).

known from the Lower Cambrian of New York, Sweden, Russia and Bohemia; from the mid-Cambrian of British Columbia and Alabama; from the Silurian, Permian, Jurassic (the renowned Solnhofen occurrences) and Cretaceous. He believed that the Ediacara fossils were probably of Early Cambrian age [although later researches showed that they were in fact of latest Precambrian, Neoproterozoic (=Vendian) age].

Preservation was discussed, a shallow-water environment while alive and rapid burial, entirely in water, being suggested. In the other cases, medusoids had been found in extremely fine-grained slates, so the preservation was unusual. Thickening of the tissues after spawning as in the case of the living *Aurelia flavida* might have caused the animal to become thin, leathery and more brittle. Many of the appendages in the umbrella region drop off in this period. In such a dried-out condition, medusae covered by sediment would have a much greater chance of preservation as fossils. *Aurelia* may also be stranded on the beach, dry out but leave the lower surface soft and turgid as in life.

It can remain buried and be dug up after quite long periods buried in sand or silt. The Ediacara medusoids were, he believed, exclusively pelagic forms. The grooves in the fossil are stained with ferruginous material or have a film of clayey material. The original sediment was fine-grained and well-sorted; the environment of entombment was intertidal flats or the strandline. Most of the animals were preserved with the exumbrella surfaces uppermost, and they were only found on the upper surface of slabs.

He then gave detailed descriptions and admittedly tentative classifications (Table 2).

Sprigg (1949) noted the problems of classification because in some cases diagnostic features were not present, whereas in others there are features preserved which indicate affinity with living organisms; he also noted that forms such as *Beltanella* and *Protodipleurosoma* may have much smaller analogues living at the present time. He redescribed *Ediacara flindersi* (now max. dimension 114 mm); *Beltanella gilesi* (now max. dimension 110 mm) (Fig. 4); *Cyclomedusa davidi* (adding two other species, *Cyclomedusa radiata*, *Cyclomedusa gigantea* max dimension >65 mm); and *Dickinsonia costata* (Fig. 5). He described two small lateral buds on *Cyclomedusa davidi*, representing a unique form of reproduction in which buds are formed with adult characteristics. The new genera described are summarised in Table 3.

Five more genera, illustrated by Sprigg (1949), *Tateana*, *Pseudorhizostomites*, *Pseudorhopilema*, *Medusina* and *Madigania*, are shown in Figs. 6 and 7, together with the anomalous budding of *Cyclomedusa davidi*.

3.2. The researches of Glaessner and Wade

In the late 1950s and 1960s, research on the Ediacara fauna was taken over by specialists, Martin Glaessner and Mary Wade. Glaessner, in his book “The Dawn of Animal Life” (1984), gave a summary of the results of researches up to that date and their thinking. Preservation of the fossils was not as faithful in morphological detail as say in the Middle Cambrian Burgess Shale, Middle Jurassic Solnhofen limestones or Eocene Baltic amber. Although the variety of components was obvious to the first observer, classification in terms of systems of living organisms was extremely difficult. The host rock is a coarser sediment than in those famous Cambrian and Jurassic localities and there has been distortion of the bodies, partial decay and various other accidents affecting preservation, all adverse factors. Accidental features are difficult to separate from biologically significant morphological characteristics. Statistical

treatment of biometric data was impossible because of distortion during fossilisation. Casts and moulds on bedding planes are such that no truly three-dimensional view is possible. Few soft parts are preserved. Comparison is limited to the preservable parts of living organisms. Structural homology must be relied on rather than functional analogy. Glaessner admitted that looking for similarities to existing taxa was preferred to erecting new high-level taxa of unknown affinities. It was not expected that this, the oldest known assemblage of Metazoans, would be entirely new. Possible relationships to living fauna are emphasised in his treatment rather than novelty. He said, in writing this, that no major changes in interpretation had been instituted in 25 yrs (this was written of course just prior to the emergence of the “Vendozoa”/“Vendobionta” concept). Glaessner gave a remarkably honest statement of his and Mary Wade’s philosophy in what may be termed the “Traditional Approach” to the Ediacara-type fauna.

The fauna list as recognised from Ediacara in 1984 was given by Glaessner in tabular form. It is not reproduced here as it was upgraded by Jenkins (1992) and his version is reproduced in Table 4.

Glaessner and Wade published extensively on the fauna from the Ediacara type area. The basis for their classification is given in Table 5, which covers the global distribution of taxa as seen at that time by Glaessner (1984). The forms were differentiated into the phyla Coelenterata, Annelida (and possibly related phyla), Arthropoda and those of which the systematic position was unknown (*Redkinia* and *Tribrachidium*). Glaessner (1984) drew a line between the Riphean (Sturtian) and Vendian (Varangian) glaciations and the time of the Ediacara faunas, and also drew a line between these faunas and the appearance of Lower Cambrian faunas. He noted that the timespan of the Ediacara faunas was 60–70 Myr, about the same as the Tertiary, Cretaceous and Jurassic. He discussed the Precambrian diversification of the Metazoa in the light of Palaeozoology and produced a diagram illustrating his concept (Fig. 8).

3.3. Fauna

Glaessner’s summary descriptions of the fauna are given below:

Coelenterata.

3.3.1. Hydrozoa

3.3.1.1. *Chondrophorina*. Only two living representatives of the Class Chondrophorina are known,

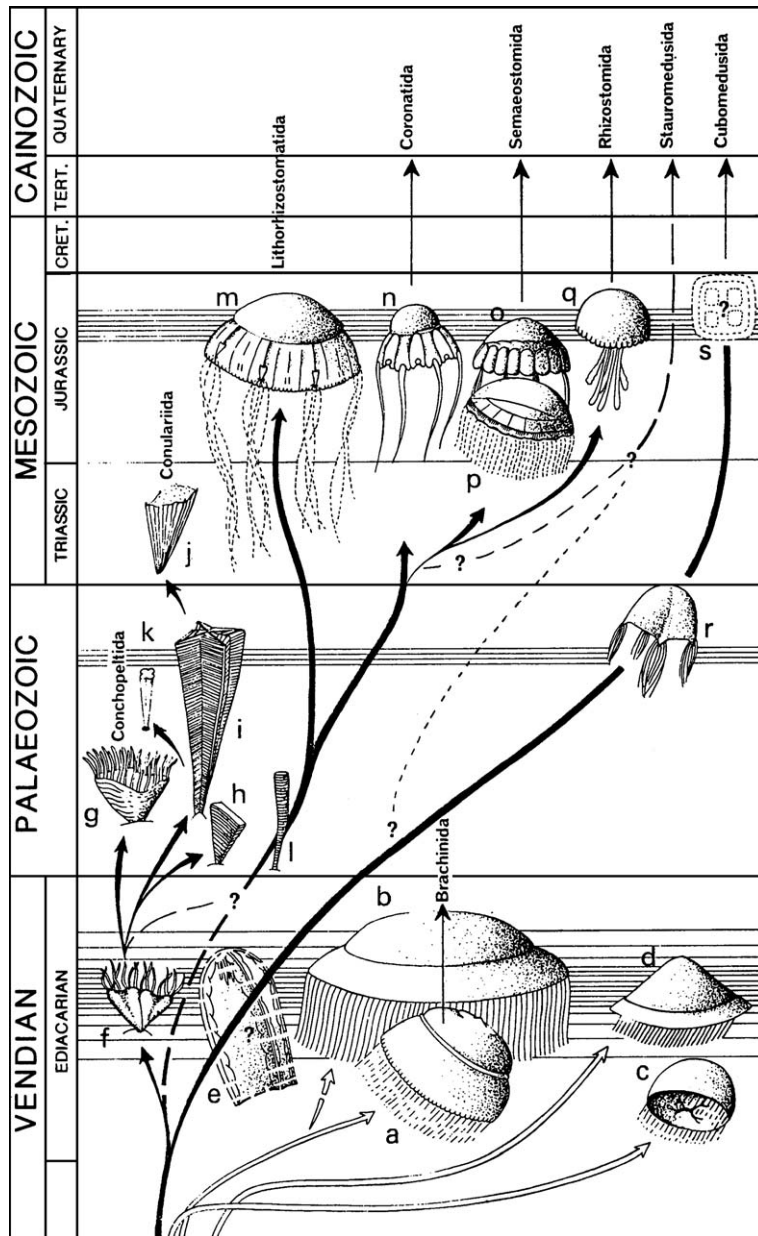


Fig. 8. Phylogenetic tree of known fossil Scyphozoa (from Glaessner, 1984. Reprinted with permission of Cambridge University Press): (a) *Brachina delicata* Wade, (b) *Ediacaria flindersi* Sprigg, (c) *Hallidaya brueri* Wade, (d) *Rugoconites enigmaticus* Glaessner and Wade, (e) *Kimberella quadrata* Glaessner and Wade, (f) *Conomeduities lobatus* Glaessner and Wade, (g) *Conchopeltis alternata* Walcott, (h) *Conuariella robusta* (barrande), (i) *Conulariina* generalised, (j) *Conulariopsis* generalised, (k) *Circonularia eosilurica* Bischoff, (l) *Byronia annulata* Matthew, (m) *Rhizostomites admirandus* Haeckel, (n) *Epiphyllina distincta* (Maas), (o) *Eulithota fasciculata* Haeckel, (p) *Semaestomites zitteli* Haeckel, (q) *Leptobrachites trigonobrachiis* Haeckel, (r) *Anthracomedusa turnbulli* Johnson and Richardson, (s) *Quadrimedusa quadrata* Haeckel.

Porpita, a radially symmetrical form, and *Veella*, with an axis of symmetry through the centre of an oval body and possessed of a diagonal 'sail' and a chambered chitinous float beneath the surface. The Ediacaran genus *Euporpita* is a radially symmetrical medusoid with various types of polyp below. *Chondroplon* has a

float chamber partly filled with sand; both it and *Ovatoscutum*, known only from casts or external moulds, are bilaterally symmetrical (not unexpected in swimming organisms, even with sails or mantle flaps). Chondrophorina float at the surface of the sea and exploit its phototropic phytoplankton. If this

attribution is correct, it indicates habitability of the surface water, availability of phytoplankton on which to feed, normal oxygen availability and salinity.

3.3.2. Scyphozoa

3.3.2.1. Vendimedesidae. A new subclass, Vendimedesidae, was established by Wade for the best known medusae from Ediacara. They were said to be characterised by a mouth which “lacked a typical manubrium or had a small conical extension or lobes separated by branching slits, the round gastric cavity extending into numerous branching radial canals”. The gonad was recognised in a lobate annulus on the outer disc, communicating with the canals. Numerous fine tentacles arose, if present, on the subumbrella edge. There is no trace of tetrameral symmetry. *Brachina delicata* was the best known species, possessing a single coronal furrow around the central disc. *Ediacara*, up to 50 cm diameter, could be of the same family, and likewise, *Hallidaya* and *Rugoconites*, with reticulate radial canals. The unique genus and species *Kimberella quadrata*, an incompletely known tetrameral form, remains problematic: almost prismatic when fossilised, it could have Cubomedusoid affinities, putting it closer to the Hydrozoa.

The conularids (subclass Conularata) were considered to be polypoid forms with chitinous epidermis and tetrameral septation. The Ediacaran fossil forms resemble juvenile living conularids. *Conomedusites* appears to be closely related to the Ordovician form *Conchopeltis* (Glaessner, 1971).

The most common medusoid fossils from Ediacara were assigned to three or four named genera, or were left unassigned, in the absence of distinctive characteristics, awaiting further study related to other fossil or living medusae. *Cyclomedusa* (Wade, 1972a) is a form with a circular outline and concentric grooves, with or without finer or coarser radial furrows. There is great variability of radial structures. There is clear evidence of flexibility, either in vertical compression of the formerly conical centre or lateral distortion of adjacent specimens. The exumbrellar side is usually preserved in the downward position as external moulds and the subumbrellar structures are not clearly recognisable. Radial splits may be due to desiccation or compression. The flexible umbrella was inferred to have had pulsating movements. The crowded multiple occurrence on bedding planes (up to 49 on a single bedding plane) suggests ability to swim in dense swarms, often drifting inshore on tidal currents. The greater probability of settling with exumbrellar side downwards was demonstrated by Wade (1968). There is no evidence of attachment in this position, but some living

medusae feed on the bottom in this position. All that is known suggests affinity with the Scyphozoa not the Hydromedusae.

Medusinites asteroides and *Mawsonites spriggi* were considered to have the same affinity, but the presence of a coronal furrow to indicate affinity to *Ediacaria* and the Vendimedesidae. *Lorenzinites rarus* was considered to be an aberrant *Rugoconites*, and to exemplify the unwisdom of naming solitary specimens.

3.3.2.2. Pteridiniidae and Charniidae. ‘Sessile colonial Cnidaria’ was the grouping Glaessner gave to the frond-like fossils common in the Charnwood Forest, England; Namibia and Newfoundland, but not very common at Ediacara. These had been described as Coelenterates (Richter, 1955), possible algae (Ford, 1958), and in great detail by Pflug (1973) as the Phylum Petalonamae. Jenkins et al. (1981) concluded that Petalonamae might cover a diversity of Classes or even Phyla. Ediacara fossils of this kind were listed under this name by Glaessner and Walter (1975, 1981), but due to misunderstanding Glaessner (1984) did not use it, but divided the frond-like forms into two families, Pteridiniidae and Charniidae. The first family was little represented at Ediacara and not well known as to their growth and functioning; however Glaessner (1984) saw “no reason to exclude them from the sessile colonial Cnidaria”. *Charniodiscus* Ford was redefined by Jenkins and Gehling (1978) as a foliate structure with median rachis, a stalk and attachment disc. Lateral structures affixed to the leaves (polyp leaves) were divided into ridges. Straight, narrow impressions were interpreted as spicules which strengthened the stalk, rachis and leaves. Resemblance was seen to the living family Pennatulacea, to which they were assigned (Glaessner and Daily, 1959). The genus *Glaessnerina* Germs was considered probably to be a junior synonym of *Charnia* Ford—it was rare at Ediacara.

3.3.2.3. Coelomata (Annelida and possible related worms). Glaessner (1984) reported that worm-like animals accounted for 25% of Ediacara collections. *Dickinsonia costata*, previously described by Sprigg (1949), he described as broadly oval commonly with up to 120 segments and flat (though some had ribbon-like bodies and 200–300 segments). He referred them to a monotypic family Dickinsoniidae. Unlike most living annelid worms, they do, Glaessner believed, have a parallel living form *Spinther alaskensis*, a parasite living on sponges. He recounted the features recognised which corrected the early attribution to the Coelenterates. He remarked that “these flat worms were not true ‘flat

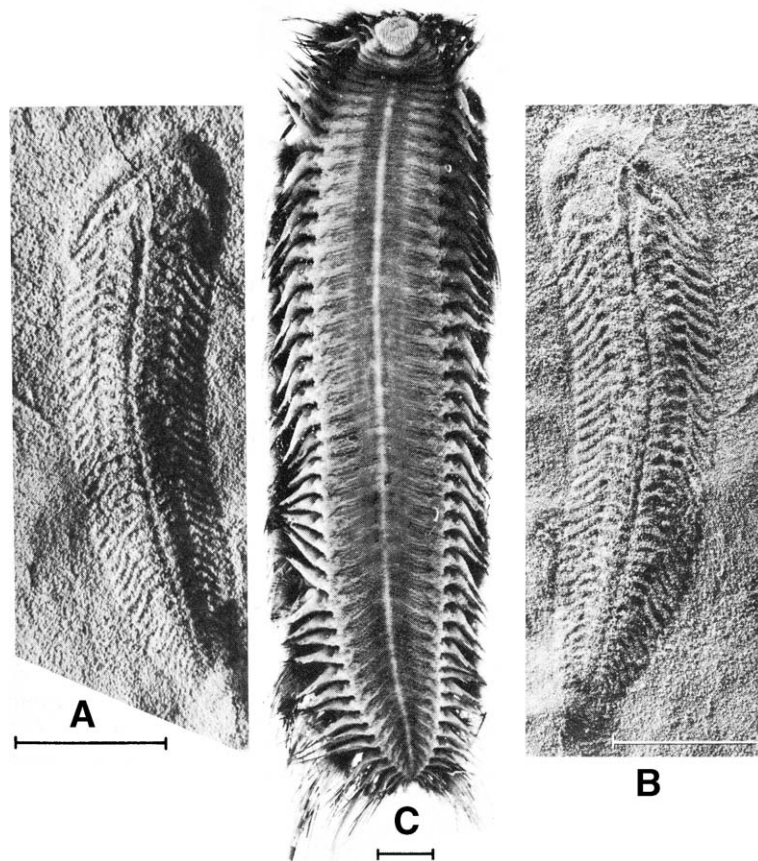


Fig. 9. *Spriggina floundersi*. Comparisons: (A) External mold, ventral side. (B) Latex cast of same specimen. (C) Living polychaete worm, *Laetmonica producta* Kinberg, ventral view (Natural History Museum, London specimen). The felt-like covering projecting around the body is characteristic of the family Aphroditidae (scale bar=10 mm). (From Glaessner, 1984).

worms' (Platyhelminthes) but had essential morphological characters of annelid worms". They were sediment and detritus feeders and according to Wade (1972b) must have been able to crawl and swim. He believed that they crawled on the sea bottom, in a world without predators (there is no evidence at all of predation). He noted that Conway Morris (1977) found "no evidence that it was a Polychaete and that its actual affinities remain uncertain". Fedonkin (1981a) in contrast assigned it to the Platyhelminthes.

Two further Ediacara fossils were assigned to the Polychaete worms, *Spriggina floundersi* and *Marywadea ovata*, but Glaessner (1984) noted that they were so unlike any living Polychaete worms in some features that some authors (e.g. Conway Morris, 1977) came to the conclusion that their affinities must remain unresolved. Birket-Smith (1981a) was impressed by similarities to arthropods. Because of discoveries of possible representatives of *Spriggina* in both South West Africa (Germis, 1973b) and Russia (Fedonkin,

1981a), Glaessner had the 25 best specimens from Ediacara re-examined in co-operation with Mary Wade and reported the following preliminary results. The body consists of a head, a trunk of up to 42 segments and a very small pygidium. The head is horseshoe-shaped with a smooth surface and smoothly curved anterior margin and pointed posterolateral projections. Its width is about equal to the anterior trunk segments, including parapodia, but its median length is greater than the body segments. The median portion of the posterior margin to the head is sharply impressed and u-shaped, and the front of the u was believed to correspond to the position of the mouth as seen in the ventral aspect. The margins of the head, although deeply impressed, are generally asymmetrical because of overlap with the first body segment. There is a narrow medial groove. The segments extend laterally with a knee-like angle into what appear to be parapodia, which end in acicular setae. The head is much larger than in living polychaetes and is sclerotised. It is not

divided by transverse or longitudinal grooves. It has no appendages such as antennae and no eyes. It grows in width from about 3–10 mm until it has 30–40 segments and from then on lengthens but does not widen. The pygidium is very small. The parapodia resemble those of living Aphroditidae (Fig. 9). They could have been used for crawling and bending the body. It was not a burrowing organism, but would have lived on and in the soft mud in which it was preserved. It probably neither had to have sense organs nor burrow for protection because of lack of predators. As the whole range of growth stages is found at Ediacara, it probably lived where it was fossilised. Glaessner considered that it was not a direct ancestor of living polychaete worms but a descendant of such an ancestor. Its body and limbs are unlike any arthropod. It was illustrated beside the living polychaete *Laetmonice* in ventral view (Fig. 9). The similar genus *Marywadea* differs in having a half-moon shaped head with pointed posterolateral projections, and long, curved dorsal setae.

3.3.2.4. Arthropoda

3.3.2.4.1. Vendomiidae and Parvancorinidae.

Two genera from Ediacara were assigned to the Arthropoda, on “indirect but convincing evidence”. The number of specimens was small and their size small, making distinction between morphological features and accidents of fossilisation difficult. *Praecambridium* was so determined (Glaessner and Wade, 1971) on account of its segmentation and the fact that the number of segments increases with size and hence with growth. Distortion without fractures showed that there was no hardened or mineralised integument. The segmentation resembles that of certain trilobite larvae and/or primitive Chelicerata. Glaessner considered that the existence of an animal in the Ediacaran fauna with such resemblance is significant.

Parvancorina minchami was similarly assigned to the Arthropoda because its remains consist of a shield-like, flat and unmineralised carapace, with traces of metameric ventral appendages, indicative of segmentation of the body although this is not evident on the dorsal surface. Something of its mobility was evidenced by varying positions of locomotory appendages. There were no antennae. *Parvancorina* was different in essential characters from *Praecambridium*, but there were similarities to Middle Cambrian and Devonian arthropods and with the larval stages of brachiopod crustaceans. Thus, *Parvancorina* and *Praecambridium* were placed, together with the related Vendomiidae, “near the point of branching of the ancestral Trilobitomorpha into Crustacea and Chelicerata”.

3.3.3. Systematic position unknown

Tribrachidium heraldicum, the last of the named members of the Ediacara fauna, could not be assigned to any known phylum. Circular, disc-shaped and deformable, three fixed angular arms arise from its dorsal surface, with a fringe of short, soft, tentacular, movable projections on one side which turns to the periphery of the disc; and with a rounded organ on the other side. The dorsal surface also carries numerous, fine, stiffly flexible, tubular spines. The three-fold symmetry is unique. There is a possible resemblance to some echinoderms and Paul (1977) thought that it might be a primitive, pre-skeletal echinoderm, resembling a soft-bodied asteroid with only three ambulacra.

3.4. Palaeobiology

Glaessner (1984) discussed under this heading the feeding habits of the Ediacara-type animals and the associated trace fossils. He assumed on general grounds that microplankton were present in the Ediacara seas, comprising a photoautotrophic microflora together with planktotrophic protozoans and metazoan larvae. None of these would have survived the prevalent conditions of sedimentation to fossilisation. Trace fossils are present but, although common, they are less in number than in the Lower Cambrian and of much smaller diversity—only six forms were recognised, none of which could be assigned to the Ediacara-type animals known from body fossils. Occurring as casts and moulds on the surface of underlying layers of silt and clay, they either form chains of pellets (e.g. *Neonereites* Seilacher, 1960) or sinuous grooves. The pellets are products of sediment feeders which passed sediment through their intestinal tract. The lines of pellets can pass into smooth ribbons. The sinuous grooves in the form of guided meanders are traces of organisms ‘grazing’ on microflora and organic detritus on the sediment surface. In contrast, gently sinuous and smooth broad bands up to 25 mm wide may cut through moulds of common Metazoa such as *Dickinsonia*, indicating formation after the basal layer of the sand was deposited and hardened, a pattern suggestive of searching for food in the clay below the sand. There were traces deposited by at least six unclassified worm-like animals. There is, however, no evidence of vertical burrows like *Skolithos* and there is no intense bioturbation of the sediment anywhere evident.

Glaessner hypothesised that medusoid Cnidaria fed on plankton and nekton, whereas the annelids probably swam or crawled slowly through the bottom water. Sluggish locomotion was all that was needed because there was no threat from predators (contrasting with the

case of living annelids). The sessile colonial Cnidaria were not fully understood, but it was suggested that they caught microplankton on the sea bottom at heights of up to 1 m. The large size of some early soft-bodied Metazoa was related to the lack of macrophagous predators. The habitats of available food-carrying niches on the seafloor were incompletely filled in Ediacara times, but were occupied when the Ediacara age was brought to a close.

3.5. Preservation

Glaessner (1984) noted the incompleteness of the palaeontological record and its gross bias with respect to size and the environment in so far as sedimentation and burial of organic remains are concerned. Bias also comes from selective collecting and description as well as the changing aims and interests of palaeontologists. He quoted the observation of Stanley (1976a,b) about overstatement of the incompleteness of the record, and

stated his belief that the fossils really supply the truth (albeit limited), the past being the key to the present and not vice versa.

Wade (1968) stated that with only two exceptions, the soft-bodied Ediacaran fauna could be grouped into two categories, resistant and non-resistant; the latter, mostly medusoids decaying and dying before diagenesis had set the enclosing sediment. Resistant animals, mostly annelids and pennatulids, but including other unique groups, were supported by the covering sediment until it had set: fossils occurred in negative relief on the base of sedimentary laminae. Where there was little clay between adjacent quartzite lenses, counterpart moulds or casts were found on the tops of underlying laminae. She believed that there was no evidence of any bodily animal living in situ (except possibly *Rangea longa*) and presented a diagram showing a medusoid settling and turning over in the process, in accordance with her belief that these organisms floated with tentacles downwards (see Fig. 172).

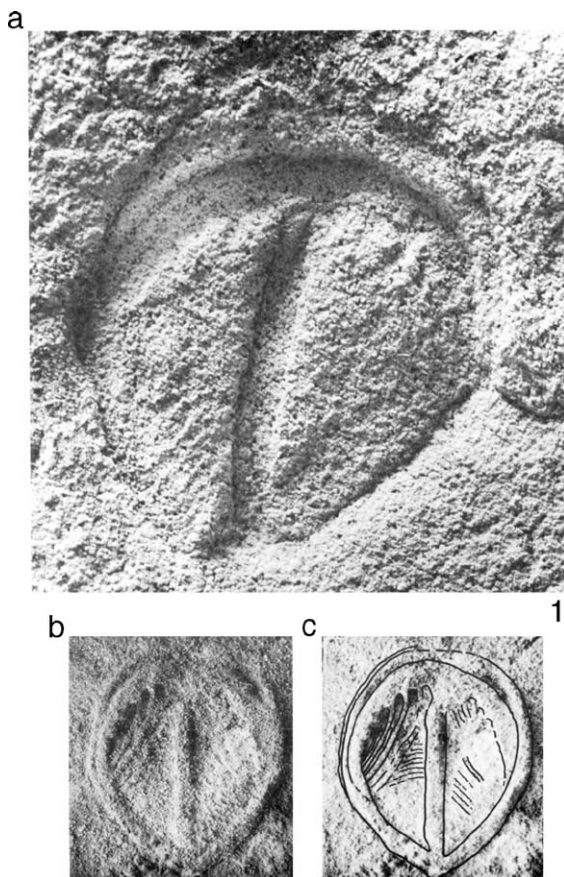


Fig. 10. *Parvancorina*. (a) External mold showing some lateral and posterior appendages ($\times 5$). (b) Latex cast showing appendages ($\times 2$). (c) Same with visible structures outlined. (From Glaessner, 1979b.)

3.6. Separate publications of Glaessner and Wade

There were many separate publications on the Ediacara fauna by Glaessner and Wade. These are summarised below in so far as they amplify the text above which was derived from Glaessner (1984).

In 1971 they described *Conomedusites* Glaessner and Wade, remarking on the similarity to an Ordovician form *Conchopeltis* and stating that both these Conulariids were polyps related to the cnidarian lineage. Wade (1971) described *Chondroplon bilobatus*, similar to *Ovatoscutum concentricum* Glaessner in its extreme bilaterality, in contrast to the two families of Phanerozoic Hydrozoan Chondrophores, and proposed a new family Chondroplidae to contain them. Wade (1972b) described the well-known *Dickinsonia* as an extinct genus of errant polychaete worms which dominated the South Australian Ediacara fauna. Like Glaessner, she compared it with the Recent *Spinther*. Freed from a reliance on Neuropodia, the worms outgrew the range of width at which such appendages could function efficiently and produced the widest worms ever known, as segment length shortened.

Glaessner (1979a) further discussed the enigmatic species *Parvancorina minchami* Glaessner (1958), based on 60 specimens from the original locality representing various stages of growth from 2 mm to about 30 mm. These are shield-like fossils (Fig. 10), quite unlike the ‘medusoids’ and occur on the lower surfaces of sandstone or quartzite beds with the convex surface invariably directed upwards. Thin films of clay

or silt separate the beds. There is secondary tectonic distortion. They are seen as external moulds, without organic material preserved. The descriptions were based on latex casts. The preservation history was outlined as settling during short periods of quiet sedimentation on smooth or gently wavy surfaces of sediment in muddy pools between sand ridges. Recurrence of the dominant high energy regime moved sand waves over these clay pans, and the sediments were reduced by compaction to thin layers between lenses of sand. The sand was of a character like that used as form sand in metal casting. *Parvancorina* and *Tribrachidium* are invariably found as impressions on the lower surfaces of sandstone slabs. The movement of sand waves was not sufficient to remove these imprints, but was able to bury and replicate the form of the organisms. Bacterial action must have affected the organic matter, but there were no macrophagous predators feeding on them. Decay products

were entirely removed by water flushing the porous sand. The shield-shaped area is described as a carapace and appendages emerge as a median series from its median zone, indicating metameric composition of the underlying body. In some specimens, there are 4–5 anterior appendages and 15–20 thread-like posterior appendages on either side of a median ridge. There is an enclosing ridge which is double in some specimens. The existence of a carapace and resemblance to other fossils supports assignment to the Arthropoda, especially to Marrellomorpha which appear to be phylogenetically related to the ancestral Trilobitomorpha. *Parvancorina* has also been found in the Vendian of northern Russia and was there assigned to the family Vendomiidae KELLER, of uncertain position within the Arthropoda. The organism was probably able to feed on small detritus particles when mud on the seafloor was stirred up by its locomotory movements, and it was suggested that it was

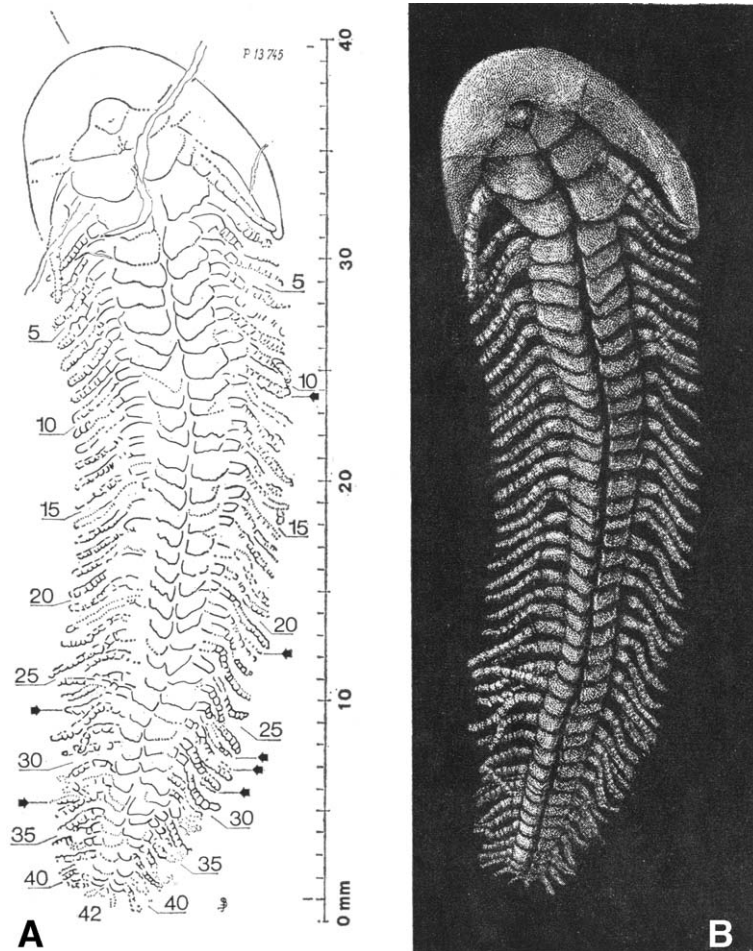


Fig. 11. *Spriggina*. (A) Detailed drawing showing structure (stumpy arrows point to “supernumery” appendages). (B) Final reconstruction (from Birket-Smith, 1981a).

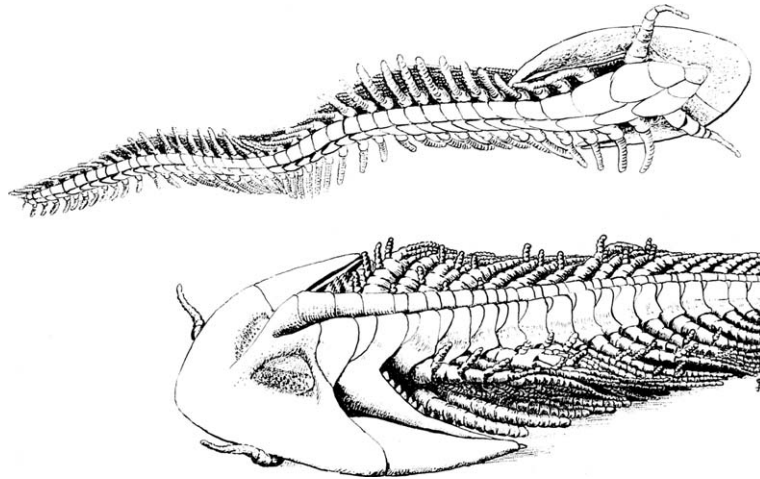


Fig. 12. Sketches of *Spriggina* as envisaged swimming and crawling in life (from Birket-Smith, 1981a).

capable of nectobenthic locomotion by swimming or crawling.

3.7. Later research

3.7.1. Detailed studies of *Spriggina* and *Praecambridium*

Birket-Smith (1981a) reconstructed the enigmatic fossil *Spriggina* by a photographic and drawing method from latex casts. He referred to the original description by Glaessner (1958), adding to it further details noted by himself. He studied the imprints of dorsal and ventral sides respectively. His main findings were:

- (1) The body was distinctly segmented, no segments being fused.
- (2) The dorsal surface was covered by a single row of cuticular, overlapping plates.
- (3) Ventrally, the body carried paired, segmental plates and should be placed in a phylum of its own.
- (4) The third and following segments carried dorsal and ventral pairs of annulated lateral appendices.
- (5) The first, strongly modified, horseshoe-shaped segment had paired dorsal depressions, possibly eyes, but no lateral appendages.
- (6) The oral opening was ventral and covered by a small prostomium.
- (7) The second segment was also slightly modified with atrophied dorsal appendices but enlarged ventral appendices, possibly used as antennae.

His final reconstruction is shown in Fig. 11. It was concluded that *Spriggina floundersi* Glaessner could be

classified neither as an annelid nor as an arthropod, according to present-day definitions. The fossil was, however compared, on account of the double, lateral rows of annulated appendages to the annelids Hesioniidae, a family of the polychaete worms. This comparison was based on dissection of *Hesione patherina* Risso, which indicated a progeniture with musculature and other structures that were essential to *Spriggina*. It might also be related to *Marywadea* Glaessner 1976 and to the fossil *Xenusion auerswaldae* Pompecki 1927, but that was only known from a single fragmentary specimen. The conclusion was reached that the trilobites developed, if not from *Spriggina*, then from one or several closely related forms. *Spriggina* should be placed in a phylum of its own. Indications are that it lived on the shallow sea bottom, consuming tiny particles living or dead. He suggested that it was capable of swimming or crawling on the seafloor (Fig. 12).

Birket-Smith (1981b) suggested that *Praecambridium* might be a juvenile *Spriggina*. He described *Praecambridium sigillum* Glaessner and Wade (1966) as an ovoid, slightly convex plate, with 3, 4 or 5 slightly elevated lobes curved across half the plate, thus indicating segmentation behind the broad anterior lobe. It was interpreted as a primitive arthropod by Glaessner and Wade (1971). The length of the fossils increases with the number of segments, and this was taken as a possible indication that it was a juvenile form. The three posterior segments were assumed to be primary. Glaessner and Wade (1971) noted the general resemblance to the protaspis stage of certain trilobites, but Birket-Smith suggested resemblance to certain recent juvenile polychaete worms and in particular to *Limulus*.

3.7.2. Sedimentological reappraisal of the Ediacara Member

Gehling (1983) enlarged the definition of the Ediacara Member, low down within the Rawnsley Quartzite, to include thick, conformable cycles of massive sandstones, siltstones and fossil-bearing thin- to medium-bedded sandstones, passing up into white cross-bedded quartzites. This package of beds ‘fills a significant erosional unconformity cutting down some 300 m into the underlying shallow water sandstones of the Rawnsley Quartzite, into the Bonney Sandstone’. Whereas the remainder of the Rawnsley Quartzite is demonstrably of shallow marine shelf origin, the Ediacara Member exhibits characteristics of mass flow and deposition below wave base. The former interpretations, based on the upper part of the Member on the western flank of the ranges (Jenkins et al., 1983), are quite untenable in the light of more recent studies. The Member is 60 m thick in the type section at Bunyaroo Gorge and equivalent thick sequences occur in the Chace and Elder ranges and also in the Heysen Range (Fig. 3). The valley-fill sequence consists of massive channel-filled sandstones locally packed with shale and sandstone clasts, massive amalgamated sandstones, khaki and maroon siltstones and fine grained sandstones passing into white cross-bedded quartzites. In the southeastern sections, there are thinly bedded turbidites, interpreted as distal according to current indicators. Shallowing-up to storm wave-base is indicated by passage into streaky sandstones and then lenticular to wavy bedded sandstones interleaved with siltstone. Here animals of the Ediacara assemblage were entombed, there they either lived or had settled by storm-surge sands. The style of fossils and trace fossils indicates that these offshore silty substrates were inhabited by benthic feeders. Mantling by sand was followed by reworking by waning storm waves. Sub-aqueous shrinkage cracks do occur but no sun desiccation cracks have been demonstrated. White cross-bedded shelf sandstones succeed the coarsening upwards cycle of siltstones and fossiliferous sandstones, and in the thicker sections, there are up to three incomplete cycles above the submarine fan complex of proximal turbidite sandstones and pelagic siltstones.

The Ediacara Member appears to be absent in the NE Flinders Ranges, where, at the time of Ediacara deposition, this region was exposed or subjected to a depositional hiatus. Of the two possible explanations for the erosional event which interrupted Rawnsley sedimentation, eustatic sea-level fall and down-faulting initiating a sub-aqueous valley incision, the latter was favoured.

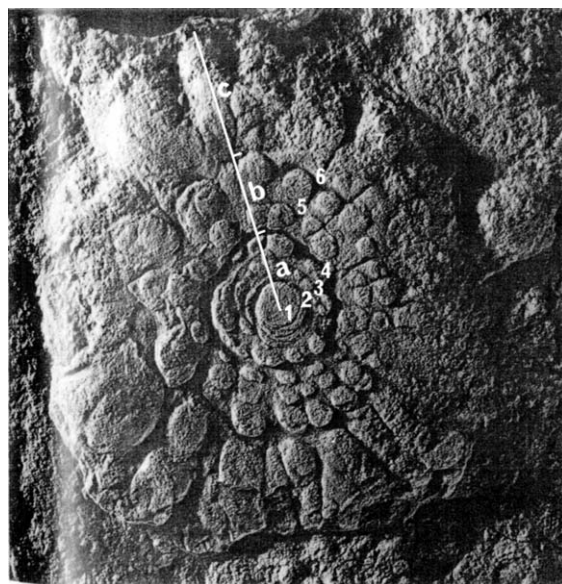


Fig. 13. *Mawsonites spriggi* Glaessner and Wade (1986) ($\times 1$) (from Sun Weiguo, 1986d).

3.7.3. Algal binding as a preservation mechanism

Gehling (1986), in a concise abstract, noted that fossils in soft-bodied Ediacara assemblages occur as sole-face impressions on sandstones. Facies analysis pointed to subtidal deposition below fair weather wave base for these beds, casts of the organisms being preserved on sharp-based massive sandstones with rippled tops, and every detail of the clayey substrates was preserved. The surface texture suggested an algal or bacterial film as responsible for the resistance to erosion by the storm-surge sands. There was evidence to support this in other shallow-water facies of the Pound Subgroup and from modern analogues on the Netherlands coast, where blue-green algae exert a sand-binding role. The paucity of surface grazing and infaunal burrowing animals ensured the preservation of induced convolutions and polygonally disrupted and rolled up algal bound sand laminae in the Rawnsley Quartzite. Algal mantling not only would have prevented storm-surge stripping but also would have provided surfaces to which low profile, sessile organisms could adhere. Vertical burrowing and active grazing by invertebrates put an end to this preservation during the Early Cambrian.

3.7.4. Detailed description of *Mawsonites*

Sun Weiguo (1986d) published a detailed description of the late Precambrian scyphozoan medusa *Mawsonites randellensis* sp. nov., and its significance in the Ediacaran metazoan assemblage. He noted that among

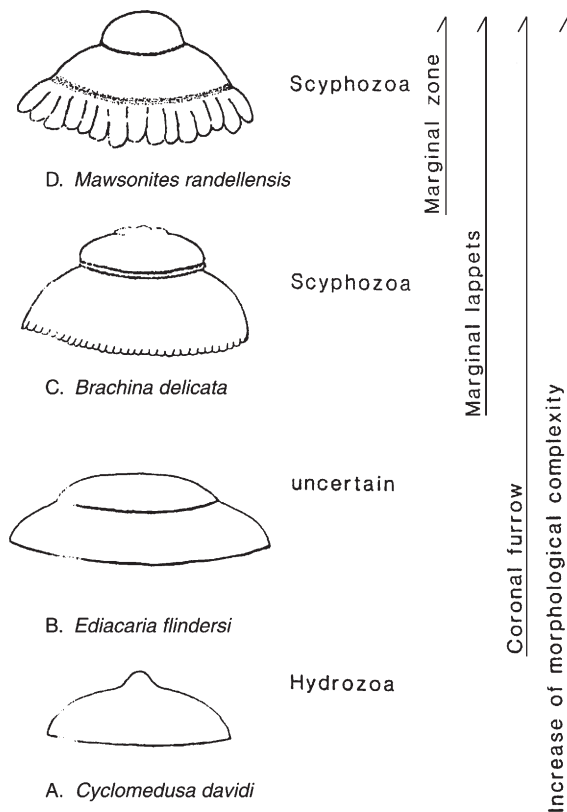


Fig. 14. Morphological diversification of medusae in the Late Precambrian Ediacara metazoan assemblage (after Sun Weiguo, 1986d).

the 2000 or so fossil specimens so far collected, medusoids comprise the majority of individuals as well as taxa, at least 10 genera and 13 species being recognised. His description of this new species was based on a new find from the Ediacara Member at the southern end of the Ediacara range, the holotype and two specimens previously collected by Jenkins. Prior to this, the monotypic genus *Mawsonites* (Glaessner and Wade, 1966) was placed under “Medusae of uncertain affinities” (Glaessner, 1979a). Now a new family, Mawsonitidae, had been erected under ?Coronitidae.

The description of the genus given was: outline circular, radially symmetrical; main umbrella subdivided by a distinct coronal furrow or a comparable structure into a central zone and the surrounding zone; marginal zone broad and deeply cleft into many prominent marginal lappets.

The type species, *Mawsonites spriggi* Glaessner and Wade, 1966 (Fig. 13) was revised as maximum known radius 75 mm, generally discoidal, three major concentric zones of about equal width, many largely deeply cleft lappets in the marginal zone. Exumbrellar surface

strongly sculptured by many large irregular bosses. *Mawsonites randellenses*, named after the site of the find close to the Randell Lookout, differed in having a smooth, discoidal main part to the exumbrellar surface, with no bosses. *Mawsonites* is distinguished from most other Ediacaran medusoids in having the marginal lappets. However, similar but very small marginal lappets are seen in the holotype of *Brachina delicata*, as illustrated by Sun Weiguo (1986d). Knowledge of it is restricted to the flattened moulds of exumbrellar surfaces. By comparison with living Scyphozoans of the Coronatae, which grow up to 150 mm diameter and possess similar lappets, and also show tetrameral symmetry, it was referred, questionably to this order, and regarded as an ancient, free-swimming scyphozoan medusa. Tentacles and other appendages, present in the modern forms, are not present in the Ediacara species, but are easily lost prior to preservation as fossils.

A diagram by Sun Weiguo (1986d) (Fig. 14) illustrated the morphological diversification of the Ediacaran medusae from South Australia. *Mawsonites* is nowadays to be found prominently displayed in museum collections, because of its size and spectacular surface structure.

3.7.5. A possible echinoderm

Gehling (1987) described the find of a small disc-like animal with pentamerous arrangement of grooves on its oral surface, preserved as an external mould on the base of sandstone beds within the Ediacara Member of the Pound Subgroup. The find was made at a locality in the eastern end of the Chace Range (Fig. 3) in the Central Flinders Ranges, 130 m above the base of the Rawnsley Quartzite. The Ediacara Member is here 152 m thick, beginning 67 m above the base of the Rawnsley Quartzite and with its top 350 m below the Lower Cambrian Parachilna Formation. The fossiliferous beds are confined to 2 or 3 intervals, each <10 m thick. The Ediacara Member, which is bounded below by erosional disconformity, here comprises a submarine fan complex, shallowing to wave base where the soft-bodied fossils were preserved. The fossils occur as impressions on the base of thin to medium bedded sandstones. Deposition is believed to have been on a storm wave base of an open marine shelf. Minute details of organisms have been moulded in the underlying clay substrate. Some beds in the sequence display current scours and groove marks documenting less common erosive events. Impressions of partly rolled-up and distorted membranous mats suggest algal mantling of clayey surfaces during fair weather as responsible for protection of such surfaces from storm events. These beds are the lowest

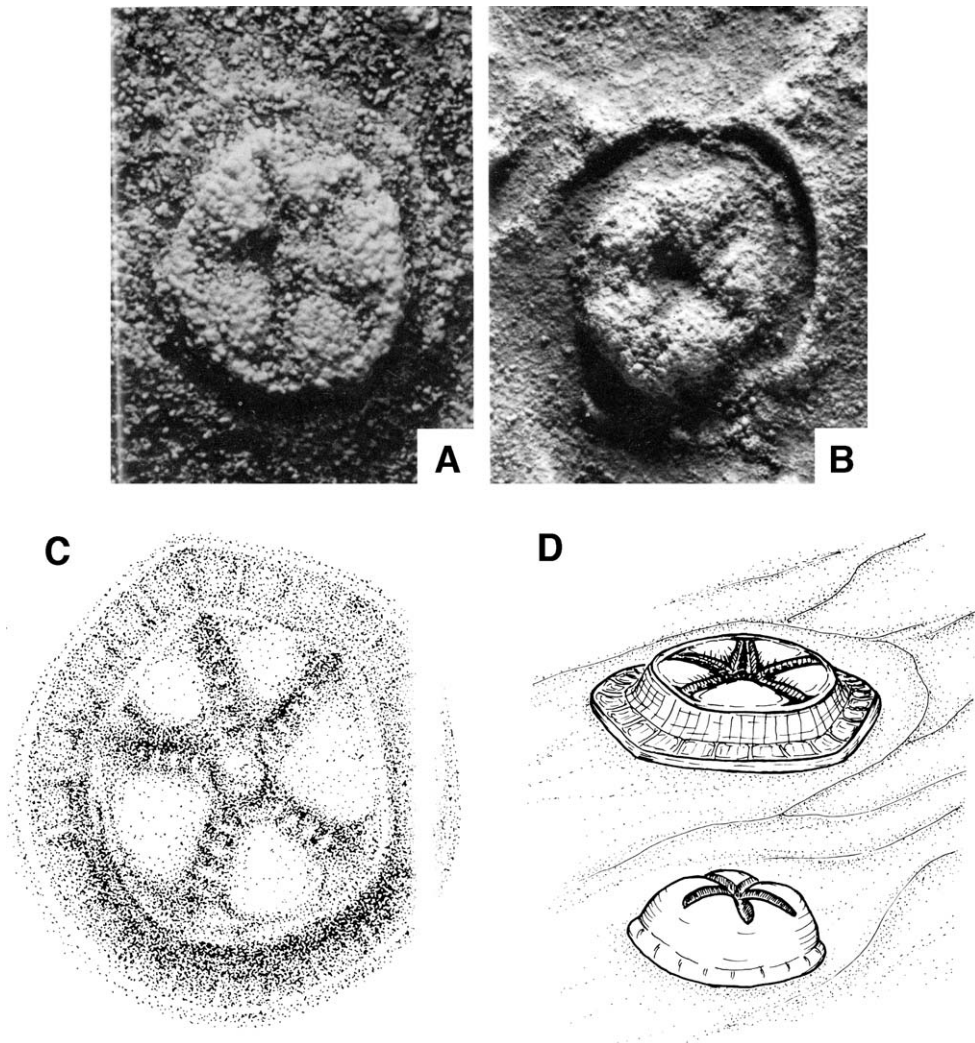


Fig. 15. *Arkarua adami* gen. et sp. nov. Oral views of silicone rubber casts from natural external molds. (A) Holotype; discoidal petameral arrangement of ambulacral grooves, showing traces of per-radial division and shallow depressions at distal ends parallel to the marginal rim, which is concave and traversed by radial ridges. The centrally placed peristomal dome is also seen ($\times 10$). (B) Paratype; discoidal to subconvex with deeply impressed marginal rim with inner and outer concentric ridges; peridomal region is depressed ($\times 6$). (C) *Arkarua adami*; interpretative sketch of the holotype in oral view. Note: 4–5 transverse ribs on ambulacral a grooves and central peristomal dome (absent in many specimens). Interambulacral regions are flat or slightly convex. Radial ribs divide the concave marginal rim ($\times 10$). (D) Reconstruction of *Arkarua adami*, oblique view of oral aspects of edrioasteroid-like echinoderm (upper: compressed discoidal state; lower: erect hemispherical state, with only a trace of the marginal rim). A contractile theca is inferred (c. $\times 10$) (from Gehling, 1987).

fossil-bearing in the section, and fossils collected from higher interval conform to other samples of Ediacara assemblages, elsewhere. Massive sandstones below are of deeper water facies. In the Chace Range, up to three shallowing-upwards cycles are represented within the Ediacara Member, whereas the remainder of the sandstones of the Rawnsley Quartzite are of shallow-water, intertidal facies.

The fossil, named *Arkarua adami* gen. et sp. nov., genus named for a legendary serpent, was described as a discoidally shaped echinoderm with a pentameral, star-

shaped depression on its oral surface, comprising ambulacral grooves which meet in a domed to depressed peristomal region (Fig. 15). Theca are of variable convex shape, polygonal to oval outline, surrounded by a marginal rim with fine radially arranged ribs. The aboral surface is unknown, this description being based on the external mould of the oral surface. 57 specimens were obtained from five separate bedding surfaces and float.

The author used the echinoderm descriptive terminology, but noted that some diagnostic features of the

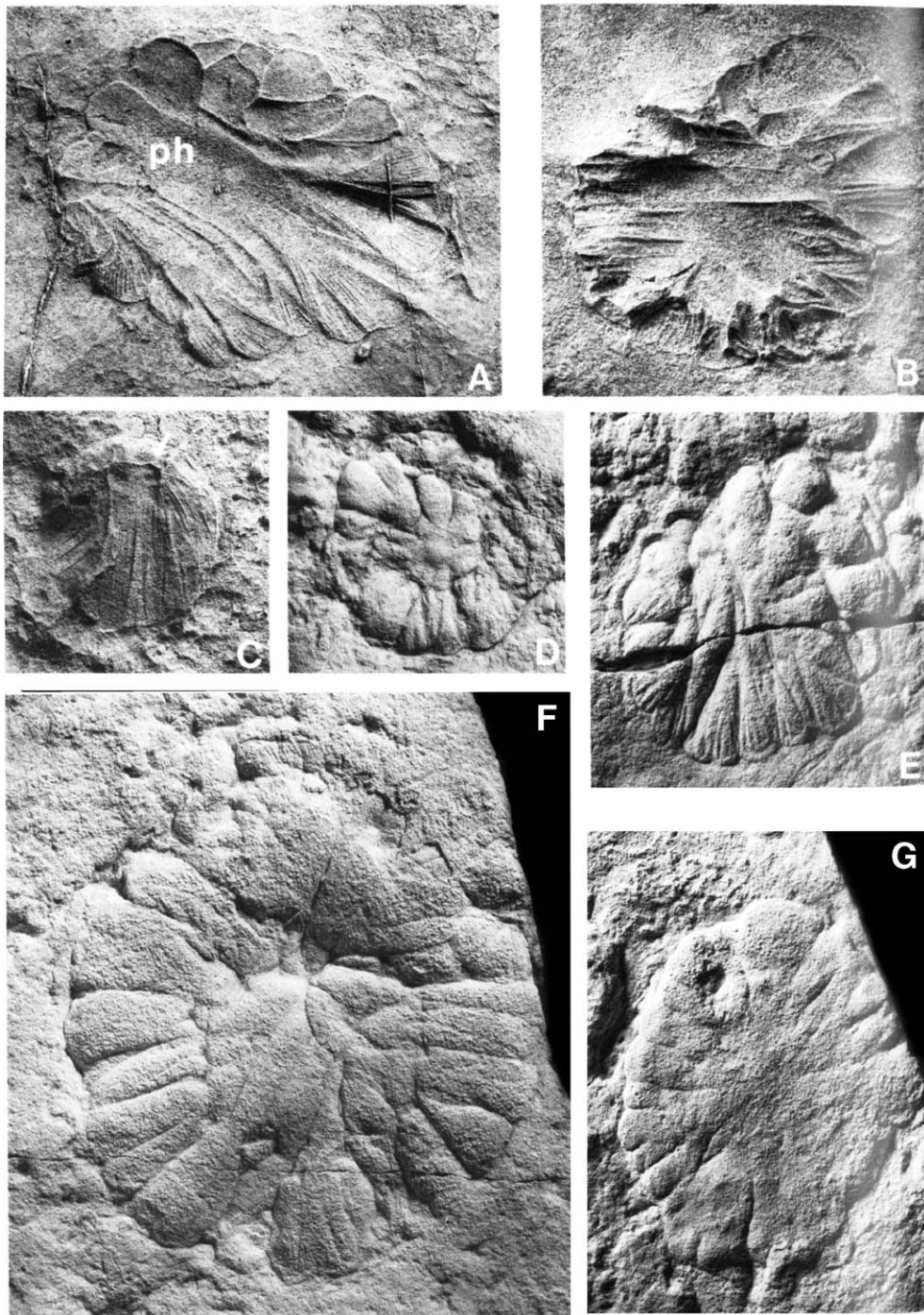


Fig. 16. *Inaria karli* gen. et sp. nov. (A) Holotype; oral surface with pharynx folded onto side (note fine rib-like impressions of muscle fibres on lobes distal to pharynx). (B) Specimen collected by R.F.J. Jenkins, oral surface with broad, laterally folded pharynx and central depression over coelenteron. (C) Juvenile, oral surface; lobes not defined, short pharynx with crescentic outline of mouth. (D) Small specimen with aboral structures predominant, well-developed lobes and faint composite, old of coelenteron. (E) Composite of collapsed oral surface mould and internal structures; note coarse fibre impressions of lobes and unmarked rim representing mesogloea and thin epidermal layer. (F) Composite mold with clear outline of coelenteron, complex impression of mesenterial walls. (G) Ovoid cast of aboral surface; radial grooves mark infolds along attachment of mesenteries to outer wall. All the above are $\times 1$ except B which is $\times 0.7$ (from Gehling, 1988).

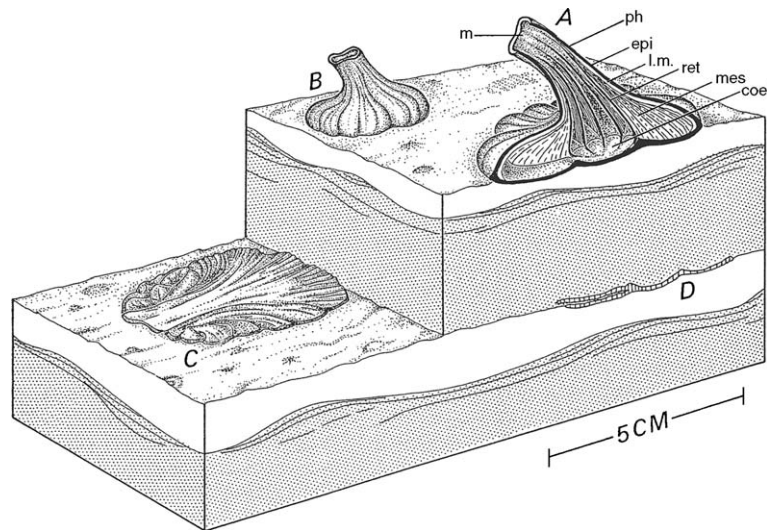


Fig. 17. Cut-away reconstruction of *Inaria karli* in life position on clayey substrate (white layers) interbedded with storm-surge sands (stippled). (A) Mature specimen, erect pharynx (ph), mouth (m), coelenteron (coel) with lobate extensions separated by mesenteries (mes), each with thickened retractor muscles (ret) on adaxial edge: two-layered body wall with simple epidermis (epi), mesogloea and gastrodermal column of longitudinal muscles (l.m). (B) Juveniles with poorly developed lobes and nesenterial grooves in outer wall. (C) Compressed specimen as it would appear in rubber cast of negative composite mold in sole of sandstone bed. (D) Sectional view of compressed specimen lying on clay substrate buried by sand (after Gehling, 1988).

Phylum Echinodermata are not demonstrable. The Pentamerous symmetry was the main reason for the allocation to this Phylum. It was assigned questionably to the Class Edrioasteroidea, on account of some resemblance. The likely relationship to the problematic *Tribrachidium heraldicum*, which occurs as small forms together with it, was noted. *Tribrachidium* has some features suggesting that it may be an Echinoderm.

3.7.6. A new fossil cnidarian of actinian grade

Gehling (1988) published a very detailed account of a new fossil, *Inaria karli* gen. et sp., nov., one of a number of fossils collected from the same locality in the eastern Chace Range of the central Flinders Ranges. It was described as a circular to oval polyp (Figs. 16 and 17) with a broad base rising to a narrow, erectile pharynx along the polar axis; column swollen aborally, similar globular in juveniles, strongly lobate in mature specimens, with gastrovascular cavity divided abaxially by mesenteries. Coelenteron axial; longitudinal gastrodermal and mesenterial muscle fibres radiate from pharynx to aboral surface; outer wall composed of mesogloea and thin epidermis; no pedal or oral disc: mouth tentacles or sting cells absent or not preserved. 51 specimens were collected from seven bedding surfaces. They are preserved as external moulds with high relief.

There is some resemblance to *Mawsonites spriggi* Glaessner and Wade (1966), mainly a superficial

resemblance in the lobate margin. Gehling interpreted it as a tentacular burrowing anemone (Fig. 18). It probably represents an early actinian that was preserved in place on a shallow shelf below fair-weather wave base. It appears to have been superseded by more evolved Early Cambrian burrowing anemones. The radial arrangement of the mesenteries within the coelenteron provides the strongest case for homology with modern actinians.

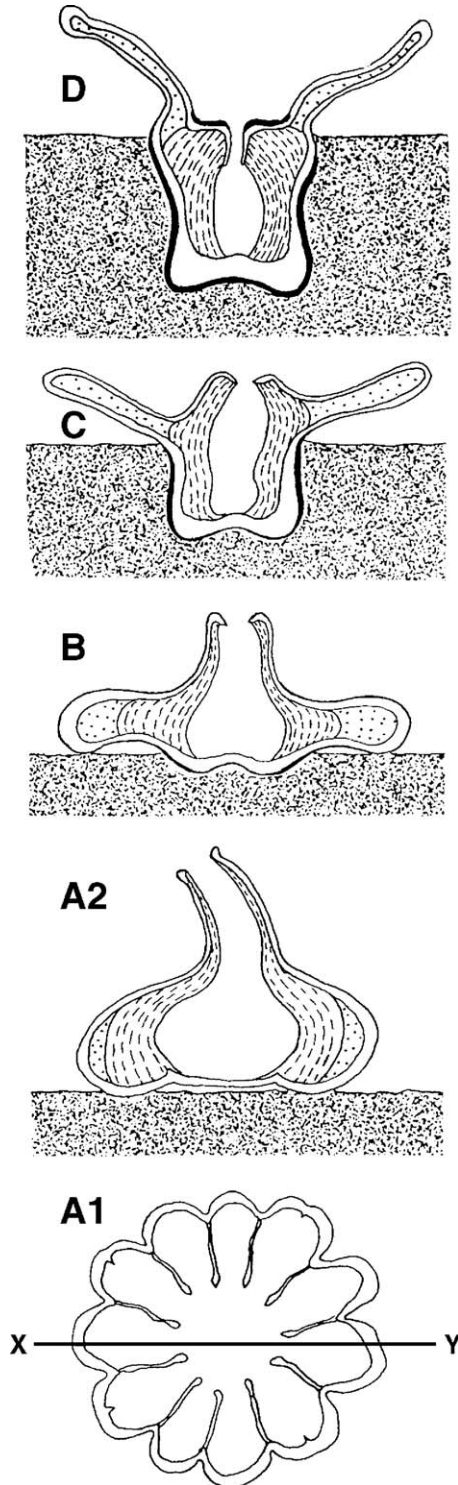
3.7.7. Sponges

Sponges, the most primitive large metazoans, were singled out as candidates for Precambrian ancestry by Glaessner (1984). Gehling and Rigby (1986) recognised casts, external and composite moulds from several localities in the Flinders Ranges, disc-shaped and preserving the characteristic spicular networks. They erected a new genus *Palaeophragmodictya*, reconstructed as a convex sponge with a peripheral frill and oscular disc at the apex.

Some of the best specimens were collected at localities, in the Chace Range but they were also found in the Elder Range, Heysen Range and Ediacara Range (Fig. 3).

Palaeophragmodictya reticulata new species (Fig. 19) is described as “a flattened, convex hemispherical sponge with a circular to oval outline; central flat-topped boss or shallow crater; surrounding field

smooth or with irregular anastomosing ridges or nodes; bordered by an 8–10 mm wide peripheral fill, sloping to form a concave rim, divided by regularly spaced radiating ridges; outer margin of frill poorly



defined. Internally, a reticulate, skeletal net, composed of primary quadrupoles, approximately 2 mm high by 3 mm wide, divided into secondary quadrules of approximately half that dimension. Radial ridges in the peripheral frill appear to be extensions of the reticulate skeletal net: spacing of ridges in frill from 2–3/cm in holotype to 6–7 cm in small paratypes". Specimens range from 10 cm to 1.5 cm maximum dimension.

They occur in close association with *Inaria karli*. They were considered to represent the first Ediacaran poriferans recognised on the basis of sandstone moulds of compressed discs bearing spicular impressions with Carboniferous hexactinellid dictyosponges, which are preserved in a similar manner. The characteristics of the fossil support the interpretation as a dome-shaped hexactinellid sponge with an osculum at the apex.

3.8. Review

A major review of the Ediacara type fauna was published by Jenkins (1992). He considered the environment of deposition of the Rawnsley Quartzite and favoured a shallow epicontinental basin with evidence of tidal sedimentation as suggested by Jenkins et al. (1983). He followed Sprigg and Glaessner in believing that fossilisation was principally linked to diurnal movement of sands during tidal deposition. Gehling (1982, 1983, 1987, 1988, 1991), on the other hand, followed some ideas of Goldring and Curnow (1967) and Wade (1968), that the remains were interred in some depth of water, in an outer shelf setting below fair weather wave base, burial being by storm-surge sands (as suggested by Mount, 1989, 1991). Seilacher (1984) accepted the same process, but added that ubiquitous wave oscillation and interference ripples are characteristic of a shore face. These ideas invoking storm deposits are contrary to the ideas of Wade (1968) who favoured an environment of lessened hydrodynamic energy.

Fig. 18. Drawing showing hypothetical development of tentacular burrowing anemone from lobate ancestor such as *Inaria karli*. Vertical section parallel to mesenterial walls showing part of inner walls (stippled) of sectioned lobes (in A2 and B) and tentacles (in C and D). (A1) Horizontal section through widest part of column showing line (X–Y) of vertical section. (A2) B, C: Hypothetical intermediate stages. A, B: Passive epifaunal 'actinians' with lobate extensions of gastrovascular system providing stable resting configuration; pharynx erect, enabling control of mouth orientation. C, D: Partly infaunal anemone, with elongation of lobes as tentacles for defence and active predation; pharynx invaginated with development of stronger retractor muscles to aid burrowing (after Gehling, 1988).

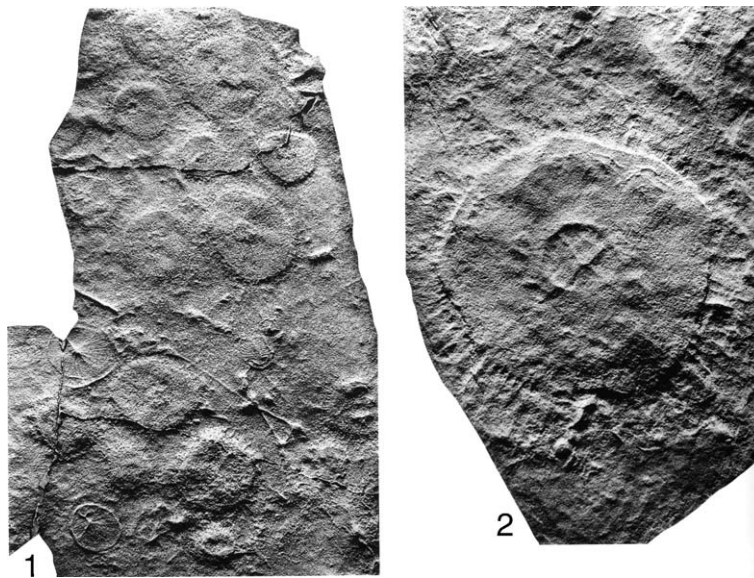


Fig. 19. *Palaeophragmodictya reticulata* gen. et sp. nov. from the Chace Range (see Fig. 3). (1) Slab bearing 15 small paratypes with smooth discs, mesa-like osculum, peripheral frill ($\times 1$). (2) *Palaeophragmodictya reticulata* gen. et sp. nov., paratype from the Heysen range (see Fig. 3), with central crater crossed by ridges; smooth disc with faint mesh ornamentation; peripheral frill of spicular ridges ($\times 1$) (from Gehling and Rigby, 1986).

Desiccation cracks had recently been found at the time when Jenkins was writing in fossiliferous beds of his “Ediacaran facies D” (Jenkins et al., 1983) in part of the Heysen Range. This would seem to support the tidal concept, the beds being subject to emergence with crinkling noted in some fossils caused by drying out. The preservation of delicate epichnial trace fossils observed was also against the storm concept. Laminal shearing in the first stage of tidal creep, gently transporting sand grains to initiate burial of organisms stuck down or clinging to gluey surfaces of drying out algal films was suggested for pelagic organisms, whereas benthic organisms must have actually lived as communities in the subtidal setting.

Jenkins provided a list of the Ediacara taxa in the type area (Table 5) and he provided some notes on certain genera and species. In the case of *Beltanella gilesi*, he noted that Nedim et al. (1991) had detected up to seven gonads and poorly preserved septa separating them, suggesting an octamerous arrangement. There were also poorly preserved tentacles evident and he suggested similarity to the order Coronata of the modern Scyphozoans.

Ediacaria was, he suggested, intermediate between a polyp and a medusa. He described the discovery of a ‘nested’ set of *E. flindersi* in the western Flinders Ranges, a central cylindrical element, filled with coarse sand (now sandstone), extending down into the

underbed and terminating in a mud clast about 0.8 cm deeper in the bed than the adjacent central extension of the disc. This was interpreted as preserving the organisms in the life position attached to mudflakes or a substrate mud layer and the organisms colonizing a shallow pool with a sandy bottom prone to rippling by currents. The creatures were apparently bowl-shaped, with a short stalk attachment, later being flattened on burial. The pool appears to have become desiccated on at least two occasions. This interpretation could apply to also to *Cyclomedusa davidi* as illustrated by Wade (1968).

Jenkins argued strongly against the idea of Seilacher (1984, 1985) that the giant fossil *Mawsonites* was not a true fossil, but a trace fossil, stating that it was clearly the cast or mould of an animal’s body. Some *Cyclomedusa* specimens showed an association with partial fronds, suggesting that they may represent anchoring devices of sea pens.

Wadea gen. nov., erected to include *Rugoconites tenuirugosus*, has a finer pattern and more radial deposition of the grooves. The holotype has a possible mould of a round mouth enclosed by a second circle (possibly a stomach) and probably was a much thinner bell than in *Rugoconites*. Wade’s indication that foam may fill the gastrovascular system of modern medusoids, or early decomposition of food material may distend the canals with gas, was said to provide an explanation why circulatory networks have acted as

resistant elements during the process of moulding these forms.

New finds of *Eoporpita medusa* (Wade, 1972a) had revealed in one specimen a central polyp seven times the diameter of the tentacle like structures ringing it. The polypoid aspect generally faces downwards, the likely stranding position of float-buoyed organisms on tidal flats. However, the three-dimensional preservation suggests possible interpretation as Actinians (Jenkins, 1989a,b). *Hiemelora stellaris* was lately located in offshore facies sediments in the Flinders Ranges and was likely Actinian. *Chondrophora bilobata* was interpreted as the float of a bilateral Chondrophoran; this and *Ovatoscutum* were compared with the modern *Verella* Lamarck 1801. *Chondroplon bilobata* was definitely not a distorted form of *Dickinsonia* Sprigg, 1947 as Hofmann (1988) had suggested.

Kimberella quadrata, reviewed by Jenkins (1984), was well established as having elongated bell shape; transversely furrowed sectors suggest strong swimming muscles. Two or three puckered gonads, were well preserved, as illustrated by Jenkins (1984). These animals were believed to be directly ancestral to sea wasps, and to have been fast-swimming pelagic predators.

Charniodiscus stalks apparently had sand-packed internal spaces, indicating hollowness in life, and a large canal may have extended the length of the stalk. The stalks may extend from a round plug of sand which presumably filled a crater when the discs had collapsed within the substrate. Discs were anchoring devices which could be worked down into the substrate where their inflation by fluid held the animal in place. The apparent flat shape of the discs resulted from compaction and they were presumably spherical in life. Stalks are up to 30 cm long and the frond grew in excess of one m tall in large specimens, which were up to 28 cm wide. Comparable organisms grew in the Mid-Cambrian Burgess Shale of British Columbia (Conway Morris, 1989b).

The extremely rare genus *Glaessneria* Germs 1983 is enigmatic; it shows resemblance to a modern sea pen, *Pennatula* Linne, 1758, and the polyps apparently needed access to free water and so projected away from the colony in life. Compression in burial could account for the zigzag overlap along the mid-line of the frond.

The find of specimens of *Rangia schneiderhoehni* in the Ediacara Member (Gehling, 1991) indicated that the Nama Group fossiliferous rocks of Namibia are of similar age to the Rawnsley Quartzite. *Pteridinium nenora* occurs below the Ediacara

Member *sensu stricto*, and is also present in North Russia (Fedonkin, 1981b) and North Carolina (Gibson et al., 1984). *Phyllozoon hansenii* is similar to *Pteridinium* but its frond seems to have been planar. It is rare at Ediacara where emergent tidal facies is represented, but is common elsewhere. It may have favoured waters a little offshore and was presumably benthic and rarely subject to stranding. Individuals may have had a weak attachment to stolons and tended to grow in clusters.

Dickinsonia has engendered much controversy. Jenkins noted that the annelid relationship had been disavowed by Fedonkin (1981a, 1985a) and Seilacher (1984, 1985, 1989), but found none of the objections substantiated. The apparent alternation of segmentation along the mid-line was consistent with flexible musculature in modern errant polychaetes. The resemblance to the modern *Spinther* Johnston 1945 was re-emphasised, the difference being only in the greater number of segments and lack of the hooks attaching the modern animal to its host. The median ridge may represent a detritus-packed intestine. Assumptions that it was a flat animal may be erroneous, the flattening may be a preservational effect of sandwiching between resistant sand layers. *Dickinsonia*, in large species, may have more than 91 segments on a weakly contracted rear end shaped like a beaver's tail and half the width of the anterior body of c. 220 segments. *Dickinsonia lissa* is, in contrast, a wrinkly contracted narrowly segmented form, of which smaller individuals seem to have inhabited extreme shallows, its flat shape favouring life in tidal pools. These were not highly active worms, but crept slowly about by expanding and contracting areas of the body, browsing on algal films and decaying sapropels at the sediment/water interface. Such a leisurely way of life adopted by these 'meaty pancakes' reflects an absence of predators. Jenkins illustrated his concept of the taphonomic changes undergone by *Dickinsonia* in a cut-away serial diagram.

Spriggina and *Marywadea*, with their large crescentic prostomia and tapered multisegmented bodies resemble trilobites (Runnegar, 1982a; Conway Morris, 1985) and have been classified by some as Arthropods (Birket-Smith, 1981a,b; Runnegar, 1992), but Jenkins believed that true limbs were not apparent in *S. flindersi* and that Birket-Smith's interpretation was overly influenced by grain boundaries in the coarse matrix. He discussed the effects of compression on burial and believed that the lateral processes could have functioned like parapodia. The animal had a quite tough and

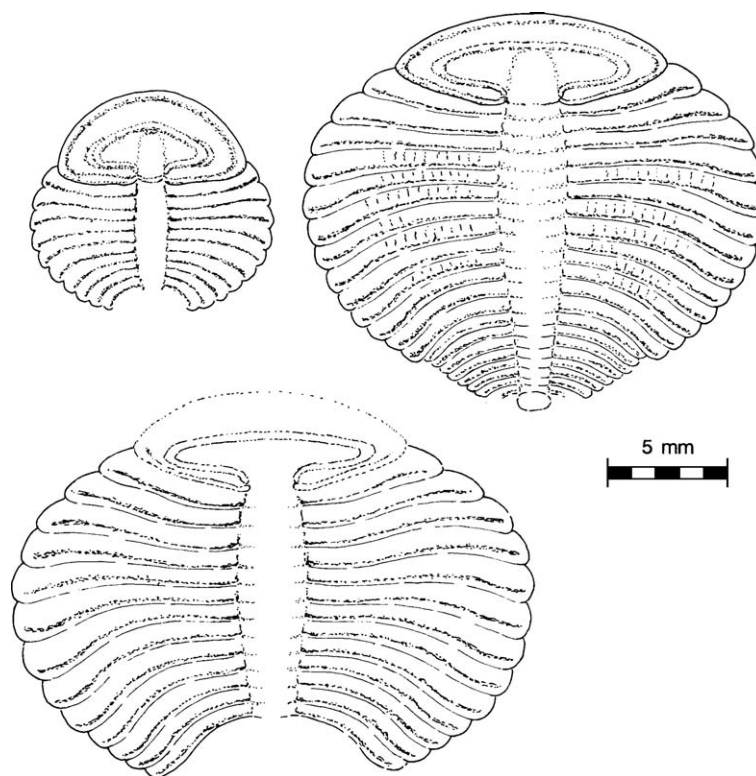


Fig. 20. Reconstructions of several examples of a recently discovered “soft-bodied trilobite” in the Ediacara Member of the Rawnsley Quartzite (from Jenkins, 1992).

resilient body. He believed that the interpretation as an errant annelid was still plausible. A large well-preserved specimen referred to as *Marywadea* (Glaessner, 1976) revealed a broad anterior end with well defined branching gastric diverticulae extending on either side of the axis. This was very similar to the arrangement in trilobites, but such ramifying gastric systems were also known in living polychaetes. They are also characteristic of *Praecambridium sigillum*, which, as Glaessner and Wade (1971) and Glaessner (1984) argued, is very likely related to the ‘trilobitoid’ *Vendia menneri* Keller, 1976 from the Vendian of North Russia. The kite or shield-shaped *Parvancorina minchami*, which ranges from 3 to 35 mm in length, is found in the Flinders Ranges as flattened forms in the top surfaces of thick mud layers within sandstone beds, the sand of which settled from density currents. This species has been compared to *Burgessia bella* Walcott, 1912 from the Mid-Cambrian Burgess Shale of British Columbia; the difference being 10 pairs of limbs on the hind axis as against 8 in the Burgess shale species.

That relatively large Arthropods were present in Ediacaran times cannot be disputed; the trace fossil *Diplichnites* Dawson, 1873 has been recorded (Gehling,

1991) and is indistinguishable from Early Cambrian examples. There are also arthropod scratches observed on lower surfaces of quartzite flags, paired—indicating double claws on each ‘telopodite’—and occurring in fan-shaped arrays up to 7 cm wide (Gehling, 1991) and 14 cm long. Whatever animal made these traces is estimated as being c. 4 cm long and having 12 or 13 pairs of limbs. Jenkins introduced these traces before introducing the possible originator, in the form of ‘a soft-bodied trilobite’ (Fig. 20; see also Fig. 169) possessing the characteristic tripartite body divisions—a semicircular cephalon with a well-marked border, conspicuous recurved eye ridges and a median glabella; a broad prothorax of 13 segments; a tapered episthrothorax of 13 segments; and a small oval pygidium, too small to show any detail. There is a raised median transverse axis and flat fields on either side of it. Distortion of the specimen indicates a degree of elasticity to the integument. This important new find does not appear to have been given a formal taxonomic description (at least nothing has been found in the present author’s thorough literature search, but it may well have appeared in an Australian publication which has evaded the search systems).

Tribrachidium heraldicum had a sack-like body, the dorsal disc bearing three crescentic arms which may have surrounded a mouth. It was an animal that probably lived shallowly buried in the upper substrate. Glaessner (1960, 1984) erected a new phylum to cover it and Jenkins agreed with this; it approaches the degree of organisation of the Echinodermata. *Arkuria adami* was considered by Jenkins to be convincing as an ancestral Echinoderm, resembling the Cambrian asteroids. There are indications that it preserved a partial skeleton of mineralised plates (Gehling, 1987).

3.9. Ediacara-type fossils in the Cambrian Uratanna Formation

Jensen et al. (1998) remarked that the world-wide occurrence of Ediacara-type fossils (from 600 to 544 Ma) is unique in consisting of soft-bodied animals, typically preserved as impressions in coarse-grained sediments. They predate the major burst of skeletonisation at the start of the Cambrian. Most of the Ediacara-type fossils have been interpreted as cnidarians, but higher metazoans such as annelids and molluscs may be present. The unique styles of preservation and difficulties in finding convincing morphology homologies with definite animals have led to some interpretations of them as non-metazoans (for example Vendobionta). In this publication, the authors reported typical Ediacara-type frond-like fossils and the discoid fossil *Kullingia* occurring together with an assemblage of Cambrian-type trace fossils in a locality to the east of Leigh Creek in the northern Flinders Ranges, where the Uratanna Formation fills megachannels within the Rawnsley Quartzite. The fossils were found on one surface 350 m above the base of the Uratanna Formation and 25 m below the top, which is marked by the appearance of the spreite burrow trace fossil *Diplocraterion* at the base of the Prachilna Formation (Fig. 3). 59 fronds were found on one surface, resembling the Namibian (Spitzkop Formation) fossil *Swartpuntia*, but differing in some aspects and requiring the erection of a new taxon.

These fossils are known to be of Cambrian age because they occur with and above an assemblage of *Treptichnus pedum*, *Taphrhelminthopsis circularis*, *Phycodes* cf. *palmyus*, *Phycodes coronatum* and *Curvolithus* sp. Trace fossils of this type first appear in the Newfoundland Cambrian stratotype section at Fortune Head above the Precambrian/Cambrian boundary which is defined by the first appearance of *Treptichnus pedum* (Narbonne and Myrow, 1988).

Kullingia is also known from the Early Cambrian of the Chapel Island Formation, Newfoundland (Narbonne et al., 1987), the Cambrian of North Sweden (Jensen and Grant, 1999) and the Ukraine (Gureev, 1985). The Uratanna Formation can be correlated regionally, stratigraphically with a formation on the Adelaide-York Peninsula which is underlain by developments of Cambrian-type small shelly fossils. It is of equivalent age to the Nenakit-Daldyn age sediments of Russia.

The initial phase of the Cambrian explosion was apparently quite protracted and many late Precambrian shelly faunas have now been recognised, composed of hexactinellids and isolated spicules (Gehling and Rigby, 1986, Brasier et al., 1997). The Uratanna Formation records the closing of the taphonomic window (i.e. the span of time characterised by unique preservational conditions), which was as important as extinction in the disappearance of Ediacara-type organisms. There is indirect evidence that Ediacara organisms occurred together with extensive microbial mats. Many of the Ediacara forms were benthic and had limited mobility or were shallowly placed in sediments or even attached to microbial mat-bound surfaces. The Ediacara-type organisms lingered in the Early Cambrian and there is no distinct cut-off; whether they evolved or simply perished is not at present known.

Droser et al. (1998) considered the role of the trace fossils in the changes through the Cambrian boundary... The increase in diversity and complexity of traces is well-documented at the Precambrian/Cambrian boundary, but other aspects are important in these changes, such as burrow size, depth of bioturbation and the amount of disturbance of the original sedimentary structures. The appearance of the boundary index trace fossil *Treptichnus* in the Pound Subgroup and Uratanna Formation also marks the development of discernible ichnofabrics. The amount and nature of bioturbation in the Early Cambrian Uratanna Formation is simple compared with typical Phanerozoic samples, yet is readily differentiated from that in the sediments of the Ediacara Member. This probably reflects the development of *Treptichnus*-type trace-making organisms. The only traces in strata below the appearance of *T. pedum* are two-dimensional and have maximum dimensions of less than 5 mm. Bedding planes of these sediments preserve discrete trace fossils but there is no resulting ichnofabric (bioturbation).

Gehling et al. (1998) added further comments related to the Uratanna finds. The apparent gap in Neoproterozoic sequences had been used to argue for extinction prior to the Cambrian explosion, but taphonomic studies suggest that the stratigraphic ranges of the biota are

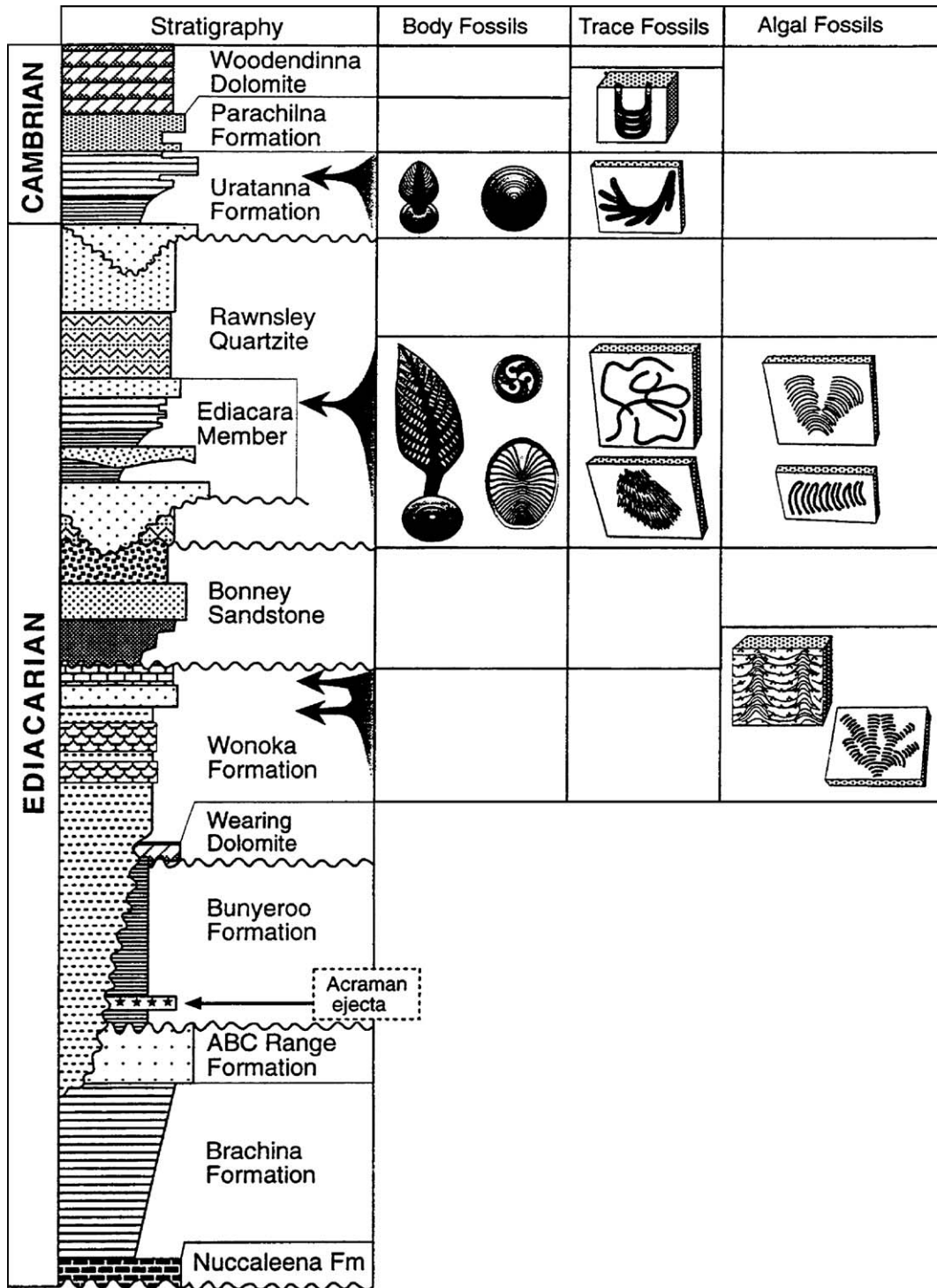


Fig. 21. Summary diagram of the stratigraphy, body fossils, trace fossils and algal fossils in the Ediacaran sections in the Flinders Ranges (after Gehling, 1983).

facies-limited. Also the ranges have been extended right up to the Cambrian boundary in Nevada and Namibia, and in the Urutanna Formation Ediacara-type fossils

have been recorded 120 m above the first occurrence of Early Cambrian type indicator trace fossils. The body fossils there were restricted to one bed where the mat

surfaces had only been penetrated to a limited extent by *Treptichnus (Phycodes) pedum*. This horizon contrasts with the fossiliferous horizons of equivalent facies within the Ediacara Member 500 m below, where trace fossils are restricted to two-dimensional styles. Whereas the Ediacaran organisms may have been driven to extinction by changing ecological patterns, more efficient processing of the sediments occupied by these soft-bodied organisms must have been a major factor in their disappearance as fossils. The buried microbial mats which formed a suitable taphonomic environment for death masks to form in the Neoproterozoic sediments were most likely largely destroyed by the Cambrian boundary revolution.

3.10. Sedimentary cycles and closing of the taphonomic window

Gehling et al. (1998) attributed the three “type-1” sequence boundaries in terminal Proterozoic–Early Cambrian succession of the Flinders Ranges, which preceded large-scale channel and valley incision, to relative falls in sea-level (Fig. 21). In each case, a low-stand sequence tract is overlain by a shallowing-upwards high-stand tract. The suggested cause is tectonic movements or evaporation draw-down of sea-level. There is limited evidence for transgressive sequence tracts suggesting rapid restoration of sea level followed by renewed progradation from north and west over an incised shelf. The Wonoka, Ediacara and Uratanna sequences represent equivalent responses to rapid drowning of a limited part of the Adelaide Geosyncline, but they are represented by taxonomically and economically contrasting body fossils. In the Wonoka sequence, there is little preserved evidence of mega-organisms; during the deposition of the Ediacara sequence, the seafloor was inhabited by passive and relatively immobile benthic organisms, sediment processing organisms being confined to two-dimensional biotopes. Buried organic remains and lamination remained undisturbed, allowing the preservation of death masks. The high-stand sequence of the Uratanna sequence recorded the last Ediacara-type fossils and the first evidence of bioturbation (burrows that penetrated below the water/sediment interface). This change indicates that the Cambrian lower boundary lies close to the disconformity at the base of the Uratanna sequence.

Recent discoveries in Nevada and South Australia show that the claimed ‘extinction’ of the Ediacara fauna well below the Precambrian/Cambrian boundary is an artifact of facies distribution. Eventually, the Cambrian

explosion of biological and ecological innovation put an end to both the ecology and the taphonomy of Ediacaran-type organisms in all but the most inhospitable environments.

3.11. Sequence stratigraphy framework

Gehling (2000) followed the above brief appraisal by a full description of the application of sequence stratigraphy to the terminal Proterozoic Ediacara Member within the Rawnsley Quartzite of the Pound Supergroup. He illustrated the positions of measured sections of the Pound Supergroup within the Flinders Ranges; and stated that the base of the Ediacara Member is a type-1 sequence boundary incised into the partly lithified Chace Quartzite Member of the Rawnsley Quartzite, of which the Ediacara Member and top half of the Rawnsley Quartzite comprise the depositional sequence. The cut down involved 250 m of relief. Impressions of soft-bodied Ediacaran organisms are preserved above the valley-fill facies on sandstone partings within upwards-shoaling delta-front environments between storm- and fair-weather wave base. There were at least four incision events, including that represented below the Ediacara Member, in the overall Neoproterozoic and Early Cambrian sequence and this has resulted in some confusion in the case of condensed sections.

Wave and tide reworked shallow-water sandstones of the remainder of the Rawnsley Quartzite represent environments not favourable to preservation of soft-bodied organisms (such preservation is extremely rare in these). They represent progradational tidal delta deposition. Recent discoveries in the Early Cambrian Uratanna Quartzite, mentioned above, have demonstrated that the preservation of the soft-bodied fossils is facies controlled and the barren section of the Rawnsley Quartzite hides the true range of the Ediacara-type taxa. The ecological revolution documented by the incoming of penetrative burrow and shelly fauna at the beginning of the Cambrian may have been a factor in both the extinction of the soft-bodied organisms and in reduced the chance of their preservation as fossils.

Distinctive microbial mat sand laminae (‘petée’ structures) occur above and below the Ediacara Member and may have assisted fossil preservation. The structures can be confused with desiccation cracks.

The definition of the Ediacara Member, by Jenkins et al. (1983), was emended to include a number of facies packages in the subsidiary type sections. A generalised sectional diagram was published and subsidiary sections for the Chace Range.

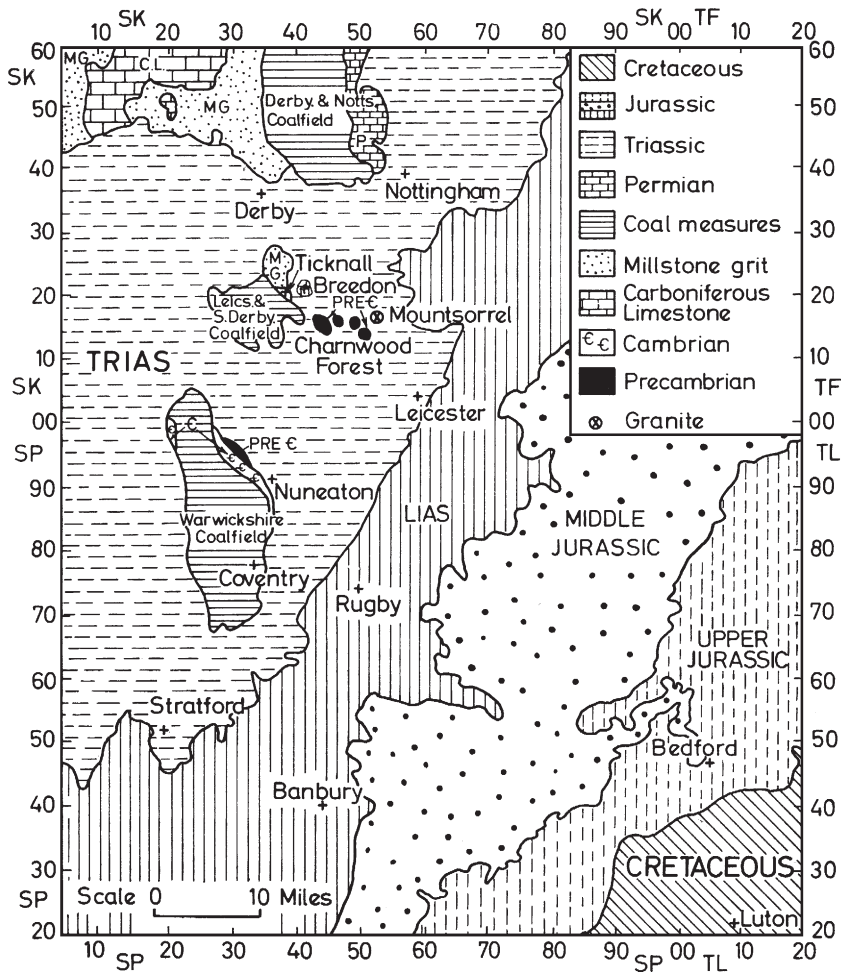


Fig. 22. Outline geological map of the East Midlands (after Evans et al., 1968).

3.12. Acritarch biozonation

Grey (1998) reported on studies of Acritarchs in the Centralian Superbasin and Adelaide Rift Complex. An older Simple Leiosphere-dominated Palynoflora is succeeded by the Ediacaran Complex Acanthomorph-dominated Palynoflora, which shows a marked increase in abundance, size, morphological complexity and taxonomic diversity, more than 40 species and 20 genera appearing for the first time in the middle “Ediacaran”, together with new body plans and new lineages of green algae. The transition coincides with a negative $\delta^{13}\text{C}_{\text{org}}$ excursion, which coincides with the Acraman impact layer (whether this is coincidental or has a bearing on the change in the biota remains uncertain). A summary is given by McKirdy et al. (1998) of research into developing a carbon isotope based stratigraphy for the

Neoproterozoic in South Australia and its possible extension as a global correlation system.

3.13. Bedding plane variation near Ediacara

Droser et al. (2003) reported that four successive thin sandstone beds 2–10 cm thick near Ediacara, when excavated, revealed quite different fossil assemblages:

Bed 1. *Dickinsonia*

Bed 2. *Aspidella* under a basal surface entirely coated with microbial or algal material: size frequency consistent with a single population.

Bed 3. Contains *Dickinsonia*, but is dominated by other taxa (*Spriggina*, *Parvancorina*, *Tribrachidium*, and *Rugoconites*)

Bed 4. Problematic mop-like structures (? A form of actinian commonly associated with disks such as *Aspidella* and *Eoporpita*) and a very large frond attached to a holdfast.

Only Bed 1 was monospecific. The beds were deposited as storm sands, stacked event sands in channels near fair-weather wave base, to thin bedded sands and silts deposited in waning storm surges below storm base.

3.14. Conclusion

Despite the proliferation of Ediacara-type fossiliferous sequences, now known in all continents save Antarctica, and the fact that some such fossils were tentatively recognised elsewhere before Sprigg's famous finds, South Australia must remain the prototype of the Ediacara-type fauna.

4. Charnwood Forest, England

4.1. Introduction

The history of the discovery of fossils in the Precambrian Rocks of the Charnwood Forest, Leicester-

shire, England, a small area in the English Midlands (Fig. 22) has been briefly covered in Section 2. Precambrian rocks have long been known here as well as nearby at Nuneaton, also further west in the Wrekin. Longmynd and Malvern Hills.

4.2. Stratigraphy

The Charnian System succession was described as follows (Evans et al., 1968):

- c. Brand Series (1000 ft)
 - Swithland slates
 - Trachose grit and quartzite
 - Hanging rocks conglomerate
- b. Maplewell Series (4500 ft)
 - Woodhouse and Bradgate beds
 - Slate-agglomerate
 - Beacon Hill Beds
 - Felsitic agglomerate
- a. Blackbrook Series (3000 ft)
 - Blackbrook Beds

Neither the base nor the top of the succession is exposed. This stratigraphy has since been revised (McIlroy et al., 1998, see below).

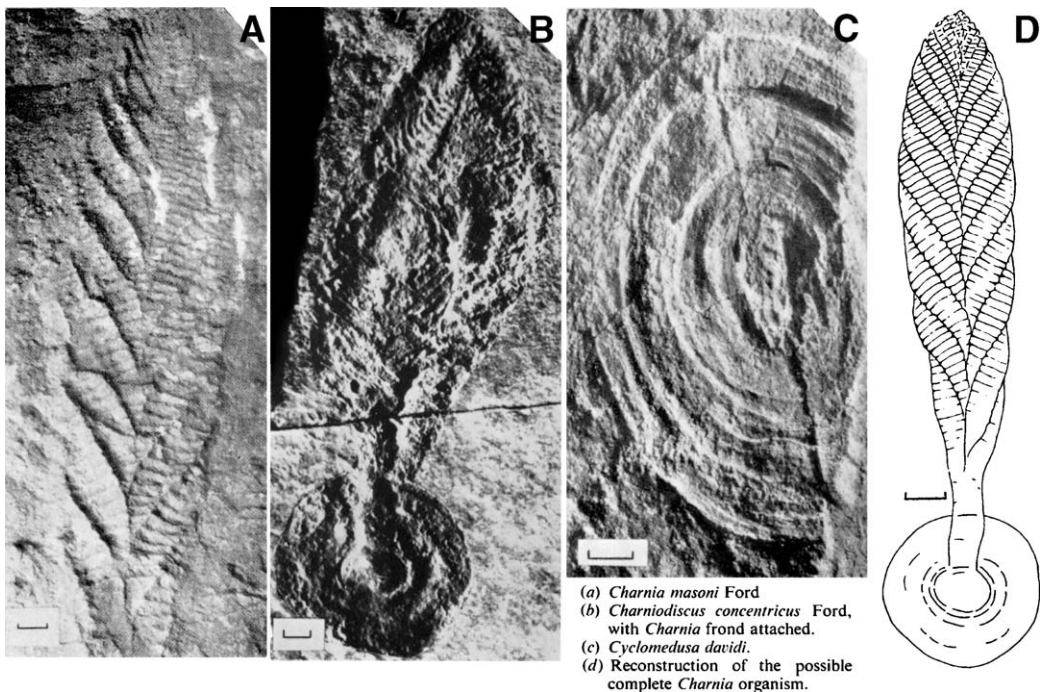


Fig. 23. *Charnia* and *Charniodiscus*; *Cyclomedusa*. (A) *Charnia masoni* Ford. (B) *Charniodiscus concentricus* Ford with a *Charnia* frond attached. (C) *Cyclomedusa davidi*. (D) Reconstruction of the possible complete composite organism seen in panel b (scale bar=1 cm) (from Ford, 1968).

The fossils are all found in the Woodhouse Beds. The sediments of the Charnian System are mainly volcani-
clastic and the impressions are on the bedding planes of
fine-grained tuffaceous siltstones. The age of the beds
was then unclear. Radiometric age dating on igneous
intrusions at Bardonia nearby in 1963 gave a minimum
age of 684 Ma (± 29 Ma) (Meneisy and Miller, 1963).
Evans et al. (1968) remarked on the considerable
thickness of Charnian rocks above the Woodhouse
Beds and the fact that there appears to have been an
erosional interval before the Brand Series was depos-
ited. Thus the age of the fossils cannot be very close to
the basal Cambrian date (nowadays taken at c. 543 Ma).
Evans et al. suggested an age of about 700 Ma, much
older than the Pound Quartzite of the Ediacara
Formation in South Australia. They believed that

Charnia/Charniodiscus (the first fossil described)
might have been a geologically long-lived organism.

4.3. The fossils

Charnia (Ford, 1958) was described as a frond-like
organism, generally 10–25 cm in length, and com-
posed of segmented lobes usually in contact laterally,
diverging alternately on either side of a sinuous axial
line the whole tapering to a pointed apex at one end
and a blunt stalk at the other. The Holotype is in the
Department of Geology, University of Leicester (Reg,
No. 2832). The lobes increase in size towards the
middle of the frond and then decrease. There is no
trace of vein structure as in a plant leaf. The holotype
is a negative impression, due to a solid body being

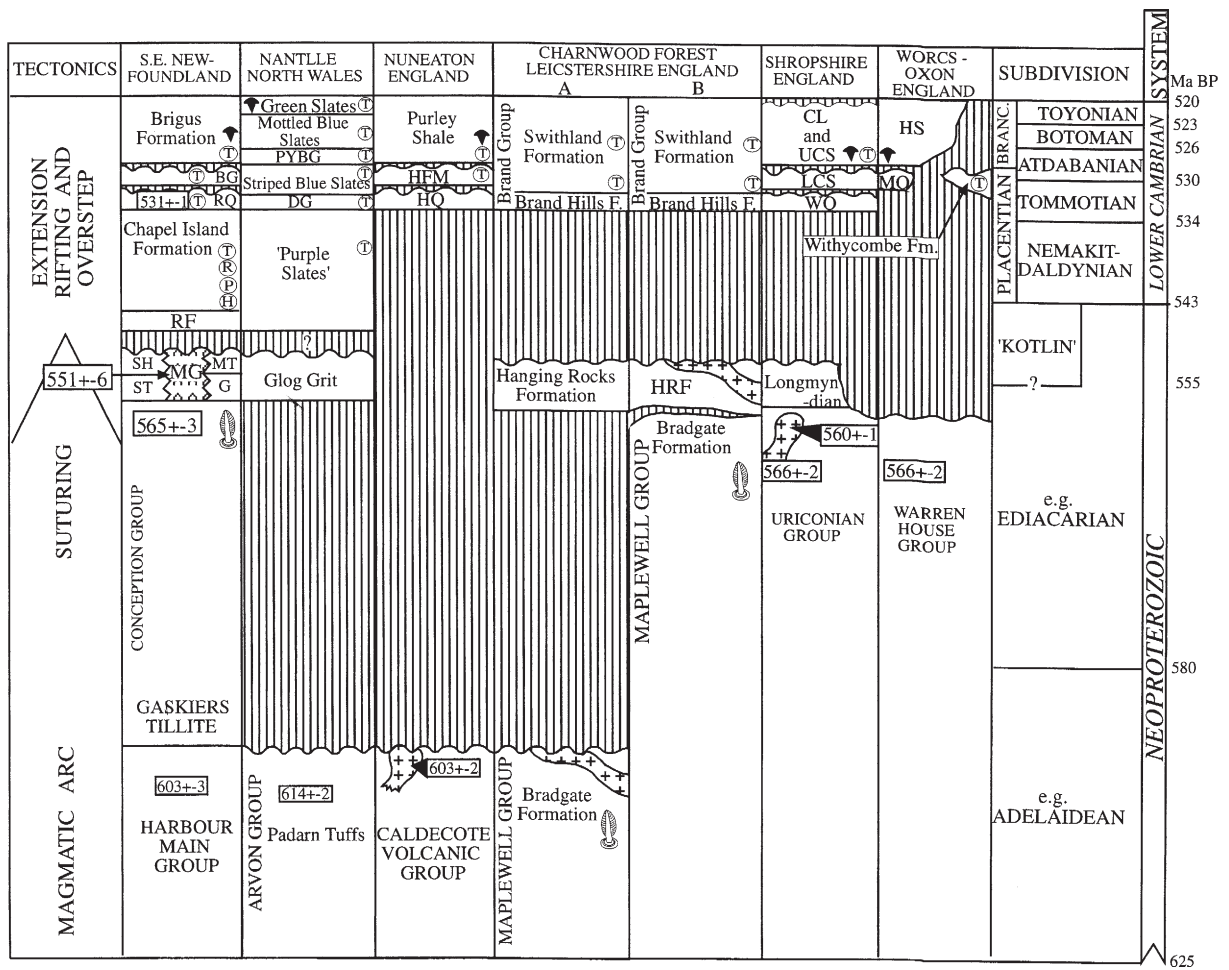


Fig. 24. Correlation of Neoproterozoic–Cambrian rocks of Charnwood Forest with those from other regions. Columns A and B give two possible schemes for the Charnwood Forest, that at the right being that favoured by McIlroy et al. (1998). Numbers=U/Pb isochron ages in Ma BP. Lithostratigraphic abbreviations are for various stratigraphic units as listed by McIlroy et al. (1998) on their caption, but this detail is not relevant here. Trace fossils, letters with circles: H=*Harlanella*; P=*Phycodes*; R=*Rusophycus*; T=*Teichichnus*. Body fossils: *Charnia* shown by symbol: First appearance of trilobite+trilobite symbol (after McIlroy et al., 1998).

	Moseley & Ford (1985)	Worssam & Old (1988)	Bland & Goldring (1995)	McIlroy <i>et al.</i> (this paper)	fossils										
CHARNIAN SUPERGROUP	PRECAMBRIAN	PRECAMBRIAN	PRECAMBRIAN	NEOPROTEROZOIC											
						Blackbrook Group	Blackbrook Group (over 1300m)	Blackbrook Group	Blackbrook Group						
						Maplewell Group	Maplewell Group	Maplewell Group	Maplewell Group	Maplewell Group	Ediacara Fauna				
												Beacon Hill Formation	Beacon Hill Tuff Formation (1100-1500m)	Beacon Hill Formation	Beacon Hill Formation
						Bratgate Formation	Bratgate Formation	Bratgate Formation	Bratgate Formation	Bratgate Formation	Ediacara Fauna				
												Sliding Stones Slump Breccia Member	Sliding Stones Slump Breccia Member	Sliding Stones Slump Breccia Member	Sliding Stones Slump Breccia Member
						Brand Hills Formation	Brand Hills Formation	Brand Hills Formation	Brand Hills Formation	Brand Hills Formation	Cambrian trace fossils				
												Hallgate Member	Bradgate Tuff Formation (190-530m)	Bradgate Formation	Hallgate Member
												Hanging Rocks Conglomerate Member	Hanging Rocks Congl. Mbr	Hanging Rocks Conglomerate Member	Hanging Rocks Formation
						Stable Pit Quartz-arenite Member	Stable Pit Quartz-arenite Member	Stable Pit Quartz-arenite Member	Stable Pit Quartz-arenite Member	Stable Pit Quartz-arenite Member	Cambrian trace fossils				
Swithland Formation	Swithland Greywacke Formation	Swithland Formation	Swithland Formation												

Fig. 25. A comparison between the stratigraphic successions of previous authors and that of McIlroy *et al.* (1998), showing the evolving concept of the contact between the Neoproterozoic and Cambrian. On the right, the distribution of the Ediacara-type fauna, simple accompanying trace fossils and Cambrian trace fossils is shown (after McIlroy *et al.*, 1998).

pressed into a soft substratum. There is no evidence of calcareous structure. The average number of segments to a frond is 13, a few show 12 or 14. Another fossil *Charniodiscus* was described as a disc-like organism, usually 5–30 cm in diameter, with a rough-surfaced central area surrounded by a smooth flange, with or without concentric corrugations. The holotype measured 6.4 cm in diameter, displayed a central boss and faint corrugations around it. Fig. 23 is Ford's (1968) illustration of *Charnia* and *Charniodiscus*; and reconstruction of the complete organism.

Another species of *Charnia* was recorded by Glaessner from the Pound Quartzite in 1959 and Evans *et al.* (1968) noted that *Rangea schneiderhoehni* Gurich, a similar form, with *Charnia*, had been allocated to the Pennatulid coelenterates ('sea-pens'). They noted that the Australian forms had since been classified as *Rangea*, *Pteridium* and *Arborea* (Glaessner, 1956), and their relationship to *Charnia* remained in doubt.

Ford (1968) also described and illustrated *Cyclomedusa davidi* from the Charnwood Forest. Boynton and Ford (1979) described from float (? derived from the Woodhouse Beds) a new arthropod imprint, *Pseudovendia charnwoodensis*, from the northeast Charnwood Forest, at Outwoods, near Loughborough. This was allocated to the Vendomiidae family,

supposedly small bilaterally symmetrical animals similar to trilobites, but lacking a hard exoskeleton. The same authors (1995) described a new frond-like form named *Bradgatia linfordensis*. They also described discoidal impressions with a slightly wavy, convex irregular rim, a inner gentle circular depression with a raised central boss: they named this *Cyclomedusa cliffi*, noting the resemblance to *Cyclomedusa cf. davidi* Sprigg of the Ediacara fauna and the Vendian *Tirasiana disciformis* Palij. They also noted and named several other discoid impressions. Most of the fossils were impressions on the upper surfaces of fine-grained sediments.

Boynton and Ford (1995) noted that there was no proof of Precambrian age for the Charnwood fossils, but that the similarity to known Ediacaran and Vendian forms strongly indicated such an age.

4.4. Recent stratigraphical revision

McIlroy *et al.* (1998) presented a revised interpretation of the stratigraphy (Fig. 24), taking the Brand Group up into the Cambrian, and noting that it contains abundant Cambrian trace fossils (large *Teichnichnus*), never found outside the Cambrian. They put the basal Cambrian boundary in or below the Swithland Formation of the Brand Group. Taking a U–Pb zircon date on

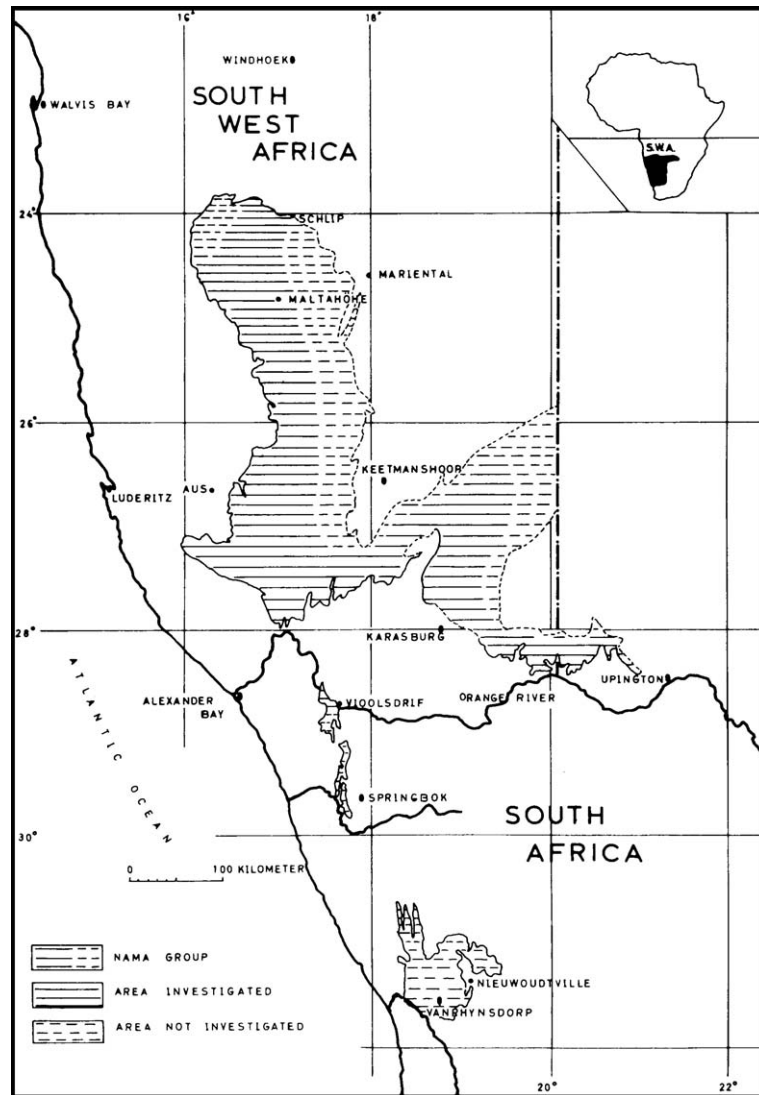


Fig. 26. Map of the known extent of the Nama Group, Namibia, with location of boreholes from which core samples were taken (after [Germis, 1972a–c](#)).

diorites beneath the base of the Cambrian at Nuneaton ([Tucker and Pharoah, 1991](#)), they give 603 Ma (± 2 Ma) as the minimum age for the Ediacara fauna in the Maplewell Group. They gave two possible age correlations with other sequences in Britain and southeast Newfoundland ([Fig. 25](#)), the first of which is based on the above age dating; the second is based on other arguments which throw some doubt on the isochron, and they suggested that the isochron needs substantiation.

4.5. Conclusion

Although the area covered by the Precambrian rocks is small and the fauna is restricted in the Charmwood

Forest, this was a historically important discovery, the first problematica being noticed as long ago as early in the 19th Century. Unlike most other developments of Vendian (Ediacaran) fossils, there is no association with any glacial horizon.

5. Namibia

5.1. Introduction

The history of finds in the Nama Group, Namibia, has been covered briefly in Section 1. The stratigraphy and palaeontology of the Nama Group ([Fig. 26](#)) was definitively covered by [Germis \(1972b\)](#), including a

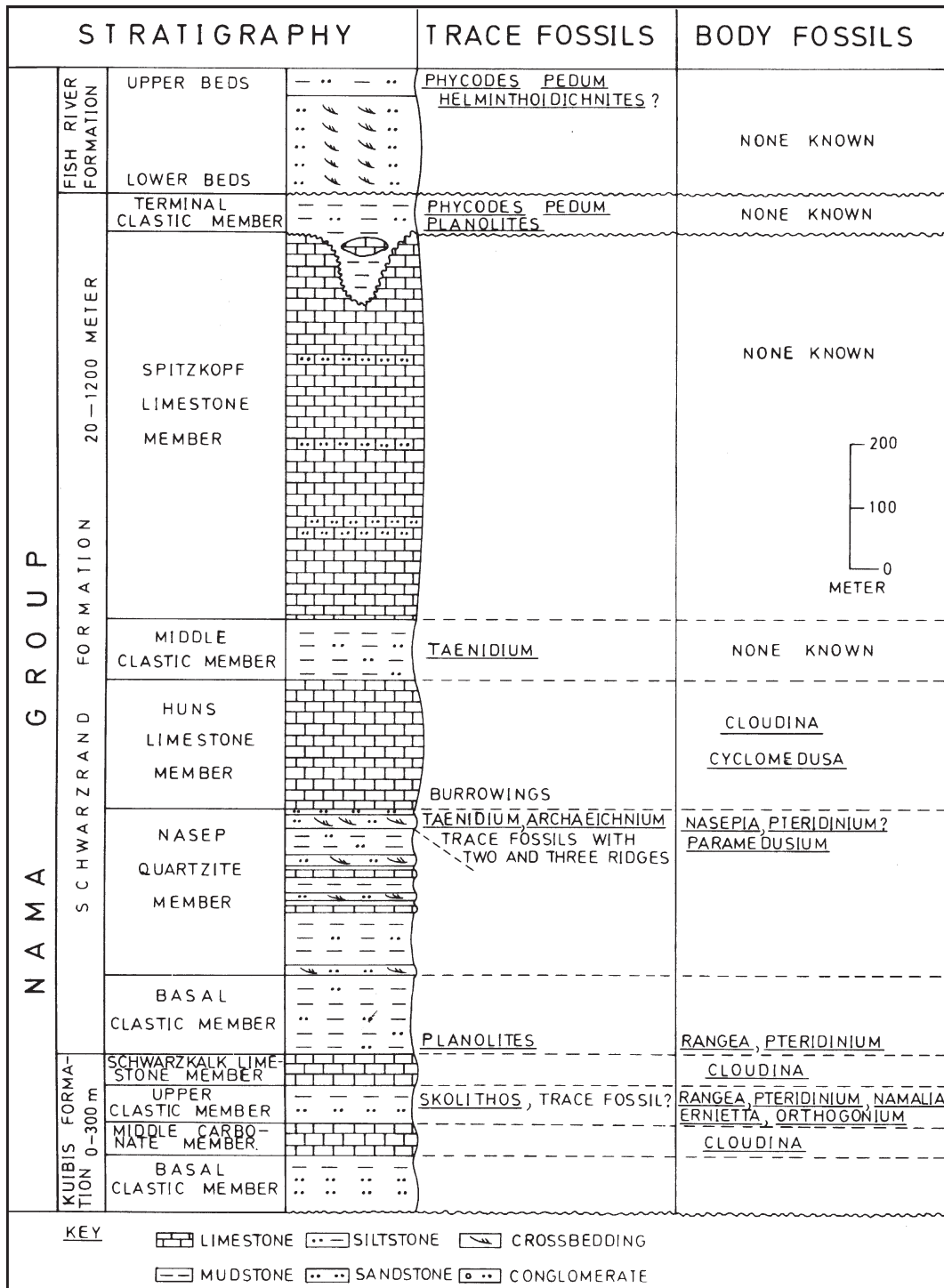


Fig. 27. Stratigraphic column of the Nama Group (after Germs, 1972a–c).

revision of the stratigraphy. The basal sediments of the Nama Group were deposited in a general eastwards transgression over the Kalahari Craton. The initial deposition, of the Kuibis Formation (Fig. 27), was of

an orthoquartzite/carbonate association, in two sub-basins separated by the E–W-trending Osis ridge. The source of the sediment supply was the Kalahari Craton. More limestone deposition occurred in the northern sub-

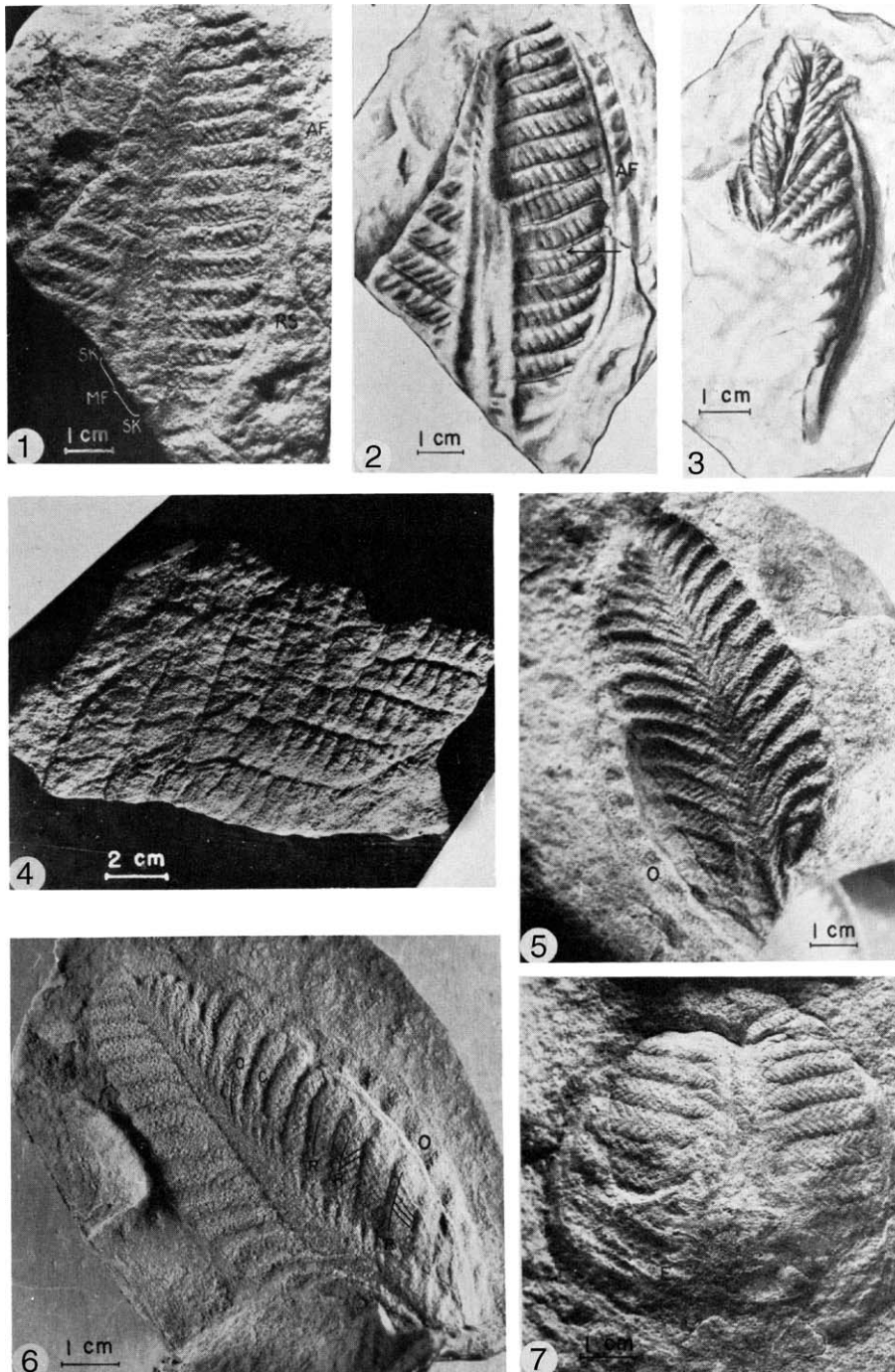


Fig. 28. *Rangea*. (1, 2, 3, 5 and 6) *Rangea schneiderhoehni* Gurich (1930), from Kuibis Formation. (4) *Rangea grandis* Glaessner and Wade (1966), holotype (renamed *Glaessnerina grandis*), from Ediacara, South Australia. (7) *Rangea schneiderhoehni*, from Basal Clastic Member of the Schwarzwand Formation (scale bar: metric). (From Germs, 1972a,b,c).

basin than the southern. The Kuibis Formation comprises two cycles away from the Osis ridge, but only one close to it. After the Kuibis deposition, the ridge disappeared, the Damara geosyncline was uplifted to the

north, west and south, and sourced the Nama Group deposits from the west in addition to the continuing sourcing from the craton. The Nama Group sediments are dominantly marine, although some fluvialite

deposition is represented, and they are specifically shallow marine. Prominent glacial deposits occur at the base of the Kuibis Formation and less well-developed glacial deposits in the terminal clastic member of the Schwarzrand Formation.

5.2. Fossils

Germes (1972a,b) provided a sectional diagram showing the stratigraphic distribution of body and trace fossils (Fig. 27). Most of the body fossils were found detrital sediments: only those found below the unconformity within the upper Schwarzrand Formation are ‘peculiar and characteristic’. Most are leaf-like bodies and are soft-bodied, but some have a skeletal structure (e.g. *Cloudina*). He described a number of body fossils, of which only *Pteridinium* and *Cyclomedusa* were at that time known from the Ediacara type-area in South Australia.

He listed the fossils with their probable Group or Phylum affinity (Table 6).

5.2.1. Petalanomae

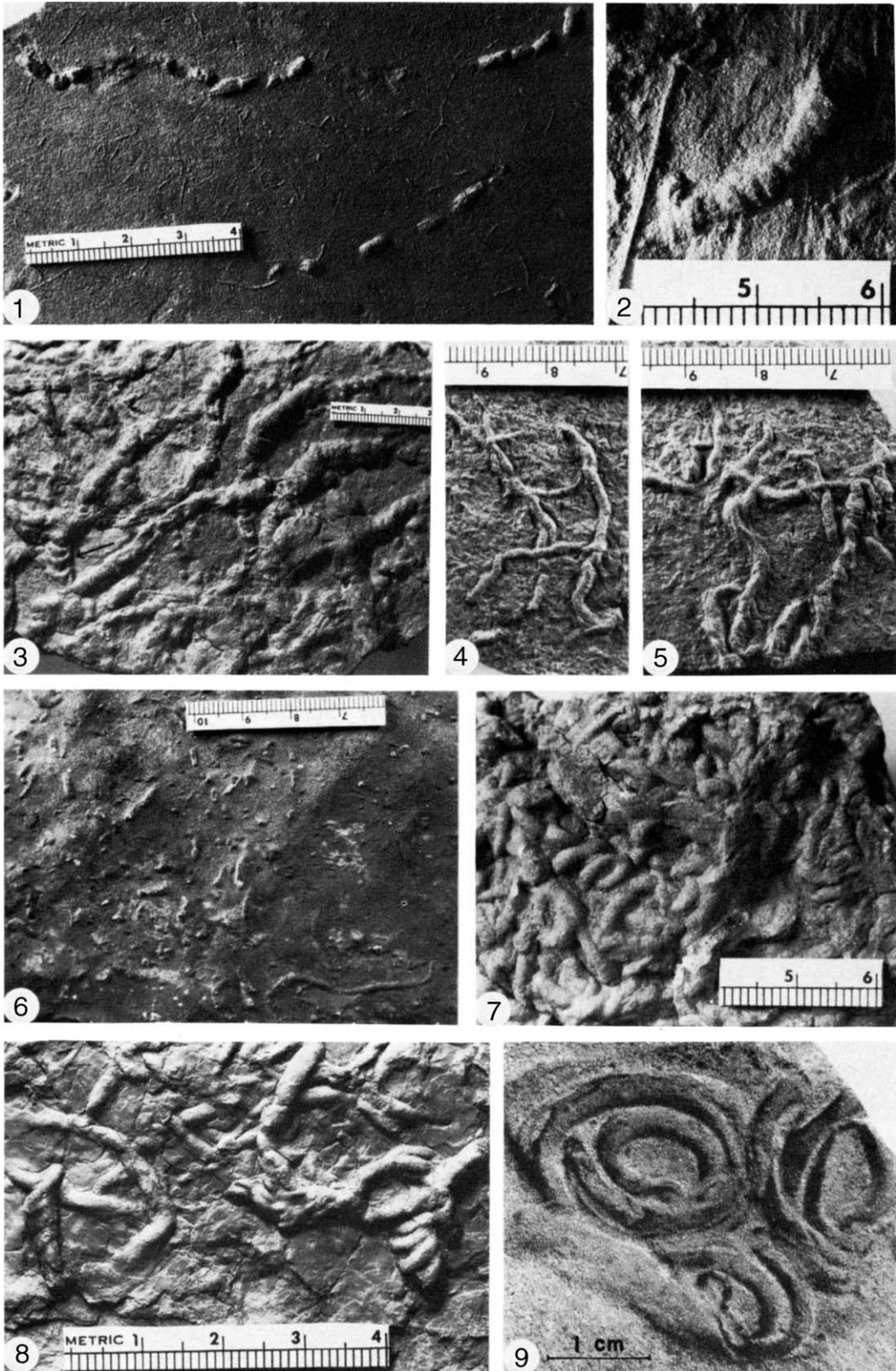
5.2.1.1. *Rangea schneiderhoehni*. Leaf-shaped main body with median field (axis) (Fig. 28). Lateral branches separated by transverse lateral furrows and subdivided by secondary furrows arising from their proximal margins. The first of Germes’s specimens was preserved as a mould and has a median line, a kind of median area, an outer furrow and an outer flange. It was 9 cm long and 4 mm wide. Primary branches are of two types; close to the median line smaller primary branches appear between the prominent ones, and form a slightly sharper angle with the median line. The prominent primary branches form angles of 45° to 50° to the median line. There were c. 16 primary branches. On one side there are secondary branches on the primary branches. The Namibian specimens differ from those described from the Ediacara type area (Glaessner and Wade, 1966) in that it has unilateral secondary branching and in the Namibian specimens there is bilateral secondary branching. The Australian specimens resemble *Charnia* Ford, 1958. It was suggested that the Australian specimens are not true *Rangea*. *Rangea* occurs in the Upper Clastic Member of the Kuibis Formation and

the Basal Clastic Member of the Schwarzrand Formation (Fig. 27).

5.2.1.2. *Pteridinium simplex* Gurich (1930). This was described as long, thin bilaterally symmetrical ‘leaves’ with transverse ribs (Hantschel, 1962), but Pflug (1970a,b) found it to be composed of three wings—the third one regularly occurring dipping down into the interior of the host rock. The three wings normally make up the body which has a complex horseshoe form built up of leaf-like bodies. The median groove separates two zones of ribbed relief, which on both sides of the axis change into relatively smooth surfaces. The ‘petaloids’ were supposed by Pflug (1970a,b) to have performed respiratory functions, their origin possibly causally connected to changes in oxygen content believed to have occurred in late Precambrian times. Pflug found that this species shared characteristics of Echinodermata, Coelenterata and Hemichordata and placed it in the new Petalonamidae, whereas Richter (1955) had related it to the Gorgonaria and Glaessner (1959) to the Pennatulaceae. *Pteridinium* is related to *Rangea*, according to Germes, but there is a significant difference in the secondary branches in two direction of *Rangea*, whereas *Pteridinium* has no secondary branches. *Pteridinium* and *Ernietta* are also related—median forms between the two can be found. *Pteridinium* occurs in the Upper Clastic Member of the Kuibis Formation, and also the Basal Clastic Member of the Schwarzrand Formation, and possibly in the Nasep Quartzite Member as well (Fig. 27).

5.2.1.3. *Ernietta plateauensis* Pflug (1966). This was described as a sessile fossil with a thick dorsal exoskeleton bending ventrally into a horseshoe form. The exoskeleton was described as built of segments oriented on either side of a zigzag median line, so that the segments fit into each other, with the segments broadening in the most elevated part of the ‘shell’. A cross-section shows filaments that, in bundles, form the skeletal structure. Pflug (1966) stated that the symmetry and segmentation was that of worms and arthropods and the filaments were similar to those of an arthropod. The organism has the appearance of a coiled-up *Pteridinium*, but *Ernietta* was interpreted as an animal consisting of a single petaloid. Some

Fig. 29. Trace fossils. (1) Discontinuous trails, Nasep Quatzite member, Schwarzrand Formation, (2)–(3) *Taenidium*, *Muensteria*, *Scolecocoprus*. Note transverse ribs in (2), (2) from same locality as (1), (3) from Middle Clastic Member of Schwarzrand Formation, (4)–(6) Worm tracks from Terminal Clastic Member, Schwarzrand Formation, (7)–(8) *Phycodes pedum* from Fish River Formation, (9) Worm tracks [*Helminthoidichnites* of Glaessner (1963)] from Fish River Formation (scale bar: metric). (From Germes, 1972a–c.)



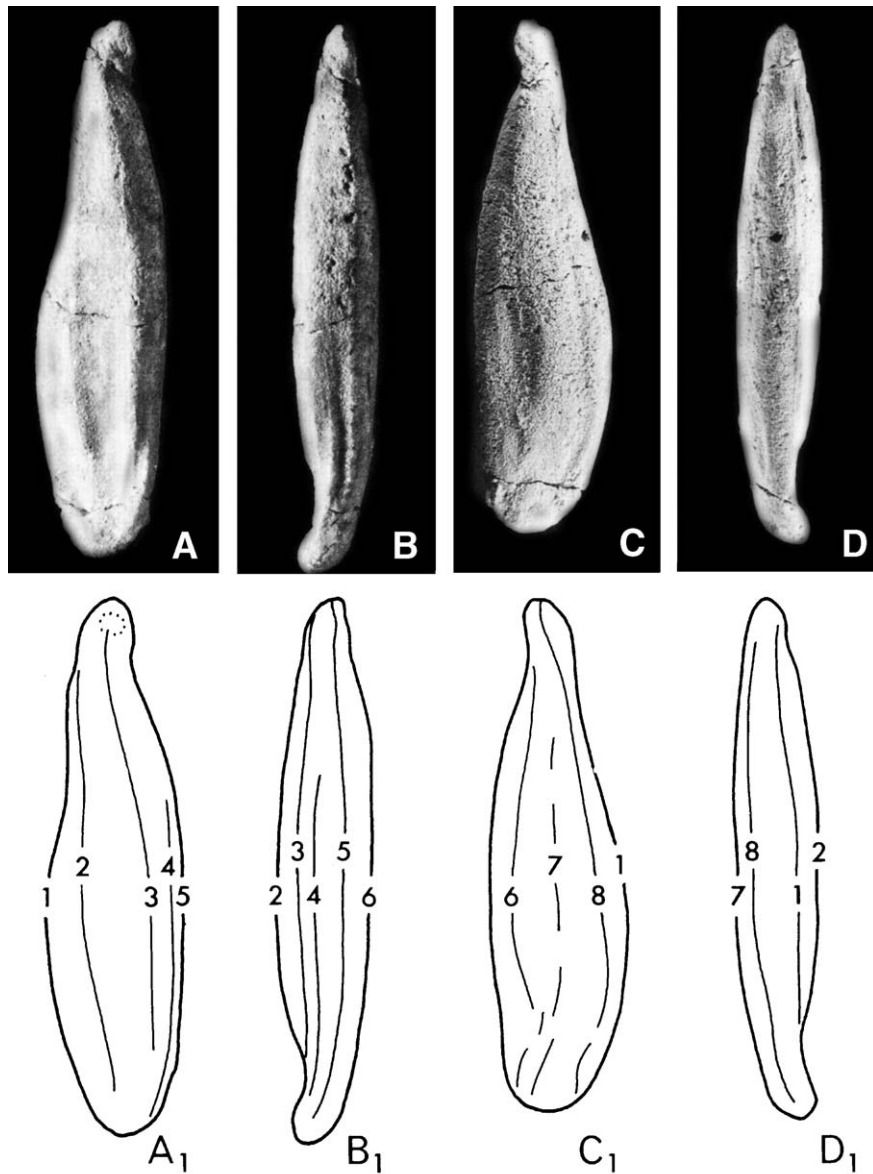


Fig. 30. *Protechiurus edmondi* gen. et sp. nov. (A–D) Different views of the natural cast. (A1–D1) Diagrams showing the positions on the above of the 8 ridges interpreted as longitudinal muscle bands. These are enhanced where the body is flattened but obscured on the inflated and stretched side (from Glaessner, 1979b).

specimens of *Pteridinium* possess a similar exoskeleton according to Pflug; however, he did not say what the exoskeleton is made up of mineral-wise. Germs recorded considerable variability in form, an original characteristic not deformational. Convexity and dimensions vary. He remarked that it and related types needed further study. *Ernietta* occurs in the uppermost part of the Upper Clastic Member of the Kuibis Formation, just below the Schwarzkalk Limestone Member, over a wide area, but, surprisingly, not in higher stratigraphical units (Fig. 27).

5.2.1.4. *Nasepia altae* new genus. This consists of leaf-like bodies, mostly elongated in one direction and mostly subparallel to the long axis. Transverse ribs may be present. The ‘petaloids’ are nearly flat or strongly convex and have a skeletal structure (Pflug, 1970a,b). It was uncertain whether an epidermis is present, as with *Rangea*. Petaloids are bundled together. A feathery structure is visible on the outer margin of one petaloid. The fossils recovered are few in number and poorly preserved, so it is uncertain whether there is a horseshoe structure as in *Rangea* and *Pteridinium*. The organism

was placed in the group Petalonamae because of the presence of bundled ‘petaloids’. It is related to *Rangea* and *Pteridinium*, but differs in the smaller size of the ‘petaloids’ and in the orientation of ribs subparallel to the long axis, whereas the ribs (branches) of *Pteridinium* and the ribs (primary branches) of *Rangea* make a greater angle with this axis. The type specimen was found in the Nasep Quartzite Member of the Schwarzsand Formation (Fig. 27).

5.2.1.5. *Namalia villiersiensis* Germs (1968). This was described as having a conical structure with longitudinal ridges, which continue a little way into the internal body. It is oval to round in cross-section. There is an outer and inner wall, with septa between perpendicular to the walls. The larger outer ridges consist of a number of fine ridges and the apex is rather blunt. Many specimens are deformed indicating a quite soft body. Germs (1968) related it to the sponges or archaeocyathids, but the discovery of *Nasepia* suggested that *Namalia* and *Nasepia* are related. Colonies of *Namalia* can be mistaken for *Nasepia*. *Namalia* may form colonies or be scattered. It has been found in quartzites of the Kuibis Formation, at one locality with *Rangea*, and possibly also with *Ernietta* in the uppermost Kuibis Formation.

5.2.2. Coelenterate

5.2.2.1. *Cyclomedusa davidi* Sprigg (1947). This medusoid occurs as circular to subcircular discs 15 to 46 mm in diameter. It was identified by Wade, but lacks the radial striae of the holotype. It might be confused with *Charniodiscus*, but occurs as casts on lower surfaces unlike *Charniodiscus*. It was found in the Huns Limestone Member of the Schwarzsand Formation (Fig. 27).

5.2.3. Archaeocyatha

5.2.3.1. *Cloudina* new genus. Sinuous calcareous tubes, composed of stacked cones giving the appearance of a double wall, the outer tube bears annular ridges and depressions and the smoother inner wall may show fine annular ridges. The inner tubes are not centrally located. Two species were recognised, *C. hartmannae* and *C. riemkeae*, the latter being smaller (up to 12 mm long) and being commonly epizoic on the other. They occur in bioherms or dispersed in the limestones, and in some cases together with stromatolites at the top of the Schwarzkalk Member of the Kuibis Formation (Fig. 27). Their occurrence with

stromatolites suggests a shallow water environment and the CaMg ratios suggest cool water. Similarities to serpulid worms and vermeitid molluscs were noted, but they were questionably referred to the Class Cribricyathae of the Archaeocyatha, although budding, probably one form of reproduction, was seen in one specimen of *C. hartmannae* and Cribricyathae display no budding. A possible relationship to the serpulids was also noted.

5.2.4. Microfossils

These were only briefly mentioned by Germs (1972b) but covered in some detail later by Germs et al. (1986).

5.2.5. Stromatolites

Stromatolites occur in all the Limestone Members of the Kuibis and Schwarzsand Formations and in some Clastic Members. They were discussed at length by Germs (1972b), but no definite taxonomic determinations were reached.

5.2.6. Trace fossils

These were also covered in a separate publication (Germs, 1972c). In the Kuibis Formation only *Planolites*-like traces were found and are restricted to the Upper Clastic Member. Some obliquely curved tubes may be *Skolithos*. The Basal Clastic Member of the Schwarzsand Formation yielded only *Planolites*-like traces near its base. The Nasep Quartzite Member yielded trails with transverse ribs, probably back-filled, *Taenidium*, *Muensteria* and *Scolecocoprurus* (Seilacher, 1971) and also *Archaeichnium haughtoni* Glaessner (1963). The Huns Limestone Member yielded vertical and horizontal burrowings, and the Middle Clastic Member the same three genera as the Nasep Quartzite Member. There were no traces at all within the Spitzkopf Limestone Member, and the Terminal Clastic Member yielded *Phycodes pedum* and also possibly *Planolites*. The presence of *Phycodes* caused this Member and those above to be placed within the Lower Cambrian. The Fish River Formation has yielded *Phycodes pedum*, as well as *Planolites* and *Helminthoidichnites*.

These descriptions of Germs (1972a,b) (Fig. 29) have been summarised in some detail because, like Glaessner and Wade’s work on the Ediacara fauna from the type-area, they represent the basic descriptions of the Nama fauna. There have been a number of revisions published in the years that followed, and many of the taxonomic attributions of Pflug and Germs have been challenged and much more has been learnt about the detailed structure of some of these forms.

In conclusion, *Germs* (1972a) stated that it seems reasonable that metazoans already lived before the late Proterozoic Numees Tillite in view of the fact that the Kuibis Formation overlies it unconformably carrying a relatively highly developed fossil fauna.

Germs (1973b) described a possible find of a Sprigginiid worm fossil and the find of a new trace fossil, *Bucholzbrunnichnus kroneri*, which resembles *Bunyerichnus dalganoi* Glaessner 1969 and *Plagiomus*, from the Nama Group. The latter was said to be important for indicating that various mollusc-like organisms lived prior to the Cambrian.

5.3. Later research

5.3.1. A possible Echiurid worm fossil

Glaessner (1979b) reported on a single specimen (Fig. 30) found in close association with *Pteridinium* in the Kuibis Formation (now Subgroup) of the Nama Formation, 35 km west of Kuibis. He based his identification on Cambrian Echiuria of America, his experience of coelenterates and annelid worms in the Ediacaran of South Australia, and comparison with living Echiuria. He described it as an Echiurid worm, named *Protechiurus edmundsi*, of a new genus and species. The material consists of one cast, composed of slightly micaceous quartzite from the collection of the State Museum, Windhoek. Approximately cigar-shaped, the greatest width is behind the mid-point and a slight constriction separates the proboscis (?) from the trunk (Fig. 30). One side is convex and the other flattened, the posterior termination being slightly turned towards the flattened side. The anterior end is twisted by 30° to the trunk. It is 74 mm long, with a maximum height (perpendicular to the width) of 19 mm, and a maximum width of 11 mm. Longitudinal ridges (probably 8 were present) mark the surface, being more prominent on the flattened side. The body was probably cylindrical prior to compression. The spatulate end has been broken off and rejoined. No internal characters are preserved and there is no organic matter.

The longitudinal ridges were interpreted as representing thickened muscle bands such as occur only in genera assigned to the family Echiuridae. The proboscis of this family is not bifid. The shape of the body and presence of longitudinal ridges support this identification. The family is related to the Annelidae, but whether they were ancestral or derived from them is uncertain. That members of this family are still living testifies to the conservative mode of life of these unsegmented, burrowing worms, which are all

marine except for some brackish water species. They dwell in shallow water and exploit the organic content of sediments as nutriment. They are less affected by anaerobic conditions than other worms. Their characteristic burrowing habit, producing branching and intersecting, multiple-walled burrows has not apparently left behind any trace fossils. With no predators, the other Vendian animals would have decomposed to provide ample food supply and this would have been added to by plant microfossils.

5.3.2. Revised stratigraphy and microfossils

Germs et al. (1986) presented the results of a study of microfossils in the Nama Group. They based this on a revised stratigraphy in which the Kuibis and Schwarzrand Subgroups replace the former so named Formations, and names are given to the subsidiary Formations and Members within them, some of the names being new. The two column diagrams covering the north and south show these changes and the stratigraphic levels at which metazoan, trace fossils and Cloudinids occur.

The lithologies in the Kuibis Subgroup vary according to distance from the Osis Ridge and, in the deeper parts of the two subbasins, sandstone units grade laterally into shale and limestone. Stratigraphic thickness of the Kuibis Subgroup varies from a few tens of metres close to the ridge to as much as 800 m away from it; also the sandstones and shales in the Schwarzrand Subgroup become increasingly immature upwards. There are several unconformities within the sequence. The Kuibis and Schwarzrand Subgroups document depositional environments from braided streams to quiet subtidal marine. Intertidal and shallow subtidal depositional environments persisted during this deposition and fluvial deposits only became significant in the upper part of the Schwarzrand deposition and became dominant in the Fish River Subgroup deposition. This latter Subgroup is a distal molasse assemblage. Throughout the entire Nama Group there is little evidence, such as turbidites, for deposition in deep water.

In general microfossils, like those in late Vendian sediments in other global developments, are poorly preserved in Nama Group sediments and this is puzzling because Riphean, early Vendian and Early Cambrian assemblages of microfossils generally exhibit quite good preservation. The following assemblage was recorded from the Kuibis and Schwarzrand Subgroups.

Leiosphaeridium spp.

Chuaria circularis Walcott emend Vidal and Ford 1985

Bavlinella faveolata (Shepeleva) Vidal 1976

Vendotaenia sp.

Filamentous sheaths

Comaspshaeridium-like microfossil.

The assemblage is remarkably simple and invariant in composition; it is dominated by sphaeromorphic acritarchs (*Leiosphaeridium*) measuring 30–70 μ in diameter. Individuals of *Chuarina circularis* are larger (114–319 μ) sphaeromorphs. *Bavlinella*, probably a cyanobacterium, occurs sporadically. Filamentous microfossils present are probably also cyanobacteria. *Vendotaenia*, present in most samples from the Nama Group, is a ribbon-like microfossil, assigned to the metaphyte algae (*Gnilokovskaya*, 1971, 1975; *Gnilovskaya*, 1976), but its systematic position remains not fully resolved. This assemblage is easily distinguished from Riphean and early Vendian biota of the East European Platform and is essentially identical with ‘post-Varangian’ (i.e. post-Laplandian), assemblages in the ‘Valdaian’ of the East European Platform. It is also similar to that of the Tent Hill Quartzite which is equivalent to the Range Quartzite, just below the Pound Quartzite in South Australia.

There is no evidence of Cambrian microfossils and the latest Proterozoic assemblage occurs in the Tses Borehole right up to the top of the Schwarzrand, but the Nomtsas Siltstones at the top do contain *Phycodes pedum*, known elsewhere only from the Cambrian: and also *Neonereities uniserialis* and *Neonereities biserialis*, known mostly from the Phanerozoic but described by Fedonkin (1976, 1977) from Vendian of the Onega Peninsula in the White Sea. The microfossils thus confirm the late Proterozoic (Vendian) age of the Kuibis and Schwarzrand Subgroups of the Nama Group, although the uppermost unit of the latter could be Cambrian.

5.3.3. General review

Jenkins (1992) published a review of Namibian occurrences, noting the revised stratigraphy based on the work of Kroner et al. (1980), Tankard et al. (1982) and Germs et al. (1986). Trace fossils in sediments to the north of the Osis Ridge suggested to Crimes and Germs (1982) that the greater part of the Nama sequence there is Cambrian, although this evidence was critically questioned by Grant (1990). Ahrendt et al. (1978) obtained a K–Ar dating of 530 Ma (± 10 Ma) for the folding and synkinematic metamorphism of these sediments. Germs et al. (1986), based on organic-walled microfossils, claimed ‘an unequivocal assignment of latest Proterozoic (“Valdaian”) age for the Kuibis

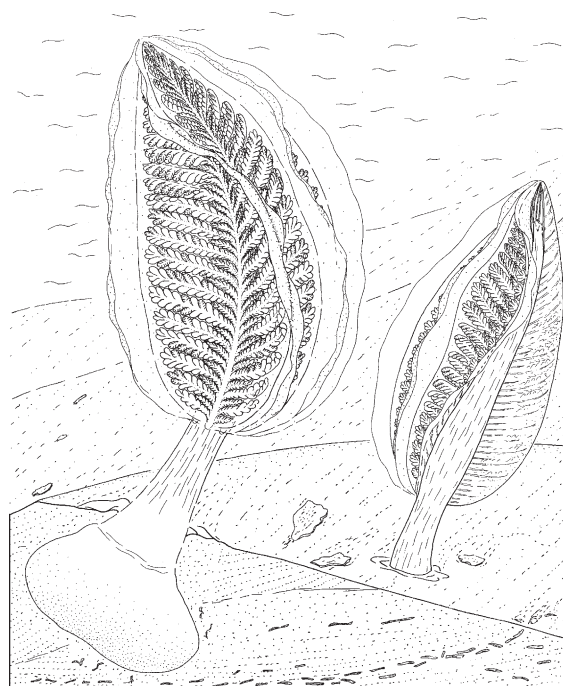


Fig. 31. Reconstruction of specimens of *Rangea schneiderhoehni* Gurich, 1926, in the inferred life position, anchored in current-bedded sand ($\times 0.52$ natural size). Ventral view on left, dorsal view on the right with tapering contractile stem well displayed. At least four fronds and possibly as many as six were clustered together back to back (from Jenkins, 1992).

Subgroup and parts of the Schwarzrand Subgroup on both sides of the ridge’. In the southern subbasin, trace fossils of the Huns Member (Fig. 27) of the Schwarzrand Subgroup seem of ‘equivocal late Valdaian/Early Cambrian kind’ and the succeeding Nomtsas Formation may be Cambrian. It was suggested that distal alluvial plain deposition in the Dabis Formation, the lower part of the Kuibis Subgroup, graded up into tidal channel fill and fan delta sandstones (indicated by large, gradationally based sigmoid foresets in the Kliphok Member), along a low energy shoreline. Mudcracks and gypsum at the top of the Kliphok member indicate tidal deposition. This is succeeded by mudcracks and salt casts in the lowest, Niederhagen Member of the Schwarzrand Subgroup. At the top of the Kliphok member and in the upper ‘shale’ of the lowermost Nudaus Formation of the Schwarzrand Subgroup, as well as in the Nasep Formation above, prominent flute casts on soles are consistent with density current deposition. Localised glaciation occurred during the deposition of the Nudaus Formation in the region of the Klein Karas Mountains according to Germs (1974) and Tankard et al. (1982).

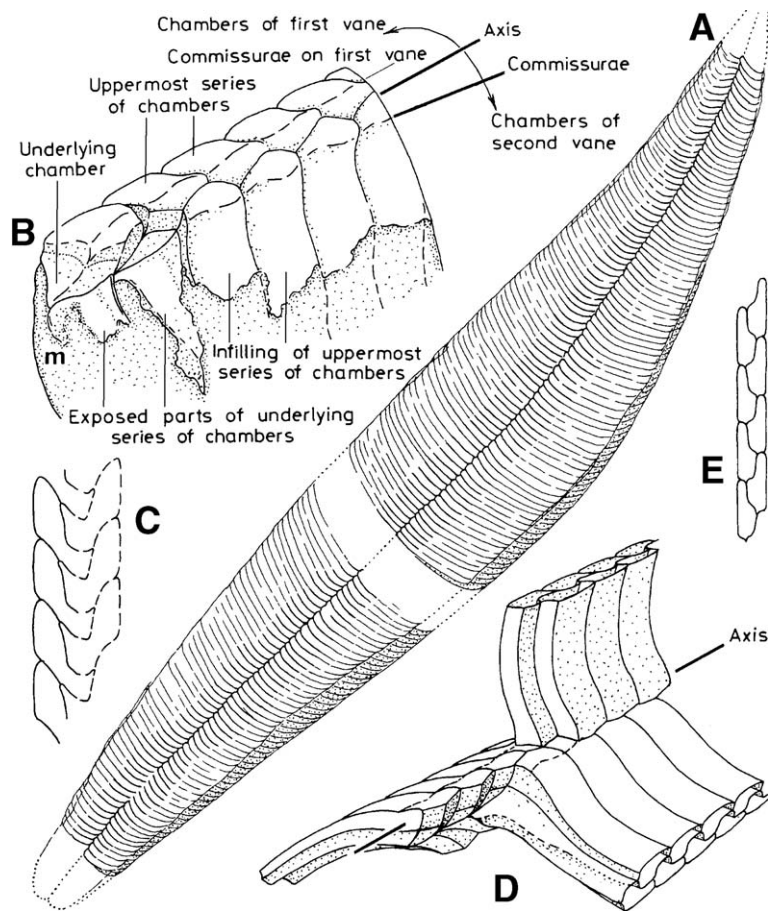


Fig. 32. Reconstruction of the frondose organism *Pteridinium simplex* Gurich (1933), Phylum Petalonamae. (A) General form of the frond ($\times 0.225$ natural size). (B) Three-dimensionally preserved specimen from the Kliphoek member of the Dabis Formation, suggesting the sectional form of the chambers close to the axis. (C) The manner in which the vanes join axially. (D, E) Section of chambers close to the edge of the vane (from Jenkins, 1992).

A peculiar aspect of the Nama assemblages of soft-bodied forms was the preservation of three-dimensional shapes. Frondose organisms lie parallel or subparallel to bedding plane; and curved or rounded forms project through relatively homogeneous, medium-grained feldspathic sandstone, in 'a rather random way'. The long fronds of *Pteridinium* are commonly twisted and buckled, suggesting envelopment in fluidised sand. *Rangaea* may have adjacent fronds separated by pods of sediment. *Ernietta*, in groups or clusters, may have bases of the sack-shaped bodies flattened at bedding planes. These patterns suggest burial by density currents generated in waves and rips during storms. Some process of fixing of moulds prior to decomposition of organic material was suggested, perhaps early precipitation of a film of mineral material in the interstices of the matrix. Possible interactions of silica and catechols, known to be

released in anaerobic decay of algae, was suggested as allowing silica solution and reprecipitation within a matter of days.

The three principal genera among the Nama fossils were then discussed. *Rangaea schneiderhoehni* seemed mainly to have been collected in storm-deposited sandstones. Composed of overlapping of conjoined fronds or 'petaloids', closely juxtaposed about a central polyp or oozoid, there is some evidence that the latter extended into a short stalk, expanding into a bulb (Fig. 31). The bulb is sediment-packed, possibly forming a weighted ballast. Four or more fronds seem to have been arranged back to back around the central polyp. There are primary secondary and tertiary branches. Similarities to *Charnia* from the Charnwood Forest and bush-like or spindle forms from Newfoundland were noted. These forms apparently derived their food in the form of suspended animal matter

through Myriad polyps. Their size must have required stiffening in the form of connective mesoglea (?) in addition to hydrostatic inflation of the colony. They are likely to have been ancestral or close analogues of the Anthozoa.

Pteridinium and *Rangea* occur in association, suggesting an overlap in environments inhabited. The main parts of the integument of *Pteridinium* tend to buckle rather than crease or fold sharply, indicating a tough, leathery consistency. The elongate, fusiform shape (Fig. 32) seems suited for life in streaming currents such as rip channels. Three-dimensional preservation is quite common and shows that the ‘frond’ consists of three half-leaf shaped fusiform elements joined at the central axis. Each ‘frond’ is composed of a series of ‘tubes, at right angles to the zigzag axial line, which may represent a septum. The tube chambers are joined by parallel lines, which probably are the traces of intervening septa or membranes. There is evidence that at least two series of overlapping chambers form each leaf-like element or vane. A polarity is indicated but neither end has been preserved in any fossil, due to damage prior to burial. It was suggested that the organism grew by adding chambers or tubes at the end of the frond.

Pteridinium was believed to be allied to the enigmatic, sack-shaped remains of *Ernietta plateauensis*, both displaying a zigzag axial suture and sub-parallel ribbing marking chambers extending from it. However, *Ernietta* is sub-cylindrical and polyp-like. Up to three layers of tubes or chambers are present in *Ernietta*, and the number seems to be the same whatever the size. The texture appears to have been flexible and soft, fine creases being in some specimens evident perpendicular to the ribbing. It was envisaged as a gregarious benthic organism, mature individuals lying close together and attached to the sea bottom (see Fig. 173). It was interpreted as of coelenterate grade by Glaessner and Walter (1975), but resembles no known present-day coelenterate. Jenkins considered neither *Ernietta* or *Pteridinium* to be coelenterates, but preferred to assign them to the Phylum Petalonamae of Pflug (1970a).

5.3.4. Extension of the range of Ediacara-type fossils in the Nama Group and accurate age-dating

Narbonne et al. (1995) reported the find of two fossiliferous levels of wave-reworked sandstones within the Spitzkopf Member of the Nama Group, 6000 m upwards from known fossiliferous beds and within a

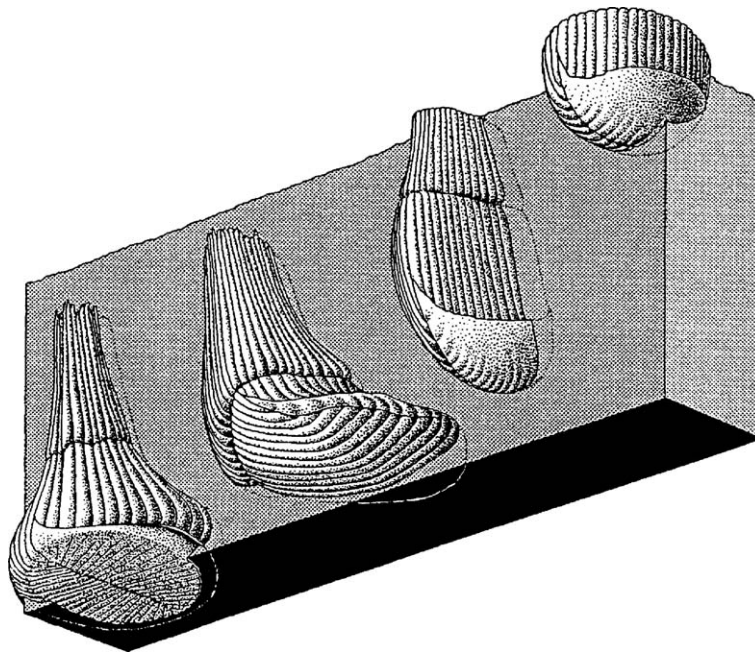


Fig. 33. Interpretation of the observed variety of shapes of *Ernietta plateauensis* Pflug (1966) from the Kliphoeck Member, Kuibis Subgroup. The diagram shows the manner in which Dzik (1999) believed that the sand-loaded membranous sacs sank in successive stages in hydrated mud. On the right, the subspherical shape is shown at the time of initial sinking, the upper part above the substrate not being preserved. In the next stage of penetration the drop-like shape is preserved, whereas in the final stage, when the organisms reaches the soft mud/firm bed boundary, the base of it is flattened, as shown at the left. Pressure from enclosed sediment produces a bulbous effect in some specimens (after Dzik, 1999).

few metres in section of the sub-Cambrian unconformity. *Pteridinium*, also known from Ediacara-type sections in Ukraine, Russia, North Carolina and NW Canada, is abundant in the form of specimens up to 30 cm long. The upper assemblage is dominated by a new Ediacaran fossil of decimeter scale with dickinsonid-like bilateral segmentation and unipolar organisation: quite complex, it exhibits features of Ediacaran taxa formerly supposed to be unrelated. The U–Pb age of the ash bed just below overlaps (within the measured uncertainties) the age obtained from Siberia for the Precambrian–Cambrian boundary of 544 Ma.

Grotzinger et al. (1995a,b), at the same time presented U–Pb age dating results which show the volcanic ash in the Spitzkopf Member to have an age of 548 Ma (± 2 Ma). Their studies of various Ediacaran assemblages throughout the World show that a number extend above this age into the Cambrian, that the so-called “Kotlin” interval” is non-existent and that there was substantial temporal overlap between soft-bodied and shelly-fauna assemblages. There was apparently slow but continuous evolution of animals from about 600 Ma (the age of the oldest fossiliferous horizons in the Kuibis Subgroup) to about 530 Ma, when the Early Cambrian explosive diversification of body plans finally occurred. A companion abstract by Saylor et al. (1995) gives details of the application of this U–Pb age dating programme to the detailed stratigraphic correlation of the two sub-basins of the Nama Group.

5.3.5. Three-dimensional preservation

Dzik (1999) recognised that, unlike the celebrated Ediacara fossils, those from roughly coeval localities in the Kuibis Quartzite of Namibia are preserved not as imprints on sandstone bedding planes but three dimensionally within the rock matrix. The most common and typical of these organisms is *Ernietta*. The original soft tissue is not preserved, *Ernietta* occurs usually within stratified sandstone or mudstone beds which apparently originated as a result of mass-flow or storm events (Jenkins, 1985). Sandstone casts of internal body cavities or collapsed bodies are preserved (Jenkins, 1992; Buss and Seilacher, 1994) The common fossils *Ernietta*, *Pteridinium* and *Rangaea* are rarely found together. Current-oriented specimens of *Rangaea*, with sand-filled basal discs and collapsed fronds, occur within beds of sandstone produced (?) by mass flows, whereas *Pteridinium* is restricted to storm sand layers with no preferential orientation (Jenkins, 1992; Seilacher, 1994). They were apparently deposited with the suspended sediment and gradually loaded with sand while sinking. *Ernietta* was deposited in reddish

mudstones with variable sand content, and had a complex preservational history which was the subject of Dzik’s study.

Ernietta has an oval body, varying from 30 to 80 mm in width. One compound specimen shows how numerous drop-like bodies penetrated the mud from the surface, blunt ends downwards (Fig. 33). They are separated now by mudstone and filled with slightly lighter, harder sandstone. Internally, the base is of quartz sandstone and above comes muddy sandstone or mudstone. The fill apparently developed in a single event. Only a single species is represented. The three-dimensional preservation is believed to be the result of sinking of the sand-filled organic skeleton into the muddy host sediment due to a density difference (Fig. 33). The wall material appears to have been proteinaeous, but of a collagenic fabric; flexible and elastic, unlike chitin. The skeleton was formed of a series of parallel chambers, which the walls of hydraulic skeleton units resembling the basement membrane of chaetognaths or the notochord sheath of chordates. The possession of such chambers was, it was suggested, widespread among the earliest fossil animals preserved in sandstone. The uprise and disappearance of the Ediacaran fauna may be in part preservational ‘artifacts’—the uprise reflecting the origin of skeletons enclosed by strong membranes, and the apparent eclipse reflecting the appearance of decomposer organisms able to disintegrate the collagenous sheaths. The Ediacaran organisms with such structure were not truly soft-bodied. The rise of the Arthropoda, the main benthic decomposers, coincided with the disappearance of Ediacaran fossils, after the late Precambrian and earliest Cambrian.

5.3.6. Calcareous fossils

Grotzinger et al. (1995a,b) reported that calcareous fossils occur in the terminal Proterozoic Nama Group in rocks below the occurrence of the trace fossil *Phycodes pedum*, widely accepted as marking the Cambrian lower boundary. They overlap with Ediacaran fossil impressions and extend between ash bands radiometrically dated at 549 and 543 Ma. At least six fossil morphologies are represented, including branching forms up to 1 cm diameter and those with hexagonal symmetry, which recalls the triradial symmetry of some terminal Proterozoic and basal Cambrian forms such as *Tribrachidium*. Other forms include open cups, possibly representative of simple vase-shaped sponges. There are also simple tubes, functionally, if not phylogenetically, related to sabellid worm tubes; and also more complex multicellular forms. Simple cups and tubes are the most numerous forms, followed by complex

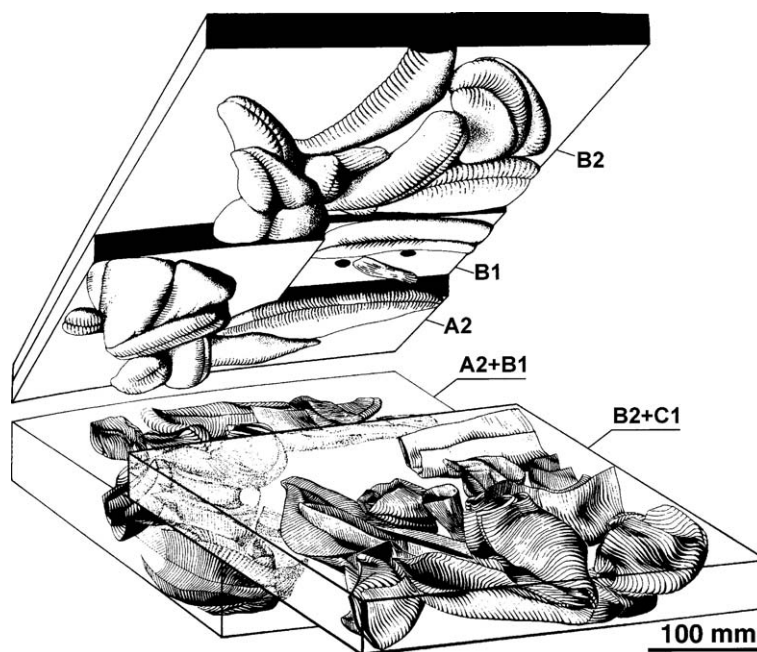


Fig. 34. Winnowed and current-collapsed preservation of *Pteridinium*, the entire triplet of vanes being tilted and coiled in the palaeocurrent direction (A). Median and lateral vanes always bulge outwards in mechanical deformation, whereas median vanes can be drape-folded (B). Stacked and imbricated individuals suggest some dragging along the bottom (C). Overturning is rare (D). l.v.=lateral vane, m.v.=median vane. Camera lucida drawings (after Grazhdankin and Seilacher, 2002).

branching and multichambered forms, and then by *Cloudina*. All these represent benthic organisms which lived in close association with reefs or biostromes, suggesting a strong substrate preference. They are rare to absent in other facies. The forms with hexagonal symmetry may be related to *Anabarites*, but most Nama calcareous fossils disappear near the Precambrian/Cambrian boundary and do not appear to be related to the Lower Cambrian (Tommotian) small shelly fossils. They remain, for the most part, as enigmatic as the Ediacaran biota.

5.3.7. Possible bilaterian body fossil

Bradley (1998) reported on a find of a new Vendian bilaterian body fossil in the form of chloritised tubes from the Klipkoek Member, Nama Group.

5.3.8. "Underground Vendobiontia"

Grazhdankin and Seilacher (2002) published a detailed study of the immobile buried life habit of *Pteridinium* and *Namalia*, based on three-dimensional preservation of fossils. The former appears to be a most puzzling creature, they remarked, constructed of a triplet of 'leaf-like' wings, the edges of which join along a common seam, a construction unknown in any other past or recent organism. The mode of preservation is

also unusual and three-dimensional, possible if *Pteridinium* had lived within the flow (Seilacher, 1992), although the preservation of the 'soft' body has been thought to be due to smothering by fluidised sand (Jenkins, 1992). The subdivision of the vanes resembles other Ediacaran forms such as *Dickinsonia* and *Rangaea* (Jenkins, 1992; Runnegar, 1995) and this subdivision was the basis for the erection of a hypothetical group of Protists, the "Vendobionta" of Seilacher (1989, 1992), with serially or fractally quilted structures. The status of that group has been questioned on the grounds of the wider diversity of Ediacaran morphologies not included, the superficial similarity to metazoan features of the Ediacaran forms and the comparison to Cambrian Burgess shale fauna members (Gehling, 1991; Conway Morris, 1993; Runnegar, 1995).

Early description of *Pteridinium* by Pflug (1970a,b) was mentioned; involving the inclusion of the canoe-shaped bodies in a new taxon, Petalanomae, carpeting the seafloor with their bottoms facing upwards; also the studies of Jenkins (1992), leading to the two-layer model of tubes alternating in cross-section. Both ends of *Pteridinium* had never been documented until the present study, and Jenkins reconstructed it as an erect organism anchored to the seafloor, a reconstruction and lifestyle consistent with a problematic alga (Gehling,

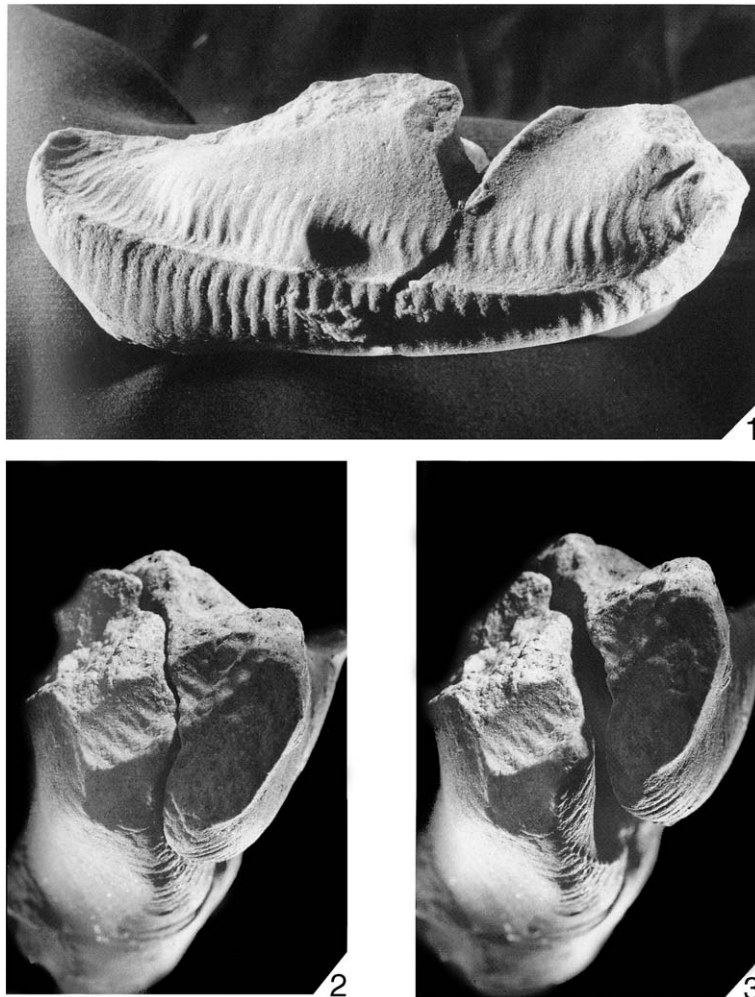


Fig. 35. *Pteridinium simplex*. Complete preservation of lateral and median vanes with both ends curved ($\times 1$) (from Grazhdankin and Seilacher, 2002).

1991; Runnegar, 1995). Fine laminations of the host rock, intersected by a vertically disposed *Pteridinium* led Crimes and Fedonkin (1996) to suggest an infaunal mode of life, as supported by the morphodynamic analyses of Seilacher (1992, 1994). The new study by Grazhdankin and Seilacher fulfilled the obvious requirements of studying larger fossil assemblages and detailed consideration of sedimentology and taphonomy. Remarkable photo-illustrations of clusters of winnowed and transported, and virgin, *Pteridinium* specimens, accompanied by drawings were presented. The explanations are complex and cannot be repeated in full here, but the very lucid conclusions are summarised below.

From the sedimentological viewpoint, the taphonomy of *Pteridinium* is seen to be controlled by its occurrence in a particular tier within a sandstone event bed. Winnowed and transported specimens (Fig. 34) are

preserved in lag deposits together with other heavy objects (clay pebbles, soft bodies of other organisms), whereas 'virgin' assemblages appear to hang from the top surfaces of sandstone units. Reconstruction of such virgin communities was possible and revealed the preservation of infaunal communities, supporting earlier assumptions (Seilacher, 1992, 1994). The underground habit of *Pteridinium* is the reason for the unusual preservation. Burial in turbidity flows, after passive transport, applies only to the winnowed assemblages, soft bodies being deformed and aligned with the current. In life, the entire boat-shaped constriction was engulfed in loose sand. The alternative hypothesis of Jenkins (1992, 1995) of both vigorous and less vigorous transport was rejected, because of the lack of folding and wrinkling of specimens in the 'virgin' assemblages, such deformations being present only in the winnowed

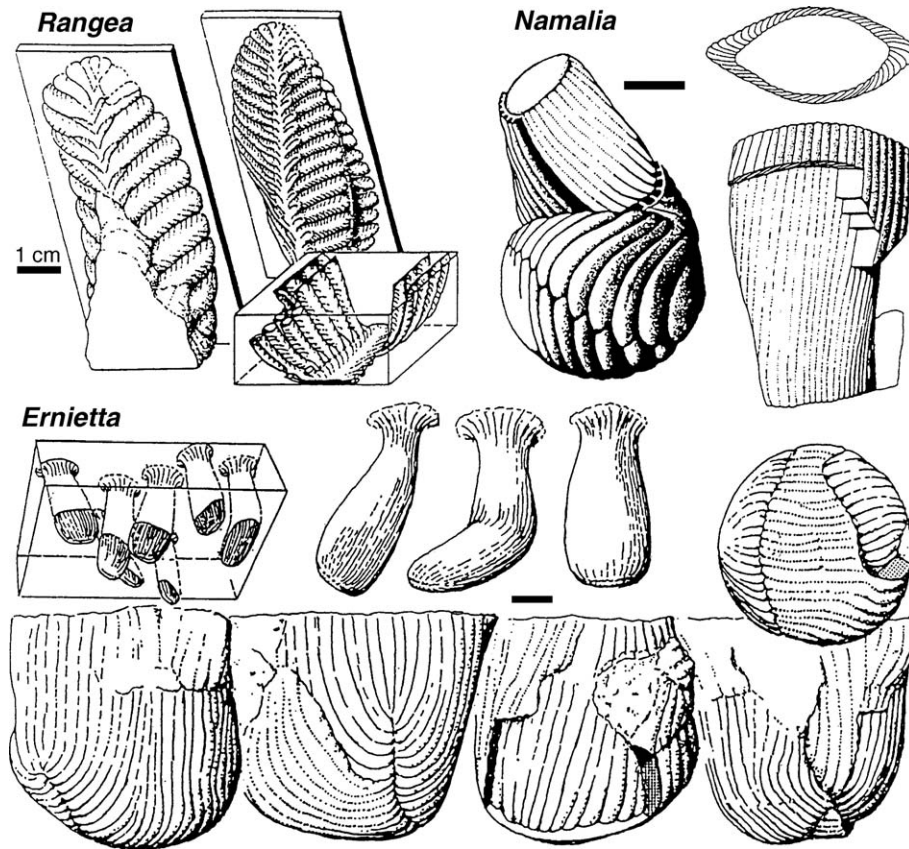


Fig. 36. Sand-filled quilts in Namibian “Vendobionts”. In vertical vanes, the sand sank into the lower parts of quilts after death and kept them from collapsing, whereas in life it probably functioned as a fill skeleton that further compartmentalized the protoplasm (after Seilacher et al., 2003).

assemblages. There are specimens in a virgin assemblage with both ends curved (Fig. 35), ruling out an anchoring device, and thus an anchored mode of life. Following this sedimentological description, the authors considered the taphonomy and concluded that each quilted vane should be considered as a collapsed pair of membranes, originally held apart by fluid pressure—the more rigid septa corresponding to the furrows. The quilt taphonomy is illustrated in Fig. 36. The reconstructed *Pteridinium* resembles a sand-filled leathery bag.

The life habits of *Pteridinium*, according to Grazhdankin and Seilacher (2002) were constrained by the details of three-dimensional preservation and lack of traces of locomotion. They envisage a boat-shaped creature, up to 415 mm long and 90 mm wide, the body of which was completely immersed in sand—convex down with the free edges of the vanes rising to the sediment/water interface. Each vane consisted of two membranes spaced by strictly parallel septa compartmentalised the fluid content. The quilts terminated blindly at both ends and hydrostatically supported the enclosing sediment; they apparently had variable

rigidity. New quilt material could possibly have formed during life by lengthwise quilt division, similar to binary cell division. However, it was noted that there are two types of quilts in the slab studied: in one quilt, they grow wider with increasing body length, and in the other, they retain the same width regardless of body length. The various morphological features (vane arrangement, quilt parameters and body shape) appear to be largely extrinsically controlled by environmental factors. Presumably all physiological functions, including obtaining food from the host sediment, were confined to a few millimetres from the sediment/water interface. A problem is how the organism entered the sediment to dwell there infaunally and these authors suggest a connection with larval behaviour and ontogeny. The results of these new observations were compared with the observations with the interpretations of Pflug (1970a,b) and Jenkins (1992). The presence of two layers of quilts as suggested by Jenkins could not be confirmed.

They also studied *Namalia* in 12 congregated specimens on a slab and 16 isolated specimens from the same

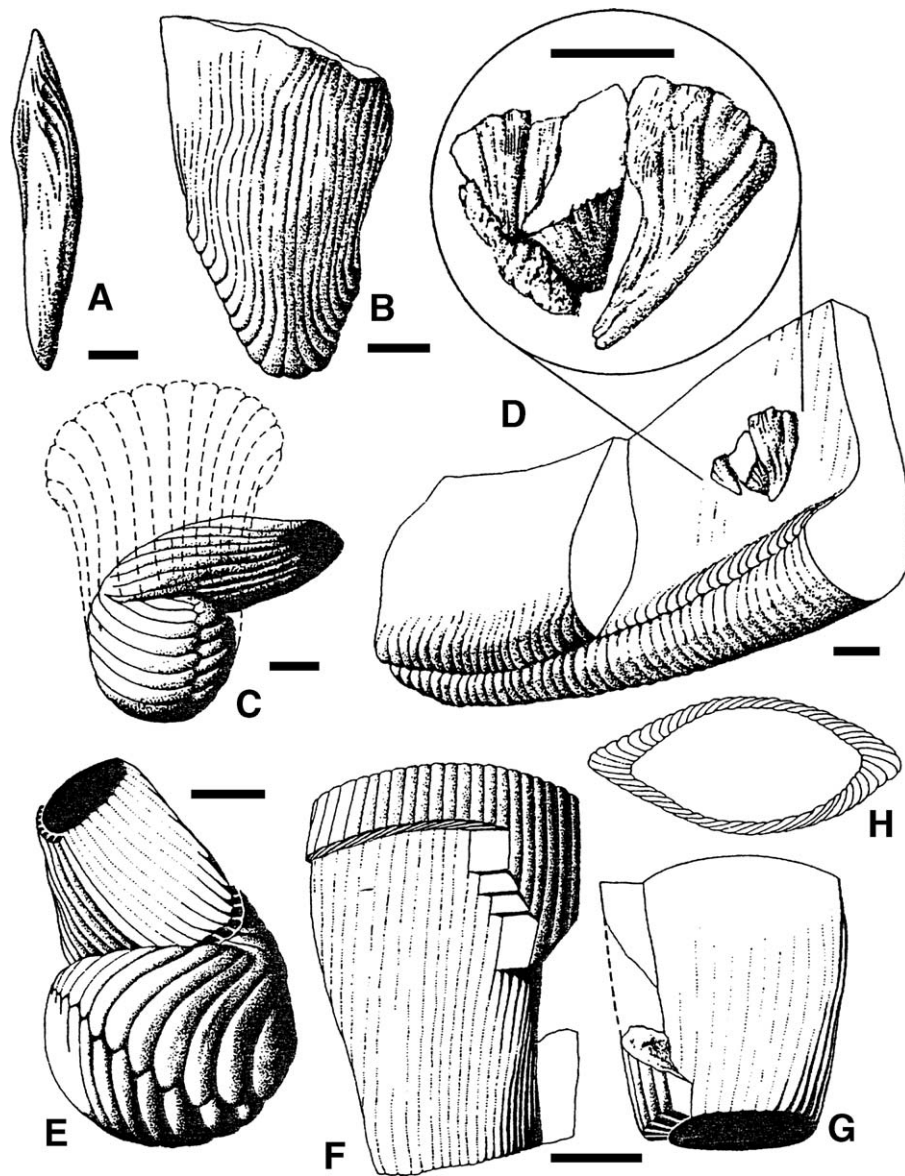


Fig. 37. Reconstructions of *Namalia*. This resembles casts of flaring upward bell shaped structures which terminate on the upper bedding plane. (A, B) Half-winnowed specimen with an undisturbed apex but top part is tipping into upstream scour. *Namalia*, a common member of *Pteridinium* communities, could have used its vanes as a starter substrate, as shown here by 3 juveniles (magnified above) (D) Each vane of *Namalia* is preserved as two walls spaced by perfectly parallel, straight structures, which also compartmentalize the sand into elongated quilts (E). This is better demonstrated in winnowed specimens because of strike-slip deformation which imbricated the septa (F–H). This suggests that sand was inside the quilted vanes during life. Camera lucida drawings (scale bar = 10 mm) (after Grazhdankin and Seilacher, 2002).

bed, in the Kliphoeck Member of the Dabis Formation. *Namalia* resembles *Ernietta*, but differs in the construction of the vanes and in having a conical shape, whereas the latter resembles a bag with a ballast of sand inside. Again there are undisturbed and winnowed specimens. The undisturbed specimens resemble the casts of a flaring-upwards, bell-shaped structure arranged normal to the bedding plane and terminating at it (Fig. 37). It

consists of two vanes, fusing outside the seam, without a sharp boundary. Each side bears parallel and evenly spaced furrows are linked to the seam in alternating fashion at right angles to form quilts, vertically elongated in life. It was concluded that *Namalia* had an underground life style, like *Pteridinium*. No evidence could be found of load-induced bag-shaped deformations as recognised by Dzik (1999) in the case of

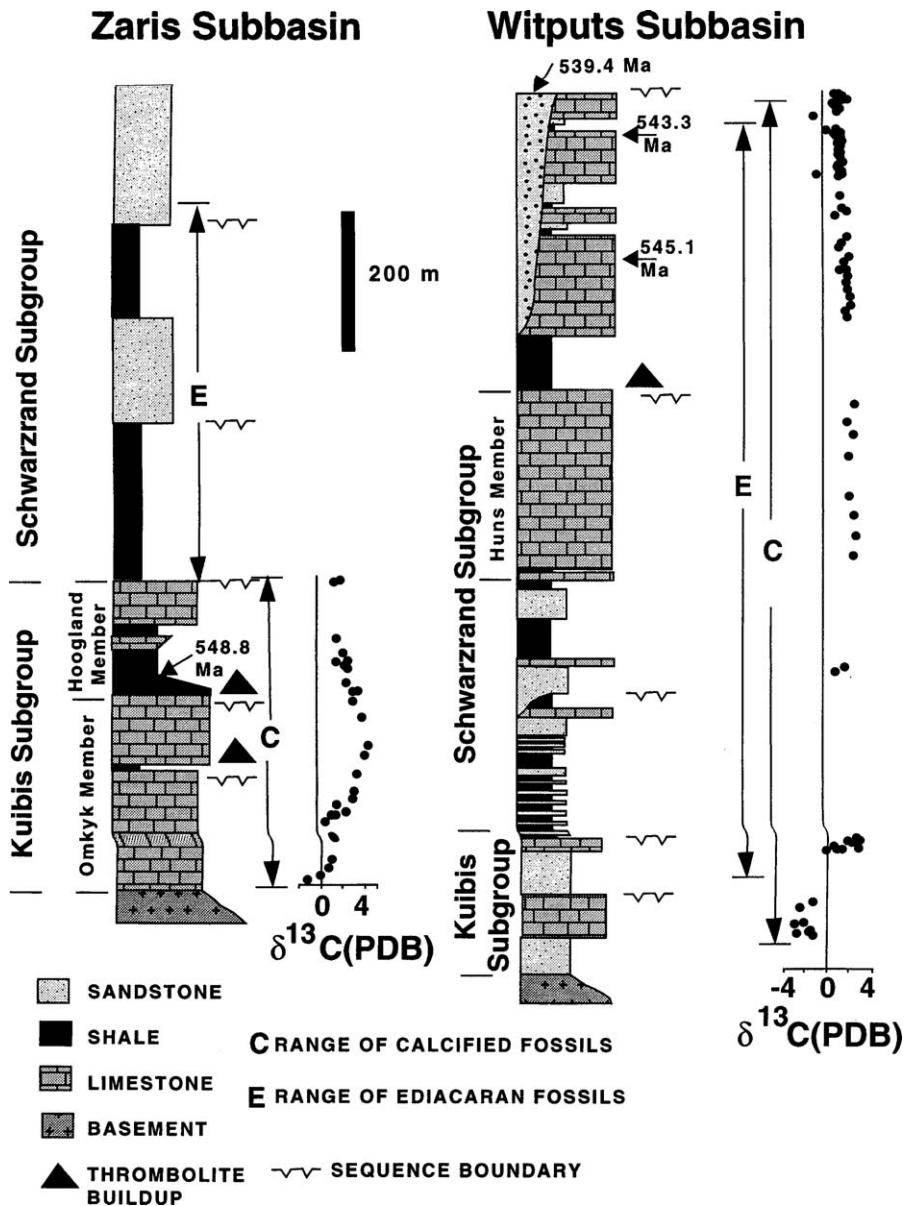


Fig. 38. Generalised stratigraphy of the Nama Group for the Zaris (north) and Witputs Sub-basins. Showing the major lithostratigraphic, biostratigraphic and chemostratigraphic attributes, and the thrombolitic complexes above the sequence boundaries (after Grotzinger et al., 2000).

Ernietta. The rounded base was thought to be the oldest part of the organism and the flaring shape was consistent with a 'sediment sticker' (Seilacher, 1999). An isolated *Pteridinium* has three small *Namalia*, with juvenile features, attached to its median vane. Again it is unclear how the organisms entered the sediment. As to the sand-filled quilts observed, the quilts were probably packed with sand during life and body fluid must have filled the sand interstices or divisions above the substrate too delicate to be preserved. The problems of interpreting *Namalia* are much the same as for *Ernietta* (Jenkins et

al., 1981; Jenkins, 1992) and *Swartpuntia* (Narbonne et al., 1997), quilts being preserved in all three as three-dimensional sand fills (Fig. 36). The possibility of a foliated quilted body with protoplasm-supported sand inside the quilts is a possible 'Vendobiont' construction that should be further tested.

These authors proposed further work of the same nature on *Rangaea* and *Ernietta*. The immobile underground life style and bizarre growth strategies of *Pteridinium* and *Namalia* make them more, not less enigmatic. It is possible that the Vendobionta represent

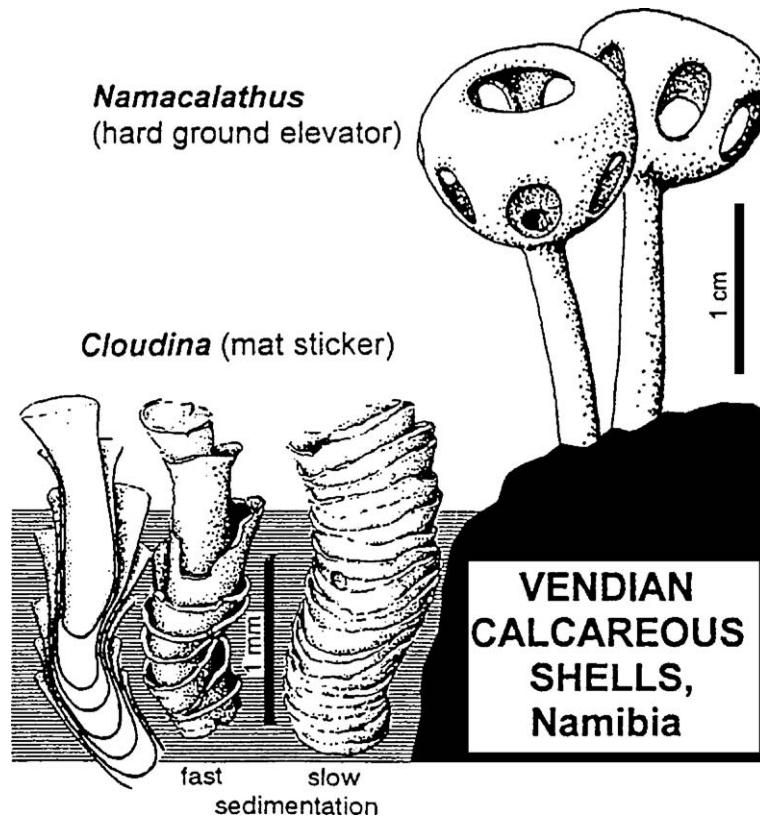


Fig. 39. Vendian calcareous shelled forms from Namibia: *Cloudina*, *Namacalanthus* (after Seilacher et al., 2003).

unicellular organisms that became extinct in the Early Cambrian (Seilacher, 1992; Conway Morris, 2000). The Vendobionta hypothesis was originally proposed to explain the unusual preservation and palaeobiology of quilted soft-bodied organisms of the Ediacara-type Precambrian biota, similarities to living creatures being coincidental and based on fabrication analogy. Vendobionts were considered as an evolutionary attempt to attain large body size by a process without multicellularity. The latest work suggests that *Petalonamae* may represent a distinct ecological grade of underground Vendobionta. A switch to this life style requires unique adaptations for gas exchange and nutrition, also problems of entering the sediment in the larval stage. This habit may have had some advantages with regard to competition for substratum and was apparently initiated in late Precambrian times prior to the initiation of a burrowing mode of life.

5.4. Calcified metazoans in thrombolite-stromatolite reefs

Attention in Namibia has lately turned to the calcified metazoans in the carbonate reefs (Grotzinger et al., 2000; Watters and Grotzinger, 2001; Wood et al., 2002).

These are composed of thrombolites (non-laminated bioherms characterized by clotted internal texture), and stromatolites (characterised by a laminated internal texture). The former occurring broadly across the carbonate ramp profile and as pinnacle reefs, whereas the stromatolite-dominated reefs occurring updip within the ramps. The reefs may form continuous horizons, patches or pinnacles. They occur in the Kuibis Subgroup of the northern Zaris Sub-basin and the Schwarzrand Subgroup above in the southern Witputs Sub-basin, including the Huns Member (Fig. 38). The age range of occurrence of mineralised fossils, determined by the U/Pb method on zircons in ash horizons, is from 548.8 Ma in the Kuibis occurrences to 543.3 Ma in the Witputs Sub-basin.

Within the thrombolite facies, the fossils occur in domal and columnar structures forming individual reefs and in trough cross-bedded interchannel fill of packstone and grainstone. The fossils occur in the form of calcareous cups, goblets and cylindrical tubes, including *Cloudina*, and their bioclastic detritus. Besides *Cloudina* (Fig. 39), which is lightly mineralised by

precipitation of calcite on an organic template, is a new taxon, *Namacalathus hermanastes*, which also has thin walls that deformed flexibly under compaction. It is believed that the original mineraliser was calcite; there are later overgrowths of euhedral calcite crystals. The organism consists of a hollow stem, open at both ends, attached to a spheroidal cup marked by circular opening with a down-turned lip and six or seven side holes) (Fig. 39). The phylogenetic attributes are uncertain, but the morphology is consistent with a cnidarian-like body plan.

This fauna anteceded the Cambrian period. Grotzinger et al. (2000) considered that the Nama Group contains at

least five taxa of calcified metazoans, including two species of *Cloudina*, *Namacalathus* and two other less determinate forms. They comprise a reefal assemblage in Nama bioherms, quite distinct from the Palaeozoic assemblages but foreshadowing Palaeozoic biology. As in the case of Uruguay (see Section 12), the fauna was already diversified by this time, late in the Vendian period.

Another genus was added by Wood et al. (2002): a ‘modular’ biomineralised metazoan, much larger than anything so far described from the Nama Group, reaching dimensions of up to 1 m across. This new fossil comes from the Omkyk Member of the Kuibis Subgroup, within the northern sub-basin (Fig. 26),

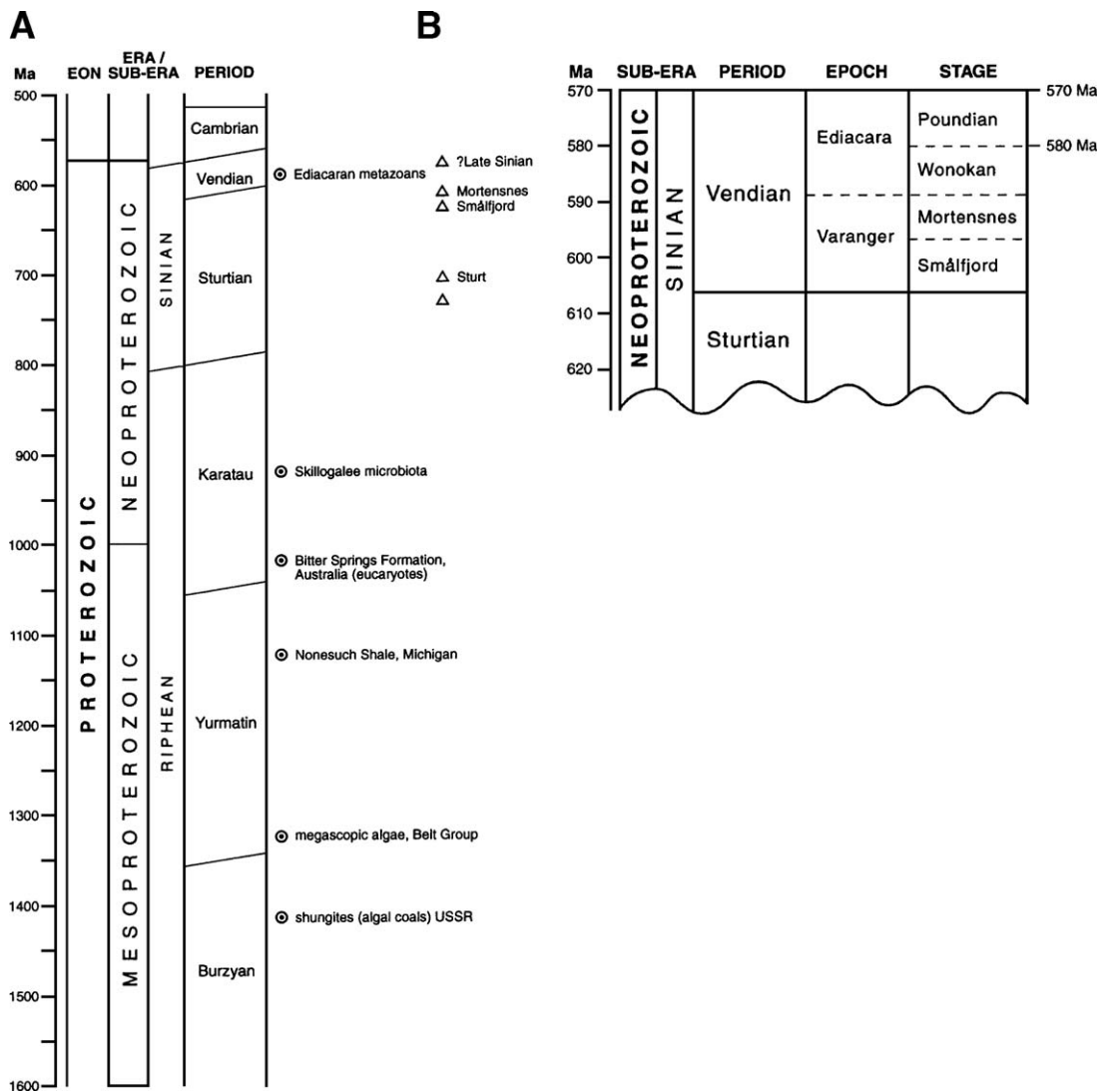


Fig. 40. Diagram based on Harland et al. (1989) showing the subdivision of the Late Proterozoic and Early Cambrian. (A) Early Cambrian extending back to the Mesoproterozoic. (B) Proposed epochs and stages of the Vendian*. *The term ‘Terminal’ Proterozoic is nowadays commonly used for the Vendian. **The base of the Cambrian is nowadays taken at 543.7 Ma; the base of the Vendian is less well radiometrically constrained but the end of the Varanger Glaciation is taken at c. 600 Ma.

beneath an ash bed dated by the U–Pb zircon at c. 548.8 Ma. It is hosted by shallow-water marine carbonate rocks and is found in pinnacle reef complexes. Named *Namapoikia* gen. nov., it has labyrinthine tubular cross-section. Cloudinid debris is associated with it. The construction is similar to that of chaetetids, a polyphyletic group calcified sponges of mid-Ordovician to Recent age range, but there are also similarities to the tetradiids, aragonitic corallomorphs of uncertain position within the Cnidaria. It is probably a representative of the poriferans or cnidarians.

5.5. Conclusion

The Nama Group occurrences in Namibia are critical to the understanding of the Vendian biota. Preservation in three dimensions of the principal body fossils has opened a window into the morphology of these organisms and their likely way of life. The study by [Grazhdankin and Seilacher \(2002\)](#) represents a major advance in knowledge. Over and above this, the outcrop of the Neoproterozoic rocks of Namibia extends over more than 500

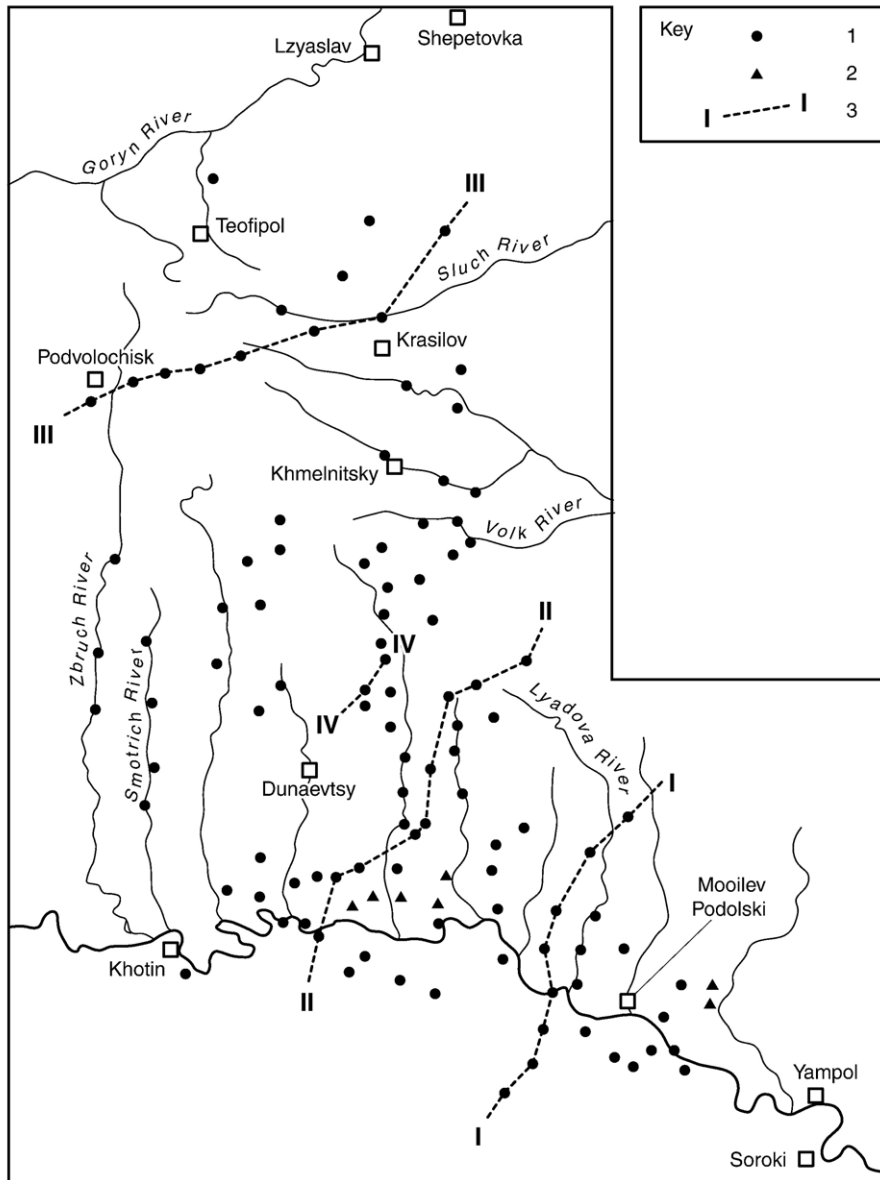


Fig. 41. Sketch map showing the distribution of boreholes and sections on which the stratigraphy of the Vendian in Podolia, west and south of Kiev in the Ukraine was based (after Sokolov and Fedonkin, 1985, English language translation 1990).

km and it is inevitable that new and informative finds there will advance our knowledge of Neoproterozoic and earliest Cambrian life in the next decades. The wealth of carbonate reefs, not as in Oman (see Section 13) associated with salt deposits, must mean that further discoveries of early mineralised organisms will be made in the future. The occurrences in Uruguay, on the other side of the opened up Atlantic, described in Section 12, should be studied in much

greater detail, for they could well be as complex as their analogues in Namibia.

6. Russia and Ukraine

6.1. Introduction

B.S. Sokolov (in Sokolov and Fedonkin, 1985) provided an appraisal of the position of the Vendian in

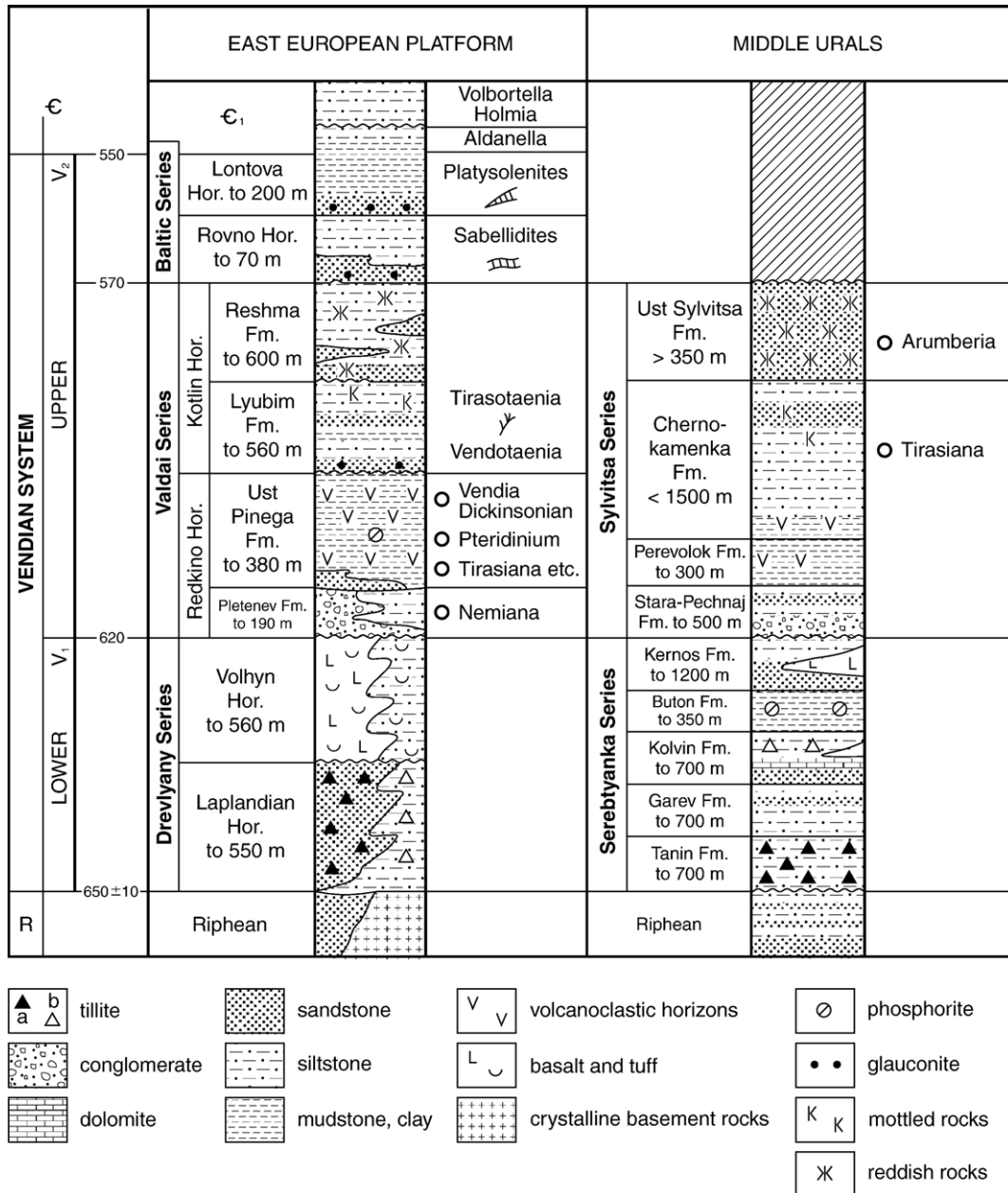


Fig. 42. Correlation between the Vendian of the east European Platform and the Middle Urals (after Sokolov and Fedonkin, 1985 (1990 English language translation).

the Stratigraphic Scale, that is as a subdivision in the Geological Column. He recognised the Vendian in 1949–50 and Keller (1963) classified it as a “Phythem” or “Protosystem”. He considered that from any standpoint it must be placed in the latest Proterozoic of the Precambrian. There is admittedly the problem of the term Sinian, used in China, which has a different range, but the Geologic Time Scale published by Harland and others for the Press Syndicate of the University of Cambridge in 1990 avoids any difficulty in this respect by inserting the Sinian as an Era and the Vendian and Sturtian beside it as Periods (Fig. 40).

Radiometric age dating of the Vendian has been bedevilled by rather wide latitudes of error in the various determinations. Sokolov accepted (in Sokolov and Iwanowski 1985) an age range from 650 Ma (± 10 Ma) to 560 Ma (± 10 Ma), and this is very near the timespan indicated by Harland et al. (1989). However, the base of the Cambrian has more recently been placed at 543.9 Ma

(± 0.3 Ma) by Bowring et al. (1993) and the beginning of the Vendian, marked by tillites, is less well radiometrically constrained, but nowadays is generally taken to be close to 600 Ma. Fedonkin (1992) accepted a timespan of about 60 Ma, which this revision implies. Although the term Vendian was erected before the term Ediacaran, meaningful scientific analysis of the Ediacaran-type fossils in the USSR appears to have been initiated later than Reg Sprigg’s remarkable discovery at Ediacara, South Australia in 1947, and the first of Glaessner and Wade’s subsequent extremely detailed interpretations and descriptions of the South Australian Ediacara fauna.

6.2. Regional geology

The Vendian has been described in its Regional Geology by Sokolov and Fedonkin (1985); and its Palaeontology by Sokolov and Iwanovski (1985)—both translated extremely well in the English language

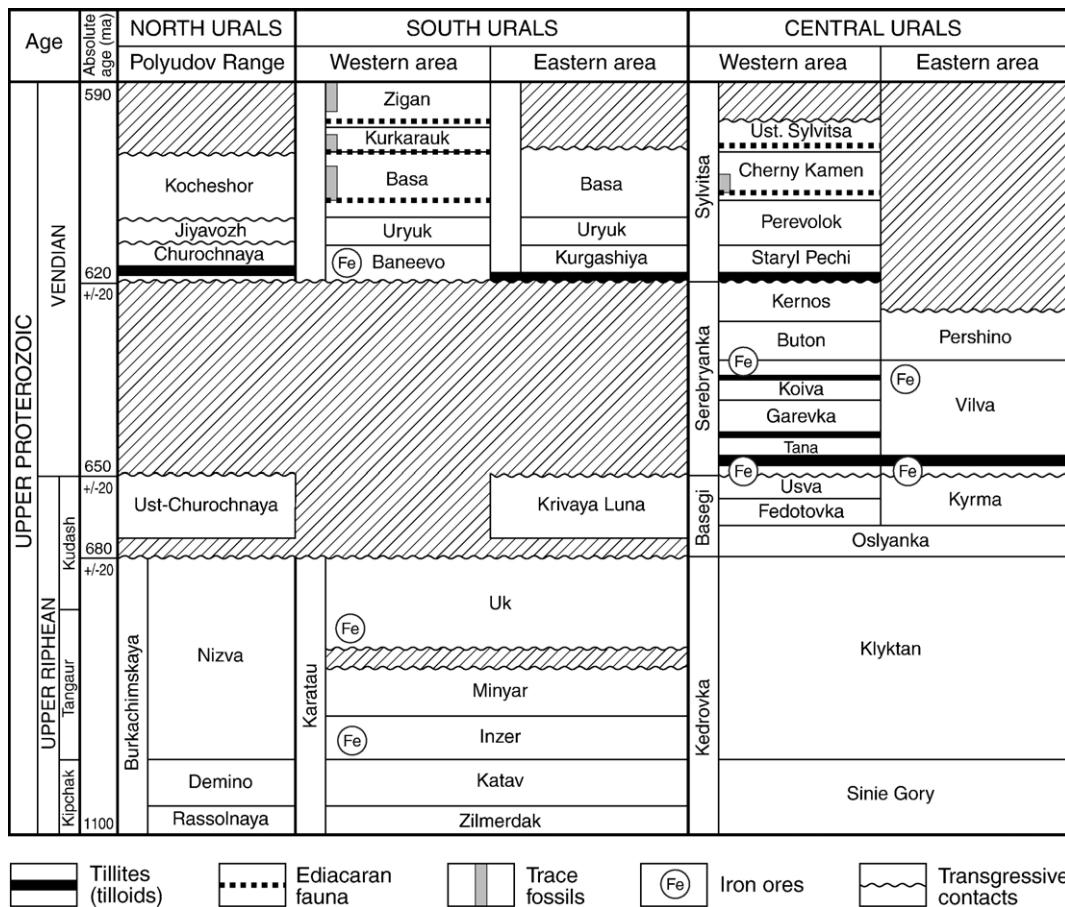


Fig. 43. Correlation of the Vendian on the Western slope of the Urals [from Sokolov and Fedonkin, 1985 (1990 English language translation). Nauka Publishers].

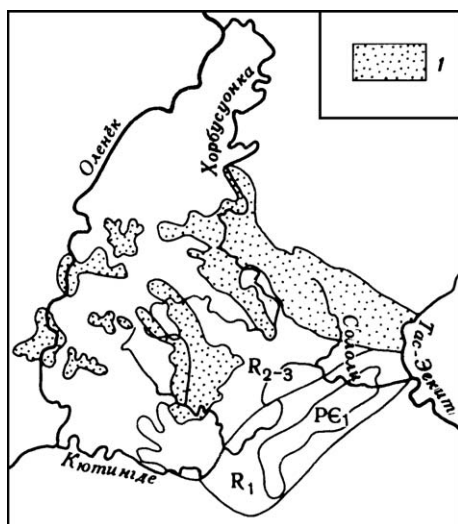


Fig. 44. Sketch map of the Olenek uplift (I=exposures of the Khorbusuonka Series) [from Sokolov and Fedonkin, 1985 (1990 English language translation). Nauka Publishers].

editions published by Springer in 1990. It is recognised in three regions of the former Soviet Union:

- The East European Platform (Russia, White Sea and Ukraine)
- The Urals (Russia)
- Siberia (Russia).

6.2.1. East European Platform

The Vendian has been recognised on the East European Platform in the Zimny and Letny Coasts of the White Sea as well as the Onega-Ladoga and Karelia regions in the northeast, and the Dniester and Goryn River basins of the Ukraine, an area referred to frequently as Podolia, in the south (E. M. Aksenov in Sokolov and Fedonkin, 1985) (Fig. 41), where natural rock exposure, deep drilling and geophysics have revealed the Vendian over an area of 2 million km²: the total maximum thickness is about 2.5 km, but is variable. In the southeastern White Sea area, the thickness is reported to be 1.5 km. The sequence is dominated by terrigenous and minor volcano-terrigenous sediments and volcanic rocks—both effusive and pyroclastic. The Vendian is divided into an upper and lower division, and the Ediacara-type fauna occurs in the lower part of the Upper Vendian. As is seen from Fig. 42, the Valdes Series of the Upper Vendian was subdivided into a lower Redkino “horizon” and an upper Colin “horizon”, the Ediacara-type fauna being largely found in the former and the upper “horizon” being characterised by the algae *Vendotaenia*, *Tyrasotaenia* and

others. This relationship has been interpreted as being due to the Ediacara-fauna initially mushrooming but having a quite short maximum development before being overtaken by adverse influences and so dwindling.

6.2.2. Urals

Vendian rocks occur in the North, Central and South Urals (Y. R. Becker in Sokolov and Fedonkin, 1985). The occurrences on the western slope are summarised in Fig. 43. The age of these deposits has been constrained by isotopic determinations on glauconitic horizons. Three glacial tillite levels are recognised below the Ediacaran fauna assemblages. Horizons with *Tirasiana* and *Arumberia* characterise the glacial levels. The Vendian is here subdivided into a lower Serebryanka division, predominantly glacial, with the upper of the three glacial divisions recognised at the top of it in all three areas; and an upper Sylvitsa division, of piedmont facies. This contains three levels of Ediacaran type fossil assemblages in the Western Urals, but only two in the Central Urals, where the Upper division, equivalent to the Sylvitsa in the South Urals is here termed the Asha division. Cyclicity is evident and geochemical evidence suggests some freshening of the water, but with intermittent approach to the normal salinity of sea water, evidenced by phosphorite and Ediacara faunas. The palaeogeography was similar to a Phanerozoic molasse basin, but there was an extensive shallow water area into which the sediments were carried in large streams to quite a distance from the source.

6.2.3. Siberia

The occurrence of the Vendian in Siberia is covered by V. V. Khomentovsky (in Sokolov and Fedonkin, 1985). He stated that the stratigraphy of the late Precambrian of Siberia is complex and not fully resolved, the Vendian Yudoma Complex (dated by isotope methods at between 670 and 570 Ma) being separated from the Riphean in the north and east, but the separation being less well defined elsewhere at the time of writing. The most important sections are in the Olenek Uplift in the northeast (Fig. 44), where the Ediacara fauna occurs within the Khatspyt Formation—the middle division of the Khorbusuonka Series, that series representing all but the top part of the Yudoman below the Cambrian boundary. This Formation is c. 150 m thick here but thins to the south. The sequence has ‘gravel stones’ at the base, as well as sandstones and siltstones, and above come thin platy siltstones together with thin platy bituminous limestones and minor grey dolomites; the stromatolite *Boxonia grumulosa* is present. More recently, Ediacaran fossils

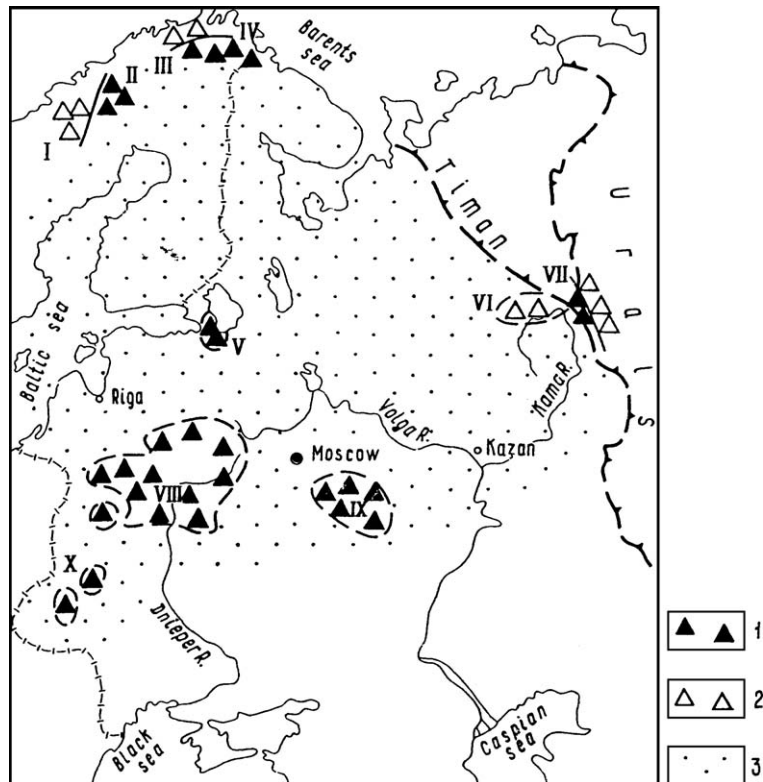


Fig. 45. Palaeogeographic map of the Laplandian glacial horizon. 1=continental tillite and tilloid, 2=glaciomarine tillite and tilloid, 3=inferred distribution of ice sheet, I–X=the various regions [after Sokolov and Fedonkin, 1985 (1990 English language translation), Nauka Publishers].

have been found at three separate horizons. In the northeast, the term ‘Sakhara’ was applied to the middle Yudomian division. The Yudomian appears to be correctly equated with the Vendian.

Ediacaran fossils have also been recorded from Ostrov Formation of the Angara River region to the southeast, in sections close to the mouth of the Irkmeer River. Sokolov recorded *Cyclomedusa* ex gr. *davidi* Sprigg from samples collected there by E. I. Chechel. There are other reported occurrences of Ediacaran fossils from the Siberian Platform, but the two localities mentioned above are the most significant *Cyclomedusa* sp., *Pteridinium* and *Baikalia* were recorded by Sokolov (1972b, 1973) from near Lake Baikal. From the River Maya, near the Sea of Okhotsk, Sokolov and Fedonkin recorded *Cyclomedusa plana* (Glaessner and Wade), and enigmatic large fossils *Suvarovella* and *Majella*, generally considered to be algae, but considered by Wade to be medusoid (Glaessner, 1984). Glaessner (1984) noted that whereas the Vendian successions of the East European platform are generally poor in limestone development, limestones and dolomites are well developed in Siberia.

6.3. Glaciation

Chumakov in Sokolov and Fedonkin (1985) provided a concise account of glaciation in the Vendian. Two Neoproterozoic glaciations are recognised in Russia and Siberia, the Late Vendian Baikonur glaciation being recognised from tillite developments in the Tien Shan and in China. The glacial deposits of the Vendian typically contain no fossils except acritarchs, so they have to be dated either by their relation to overlying and underlying formations or by radiometric (isotopic) methods. The principal glaciation of the Vendian is the ‘Laplandian’ (Fig. 45), originally distinguished in Scandinavia under the name ‘Varanger Ice Age’ (Kulling, 1942); the original name was dropped on account of duplication with the Varanger System or Group (although it is still widely used). The deposits of this glaciation are low in the Vendian succession beneath the Valdai Series that contains the Ediacaran assemblages (Fig. 42). An age of 654 Ma (± 23 Ma) was derived by Pringle (1973) on the lower part of the second unit of the interglacial Nyborg Formation in Finnmark, and Chumakov accepted an

age range of 630–670 Ma. There are two separate Laplandian glacial stages defined. The wide development of these glacial deposits was illustrated by Chumakov and the existence of a parallel glaciation (Marinoan) in the Southern Hemisphere. This is the glaciation which has given rise to the “Snowball Earth Concept” (Hoffman and Schrag, 2000; Fairchild, 2001). The Sturtian glacial deposits of Australia were placed by Chumakov in the Riphean.

At the present state of knowledge, there is considerable variation in age determinations for the late Precambrian glaciations and there is some evidence of diachroneity. One explanation for this diachroneity is related to plate movement. Because of the considerable timespan occupied by some glaciations, different regions became glaciated at different times (see for example Deynoux et al., 1978; Frakes, 1979). This appears to be well established in the case of the late Palaeozoic glaciation, but is difficult to apply to the early Vendian glaciation because there is evidence that

the climate changed rapidly from tropical to glacial and back, and that glaciation occurred well away from the polar latitudes. Chumakov in Sokolov and Fedonkin (1985) suggests that an alternative explanation related to different distances from glaciation centres and degree of preservation should be added to plate-movement-related pole wandering. The complication of diachroneity is not really important in the context of the faunal assemblages, except that it implies that a perfect global match of radiometric ages for the Laplandian equivalents globally need not necessarily be expected.

6.4. Ediacara-type faunas

Fedonkin in Sokolov and Iwanovski (1985) gave an account of the ‘multicellular fossils’ found in various sites in the then Soviet Union: the southeastern White Sea area, the Dniester basin of Podolia (Ukraine) and the Olenek Uplift, Siberia. In this study, he noted the

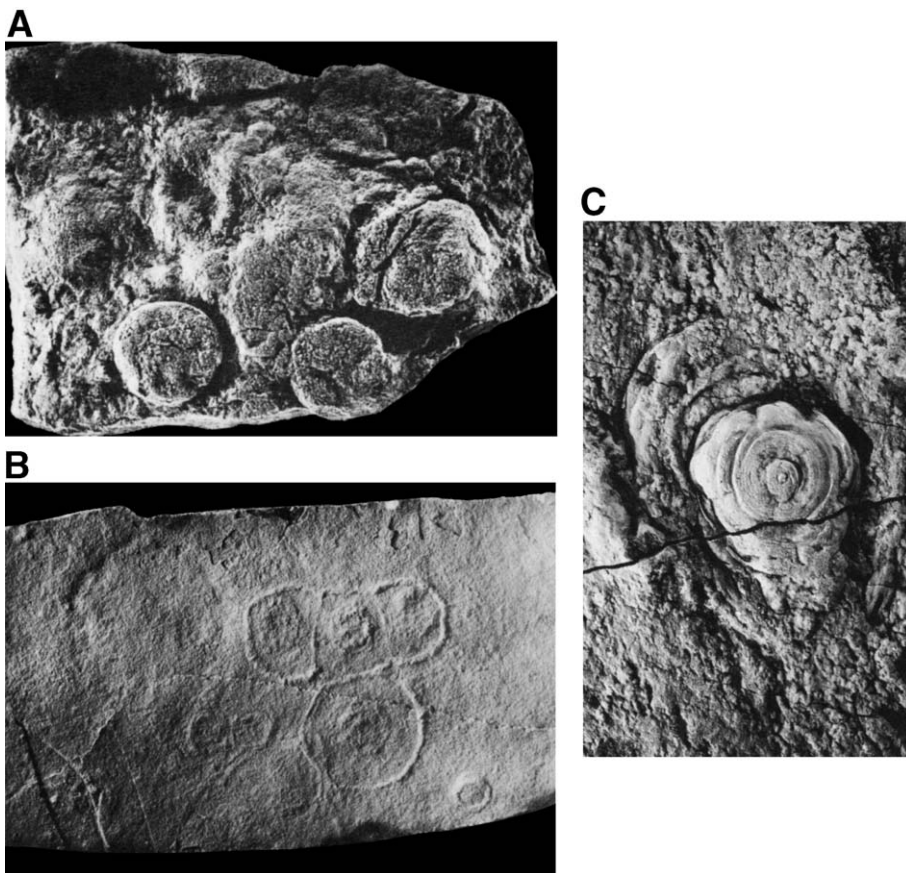


Fig. 46. (A) *Nemiana simplex* Palij, from the White Sea Region ($\times 1$). (B) *Paliella patelliformis* Fedonkin, from the Olenek Upland, Siberia ($\times 0.7$). (C) *Tirasiana cocarda* Becker, from the Cherny Kamen Formation, Urals ($\times 0.9$) [from Sokolov and Iwanovski, 1985 (1990 English language translation). Nauka Publishers].

widespread excellent fossil preservation and the fact that he checked with Australian identifications. There is an absolute dominance of soft-bodied organisms, tubular forms with mineral skeletons (e.g. *Cloudina*) only appearing towards the close of the Vendian in the Nemakit-Daldyn Horizon, Siberia (probably a little later than in Namibia). He regarded these as atypical of the

Vendian and to have been precursors of the explosion of skeletal Metazoa at the very beginning of the Cambrian.

The lack of skeleton results in some unusual effects in the Vendian organisms:

- (1) Uniquely, all Vendian megascopic organisms have more or less equal preservation potential, whereas,

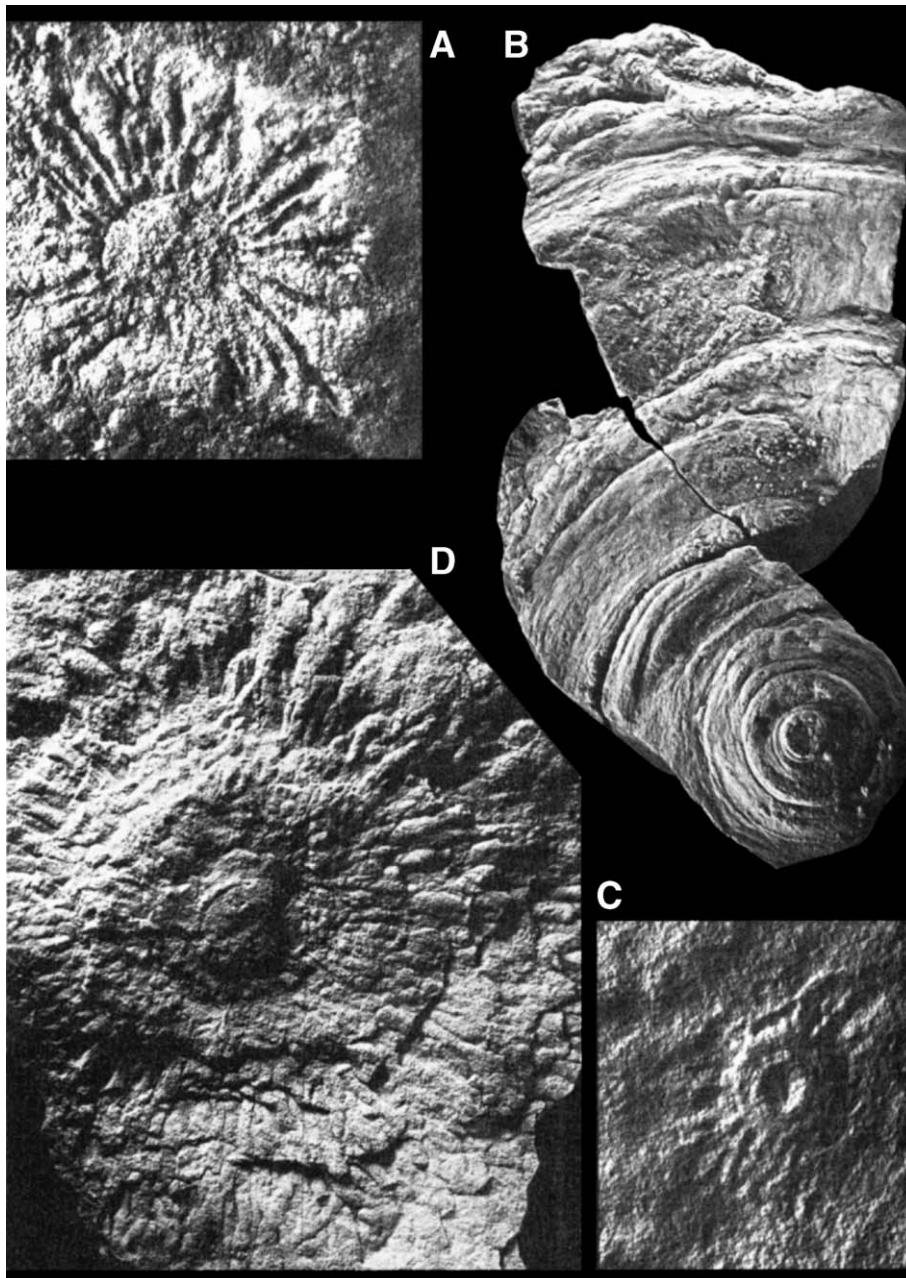


Fig. 47. (A, C) *Hiemalora stellaris* Fedonkin ($\times 1$, $\times 1.3$). (B) *Cyclomedusa* sp., fragment of aboral side ($\times 0.9$). (D) *Eoporpita medusa* Wade, oral side ($\times 1$) (A, B and D are from the Ust–Pinega Formation, Winter Coast; C is from the Mogilev Formation, Ukraine) (from Fedonkin, 1992).

afterwards, skeletal organisms were preferentially preserved. The preservation potential of soft-bodied organisms as fossils depends on mechanical properties of the tissue as well as size, morphology and ecology.

- (2) Soft tissue of organisms may be preserved, allowing determination of their internal structure.
- (3) The Vendian organisms apparently became denser than their predecessors. They could secrete scleroproteins (e.g. *Redkinia spinosa* from the

Valdai Series of the Russian Platform, which is composed of chitinous matter).

- (4) Gigantism is evident (e.g. specimens from Russia, South Australia and Newfoundland up to one metre across: for example, *Dickinsonia*, *Ediacaria* and *Mawsonites*; and a specimen of *Charniodiscus* preserved at Adelaide, 1.2 m long). This feature of gigantism is related to vast, warm epicontinental seas in the Vendian with immense masses of primary food such as phytoplankton available. Only some of the groups exhibit gigantism and these are the ones with no known descendants. Sokolov (1976) related this phenomenon to the ecogenetic or phylogenetic termination of evolution of such groups.
- (5) The Vendian fauna is characterised by high morphological differentiation into taxa of high rank, which is attributed to prior diversification of the main Metazoan lineages. Diversification at species level appears to have been limited.
- (6) Despite the excellent preservation, classification has performed to rely on comparative anatomy methods, analysis of promorphology, body-plan.
- (7) There is (in Fedonkin's opinion) a dominance of Coelenterates, an artifact of their greater body size. This may have influenced their chances of preservation and they may have diminished the population of smaller organisms by using them as food sources.
- (8) We can rule out long distance transport of the fossil organisms from where they lived.

Fedonkin suggested that the Vendian fauna should be regarded as descendants of older Precambrian Metazoans, still unknown to us, rather than ancestors of the Phanerozoic fauna. He accepted that classification is bedevilled by uncertainties, but followed a traditional system of classification, as developed by Glaessner and Wade in Australia for the Ediacara fauna. He subdivided on the basis of promorphology–symmetry of body plan.

6.4.1. Radialia

Fedonkin considered symmetry, commencing with those with a symmetry axis of infinitely high order, which he divided into two subdivisions. The first, undifferentiated forms (Table 7) include *Nemiana*, *Paliella*, *Beltanelliformis* and *Tirasiana* (Fig. 46A,B, C). He believed that these convex discoid casts represent sedentary forms, solitary polyps with central mouths. He divided the next subdivision, characterised by concentric differentiation of the body, into three further subdivisions—Oligocyclic, Polycyclic and those with a

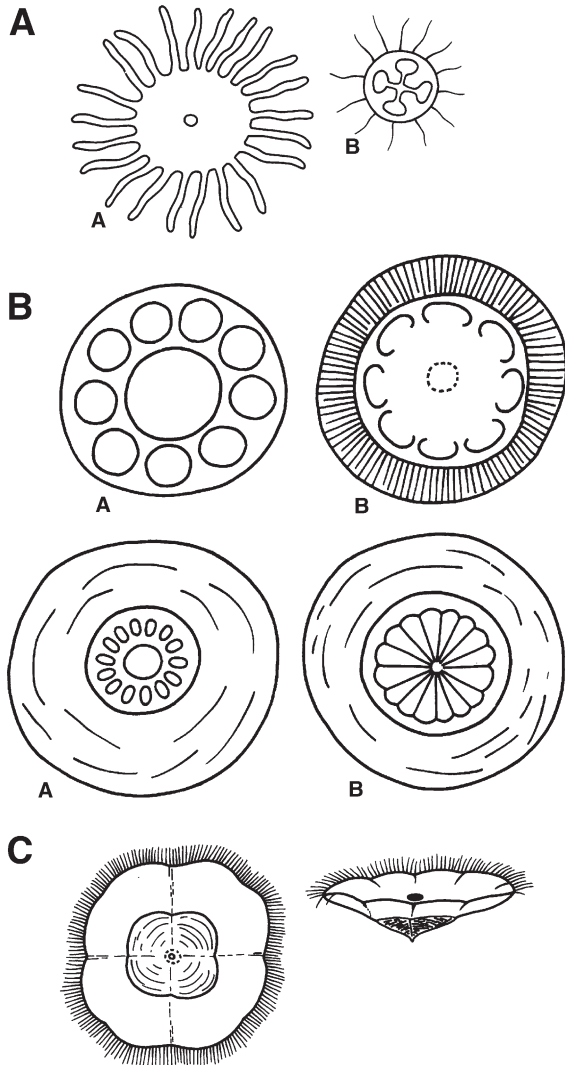


Fig. 48. Symmetry groups of soft-bodied Vendian organisms as subdivided by Fedonkin. (A) Some forms with radial symmetry of variable order, believed to be planktonic: *Hiemalora stellaris* Fedonkin; *Stauridinia crucicula*. (B) Body plan of medusae with characteristic radial symmetry of variable order: *Elasenia aseevi* Fedonkin; *Armillifera parva* Fedonkin. (C) Symmetry as B: *Evmiakisia aksionovi* Fedonkin; *Bonata*. Bottom line: Fourfold symmetry: *Conomedusinites lobatus* Glaessner and Wade, aboral side and reconstruction (after Fedonkin, 1992).

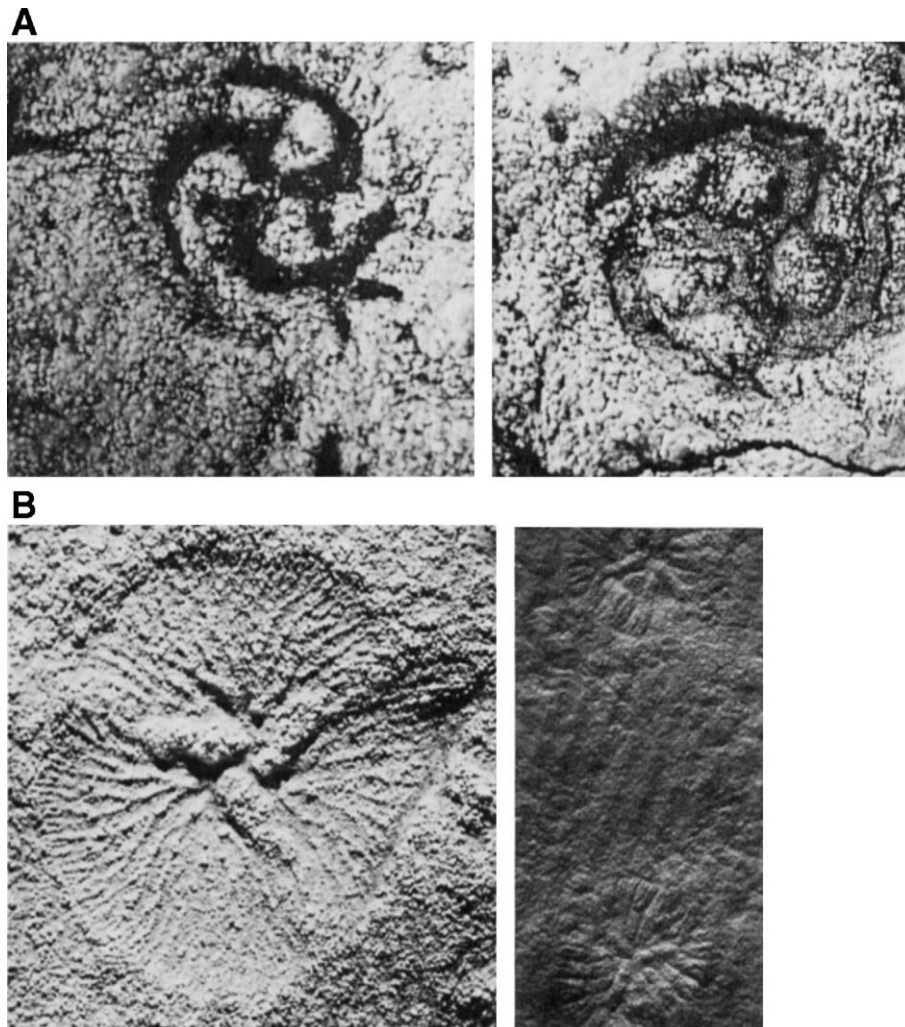


Fig. 49. *Tribrachidium heraldicum* Glaessner, aboral and oral surfaces, from the White Sea Region ($\times 2.5$, $\times 4$). Below: *Albumares brunsaе* Fedonkin ($\times 5$); *Anfesta stankovskii* Fedonkin ($\times 1$), both from the White Sea region (from Fedonkin, 1992).

constant number of concentric rings (the number does not change in ontogeny in contrast to the case of Polycyclic forms: it is considered that these possessed functionally differentiated concentric rings). The first sub-division is represented by *Cyclomedusa plana* (Fig. 47B), which may be a simple form or have radial furrows. There is evidence supporting a fixed mode of life, but also evidence from the White Sea occurrences supporting a swimming mode of life in adult life. His second sub-division is represented by *Euporpita* (Fig. 47D) and his third by *Ediacaria*, one of the largest Vendian medusoids, considered to have been in sedentary form. All these forms are classified as Cyclozoa, a separate class of the Coelenterata. Those with symmetry of uncertain order are not further subdivided and may combine radial and concentric

body plan. Forms with such symmetry were more widespread in the Vendian than in the Palaeozoic or at the present time. They include *Hiemalora* (Figs. 47A,C and 48A), also *Elasenia*, *Armillifera*, *Evmiaksia* and *Bonata* (Fig. 48B,C). They increase the order of rotation symmetry, that is new divisions (“antimeres”) are added during growth, but not in a regular position. This form of addition is considered to be very primitive. He considered them as a special class of coelenterates, the Inordoza. Those with radial symmetry of a stable order he subdivided into three-fold, four-fold and six fold symmetry. Such forms are quite rare in the Vendian, 3-fold symmetry forms being the most common of them. Trilobal medusae are regarded as a separate class, the Trilobozoa, which includes *Tribrachidium*, *Albumares*, *Anfesta* (Fig. 49) and *Skinnera* (Glaessner and Wade,

1966, Wade, 1969; Keller and Fedonkin, 1976; Fedonkin, 1981a,b, 1983a,b). There is no certainty that these are Coelenterates and Runnegar (1998) suggested placing this group in a separate phylum. Forms with fourfold symmetry include *Conomedusites* (Fig. 48), *Kimberella*, *Ichnusa*, *Persimedesites* and *Stauridina* (Glaessner and Wade, 1966; Wade, 1969, 1972a; Hahn and Pflug, 1980; Debrenne and Naud, 1981; Fedonkin, 1983a). Only *Pomorina* displays sixfold symmetry. Fedonkin's symmetry classification is summarised in Table 7 and a suggested development sequence of forms with a concentric body plan, moving towards bilateral symmetry was illustrated by him. He also listed the geographic distribution of remains of non-skeletal Vendian organisms (Table 8).

Promorphological study of the Radialia was considered by Fedonkin to open the possibility of understanding the earliest evolutionary stages of the Coelenterata; the wide distribution in the Vendian of forms with symmetry axis of an infinitely high order and concentric body plan would seem to justify them forming a group of high order and the erection of the class Cyclozoa, dominant in the early evolutionary stages of the Radialia. However, we see other evolutionary trends in the Vendian Coelenterata, which became dominant in the Phanerozoic. We can regard the Vendian to a great extent as the time of phylogenetic closure of this class, being forced out in both benthic and pelagic regions by more highly organised radial Cnidarians. The development of radial and concentric body plane in this class in the Vendian was regarded by Fedonkin as indicative of evolution, providing one more degree of freedom in the direction parallel to the axis of symmetry. Variable radial symmetry is abundant and diverse in the Vendian, but rare in living forms of Radialia,

suggesting that it represents an evolutionary stage. The Vendian Radialia were regarded as representing an early evolutionary stage in the development of the modern Cnidaria.

Fedonkin suggested that analysis of the promorphology of the Radialia provides the possibility of emplacement of symmetry in the Articulata, not previously predicted theoretically. This possibility may have been realised in the early stages of metazoan evolution.

6.4.2. Bilateria

Fedonkin classified the Bilateria into two subdivisions, the second having three further subdivisions (Table 7). The Bilateria are more abundant than Radialia in the modern animal kingdom, but the reverse was the case in the Vendian. He believed that this supported the idea of affinity of the primitive groups of Bilateria of the Vendian with the Coelenterata. He suggested also that the abundance, diversity and large dimensions of the Vendian coelenterates indicate that they could be regarded as the oldest type of the Eumetazoa. Radially symmetrical organisms completely dominated the animal world during the earliest, possibly very short stage of evolution of the multicellular animals. He cited evidence from the Conception Group, Avalon Peninsula, and Newfoundland that Bilateria appeared late in the Vendian, and only Radialia being present early on.

His promorphological analysis of the Bilateria does, he believed, allow one to outline the major, earlier unknown lineages, because the Vendian Bilateria are so far the oldest organisms recognised in the fossil record belonging to this Metazoan division. Many genera in the group are monotypical and represented by only a few specimens. This means that corrections of the analysis may be needed when new genera are found.

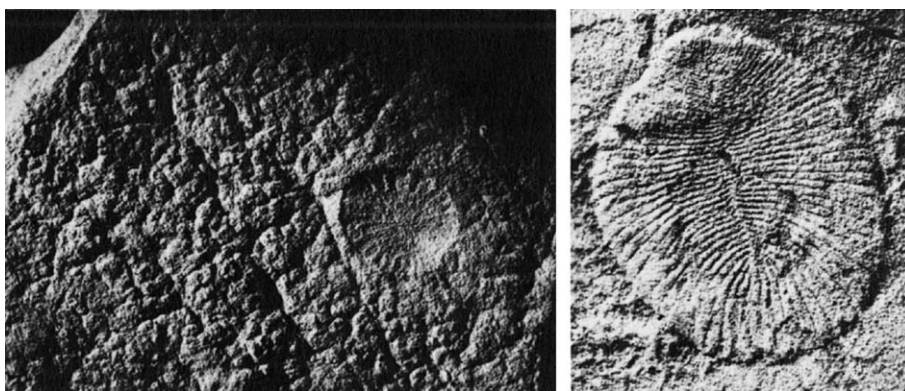


Fig. 50. *Dickinsonia costata* Sprigg: left, juvenile individual on a wrinkled surface that probably represents a microbial mat that covered the surface of the sediment after burial of the animal; right, adult (both $\times 1$) (from the White Sea Region). (From Fedonkin, 1992).

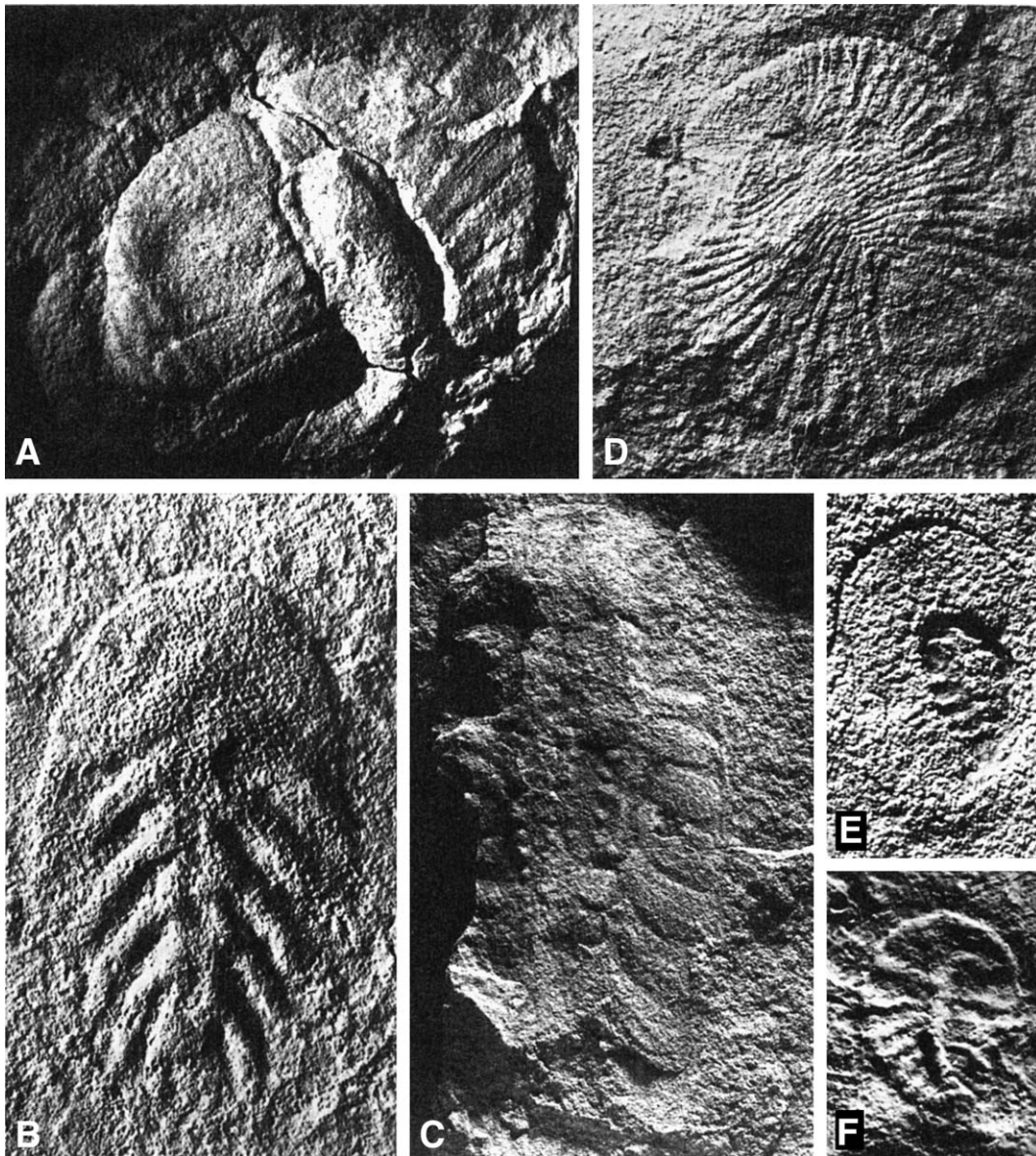


Fig. 51. Metamerical forms. (A) *Mialsemia semichatovi* Fedonkin ($\times 1$). (B) *Vendia sokolovi* Keller ($\times 5$). (C) *Bomakellia kelleri* Fedonkin ($\times 0.7$) (from the Ust–Pinega Formation, Summer Shore, White Sea Region). (D) *Dickinsonia costata* Sprigg ($\times 1$). (E) *Onega stepanovi* Fedonkin ($\times 5$). (F) *Vendomia menneri* Keller ($\times 5$). A, B, D from the Ust–Pinega Formation, Winter Coast, White Sea Region; C, E, F from the Ust–Pinega Formation, Summer Shore, White Sea Region. (From Fedonkin, 1994.)

However, the general body plan of these animals is usually quite distinct. Superficially, the Vendian Bilateria are dominated by diverse segmented forms, not all of which can be classified under Articulata. There are some grounds to recognise a large group close to the Articulata, representing an important link on the way to the latter. Unsegmented forms are rare in the Vendian.

Platypholinia pholiata may be the simplest form among the Vendian Bilateria: it occurs as flat, slightly

tapering leaf-shaped imprints about 70 mm long \times 35 mm wide. The non-tapered end is rounded, and a median furrow and sub-parallel lines run inwards from the slightly bifid tapered end. Only three specimens are recorded from the Zimny Coast on the White Sea. He regards it as primitive and enigmatic, but assigns it questionably to the Plathelminthes (flatworms). Another leaf-shaped fossil with both ends sharp, *Vladimissa*, is represented by a single specimen from the Zimny Coast: this too is tentatively assigned to the Plathelminthes.

To the Polymerous subdivision of the segmented forms of the Bilateria, is allocated *Dickinsonia*, of which, at the time of writing, five species were differentiated among the 400 specimens collected in South Australia. Four of these species are known in the Vendian of Russia and the Ukraine (Figs. 50 and 51D). *Dickinsonia* has a thin flat body, ovate or elongate and leaf-shaped. The state of preservation suggests that even the largest specimens are no more than 3 mm thick. There are a large number of similar segments (“polymerous, homonomous metamerism”). The growth zone is situated at the posterior end. The segments are arranged alternately, not corresponding on opposite sides of the median ridge (Fig. 50), unlike living and known Phanerozoic representatives of the Articulata (in later publications he referred to this as a “plane of glide or slide symmetry”). Fedonkin believed that *Dickinsonia* represents an independent and specific branch of Metazoan evolution on the way to Bilateria, and simultaneously Articulata. He added later that they are not true Articulata, but there is no evidence of analogy to the Platyhelminthes. He placed them in a Phylum “Proarticulata”.

The Sabelliditids occur in the form of thin, extremely long, elastic, solitary chitinous zooid tubes. They have a cylindrical tube shape, with no articulation or branching that is typical of annelids. The tubes show gradual transition from wrinkled to smooth portions. Some representatives have “collars” terminating the tubes. This feature is shared with the Pogonophora, which are known as fossils from the Ordovician, Silurian, Oligocene and Pliocene and as living forms, and Sokolov (1972a) interpreted them as fossil Pogonophora. Sabelliditids are abundant in the Cambrian/Precambrian boundary beds and appear to be an exception to the cut off of Vendian forms at the base of the Cambrian. Sokolov believed that they occupied non-agitated shelf or epi-platform seas at the commencement of the expansion of archaeocyathans and trilobites, and that those organisms drove them to deeper sea zones, where they evolved slowly to the modern Pogonophora. The Vendian–Early Cambrian Sabelliditids constitute two families, the Sabelliditidae including *Sabellidites*, *Parasabellidites*, *Paleolina* and the Saarines *Saarina* and *Caluptrina*.

The Oligomerous segmented forms are mostly forms with a small number of segments (metameres). The family Vendomiidae includes five monographed genera, *Praecambrium*, *Vendia* (Fig. 51B), *Vendomia* (Fig. 51F), *Pseudovendia* and *Onega* (Fig. 51E). The first genus is not found in the Vendian of Russia and the Ukraine: it has been the source of prolonged

argument about its status. *Vendia* is preserved as a flat, ovoid impression, 14 mm long × 8 mm wide in the holotype. The body was flat and undivided, but there is a well-defined median ridge. The anterior or cephalic area is horseshoe-shaped. There are five segments or lateral branches, diverging outwards and backwards and alternately arranged on either side of the median ridge. This “staggering” of the lateral outgrowths appears to real and not a slight, oblique distortion, as has been suggested by some authorities. It is a common feature of Vendian segmented Bilateria. Fedonkin believed that it is a primitive feature related to initial ancestral radiation. *Onega* is a similar organism with five staggered lobes or segments, separated by a deep furrow. *Vendomia* displays even more similarity to the Arthropods; 4 mm long, its drop-shaped body, consists two-thirds of a horseshoe-shaped head, with two depressions “equating to eyes”. Six paired segments arise from the median ridge, which “resembles the rachis in trilobite”. It closely resembles larval trilobites. Fedonkin quoted Termier and Termier (1976) who believed that the Vendian/Ediacaran fauna was rich in nymphoids, adults whose body plan resembled larvae of later known Metazoa. *Parvancorina*, studied in numerous specimens by Glaessner, is recorded from the Vendian of the Zimny Coast, and has the form of a shield-like impression enclosing an anchor shaped ridge: there is evidence of a metamorous (segmented) body under a carapace. Fedonkin placed *Vendia*, *Onega* and *Vendomia* in a separate class (Vendiamorpha) of the Phylum Proarticulata, whereas he placed *Parvancorina* in the Arthropoda, but thought it close to the divergence of the Trilobitomorpha but not in a direct lineage.

Spriggina is rare in the Vendian of Russia. Fedonkin noted the resemblance to living animals, but also the resemblance of the horseshoe-shaped head to some Trilobitomorpha. He mentions Birket-Smith's (1981a) conclusion that trilobites may have derived from it or else some very closely related forms. *Bomakellia* (Fig. 51C), a large trilobite-like form with a half-moon shaped head and spindle-shaped trunk bearing ovoid lateral appendages, and rows of bosses, is also allocated to the Arthropoda, as is *Mialsemia* (Fig. 51A), ovate and wider than long, with a half-moon-shaped head and two rows of opposite, lateral appendages; long and petaloid, with two-pennate sculpture. The largest appendages are in the middle and they decrease in size towards both ends. There is the suggestion of the existence of a carapace. *Spriggina*, *Bomakellia* and *Mialsemia* were allocated by Fedonkin to the Class Paratrilobita of the Phylum Arthropoda.

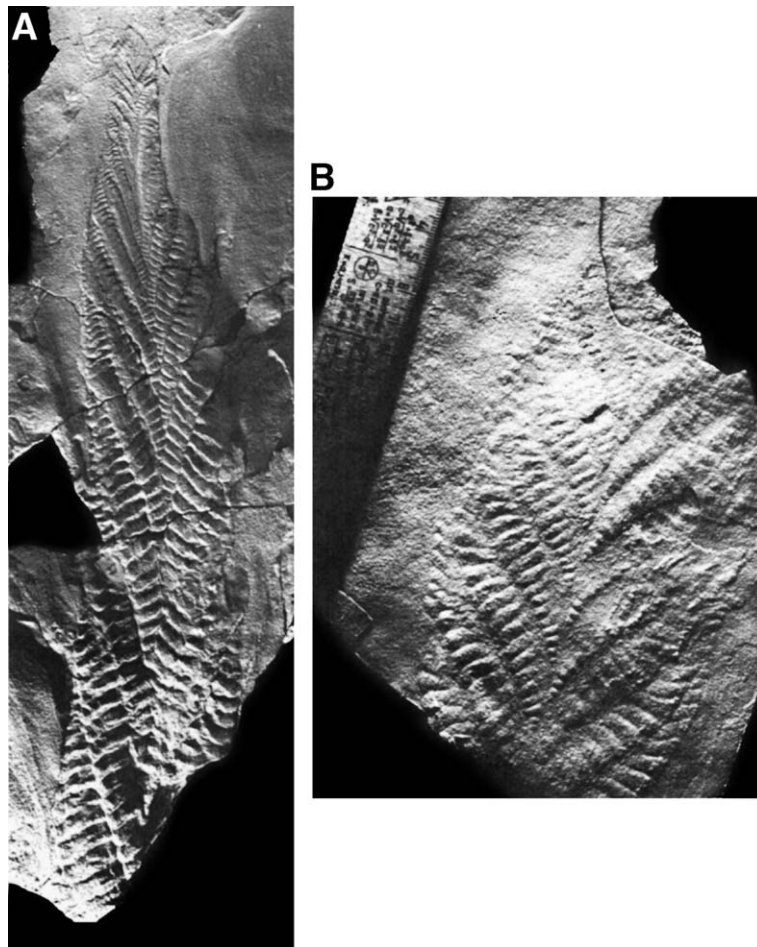


Fig. 52. (A) *Charnia masoni* Ford, fragment of a large colony, and upper terminal part of the same specimen ($\times 0.7$, $\times 3$): (from Ust–Pinega Formation, Summer Shore, White Sea). (B) *Charnia masoni* Ford ($\times 0.6$), Olenek Upland, Siberian Platform (from Fedonkin, 1992, 1994).

6.4.3. Petalonamae

Fedonkin in Sokolov and Iwanovski (1985) placed a number of fossil genera under the “Colonial Forms and Petalonamae”. The former are not as diverse as are Phanerozoic colonial forms. The Vendian fossils include frond-like or pennate organisms bearing a resemblance, which may be superficial, to modern Anthozoa (Alcyonaria and Pennatularia). The most commonly preserved part is the basal attachment disc or the base of the main axial structure, on the bottom surface of beds—typically the lower bedding plane surface of sandy slabs as furrows which radiate outwards from a centre of variable shape. As they radiate they split and become shallower. No outer edge is generally observed, although there are exceptions. *Pseudorhizostomites howchini* Sprigg is typical, also *Charnia*, both being recorded in the Vendian of Russia (Fig. 52A,B). The former measures about 5.7 cm in diameter. The possibility of

hydrozoan coelenterate affinities was suggested. However, the discoid basal attachment is unlike the attachment shapes of Pennatularia.

The Phylum Petalonamae of Pflug (1972a,b) was taken to include those forms of which the systematic position remains uncertain. Fedonkin placed only *Pseudorhizostomites* under the Arthropoda in his detailed descriptions: other problematica of this frond-like and pennate character he put under the Petalonamae; in which he includes *Charnia* (found on the Zimny Coast and Olenek Uplift, Fig. 52); *Pteridinium* (White Sea) (Fig. 51C), *Vaizitsinia* (White Sea), *Inkrylova* (Onega Peninsula, White Sea, characterised by a bag-shaped body, and flat symmetrical segments detaching from the median furrow and not varying in width, possibly bilaterally symmetrical), *Archangelia* (Onega Peninsula, White Sea; also ? bilaterally symmetrical), *Podolimerus* (Dniester basin, Podolia, holotype only of two impressions), *Valdaina*

(Zimny Coast, a bipinnate, leaf-shaped form up to 70 mm long), *Ramellina* (Zimny Coast, a small bipinnate form), *Vaveliksia* (Dniester Basin, Podolia, a problematic organism with a small attachment disc and obconical body attached to it forming an “ampular” sac—a primitive form with possible coelenterate and hydrozoa affinities), *Zolotytsia* (Zimny Coast and Podolia: a form consisting of two rows of ovate bodies separated by a deep axial groove, and lateral grooves), and *Lomozovis* (Dniester Basin, Podolia, a large dendritic colonial organism, with a small discoid attachment).

6.4.4. Summary

Fedonkin in his systematic descriptions thus adopted the following classification:

Phylum: Coelenterata
Class: Cyclozoa

Class: Inordozoa
Class: Trilobozoa
Class: Conulata
Class: Scyphozoa(?)
Phylum: Plathelminthes (?)
Phylum: Proarticulata
Class: Dipleurozoa
Class: Vendiamorpha
Phylum: Arthropoda
Class: Paratrilobita
Phylum: Petalonamae.

He listed the following characteristics of the Vendian fauna:

- (1) Lack of sclerotised tissues in most invertebrates.
- (2) High diversity of life forms.
- (3) Significant differentiation level of taxa of high rank and insignificant at specific level, suggesting

Table 9

List of trace fossils [after Sokolov and Iwanovski, 1985 (1990 translation), Nauka Publishers]

	Vendian			Cambrian		
	Volyn series		Valdai series	Baltic series		
	1	2	3	4	5	6
<i>Harlaniella podolica</i> Sokolov			_____			
<i>Palaeopascichnus delicatus</i> Paliĭ		_____				
<i>Palaeopascichnus sinuosus</i> Fedonkin		_____				
<i>Cochlichnus</i> Hitchcock				_____		
<i>Neonereites uniserialis</i> Seilacher				_____		
<i>Neonereites biserialis</i> Seilacher				_____		
<i>Neonereites renarius</i> Fedonkin			_____			
<i>Nenoxites curvus</i> Fedonkin			_____			
<i>Vendicus vendicus</i> Fedonkin		_____				
<i>Vimentes bacillaris</i> Fedonkin			_____			
<i>Intrites punktatus</i> Fedonkin			_____			
<i>Bilinichnus simplex</i> Fedonkin et Paliĭ				_____		
<i>Didymaulichnus tiransensis</i> Paliĭ					_____	
<i>Bergauera</i> Paliĭ				_____		
<i>Bergaueria major</i> Paliĭ				_____		
<i>Gordia</i> Emmons				_____		
<i>Skolithos</i> Haldemann		_____				
<i>Skolithos linearis</i> Haldemann					?	_____
<i>Diplocraterion parallelum</i> Torell				?		_____
<i>Rhizocorallium</i> Zenker						_____
<i>Teichichnus</i> Seilacher				_____		
<i>Treptichnus bifurcus</i> Miller				_____		
<i>Treptichnus troplex</i> Paliĭ				_____		
<i>Phycodes pedum</i> Seilacher				_____		
<i>Aulichnites</i> Fenton et Fenton	_____					? _____
<i>Planolites</i> Nicholson	_____					_____
<i>Gyrolithes polonicus</i> Fedonkin				_____		
<i>Rusophycus</i> Hall				_____		
<i>Cruziana</i> d’Orbigny					_____	_____

1=Drevlyany, 2=Redkino, 3=Kotlin, 4=Rovno, 5=Lontova, 6=Talsy.

that there was a pre-Vendian stage of Metazoan history, although not necessarily of long duration.

- (4) Prevalence of coelenterates (due to relatively large dimensions, and abundance of sedentary forms, which may be a factor of preferential preservation).
- (5) Presence of all ecological groups: stationary and vagile benthon, nekton, plankton and pleuston.
- (6) Preferential occurrence of benthon and other groups of normal, marine, shallow-water environments.
- (7) Similarity of Vendian (Ediacaran) faunal assemblage in all parts of the world, due to the absence of strong ecological barriers during the Vendian post-glacial transgression.
- (8) Presence among Vendian Metazoa of adults resembling in body plan the larval stages of organisms known from later geological periods.
- (9) Gigantism evident in the most primitive solitary organisms, followed by decrease in body size. The larger body forms are preferentially preserved.
- (10) Very variable symmetry and architectonics, some examples being unknown or rare in the Phanerozoic (e.g. concentric symmetry of the cyclomeric coelenterates, three-fold radial symmetry).
- (11) First traits of an organic skeleton and the development of a mineralised skeleton at the close of the Vendian in some groups.
- (12) Absence among Vendian soft-bodied animals of obvious ancestors of the minute skeletal organisms which appear at the Tommotian level of the Early Cambrian.
- (13) Low activity of vagile predators and necrophages.
- (14) Short trophic (food) chains.
- (15) Low specific weight of infauna in benthic communities of the Vendian sea with sharp predominance of sestonophages (suspension feeders) and detritophages.

Fedonkin's list of species recognised in the Vendian of Russia and the Ukraine is given in [Table 8](#).

Becker in [Sokolov and Iwanovski \(1985\)](#) gave a few detailed descriptions of forms from the Urals.

6.5. Trace fossils

Fedonkin in [Sokolov and Iwanovski \(1985\)](#) lists the trace fossils recorded in the Vendian of Russia and the Ukraine ([Table 9](#)) and their distribution in time in the Volyn, Valdai and Baltic (Cambrian) Series. They constitute one of the few transit groups at the Precambrian/Cambrian boundary. They are, he consi-

dered, important for their heuristic (discovery) value for palaeontology and palaeoecology, particularly in relation to the early stages of evolution, but not for stratigraphic usefulness. They provide information on amount, diversity, biotype density, general dynamics of populations, and feeding, and, especially, on movement modes. In the case of the Vendian, they provide information on the time of appearance of the first benthic Metazoa in the geological record and the history of habitation of the seafloor.

Unfortunately, in the oldest Precambrian, trace fossils are rare, morphologically fuzzy and of dubious identification as traces. Thus, knowledge of pre-Vendian palaeoichnology is limited. The overwhelming majority of Precambrian trace fossils are in Vendian strata. This proliferation compared with older rocks may be related to the limitation of the shelf zone globally during the Laplandian (Varanger) glaciation and earlier, life being mainly confined to the pelagic region, and the favourable conditions provided by the succeeding epoch of transgression and wide, shallow epiplatform seas—extensive shelf zones. The trace fossils which appear in the mid-Vendian record one of the most important population and taxonomic novelty outbreaks in the geological record—documented, unlike the outbreak at the base of the Cambrian, by abundant remains of non-skeletal fauna and trace fossils.

During the Vendian, there was progressive increase in both abundance and diversity of forms. Trace fossils from the Vendian (post Laplandian tillites) reveal a highly organised vagile benthos, of organisms that moved through the shallow subsurface layer by peristaltic changes in shape of the entire body, like living annelid worms, passing sediment containing organic matter through their digestive canal. Motions of the ventral part of the body were most common in the Vendian, but wavelike curvings of the body are also recognised. A peculiarity of the Vendian is tracks with repeated symmetry elements, produced by repeated moves forwards by mud-eaters. Transverse movements of the anterior body are also recorded, and movement by alternate right and left turns. The record of trace fossils suggests that there was a quite fast pre-Vendian evolution of the vagile benthos, compared with pelagic and sedentary forms.

Fedonkin then considered individual genera and species from the White Sea and Podolia regions. Grazing trails are the most abundant and diverse group. As a rule the organisms did not cross their own trail, and moved essentially horizontally. Among the grazing trails (group Pascichnia), the genera

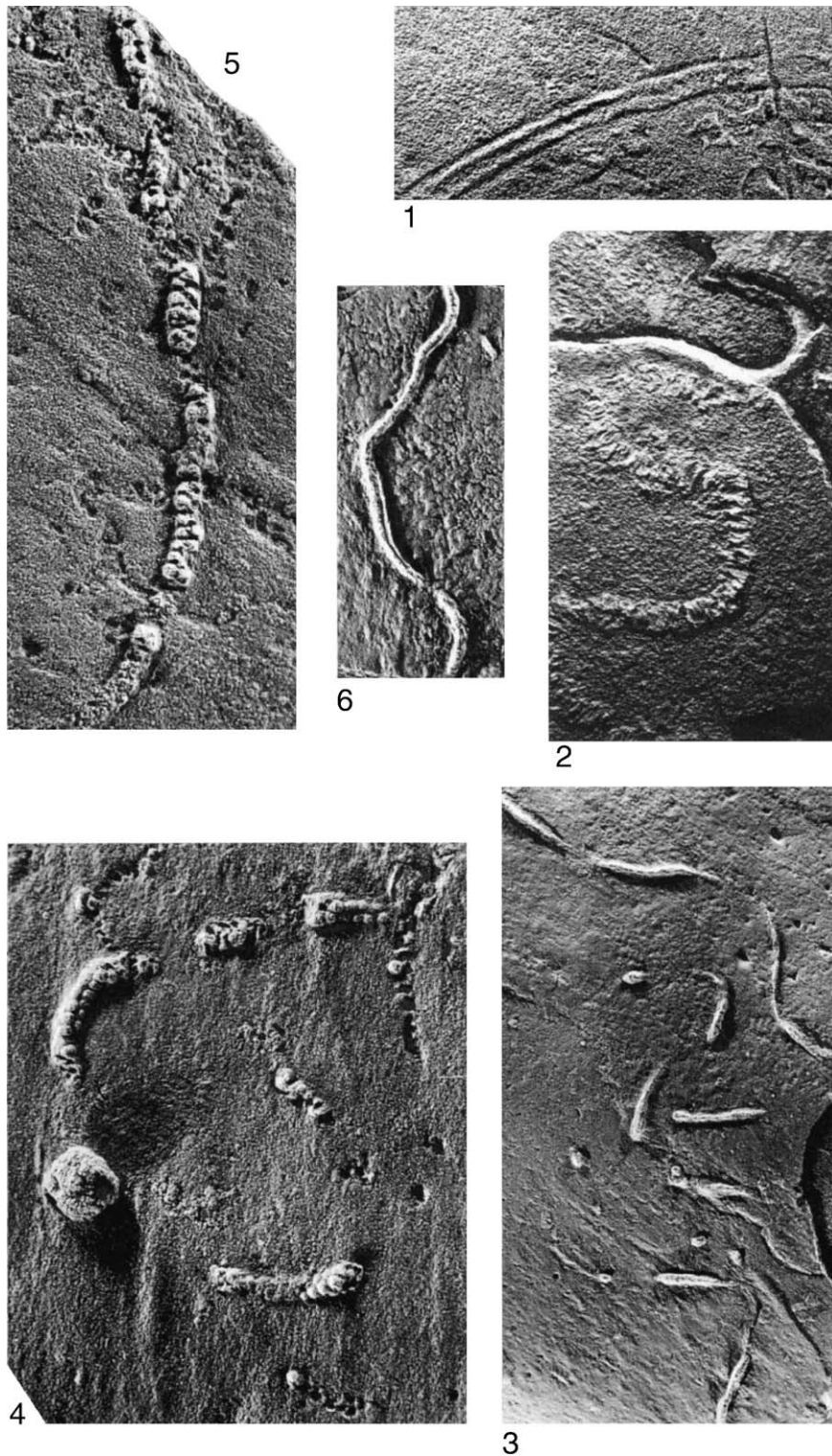


Fig. 53. Trace fossils from the Ust–Pinega Formation, Letny Coast, White Sea Region: (1) Double crawling trail left behind by an animal in the course of passing by ventral peristalsis (pedal wave). (2) *Nenoxites curvus* Fedonkin (holotype). (3, 6) *Planolites serpens* (Webby) (positive hyporelief). (4, 5) *Neonereites biserialis* (Seilacher) (positive hyporelief) (all are $\times 0.9$) [from Sokolov and Iwanovski, 1985 (1990 English language translation). Nauka Publishers].

recorded include *Ilmenites* (densely meandering burrows), *Aulichnites* (two gently sloping ridges separated by a groove, preserved in sandstone beds), *Bilichnus* (two parallel grooves, a trail produced by peristaltic ventral movements), *Nenoxites* (meandering ribbon-like traces with transverse “rugae”, related to the mud-collecting process, sediment saturated in organic matter), *Palaeopascichnus* (narrowly arched grooves, representing movements across the direction of motion), *Harlaniella* (preserved in positive hyporelief as obliquely hatched ridges, attributed to a worm-like organism), *Planolites* (subhorizontal dwelling burrows of circular cross-section), and *Neonerites* (preserved as small round pellets, the substrate surface being subjected to biological processing and repleted with faecal pellets, as the organism moved). The proportion of dwelling burrows (Group Domichnia) is low, as in the Phanerozoic; fine inclined dwelling burrows, *Skolithos*, are recorded of a worm-like organism from a densely populated occurrence on the Zimny Coast (20–30 individuals/dm²). Resting tracks (group Cubichnia) are rare in the Vendian; they include *Vendichnus* (trail of two wing like dents separated by a ridge and are oriented parallel to linear current marks, indicating response to the water stream); these trails resemble those ascribed to trilobites, particularly *Ixalichnus*, and this suggests that they were produced by nektonic (swimming) organisms, rather than seafloor crawling organisms because no similar crawling traces have been found. Some of these trace fossils are illustrated in Fig. 53.

There is a lack of correlation with known mollusc traces, because most Vendian traces were made by mobile benthic forms, not nektonic or sedentary. The predominance of group *Pascichnus* indicates that most of the vagile benthos was of microphage affinity, feeding on small nutrient particles collected from the soil.

The trace fossils can even be used for distant correlations of Vendian deposits, based on the presence of similar populations of forms. A striking change in character is recorded at the Vendian–Cambrian boundary, at the level at which the maximum abundance of sabelliditids occurs. Many hitherto unknown taxa appear—large, flat spiral forms, large, fairly deep, morphologically complicated feeding trails, spreiten burrows and vertical spiral feeding trails. These appear alongside the subhorizontal and shallow traces characteristic of the Vendian. It is suggested that interspecies competition became more intense, together with predation of the benthic population: better aeration due to a greater oxygen content in the atmosphere may have

allowed deeper penetration, new niches being actively colonised. Arthropods took a leading position in the trace formation of the offshore areas in the Atdabanian, although tracks of unknown arthropods do occur in the Tommotian. The similarity between Lower Cambrian traces in different parts of the world is remarkable, and indeed these traces in their appearance provide a useful marker of the boundary.

6.6. Plants, microfossils, calcareous algae and stromatolites

Sokolov and Iwanovski (1985) provided details of the fossils other than Metazoa recorded in the Vendian of Russia and the Ukraine.

6.6.1. Plants: Metaphytes

Gnilovskaya (in Sokolov and Iwanovski, 1985) described Vendian Metaphytes: only in the Vendian at 600–580 Ma do ribbon-like ‘macrophytes’ (or ‘megaphytes’) appear in abundance over large areas. Non-mineralised, megascopic, ribbon-like fossils are very common in the Vendian of the East European Platform, in Poland, Byelorussia, the Ukraine, Moldavia, Central Russia, the St. Petersburg District, Baltic District and Siberia—although in the latter case they have not been systematically studied. They are classified as Vendophyceae and they contain two orders: Eohohyniales (bushy, intensely branching forms) and Vendotaeniales (ribbon-like forms).

The Vendotaenids can be separated into three successive floras in the Vendian:

- (1) Redkino flora: *Eoholynia*, *Orbisiana*, *Caudina*, tendrils of *Helminthoidichtes*, *Leiothrichtoides*.
- (2) Kotlin flora: *Vendotaenia*, *Kanilovia*, *Aataenia*, *Leiothrichtoides*, *Sarmenta*, *Primoflagella*.
- (3) Rovno flora: *Tyrasotaenia podolica*, *Tyrasotaenia tunguska*, *Dvinia*.

6.6.2. Microfossils

Sokolov and Iwanovski (1985) included a lengthy chapter on Vendian microfossils, in seven sections authored by various authorities. Microfossils are rare in the early Vendian Laplandian deposits (coeval with the glaciation). The post-Laplandian Vendian rocks of the Redkino and Kotlin horizons, in contrast, yield abundant microfossils, filamentous acritarchs, small acritarchs with processes and small spores with a tetrad scar. The Rovno horizon is marked by the appearance of characteristic forms, with cone-like walls, ovate and the increase in number of certain

Table 10

Stratigraphic distribution of plant microfossils ('microphytes') in the Vendian of northwestern Archangelsk [after Sokolov and Iwanovski, 1985 (1990 translation), Nauka Publishers]

Vendian							Kotlin Horizon	Microfossils
Redkino Horizon								
Tamitsa Beds	Lyamitsa Beds	Arkhangelsk Beds	Verkhovsk Beds	Syuzma Beds	Vaizitsa Beds	Zimnie Gory Beds	8	9
1	2	3	4	5	6	7		
x	x	x	x	x				<i>Kildinella sinica</i> Tim.
x	x	x			x	x		<i>Kildinella hyperboreica</i> Tim.
○	○	○		○		○	○	<i>Leiosphaeridia minor</i> Schep.
○	○	○		○		○	○	<i>Leiosphaeridia aperta</i> Schep.
		○	○	○	○	○	○	<i>Leiosphaeridia pelucida</i> Schep.
		○	○	○		○	○	<i>Leiosphaeridia culta</i> Andr.
○	○	○	○	○				<i>Leiosphaeridia laccata</i> Aseeva
		○	○	○				<i>Leiosphaeridia bituminosa</i> Tim.
				○	○	○	○	<i>Leiosphaeridia effusa</i> Schep.
				○		○		<i>Leiosphaeridia gigantea</i> Schep.
x	x	x	x					<i>Protosphaeridium densum</i> Tim.
○	○	○	○	○				<i>Trachysphaeridium Laminaritum</i> T
							○	<i>Trachysphaeridium magnum</i>
								Schep
	○	○	○	○	○	○	○	<i>Trachysphaeridium bavlnense</i>
								Schep.
		○		○		○		<i>Trachysphaeridium partialum</i>
								Schep.
		○				○		<i>Stictosphaeridium pectinale</i> Tim.
		○				○		<i>Stictosphaeridium sinapticuliferum</i>
								Tim.
○	○	○				○	○	<i>Stictosphaeridium implexum</i> Tim.
x	x	x	x	x		x		<i>Favosphaeridium favosum</i> Tim.
						x		<i>Stratimorphis plana</i> As.
		○	○	○	○	x	○	<i>Orygmatosphaeridium</i>
								<i>rubiginosum</i> .
x	x	x				x		<i>Podoliella regulare</i> Tim.
				x	x	x		<i>Bavlinella faveolata</i> Schep.
		○	○	○			○	<i>S. sorediforme</i> Tim.
		x	x			x		<i>Synsphaeridium bullatum</i> Andr.
		○				○	○	<i>Synsphaeridium conglutinatum</i>
								Tim.
			○			○		<i>Symplastosphaeridium</i> sp.
x	x	x	x			x	x	<i>Nucellosphaeridium</i> sp.
		x	x					<i>Pterospermopsimorpha insolita</i> Tir
	x	x						<i>Volyniella valdaica</i> (Schep.) As.
							x	<i>Volyniella</i> sp.
				x		x		<i>Leiominuscula minuta</i> Naum.
		x	x			x		<i>Gloeocapsomorpha</i> sp.
				○		○	○	<i>Leiotrichoides typicus</i> Herm.
								<i>Leiotrichoides</i> sp.
							○	<i>Polytrichoides lineatus</i> Herm.
							○	<i>Tortunema sibirica</i> Herm.
							○	<i>Oscillatorites wernadskii</i> Schep.
							○	<i>Oscillatoriopsis magna</i> Tynni et Bo
							○	<i>Oscillatoriopsis constricta</i> T.et B.
							○	<i>Oscillatoriopsis rhomboidalis</i>
								sp. nov.
						○		<i>Oscillatoriopsis funiformis</i> sp. nov.
						x		<i>Palaeolyngbia</i> sp.
		x	x	x	x	○		<i>Rudnjana</i> Golub

○=abundant, ×=rare.

Table 11

Vertical range of characteristic Vendian and Lower Cambrian microfossil species on the East European Platform [after Sokolov and Iwanovski, 1985 (1990 translation), Nauka Publishers]

Pachelma Series	Lapladian		Vendian			Cambrian	Species
	Lapladian type	Volyn type	Redkino	Kotlin	Rovno	Lontova	
●							<i>Brochopsophsphaera minima</i> Schep.
●			x	x		x	<i>Kildinella hyperboreica</i> Tim.
●	●		x	x			<i>Killdinella sinica</i> Tim.
●		●	●	●	●	●	<i>Leiosphaeridia aperta</i> Schep.
●			●	●	●	●	<i>Leiosphaeridia pelucida</i> Schep.
●		●	●	●	●	●	<i>Leiosphaeridia minor</i> Schep.
x			x	x			<i>Leiosphaeridia gigantea</i> Schep.
●		●	●	●	●	●	<i>Oscillatorites</i> div. sp.
●				●			<i>Leiosphaeridia warsanofiewae</i> Naum.
○			●	●	●	●	<i>Leiotrichoides typicus</i> Herm.
○			●	●	●	●	Fragment of non-septate, smooth filament
		●		●	●	●	<i>Leiosphaeridia parva</i> As.
		●	●	●	●	●	<i>Orygmato-sphaeridium rubiginosum</i> Andr.
			●	●			<i>Rudnjana</i>
				●			<i>Leiosphaeridia effusa</i> Schep.
				●			Filament fragment with a rhomboid pattern
				x			<i>Ambiguaspora pervula</i> Volk.
				x			<i>Micrystridium</i> sp. 1
				x	●	●	<i>Leiosphaeridia bicrura</i> Jank
				x	●	●	<i>Micrystridium tornatum</i> Volk.
					●	●	<i>Leiosphaeridia dehisca</i> Pas'k.
					●	●	<i>Ceratophyton vernicosum</i> Kirjan.
					●	●	<i>Ceratophyton duplicum</i> Pas'k.
					●		<i>Teophipolia lacerata</i> Kirjan.
						●	<i>Granomarginata squamacea</i> Volk.
						●	<i>Granomarginata prima</i> Naum.
						●	<i>Leiomarginata simplex</i> Naum.
						●	<i>Tasmanites tenellus</i> Volk.
						x	<i>Pulvinosphaeridium antiquum</i> Pas'k.

● = common, × = rare, ○ = occurrences reported from other regions.

forms. The upper boundary of the Vendian is again characterised by the appearance of characteristic forms including those with pore canals. Sokolov and Iwanovski (1985) provided tabulations of the plant microfossils representative of the Redkino and Kotlin horizons in the northwest Archangelsk district (Table 10); and the vertical range on the East European Platform (Table 11).

6.6.3. Calcareous algae

Calcareous (carbonate secreted) algae occur in mass abundance in the upper Nemakit-Daldyn division of the Vendian on the Siberian Platform, and were described by L. G. Voronova and V. A. Luchinina in Sokolov and Iwanovski (1985). There are no descriptions from the East European Platform, where they are presumably not present or extremely rare. They have been possibly recorded from the Riphean, when the carbonate sheath presumably first developed, but

appear suddenly in the late Vendian, and from then on became major bioherm builders. They were first described from the Nemakit-Daldyn division on the Anabar Massif by Voronova and Missarzhevsky (1969), four genera being then recognised. At the time of writing by Voronova and Luchinina, nine genera were known: *Renalcis*, *Korilophyton*, *Girvaninella*, *Proto-tonella*, *Gemma*, *Botomaella*, *Gemma*, *Subtrifloria* and *Botominella*. Many other occurrences are now known from many other locations on the Siberian Platform, and another genus *Obruchevella* is also mentioned. The assemblage is not diverse. Such assemblages are of rare occurrence outside the Siberian Platform.

6.6.4. Stromatolites

Stromatolites, laminar, biogenic sedimentary structures attached to the substrate, and attributed to the subsurface activity of blue green algae and bacteria

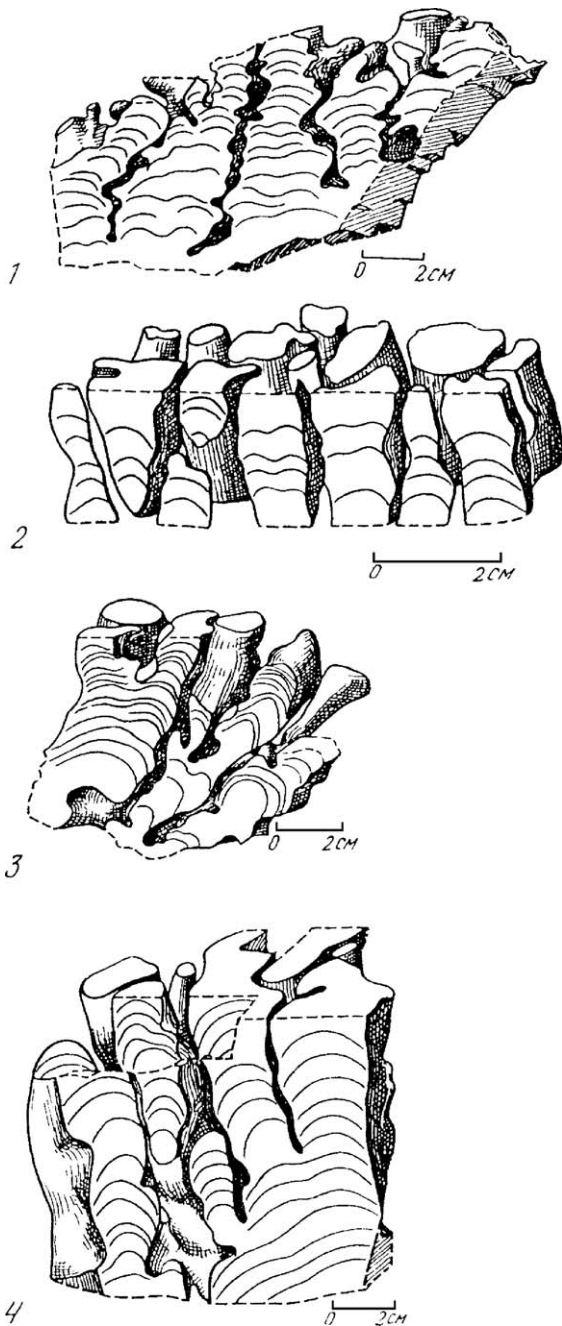


Fig. 54. Characteristic Vendian stromatolites [after Sokolov and Iwanovski, 1985 (1990 English language translation). Nauka Publishers].

which trap fine detritus and precipitate calcium carbonate, are absent from the Vendian stratotype in the East European Platform but present in Siberia in the Yudoma deposits. They are described by a number of authors in Sokolov and Iwanovski (1985). The character of the Vendian stromatolites is markedly

different from those of the underlying Riphean or the Cambrian. They were described in a monograph (Semikhatov et al., 1970). At the time of writing, 30 forms were known separated into 12 groups, the most common genera being *Boxonia*, *Paniscollenia* and *Colleniella* (Fig. 54). It is difficult to use stromatolites for subdivision and correlation of the Vendian, because of present poor knowledge concerning them, although some such use has been made in the case of the Yudoma division.

In the late Vendian there were major changes in stromatolite structures and the bioherms are mainly of calcareous algae. Stromatolites have not, however, entirely disappeared, and at the Kotnui River, Siberia, small branching stromatolites occur together with *Renalcis*, the only known case of stromatolites and calcareous algae occurring together. Later on, algae acquired a leading role in bioherm building, stromatolites becoming less common. Such bioherms are widely distributed throughout the Anabar sections. At the Cambrian boundary, all species forms disappear (with a single exception) and new ones take their place, including new species of Vendian genera; two new groups occur in the lowermost Cambrian.

6.7. Summary

Sokolov and Iwanovski (1985) illustrated the Vendian biostratigraphy of the Russian Platform, of the Olenek Uplift, Siberia, and suggested Vendian sectional correlations, summarising the state of knowledge and interpretations of the Vendian in Russia and the Ukraine at the time of writing in 1985. Their summary for the Siberian platform is given in Fig. 55.

6.8. Later discussions of the Vendian biota

6.8.1. Morphology, ecology and preservation

Fedonkin (1985b), in a publication which repeated some of his observations in Sokolov and Iwanovski (1985) but amplified them, suggested that the unique appearance of Vendian metazoans in the fossil record is controlled by taphonomic and ecological factors as well as the level of morphological and physiological organisation. It is a global fauna, at a special stage of evolution, with world-wide distribution, similar ecological aspects, similar levels of organisation and the co-occurrence of species far apart, even in palaeogeographical reconstructions. Soft-bodied animals predominated and had more or less equal preservation potential. They make their appearance stratigraphically directly

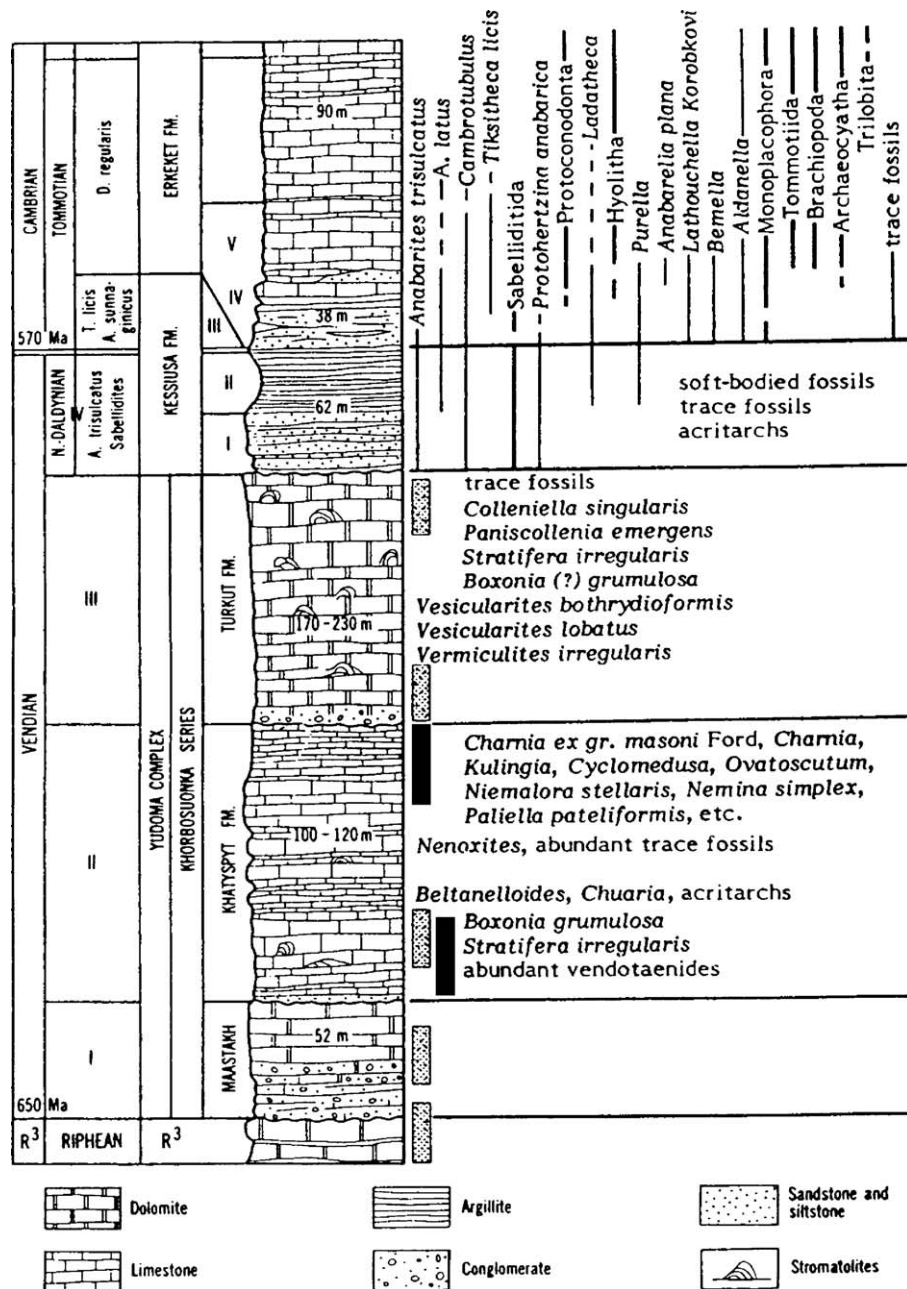


Fig. 55. Vendian biostratigraphy of the northern Siberian Platform (Olenek Uplift). Distribution of the Ediacaran-type fauna and shelly fauna including those from the Anabar massif is shown [after Sokolov and Iwanovski, 1985 (1990 English language translation), Nauka Publishers].

above the Varangian (Lapländian) tillites, in the first of the Vendian marine deposits.

He recognised an extinction event prior to the beginning of the Cambrian period—one of the causes may have been ecological competition with more progressive lines of Metazoa that extended into the Phanerozoic for food resources and habitat. Though soft-bodied animals persisted into the Phanerozoic, they

declined in the fossil record due to predators, necrophagous animals and progressive colonisation of the seabottom by other animals, also the destructive effects of bioturbation on potential fossils and sediments. The most characteristic elements of the Vendian–Ediacaran fauna, including the main groups of the Radiata, particularly those with symmetry of an infinitely high order disappeared.

Because soft bodies decay and mechanically destruct rapidly, they must, where preserved as fossils, be close to their burial sites, and transport any distance as fossils is precluded; the predominance of imprints and moulds also precludes this.

Imprints in positive and negative relief occur in finely laminated clastic rocks, alternations of quite coarse-grained sediments with fine siltstones and clays. Rapid, sudden accumulation is inferred. Fossils also occur in non-laminated clayey sediments of proximal turbidite origin—for example, in the Ust–Pinega Formation of the North Russian Platform (Keller and Fedonkin, 1976) and thin bedded bituminous dolomites of the Khatspyt Formation of the North Siberian Platform (Sokolov and Fedonkin, 1984). Almost all deposits with these fossils are in shallow-water environments, most of the organisms were living in the sub-tidal zone, but there were exceptions living in deeper water.

Concerning problems of classification, Fedonkin again discussed body plan analysis, especially symmetry analysis, one of the methods of comparative anatomy useful if applied to Vendian organisms. He remarked that:

- (1) In low rank Metazoa, symmetry features vary very widely and allow recognition of low rank taxa.
- (2) The number of characteristic morphological features that can be used for systematisation is small in the case of Vendian metazoans.
- (3) The vast majority cannot be placed in existing classification systems of the Metazoa.
- (4) The prevalence of Coelenterates is to some extent an artifact of their higher preservational potential.
- (5) Some forms had thick mesoglea and were thus resistant enough to produce a permanent structure after burial.
- (6) Forms with attachment processes are preserved in sediment in the life position.
- (7) These organisms lived at the end of the trophic chains, which seem to have been very short in this period.

Abundance, diversity and large size indicate that the Vendian animals were the oldest group of the Metazoa. During the earliest stage of evolution of the Metazoa, which may have been short, the animal world consisted entirely of Radialia? This ‘apparently fantastic supposition is based on retrospective extrapolation, but is palaeontologically supported by the Vendian fossil record’. This concept of the primacy of radial symmetry is supported by many authorities and

the fossil record supports this concept based on comparative anatomy.

If the assumption is made that the palaeontological record reflects the ratio of major groups in the Precambrian world, then, during the Vendian, bilaterally symmetrical animals were in the minority (Fig. 56A). The main reason for this may be the priority of radial symmetry in metazoan evolution. If the assumption is correct, the earliest radiation of multicellular organisms involved symmetrical diversity and some of the various body plans became fixed in higher taxa. A more advanced diagram illustrating the theoretical possibilities of development of bilateral body plan from radial, based on study of the Vendian organisms, was presented (Fig. 57).

Fedonkin discussed the imperfect ‘glide symmetry’ of many of the Vendian most primitive segmented forms, which he believed marked an important stage in evolution towards the Articulata.

He concluded that the Vendian was a terminal period of the pre-Palaeozoic era, comparable in importance and evolutionary events with any other era. During the

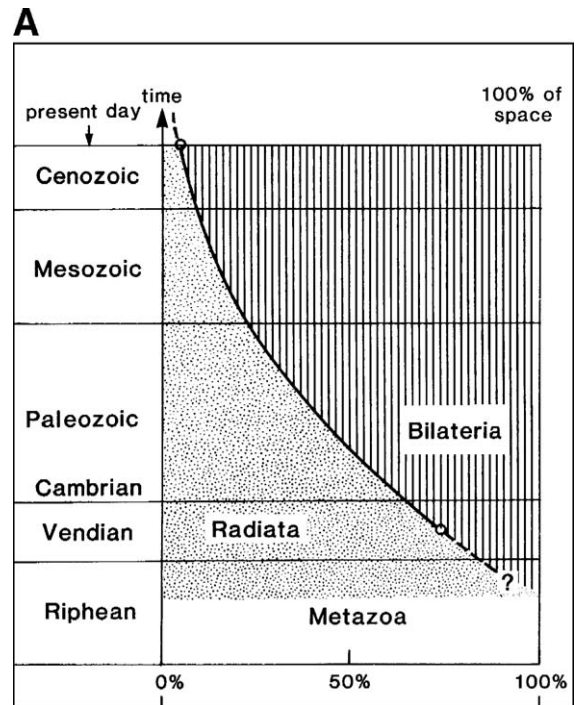


Fig. 56. (A) Comparison of the abundance of Radiata and Bilateria at the present day and the Neoproterozoic record allowing a retrospective extrapolation which supports the idea of the primacy of radial symmetry and the coelenterates being the oldest group of the Metazoa. (B). Development of major groups of organic life in the Vendian and Early Cambrian [after Sokolov and Iwanovski, 1985 (1990 English language translation). Nauka Publishers].

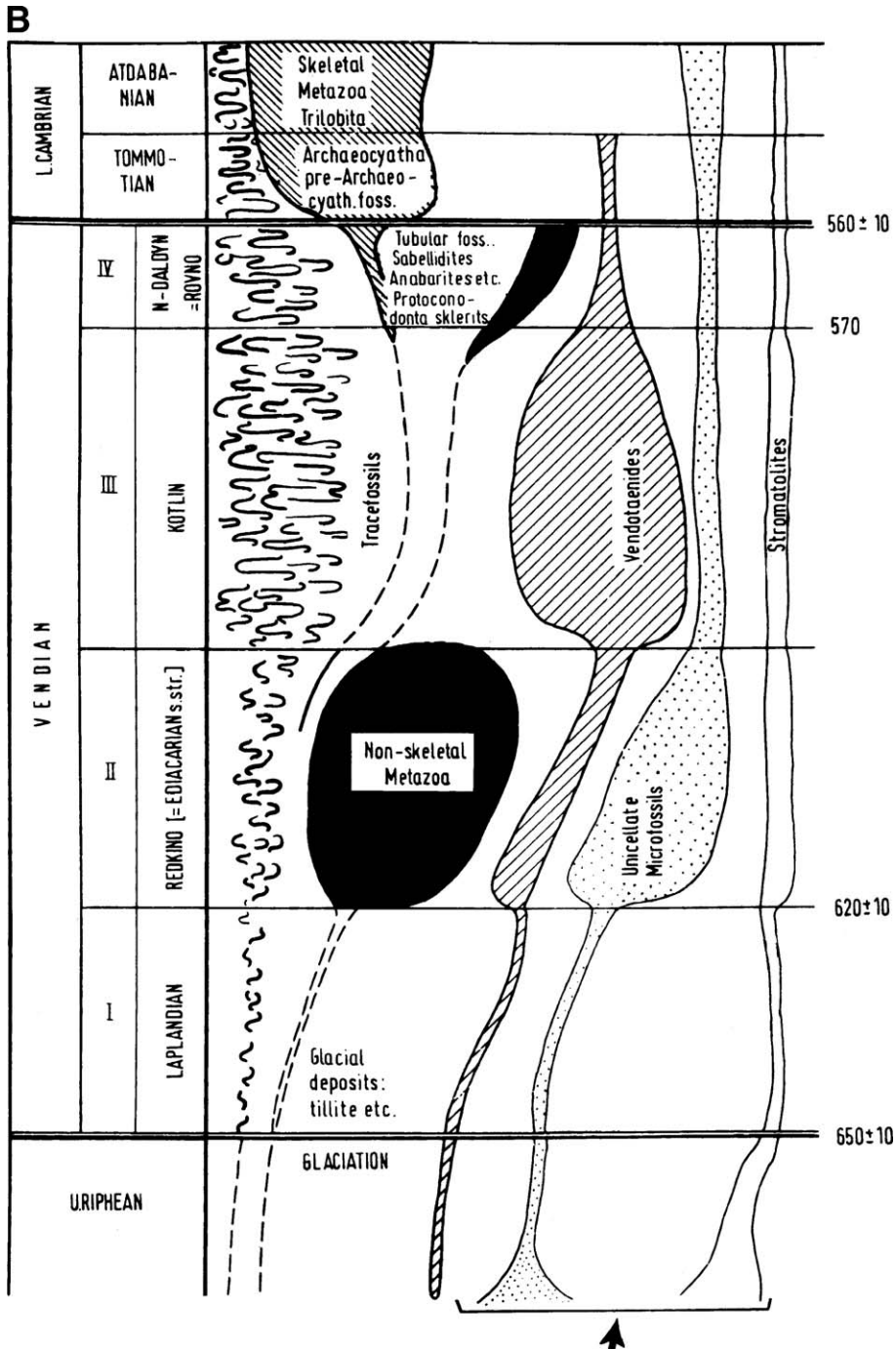


Fig. 56 (continued).

Vendian, many new groups of organisms appeared and are preserved as fossils and they became extinct by the end. There are indications of significant pre-Vendian development of Metazoa and search for even older fossils in earlier periods is both necessary and will

possibly require change in definition of the lower boundary of this terminal Precambrian system. He warned that further studies of Vendian assemblages from various regions globally may also necessitate biostratigraphic changes.

6.8.2. Vendian faunas and the early evolution of the Metazoa

Fedonkin (1992) presented a further synthesis of his observations and ideas. This to a considerable extent repeats previous statements and only new developments and observations are reproduced here. He reiterated his belief that there are few if any trustworthy fossil remains of multicellular animals older than 650 Ma, but noted that enigmatic bedding plane markings resembling strings of beads had been found in rocks dated at some 1300 Ma in Montana (Horodyski, 1980). These have in fact been named subsequently as *Horodyskia moniliformis*; and similar bodies have been found SW of Newman, Western Australia, in Proterozoic rocks of the Collier and Manganese Groups of the Bangemall Supergroup, dated at 1211–1070 Ma by high resolution ion microprobe on zircon and baddeleyite. These, if organic, are, however, thought likely to be metaphytes, not animal fossils, and have affinities with brown algae or seaweeds.

Fedonkin noted that there were now about 50 species of Vendian body fossils and 20 trace fossil forms known from the White Sea region of north Russia, most from unaltered clayey siltstones of the Ust–Pinega Formation in the Redkino Regional Stage. The abundance there was attributed to greater diversity of facies than other fossiliferous localities. The Dniester Basin, Podolia, Ukraine had yielded 10 species in common with the Ediacara type assemblage from South Australia. He noted the unique occurrence in the Khatspyt formation, Olenek Uplift, where the fossils were within thin, laminated bituminous limestones, not clastic sediments (Vodanyuk, 1989; Fedonkin, 1990).

He suggested that the intensive erosion of land not protected by vegetation and the development of gigantic tidal flats in which dead or living organisms were rapidly buried were major factors in the unusual preservation of the Vendian organisms as fossils. Absence of filter feeders, which cleanse marine water—sponges, archaeocyatha and brachiopods appeared later in the Early Cambrian radiation—was another major factor (it is, however, pertinent here to note that sponge spicules have been recognised in Vendian deposits in Mongolia by Brasier et al., 1997). Turbidity will have restricted warmth and lighting to the surface layer of the water, which will have been enriched in oxygen by the photosynthetic activity of planktonic algae and cyanobacteria, whereas the water below remained cold and poorly oxidised. Mixing of these two water levels will have been slow. Bottom water, where relatively deep, did not favour life and there was less decomposition of buried organic matter there. There will also have been increased cementing

and lithification diagenesis due to the abundant clayey particles in the water and sediment. The most important biotic influences were:

- (1) high benthic population density in zones with active hydrodynamic conditions
- (2) numerous attached forms
- (3) low scavenger and vagile predator activity
- (4) little processing of sediment by deposit feeders and other bottom animals
- (5) because of weak biological processing of sediment, cyanobacterial mats may have developed on the sediment surface and might have stabilised the sediment and prevented the destruction of biogenic structures in littoral shallow-water
- (6) such mats may have hindered aeration and escape of decay products from the sediment
- (7) traces of decomposition are not commonly seen in Precambrian fossils, indicating rapid and early diagenetic lithification.

The type of imprint and mould preservation of fossils is not seen in the case of later skeletal fauna. In such preservation, only one side of the organism may be preserved as a fossil, the connection of the two sides is commonly not possible and, as a result, different sides of the same animal may be allocated to separate taxa. Different decay states may also have multiplied the taxa, although this may be a minor factor because signs of decay are not commonly seen in these fossils. In some cases, thin soft-bodied organisms left imprints preserving details of inner anatomy, for example gastrovascular systems, as in the case of *Albumares brunsa*. Such preservation may be due to high protein content, but the mechanical resistance could also have been provided by maintenance of turgor by gases or fluids formed by decomposition, retained within the canals until the imprint was achieved. This effect may also have produced complicated moulds in which two or more microbedding planes are preserved (Wade, 1968).

The fossil record of the Vendian metazoans virtually ends well before the base of the Early Cambrian, and the almost complete termination is separated from it by quite thick deposits. Rare imprints of medusoids do however occur in the upper part of the Vendian [here it should be noted that the base of the Cambrian has been subsequently adjusted at or near the base of the Rovno Horizon/Nemakit-Daldyn Horizon of Siberia (e.g. see Knoll et al., 1995 summarised below)]. The disappearance of many

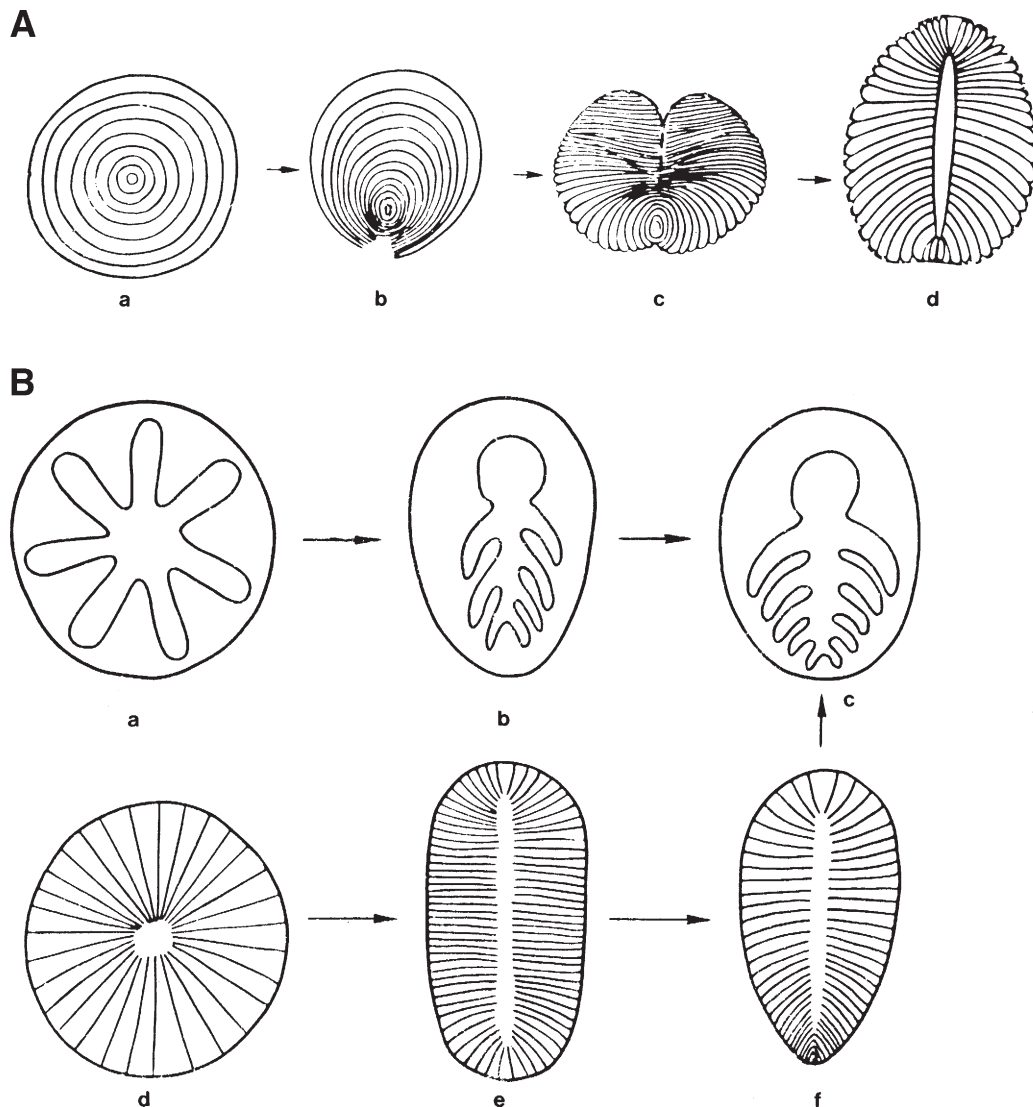


Fig. 57. Theoretical possibilities of deriving bilateral metameric forms from (A) Cyclozoans (concentric body plan) and (B) Inorozoans (radial body plan), possible related processes at very early stages of metazoan evolution. A a=*Kullingia*; b=*Ovatoscutum*; c=*Chondroplon*; d=*Dickinsonia*. B a=*Bonata*; b=*Vendia*; c=*Praecambidium*; d=*Irridinitus*, e=intermediate forms; f=*Dickinsonia* (after Fedonkin, 1992).

Vendian (Ediacaran) forms and decrease in body size of other groups may be extinction-related, but may equally be related to change in taphonomic processes, coupled with increase in activity of destructive animals, change in other populations [e.g. cyanobacteria replaced by eukaryotic algae and benthic invertebrates, the appearance of a meiofauna (1 mm–0.1 mm dimensions) promoting aeration and transportation of decay products, the strong increase in megascopic vagile invertebrates as indicated by the trace fossil population change].

Discussing the fossil systematics, Fedonkin mentioned the differences of opinion concerning “colonial

forms” and Petalonamae. A large part of the Vendian Fauna consists of colonial forms, with high integration of colonies and absence of signs of functional polymorphism of the zooid; there are dominant double-pinnate forms, as well as fan- and comb-shaped colonies. The former may have attachment discs, or be pelagic. He believed that these can only be assigned to the Coelenterata. Glaessner (1979a) considered the colonial forms such as *Charniodiscus*, *Vaizitsinia* and *Rangaea*, characterised by monopodial growth, as well as *Charnia* and *Glaessnerina* with simpodial growth, to be Problematic Coelenterata, uniting them with other leaf-shaped, ribbed organisms in the group Petalonamae,

separated as a phylum (Pflug, 1970a,b). In contrast, Fedonkin believed that they should be separated from the Petalonamae, fossil organisms which are enigmatic in many respects—that is, separated from *Pteridinium*, *Ernietta*, *Baikalina*, *Namalia*, *Nasepia*, *Inkrylovia*, *Valdainia* and *Podolimerus*. These are all of unsystematic position, although many share some common features—leaf- or bag-shaped body, primary segmentation or ribbed surface without any trace of secondary division. Glaessner and Walter (1981) and Glaessner (1984) would assign them to the “Coelenterates of uncertain position”. It has also been suggested that some of them have a structure similar to that of an air mattress that permitted a high inner pressure of body fluid (“hydrostatic skeleton”) and that these animals may have utilised liquid organic matter absorbed from water through their body integuments (Seilacher, 1984; Gould, 1984). The Petalonamae could be related to the Tunicata (Sokolov, 1976; Chistiakov et al., 1984). Fedonkin believed that there was no reason to attribute the Petalonamae to anything but the Diploblastica (sponges and coelenterates).

Solitary bilateral organisms were further discussed. The overwhelming majority of bilateral metazoans are represented by flat-bodied forms. Segmented organisms predominate including polymeric and oligomeric creatures with signs of homonomous and heteronomous metamerism as well as imperfect segmentation and symmetry of a sliding (or gliding) reflection. Very few forms have been identified as non-segmented bilateral metazoans [examples of these are *Protechiurus* (Glaessner, 1979b); *Platypholinia* and *Vladimissia* (Fedonkin, 1985a,b,c)]. They are represented only by unique specimens or by specimens with obscure morphology, making determination difficult.

Most Bilateria have peculiarities not commonly observed in multicellular animals of later epochs, and the most important of these is the plane of sliding (or gliding) reflection symmetry characteristic of primitive Vendian Bilateria, especially polymeric forms with homonomous metamerism (for example, Dickinsonidae) or oligomeric forms with evidence of cephalisation (for example, Vendomiidae). The former was referred to an independent branch of the most primitive Bilateria. Fedonkin (Fig. 57) has illustrated the possibility of deriving these from the most archaic Radialia possessing an axis of rotation of an infinitely high order—*Kullingia*–*Ovatoscutum*–*Chondroplan*–*Dickinsonia*: or those with an axis of variable order—*Irridinites*–intermediate forms—*Dickinsonia*. They may be a branch of the Bilateria that

separated earlier than others. It became extinct in the Vendian and is placed not in the Coelenterata but with primitive Bilateria in the Phylum Proarticulata (Fedonkin, 1983a).

Turning to the animals with flat oval bodies and large cephalic areas, Fedonkin assigned them to an independent group of the Bilateria, the Vendomiidae. This group includes *Praecambridium*, *Vendia*, *Vendomia* and *Onega* (Keller and Fedonkin, 1976). Segments on either side may be placed opposite one another or alternate. In *Vendia*, the plane of slide symmetry reflection within the area of the segments suggests that the group is archaic, a special branch in the ancestry of the Articulata. Only *Vendomia* of these can be attributed to normally segmented animals and even compared with trilobite larvae. The other three small Vendomiids seem to be adult forms.

Fedonkin mentioned *Spriggina*, suggesting that its may have a thin carapace like *Bomakella* and *Mialsemia*, a form with a small cigar-shaped body with lateral, flat feather-like appendages, and covered by a wide carapace. Each these forms is represented by single specimens from the Ust–Pinega Formation of the Redkino Horizon on the White Sea Coast.

Fedonkin’s concept of the development of life in the Vendian and Early Cambrian is illustrated in Fig. 56B.

6.9. Further researches on Siberian occurrences

A later revision of the stratigraphy of the Vendian in Siberia was published by Khomentovsky (1986). The Yudoman deposits of the Siberian Platform differ greatly in composition and structure and four facies provinces were recognised there:

Yudoma–Anabar Province
Baikal–Patom Province
Yenisey–Prisayan Province
Interior Province.

Local stratigraphy charts were presented for them and it was shown that the Vendian System of Siberia comprises three horizons or stages, the lower two, Yukand and Sakhara Stages, being defined mainly on lithostratigraphic data whereas the upper Nemakit-Daldyn Stage was substantiated by palaeontological data, on the basis of which it was subdivided into two zones: *Anabarites trisulcatus* and *Purella antiqua*. The boundary of the Lower Cambrian Tommotian stage was shown in the type section to conform to the base of the Pestozvet Formation, which divides the *Anabarites sunnaginicus* zone from the *P. antiqua*

zone (it should be noted here that in the latest revision, mentioned in the publication by Knoll et al. summarised below, the base of the Cambrian is placed at or near the base of the Nemakit-Daldyn stage, which, in another publication by Bowring et al. (1993), was referred to as the Manakayian; added as an extra stage beneath the Tommotian at the base of the Cambrian; the name coming from the Manakay Formation in which skeletal fossils first appear in the northern Yudoma-Anabar Province.

6.9.1. Stratigraphic revision utilizing bio- and chemical stratigraphy

Fossils are not as diverse in the Proterozoic Eon as in Phanerozoic strata and turn over rates appear to have been lower. Knoll et al. (1995) argued that secular variations in C and Sr isotopic composition in carbonates (Kaufman and Knoll, 1995) provide an important means of correlation Proterozoic sequences. Fossils and isotope chemostratigraphy provide reliable tools for both intra- and inter-basinal correlation (Knoll and Walter, 1992; Narbonne et al., 1994). Biostratigraphy is sensitive to facies distributions and chemostratigraphy to hiatuses. The authors used the outcrops in the Khorbusuonka Rover on the Olenek Uplift in NE Siberia to demonstrate this. They are unique in the dominance of carbonate sediments among Vendian sections with Ediacara-type fossils: this wealth of palaeontological data caused Sokolov (Sokolov and Fedonkin, 1984) to select it to epitomise the Vendian equivalent in Siberia to the East European Platform sequences, correlating the Mastakh, Khatspyt and Turkut Formations with the Volyn (Laplandian), Redkino and Kotlin stages of that Platform. The succession contains vendotaenids, small shelly fossils, trace fossils and acritarchs besides Ediacara-type soft-bodied fossils.

Due to faulting, these measured sections had to be pieced together in a composite section. U–Pb ages have been determined for the upper part of the section (Bowring et al., 1993). The Riphean–Yudoman boundary is marked by a marked break which Shenfil (1992) interpreted as an angular unconformity: at the four locations where it was observed different facies underlie it. Locally, quartz pebble conglomerate fills a scoured surface. Above it, the Mastakh Formation is 40 m thick and consists of desiccation-cracked, microbially laminated fine dolostones with chert nodules. This is overlain abruptly at the top by red basal sandy siltstones of the Khatspyt Formation. The sedimentology of the Mastakh Formation is consistent with deposition on regionally extensive tidal mudflats. Irregular lamination

of the dolomites and poorly preserved fossil filaments indicate that the mudflats were colonised by microbial mats. No evaporite minerals are preserved, but the ‘cauliflower’ chert concretions may have replaced anhydrite. Sedimentation was limited to aggradation of tidal mudflats during an early high-stand. The early post-Riphean deposits appear to have been lost by erosion.

The Khatspyt Formation can be subdivided into a Lower Member of poorly exposed, thin-bedded siltstones, fine cross-stratified sandstones and quartz pebble conglomerate, up to 25 m thick: and an Upper Member of laminated and massive limestones, minor dolostones and rare black shales, up to 160 m thick. The upper contact is gradational with the Turkut Formation. The sedimentology is consistent with a transgressive and deepening sequence flooding the exposed Mastakh surface. The siliciclastic Lower Member is of outer shoreface facies, with deposition above storm wave base, whereas the Upper Member represents continued subsidence to basinal depths with fall-out of suspended carbonate muds in a distal basinal setting. There is some evidence of debris flow activity on the slope. The setting is envisaged as a carbonate ramp rather than a rimmed shelf. There is a possibility that there was basin anoxia when the Upper Member was deposited.

The Turkut Formation represents the highstand deposition. It consists of thickly laminated dolostones and minor finely laminated limestones, up to 70 m thick. At the top there is dolomite intraclast-oid grainstone, with some pores filled with bitumen, and biostromes of small irregular columnar stromatolites, a few centimetres wide. There is a karstic surface at the top. The Turkut Formation is taken to represent shallowing from a basinal to shallow ramp environment. The grainstones and stromatolites represent progradation of more proximal up-dip ramp environments, including shoals, and this culminated in a subaerial karstic environment. Collectively, the Khatspyt and Turkut Formations form a single sequence. The upper boundary coincides closely with the position now accepted for the Proterozoic–Cambrian boundary (Fig. 58).

The Kessyusa Formation, up to 50 m thick, is a diverse assemblage of siliciclastic, carbonate and volcanic facies. At the base is a sequence boundary defined by a basal quartz pebble conglomerate up to 3.5 m thick, filling in irregular topography on the underlying Turkut Formation, and it has an abrupt karstic contact with maroon, hyolithid wackestones of the Erkeket Formation. Siltstones just above the basal

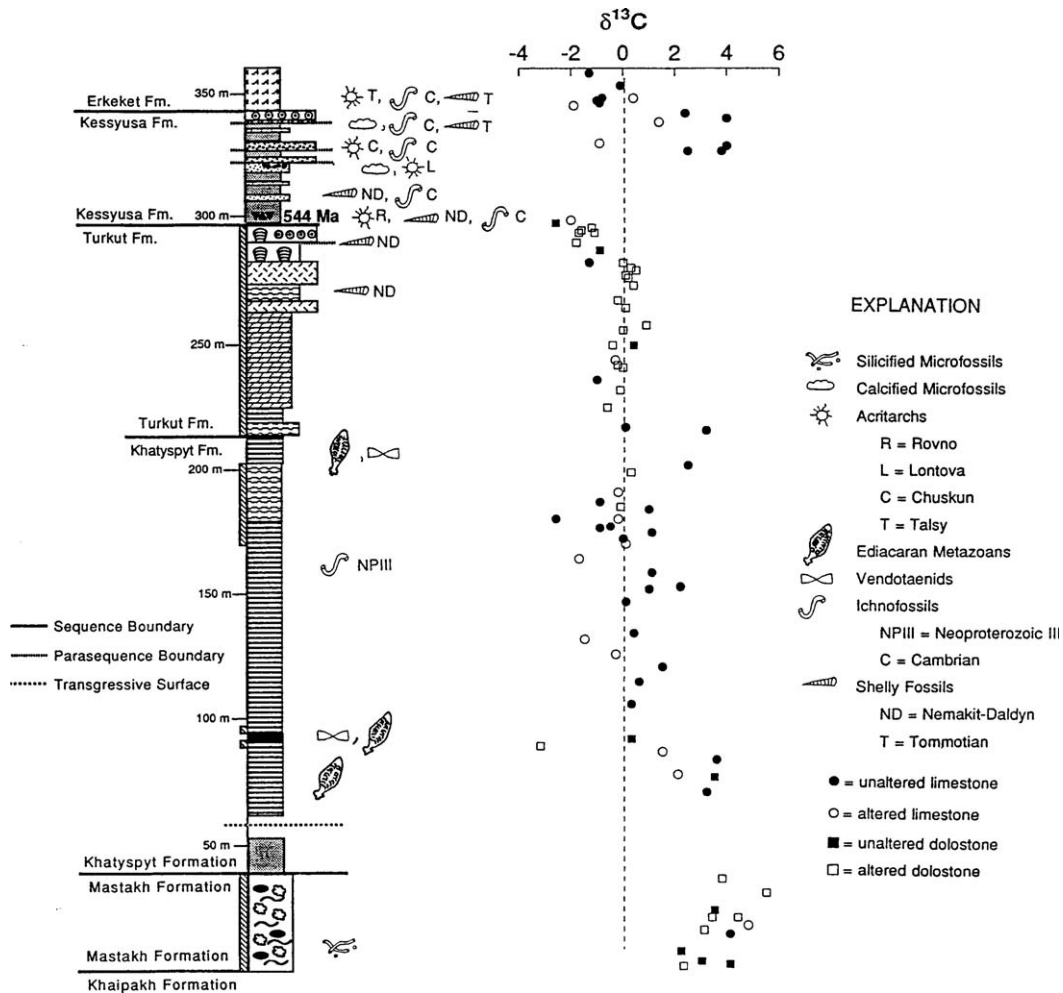


Fig. 58. Carbon-isotope and biostratigraphic data for the terminal Proterozoic and basal Cambrian succession along the Khorbusuonka River, Olenek Uplift, northern Siberia (after Knoll et al., 1995).

conglomerate of the Kessyusa Formation contain shelly invertebrate fossils representing the *Anabarites trisulcatus* zone of Missarzhevsky (1989a,b), and they are associated with a volcanic breccia, from which magmatic zircons yielded an age of 543.9 Ma (± 0.3 Ma) (Bowring et al., 1993). The breccia is probably related to the numerous kimberlitic pipes which cut the Turkut Formation but not the Kessyusa Formation. The sedimentology suggests that this Formation represents maximum flooding of the shelf or initial highstand progradation. The upper boundary is a significant sequence boundary.

The Erkeket Formation was only examined in its basal development. There it consists of monotonous, maroon to mauve, argillaceous, fossiliferous lime mudstones and wackestones, with large hyoliths locally abundant. Bioturbation and large, simple bedding-

parallel traces are common. It represents deposition on an open, shallow-marine carbonate platform, with storms concentrating fossils in lag deposits by winnowing. It represents onlap of the Olenek Platform following sub-aerial exposure of upper Kessyusa rocks.

6.9.2. Biostratigraphy

Prokaryotes, protists and stromatolites: the carbonates of the Mastakh Formation contain poorly preserved sheaths of mat-forming cyanobacteria, an abundant but de-pauperate assemblage, of no use in constraining the age. The Lower Kessyusa siltstones contain leiospherid acritarchs, an assemblage that implies correlation with the Lower Cambrian Lontova Horizon on the East European Platform. An assemblage of calcified microbes in Kessyusa

Table 12

Ediacaran metazoans identified from the Khatspyt Formation, Khorbusuonka River, northern Siberia (after Knoll et al., 1995)

<i>Nemiana simplex</i> Paliž
<i>Ediacaria flindersi</i> Sprigg
<i>Kullingia concentrica</i> Foyn and Glaessner ^a
<i>Hiemalora stellaris</i> Fedonkin
<i>Hiemalora pleimorphus</i> Vodanjuk
<i>Glaessnerina longa</i> (Glaessner and Wade) ^a
<i>Aspidella costata</i> Vodanjuk
<i>Aspidella hatsypytia</i> Vodanjuk
<i>Anabylia improvisa</i> Vodanjuk
<i>Charnia masoni</i> Ford
<i>Ovatoscutum concentricum</i> Glaessner and Wade
<i>Patiella patelliformis</i> Fedonkin
<i>Khatsypytia grandis</i> Fedonkin
<i>Beltanelloides</i> sp.
<i>Cyclomedusa</i> sp.

Data from Fedonkin (1987) and Vodanyuk (1989).

^a Species identified provisionally.

carbonates is consistent with the observation of Riding (1991) that calcified cyanobacteria increased in abundance greatly near the beginning of the Cambrian Period. Stromatolites are not abundant in this succession, but *Boxonia grumulosa* and *Stratifer irregularis* occur in the Mastakh Formation and again with other forms in the Turkut Formation. The assemblage is characteristic of terminal Proterozoic (Vendian) carbonates.

Ediacara-type fossils comprise 15 taxa (Table 12), most from a 1-m-thick horizon near the top of the Khatspyt Formation (Fig. 58). They stand out in positive relief on tops and bottoms of millimetre-scale laminae of carbonaceous limestones. Preservation may be related to early cementation. The taxa are mostly widespread components of Ediacaran faunas, and most are simple medusiform remains, *Charnia masoni* being the exception.

Trace fossils density increases markedly through the Kessyusa Formation with *Planolites* sp. and *Didymaulichnus* spp. appearing in its upper part. There is increased density again through the Erkeket Formation in the form of horizontal tracks. *Phycodes pedum* has been reported from the lower Kessyusa Formation, the trace fossil of which the appearance marks the Cambrian lower boundary in the GSSP section in Newfoundland.

Small shelly invertebrates appear first 30 m below the Turkut–Kessyusa Boundary in the form of *Cambrotubulus* sp. A more diverse fauna including *Anabarites trisulcatus*, *Cambrotubulus decurvatus* and *Protoherzina anabarica* (Fig. 59) appears just above the base of the Kessyusa Formation. This assemblage

defines the *Anabarites sulcatus* zone, the lowermost of the four zones in the Nemakit-Daldyn or Manykai Stage (Missarzhevsky, 1989a,b). There are divergences of opinion about the duration of this zone, and some authorities place it in the Tommotian whereas others place it in an initial Cambrian Manykai Stage. All authorities agree that it marks the beginning of the Nemakit-Daldyn Stage. Thus small shelly fossils indicate that the beginning of the Cambrian in the Kharbusuonka River Section must be placed at or near the beginning of the Nemakit-Daldyn Stage, which was formerly assigned to the uppermost Proterozoic (i.e. the erathem boundary lies within the upper Turkut or lower Kessyusa Formation). This was confirmed by the find of small shelly fossils of Missarzhevsky's Nemakit-Daldyn (Manykai) Stage, equivalent to the

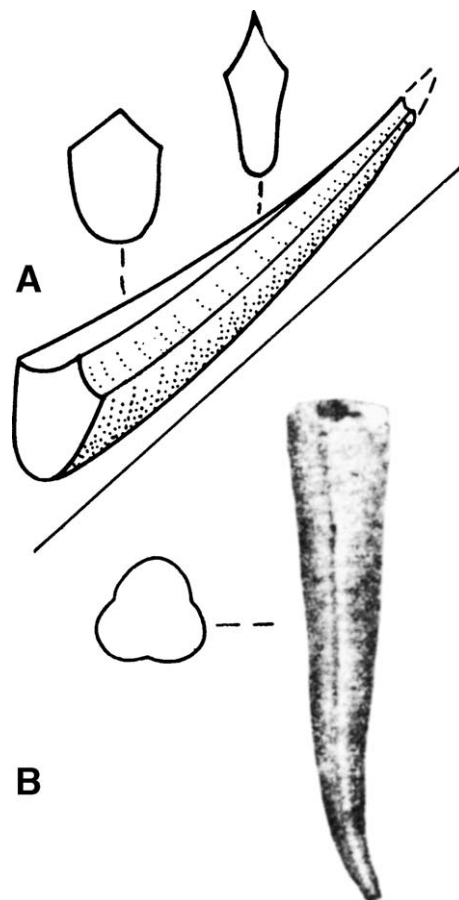


Fig. 59. Pre-Tommotian small shelly fossils: (A) *Protoherzina anabarica* Missarzhevsky; oblique view and transverse sections, length 1.25 mm (from northwest slope of the Anabar massif). (B) *Anabarites trisulcatus* Missarzhevsky; incomplete tube and transverse section, length 3 mm (from Yudoma River, eastern Siberia). (Drawings from Glaessner, 1984 after Missarzhevsky).

Purella antiqua zone of Khomentovsky and Karlova, 1993). In the Upper Kessyusa beds; and shelly fossils of the lower Tommotian Stage in the uppermost 10–15 m of the same formation. The basal Erkeket Formation contains a shelly fauna compatible with assignment to the Upper Tommotian Stage and fallotaspid trilobites occurring 14 m above the base of the Erkeket limestones.

6.9.3. Chemostratigraphy

The plot of Carbon isotope variations (Fig. 58) shows distributions of variations in the stratigraphic section similar to those recorded elsewhere in other terminal Proterozoic–Cambrian sections and confirms the deductions drawn from the biostratigraphy. An important aspect is that it shows that the Mastakh transgression substantially postdated the melting of the Laplandian (Varanger) ice sheets. Also, it indicates that the basal transgression of the Vendian over Riphean deposits is of varied ages and the transgressive packages should not be correlated in geological time.

6.9.4. Conclusions

An important conclusion of Knoll et al. (1995) was that small shelly invertebrates (*Cambrotubulus*) predate the initial Nemakit-Daldyn boundary and corre-

late chemostratigraphically with strata beneath the interpreted base of the Cambrian in eastern North America.

The Khorbusuonka Section is thin compared with sections in Newfoundland, northwestern Canada and South Australia, yet it displays nearly all the palaeontological and C-isotopic events recorded in those much thicker sections. Bio- and chemostratigraphic events do not generally coincide with sequence boundaries, suggesting that sequence development is not the principal control on fossil and isotopic excursion distribution. This exercise does show that combination of palaeontology and isotopic chemostratigraphy provide a good framework for correlation in the terminal Proterozoic (Neoproterozoic III of Plumb, 1991). The sequence is not a good candidate for a GSSP covering the terminal Proterozoic, because it contains neither the Varanger (Laplandian) tillite nor the distinctive C-isotope excursion which marks the immediate post-glaciation carbonates, nor has it yielded post-Varanger acritarch biota as found elsewhere (Zhang and Walter, 1992). Nevertheless, it is a significant reference region for studies of the terminal boundary of the Vendian period. The three units defined in Olenek data can be correlated among basins based on acritarch flora and C-isotope excursions, soft-bodied metazoans and trace fossils.

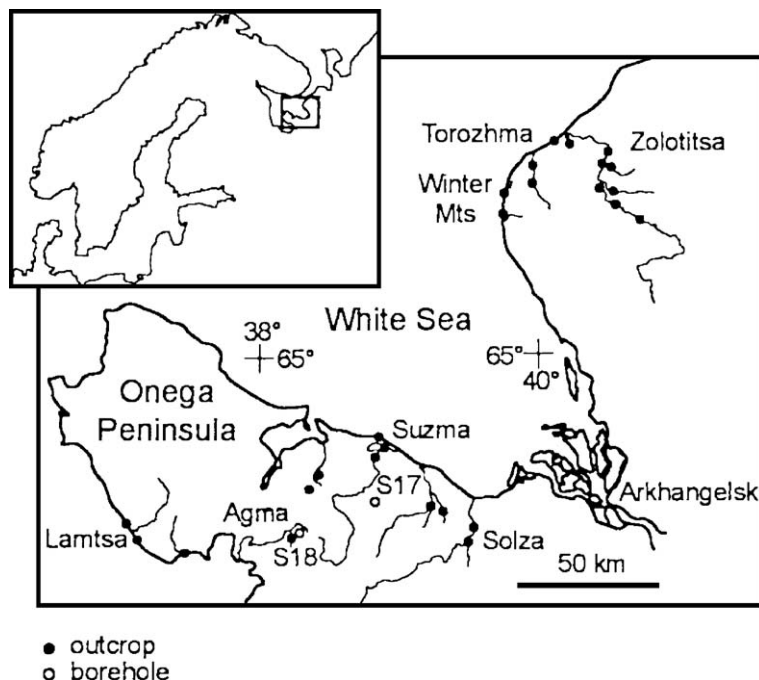


Fig. 60. Location and stratigraphy of the Vendian in the White Sea area of Northern Russia (after Grazhdankin, 2004).

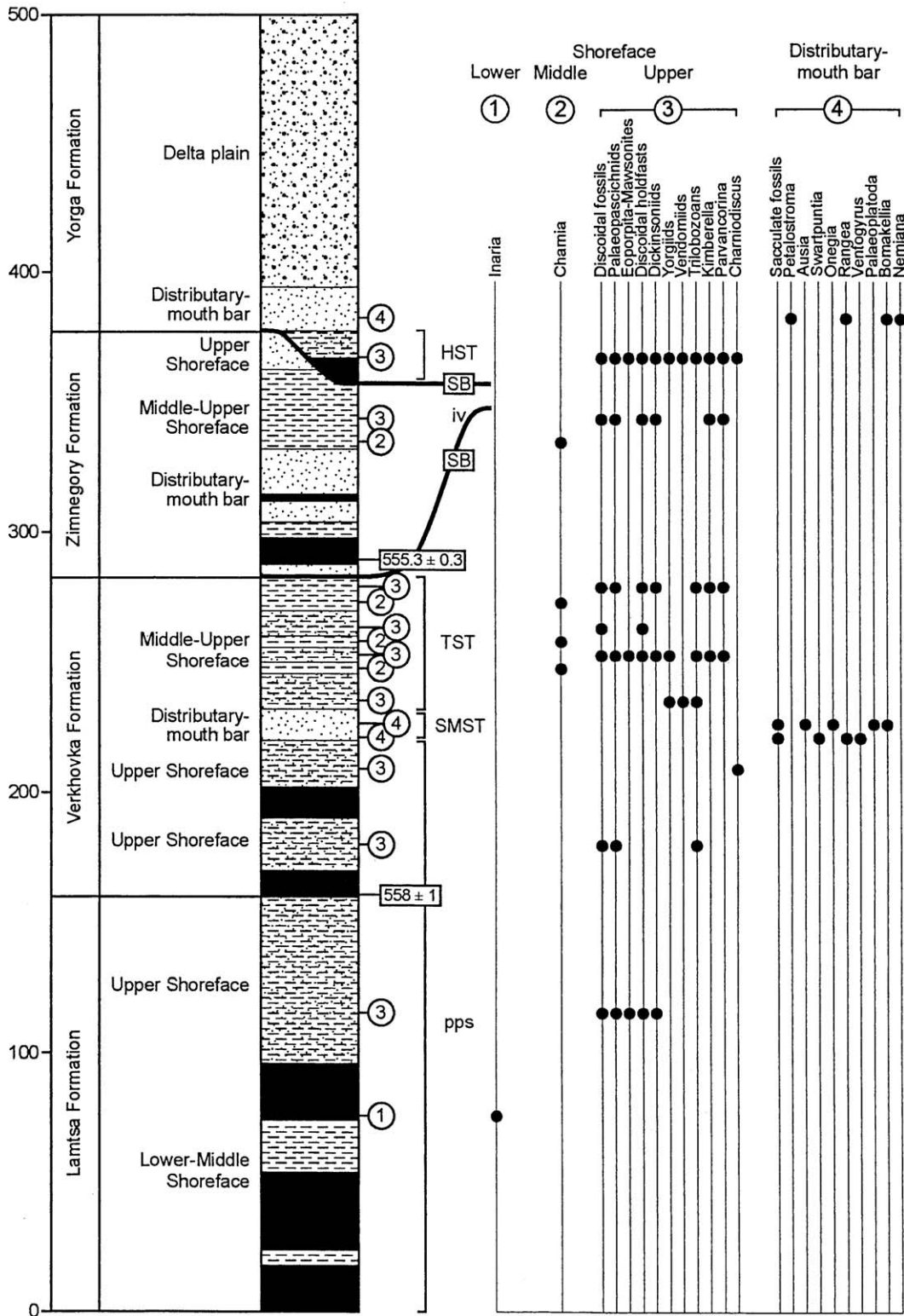


Fig. 61. Generalised section of the Vendian in the White Sea area showing lithofacies, sedimentary environments and sequence stratigraphy, also U–Pb zircon dates on tuff beds and distribution of in situ fossil assemblages. SMST=shelf–margin systems tract; TST=transgressive systems tract; HST=highstand systems tract; pps=progradational parasequence set; iv=incised valley fill (after *Grazhdankin, 2004*).

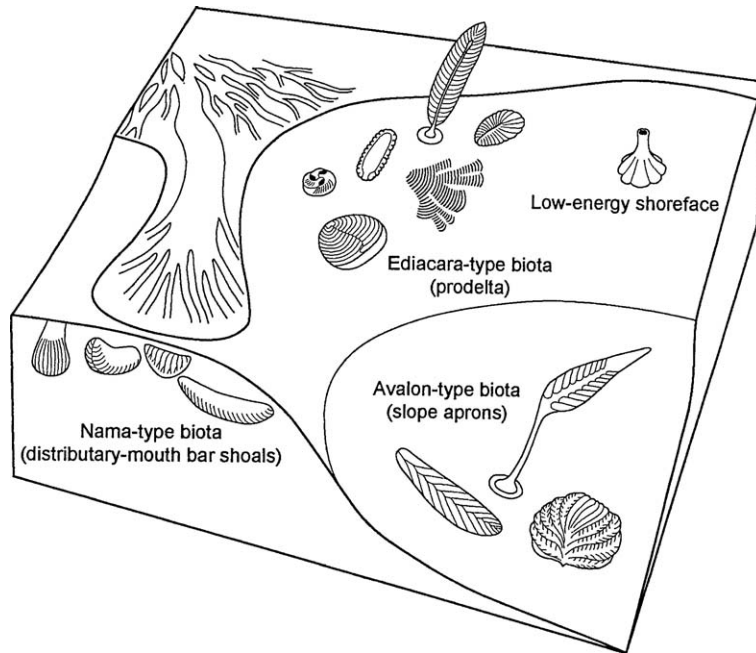


Fig. 62. Schematic diagram of ecological distribution of Ediacaran biotas (after Grazhdankin, 2004).

The three subdivisions coincide broadly, but not precisely, with the Volyn, Redkino and Kotlin intervals of the East European Platform. As stratigraphic correlation of the terminal Proterozoic

improves, based on this combination of tools, so will our understanding of the profound biological and biological events that marked the transition to the Phanerozoic world.

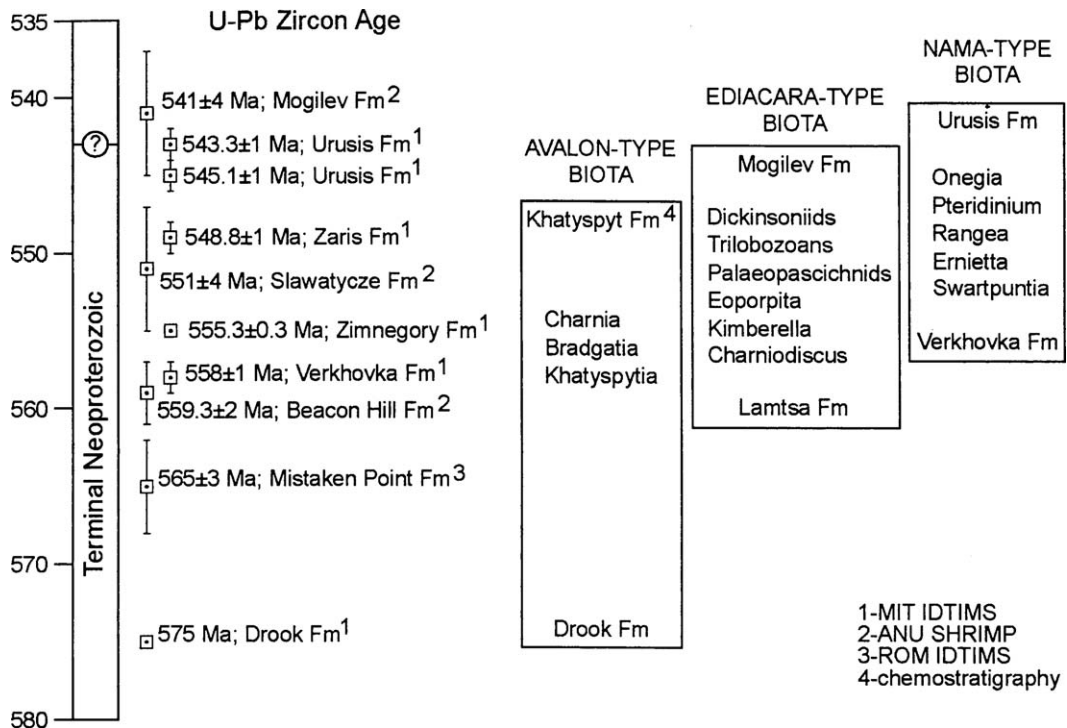


Fig. 63. Examples of geographical provinces with the three different ecological types of Ediacaran biota (after Grazhdankin, 2004).

6.10. New research: the Winter Coast, White Sea

Grazhdankin (2004) noted that here is a wide range of lithofacies in the siliciclastic sequence of the White Sea area (Figs. 60 and 61). He listed four taxonomic assemblages, each characterizing a different lithofacies (Fig. 62):

- (1) Monospecific *Inaria* assemblage in lower shoreface muds
- (2) *Charnia* assemblage in middle shoreface siltstone/shale couplets
- (3) *Dickinsonia*–*Kimberella* assemblage in pro-delta interstratified sandstone and shale
- (4) *Onegia*–*Rangaea* assemblage in channelised sandstone beds of distributory mouth bar.

There is a strong correlation between taxonomic position/biostrat features/palaeoecological content. Facies controlled distribution is also seen in other Ediacara-type assemblages. There are three types of biota:

- (1) Avalon-type biota—deep marine habitats
- (2) Ediacara-type biota/microbial biofilms—shallow marine pro-delta settings
- (3) Nama-type infaunal biota—distributory mouth bar shoals.

There is marked degree of ecological sensitivity and ecological specialization. This refutes any suggestion of biogeographic provinciality and casts doubt on evolutionary change as the agent determining the taxonomic content in any assemblage (Fig. 63).

6.11. Conclusion

The nature of the literature base on the Russian and Ukrainian occurrences has to some extent constrained the format used here, as has the need to utilise English-language translations, although these are of high quality. Nevertheless, the text above represents the salient facts and interpretations made in these remarkable and prolific regions of development of Vendian sequences and Ediacara-type faunas.

7. Newfoundland, Canada

7.1. Introduction

The discovery of the Ediacara-type fauna at Mistaken Point in the Avalon Zone of Newfoundland (Anderson and Misra, 1968, Misra, 1969, 1971) has been briefly

mentioned in Section 2. This is unquestionably a major province with some 30 genera recognised and more than 20 fossil localities depicted (Anderson and Conway Morris, 1982) (Fig. 64). The fauna differs significantly from those described from other regional sites, differences which Anderson and Conway Morris attributed to it being older and of a different environment of deposition. However, the difference in the proposed age (Latest Riphean as against Vendian) is not yet accepted (Myrow, 1995; Clapham et al., 2004), but it is of a deeper, slope environment—a similar environment to that recognised in the Sekwi Brook, NW Canada, faunas by Narbonne and Aitken (1990). *Charnia masoni* is present; however, all but possibly two more of the 30 genera were not known outside Newfoundland, according to Anderson and Conway Morris (1982), and there are unfamiliar forms amongst the dominant frond-like forms: pectinate, bush-like, spindle-shaped and star-shaped.

7.2. The setting and age dating

A more up to date review of the setting was given by Myrow (1995) (Fig. 65). The sediments and volcanic rocks were interpreted as deposits of ensile rift basins associated with a continental arc setting and the 7500 m of volcanoclastic strata were reported to include submarine fan and slope deposits, passing upwards into a prograded wedge of deltaic and fluvial deposits, a flysch to molasse progression. The Ediacara-type fauna is within the upper part of the Conception Group and the lower part of the St Johns Group, both of which are fan deposits. There are ash beds intercalated in the sequence from the lower part of the Conception Group to the basal Signal Hill Group, which is molassic (Fig. 65). The Gaskiers Formation is a tillite horizon, representing the Varangian (=Laplandian) Glaciation and is below the Mistaken Point Formation which carries the fauna (Fig. 65).

Clapham et al. (2004) note that two fossiliferous horizons at Pigeon Cove near Mistaken Point are dated at 565 (Benus, 1988) and 575 Ma (Bowring et al., 2003), and are the oldest known diverse Ediacara-type assemblages. Nevertheless, the Conception Group fauna is of Vendian age, like the occurrences in the Ediacara type area in Australia and the fossiliferous strata of the East European Platform in Russia and Ukraine and those in Namibia.

7.3. The fauna

Conway Morris (1989a) remarked that, despite Ediacaran biotas having a worldwide distribution,

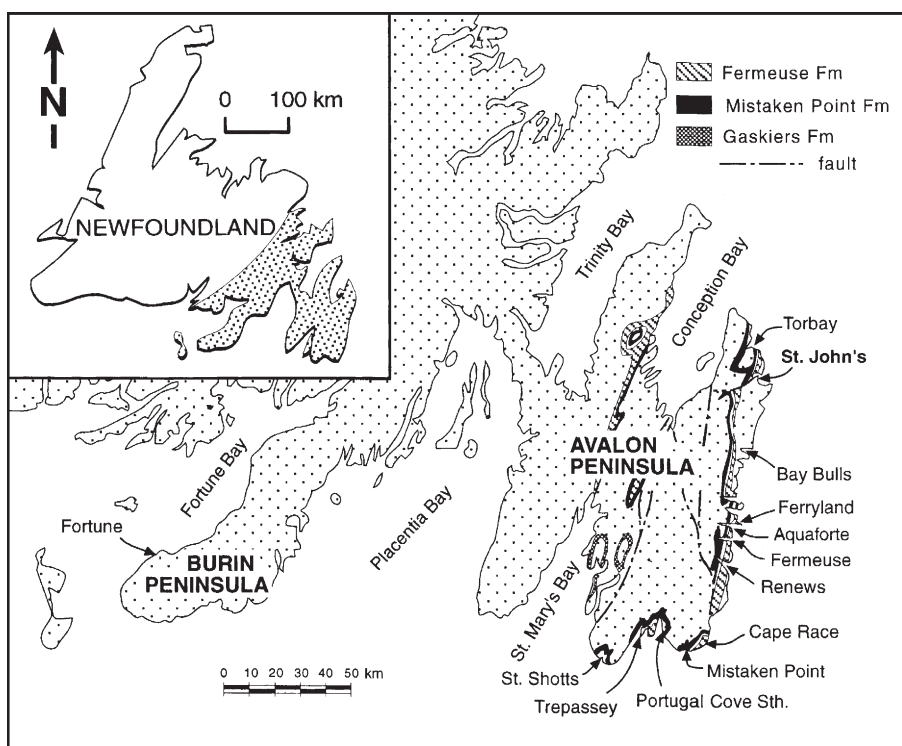


Fig. 64. Location map showing the Avalon and Burin Peninsulas, Newfoundland and outcrops of the Neoproterozoic Fermeuse, Mistaken Point and Gaskiers Formations, also major fault lines (after Gehling et al., 2000).

those from SE Newfoundland appear to be endemic, apart from some striking similarities to the Chamwood Forest fauna, notably in its occurrence in a single terrane and in its sedimentology. He suggested biogeographical isolation or deeper water sedimentary facies as the cause of the different character of the Avalon Zone fauna, but the case for such an explanation seems to be weakened by the ‘medusoid’-dominant nature of the Sekwi Brook fauna of the Mackenzie Mountains (Narbonne and Aitken, 1990), which is of similar deeper water facies. Conway Morris noted the presence of medusoid-like elements as low as the Drook Formation of the Conception Group (Fig. 65) and the presence of the problematic *Arumberia* in the Signal Hill Group. Examples of the fauna from Conway Morris (1989a) are illustrated in Fig. 66.

7.4. A later review

Jenkins (1992) published a review of the main Ediacaran occurrences which included the Avalon occurrences and a large-scale sectional diagram showing the stratigraphic positions of the metazoan, body fossil, microfossil and trace fossil occurrences

(Fig. 67). Metazoan fossils occur in the Briscal and Mistaken Point Formations of the Conception Group, and also in the Trepassy and Fermeuse Formations of the overlying St Johns Group. At Mistaken Point, the dominant host rocks are cyclic, medium-bedded turbidites and Jenkins suggested a continental terrace setting, and noted that Pickering (1983, 1985) had suggested that it is an outer fan deposits of lobe-hinge setting. At Mistaken Point, the sandier beds of the Trepassy Formation are probably lobe-fringe and fan-fringe deposits. At Cape Race, slumped deposits of the Fermeuse Formation resemble ‘fan lateral margin’ deposits; illustrated by Pickering (1983). On the other hand, the higher parts of the succession are progradational and generally indicate shallowing upwards.

The evidence suggests that the Avalon fossils are benthic taxa. There is no support in the field evidence for the idea of McMenamin (1987) that they relate to hydrothermal vents and chemotropic metabolism. They must also have lived below the photic zone, which is contrary to the suggestion of Seilacher (1984, 1989) that they were photosynthetic symbionts. The fauna includes large animals up to 50 cm diameter, for

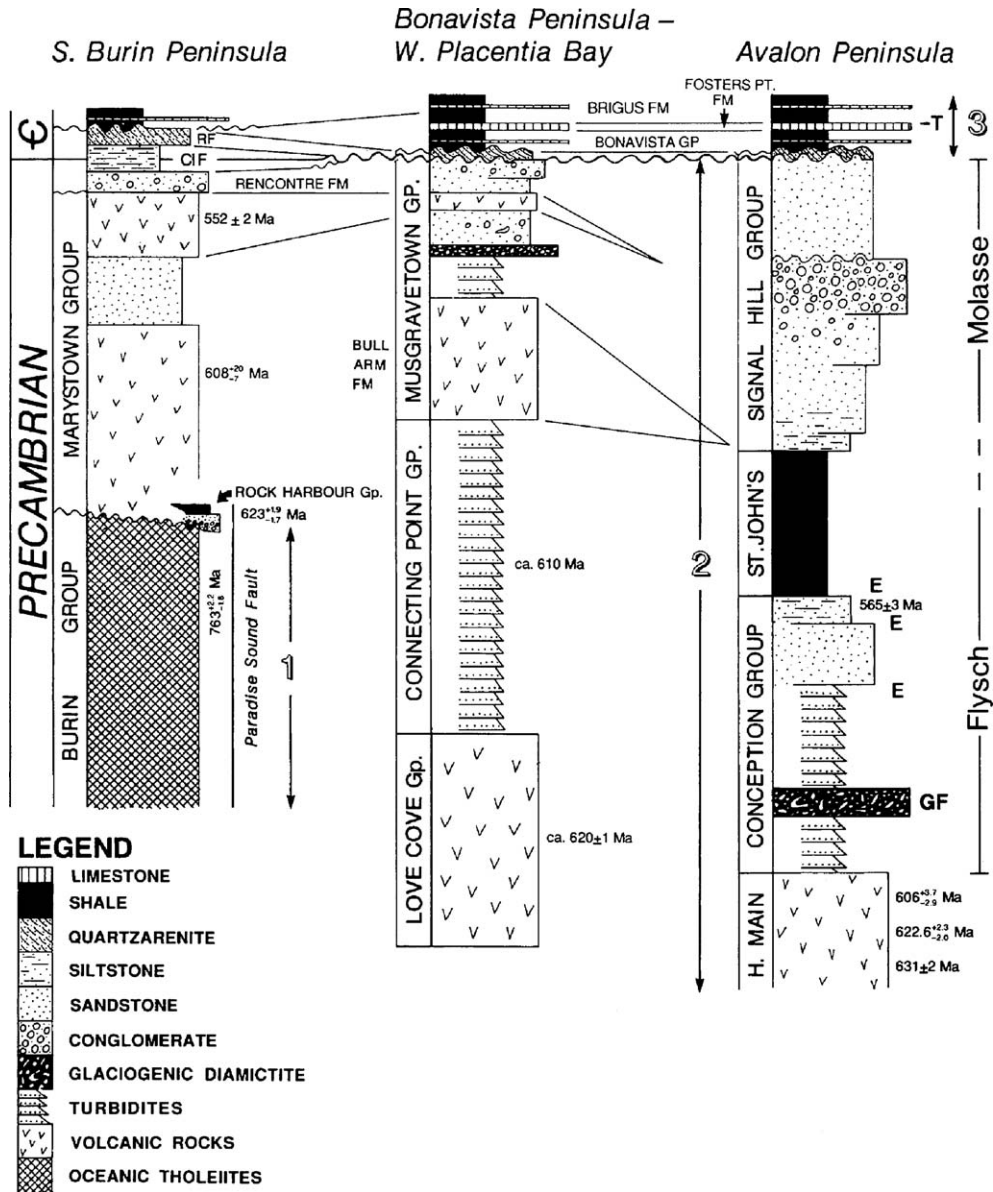


Fig. 65. Correlation chart of sections from the southern Burin Peninsula, Bonavista Bay–West Placentia Bay and the Avalon peninsula. The Gaskiers Formation (GF) is a late Precambrian glacial diamictite unit. The Precambrian–Cambrian boundary (heavy line) occurs within the Chapel Island Formation, below the Random Formation. E=occurrence of Ediacara-type fossils; T=the first occurrence of trilobites. 1, 2 and 3 indicate the lower, middle and upper stratigraphic assemblages referred to by Myrow (1995).

which bottom waters must have been sufficiently oxygenated to maintain heterotrophic metabolism, and there must have been some form of adequate suspended nutrient.

Except for few taxa such as *Charniodiscus* recognised elsewhere, none of the taxa had apparently been named formally by 1992, when Jenkins was writing. However, according to Anderson (1978), there were some 20 genera and Anderson and Conway Morris

(1982) indicated more, 30 genera. Jenkins listed five main types:

- (1) Spindle-shaped, in the upper part of the Mistaken Point Formation
- (2) Complexly branched ('bush-like'), numerous fronds joined by branching or zigzag connections (? 'pectinate' of Misra, 1969). Upper Mistaken Point, Trepassy and lower Fermeuse Formations.

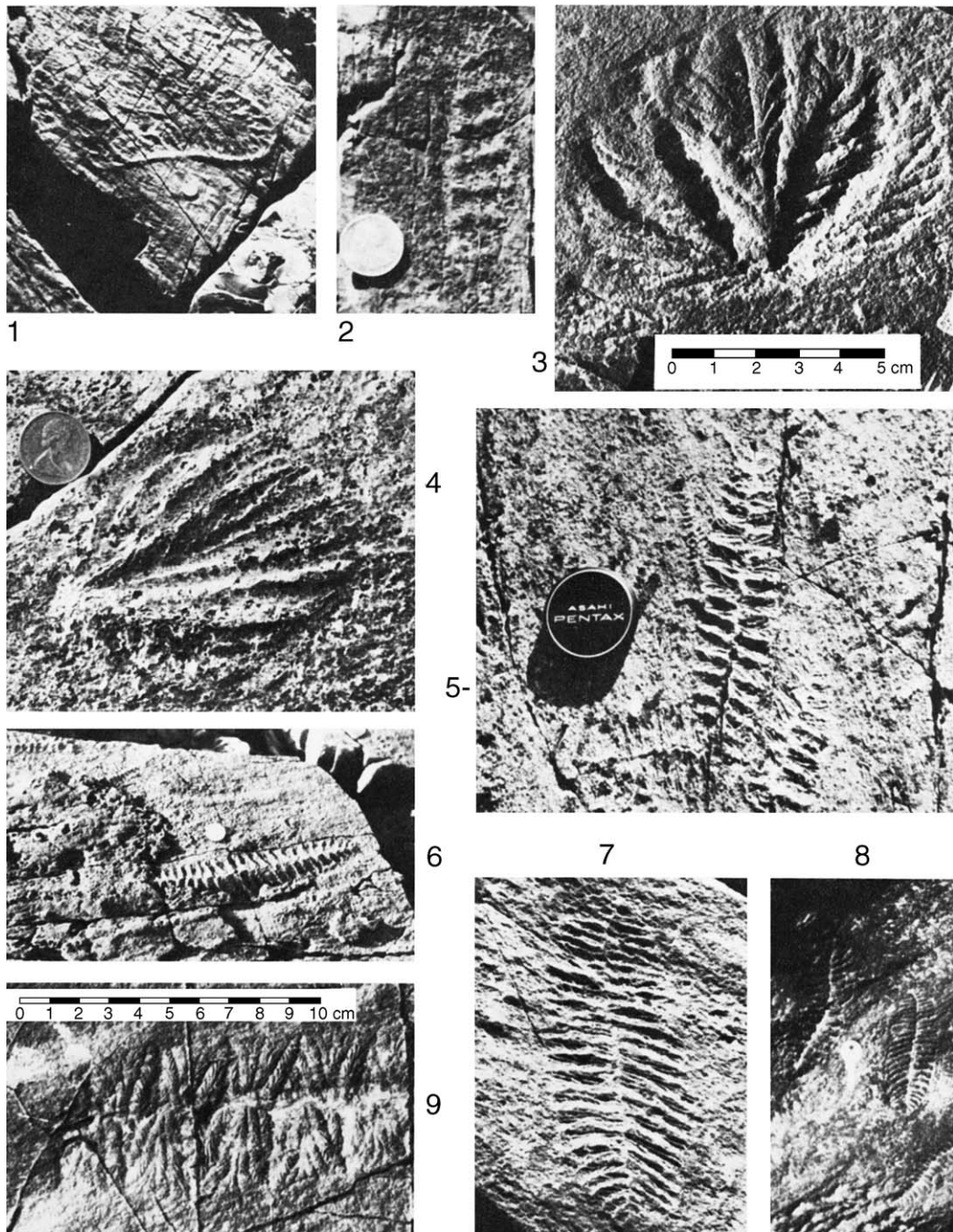


Fig. 66. Various frondose Ediacara-type fossils from the Avalon Peninsula. (1, 2) Pectinate form: 1=large specimen with more than 17 branches, looped appearance probably arose during burial (25 cm long); 2=juvenile with only seven branches ($\times 0.5$). (3, 4) Bush-like form, under-surface exposed after overturn, best observed if viewed upside down; meridional corrugation and arrangement of oblique bars evident, although much disturbed by compaction: 4=specimen showing typical appearance. (5–9) Spindle-shaped form: 5=large specimen, partly overlying smaller and fragments of others (lens cap diameter: 5.4 cm); 6=oblique view; 7=specimen about 12 cm long, fully contracted with ends drawn in, making them rounded in stead of pointed; 8=contracted specimens grouped together; 9=mid-portion of a large specimen in an expanded state with several groups of branches spread out axially; the arrangement of branches in groups and thecae of the branches can be clearly seen (from [Anderson and Conway Morris, 1982](#)).

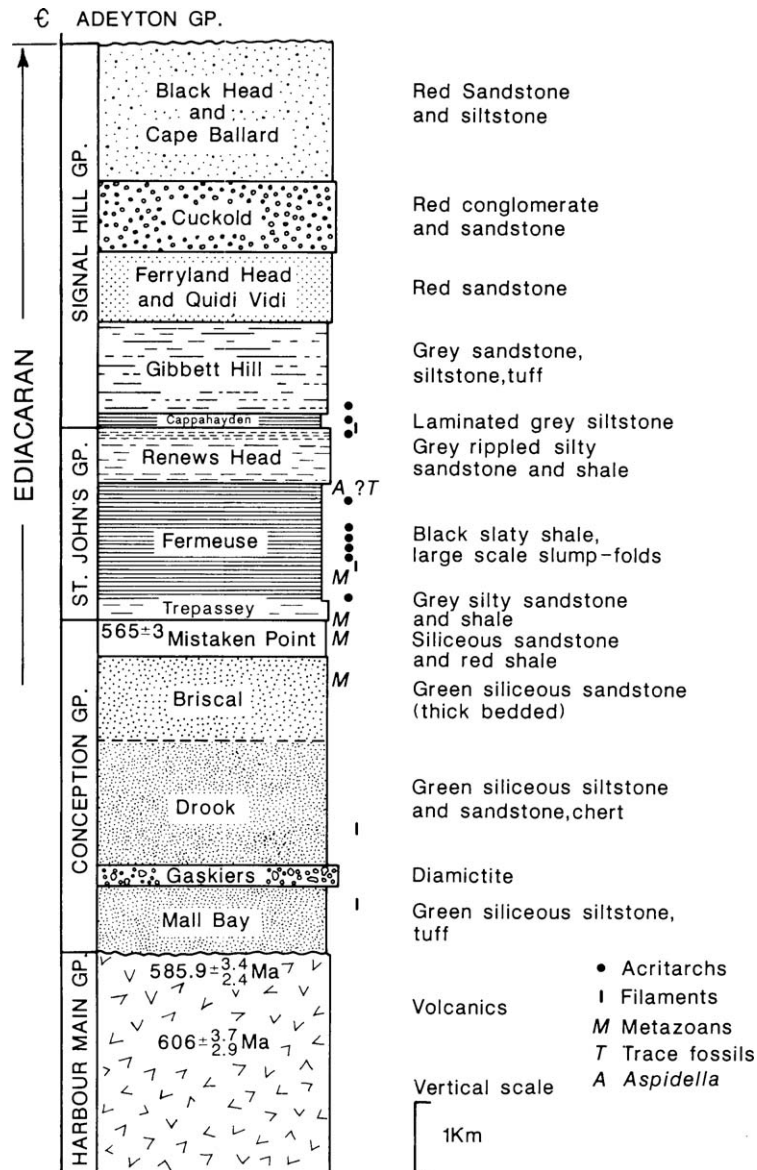


Fig. 67. Late Proterozoic stratigraphic succession, Avalon Peninsula, with levels of fossil finds (after Jenkins, 1992).

- (3) Singly frondose, with stalks expanded basally and terminating in a disc. Upper Mistaken Point, Trepassey and lower Fermeuse Formations.
- (4) Discoidal, with either radial or irregular 'lobes'. Briscal, Mistaken Point and Trepassey Formations.
- (5) Discoidal with strongly developed annulations, as illustrated by Anderson (1978). ? Mid-Fermeuse Formation.

The star-shaped form from the Trepassey Formation (Anderson and Conway Morris, 1982) is accompanied by unusually dark material in the sediment, and

Jenkins concluded that it is likely to be a trace fossil. The discoidal, annulate organism (5) was compared with *Cyclomedusa davidi* Sprigg (1947). The deep impression suggests that like that species it was probably buried during life, and resulted from the impact of a ringed, cone-shaped form of polyp-like aspect, but the annulation is stronger developed and more regular.

Jenkins (1992) accompanied his review by a set of drawings which show how he believed that the Avalon organisms would have looked in life, in situ on the sea bottom (Fig. 68).

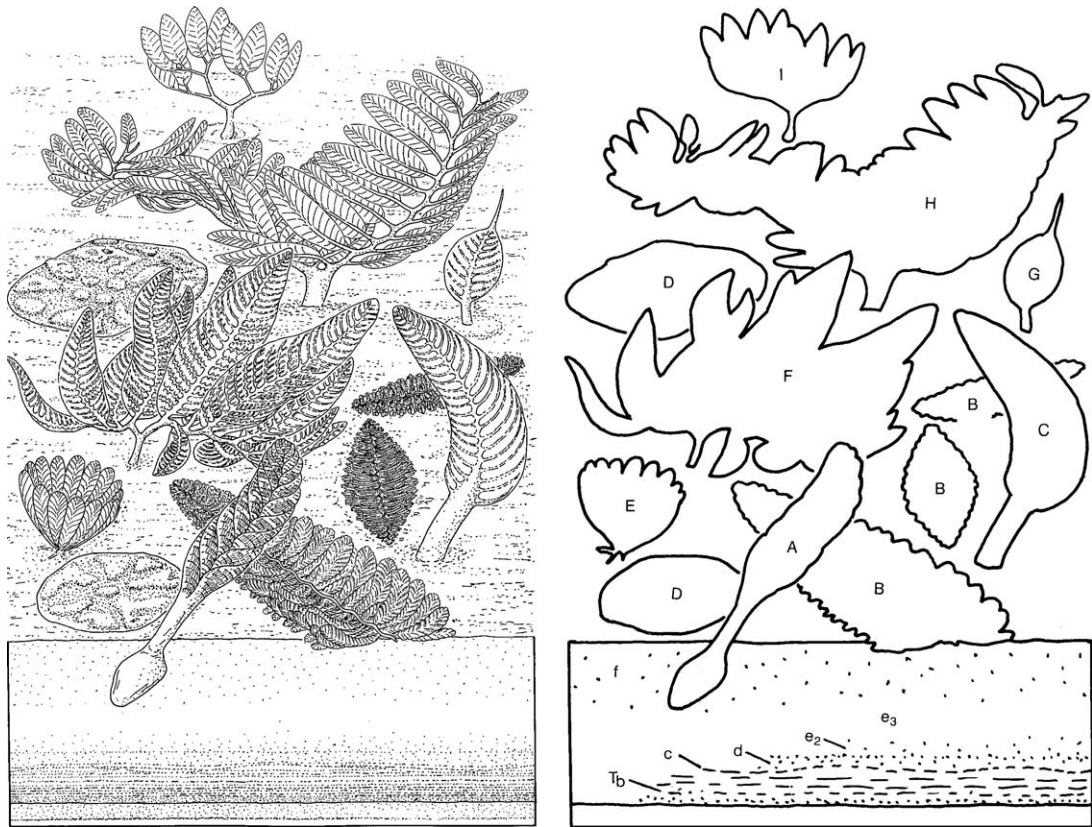


Fig. 68. Reconstruction of life forms from the upper part of the Mistaken Point Formation, Avalon Peninsula, portrayed at approximately one-third of natural size. (A) *Charnia masoni* Ford (1958). (B) Spindle-shaped fossils. (C) *Charniodiscus concentricus* Ford (1958). (D) Lobate discoidal remains. (E) Bush-like fossils. (F) Branched frondose fossils showing coarse secondary structures, resembling *Glaessnerina* Germs, 1983. (G) *Charniodiscus* Ford (1958). (H) Dichotomously branched frondose organism. T_{b-f}=Bouma divisions of turbidite substrate (after Jenkins, 1992).

7.5. Re-appraisal of *Aspidella*

Gehling et al. (2000) revised the interpretation of *Aspidella terranovica* Billings (1872), discovered in the late Neoproterozoic Fermeuse Formation about 1 km in section above the famous Ediacara-type assembly at Mistaken Point, in section; and several km below the base of the Cambrian (Billings, 1872). This find of discoidal forms caused much concern, being well below the local trilobite-bearing ‘primordial strata’, with separation by marked unconformity. Non-biological explanations were subsequently favoured because, until 50 yrs ago, the Precambrian was thought not to contain microfossils or megafossils (though stromatolites were recognised)—interpretations of *Aspidella* ranged from a fossil mollusc or ‘medusoid’; a gas-escape structure; a concretion; to a mechanical suck mark. No similar fossils had ever been recovered from the Phanerozoic. Gehling et al. weighed the evidence in

an attempt to distinguish between biogenic and inorganic origin

7.6. Field occurrence

They were aided by field study of a new roadside exposure at Ferryland (Fig. 64), where large numbers of *Aspidella* resembling the holotype occur in thinner beds of the same facies as large convex specimens. Many other sites where *Aspidella* occurs were recognised and the original find site is still exposed. The best site is just north of Aquafort Harbour (Fig. 64), where tens of thousands of specimens occur on the surface of east-dipping beds.

The Newfoundland rocks are highly cleaved and the best specimens are obtained where cleavage and bedding almost coincide and the sand content is highest. Cleavage is only apparent in shale beds and is insignificant in sandstone beds. Thin sandstone beds

alternating with shale are the optimum lithology for fossil collecting.

7.6.1. Stratigraphy and lithology

The apparently continuous Neoproterozoic sequence on the Avalon Peninsula is illustrated in Fig. 69. Two sections were measured near Ferrylands. Geochronological U–Pb determinations on basement rocks of the Harbour Main Group below the Conception Group have fixed the maximum age of the Gaskiers Formation at 606 Ma (± 3.7 Ma) (Krogh et al., 1988) and the most populated bed in the Mistaken Point Formation is covered by an ash bed dated at 565 Ma (± 3 Ma) (Benus, 1988). The Signal Hill group (Fig. 69) is correlated with the Rencontre Formation on the Burin Peninsula (Fig. 64) and this is overlain by the Chapel Island Formation in which the Precambrian–Cambrian Boundary was designated by the appearance of the trace fossil *Phycodes pedum* in the lower part of Member 2, in the Global Stratotype Section and Point (GSSP) The *Aspidella*-bearing rocks are therefore of unquestionable Neoproterozoic age. The range of *Aspidella* is from the

top of the Drook Formation of the Conception Group to the Renewes Head Formation of the St. Johns Group (Fig. 69). The upper, lithologically more varied, part of the Fermeuse Formation contains the best specimens. *Aspidella* is rare in the Mistaken Point Formation in the fossil beds covered by volcanic ash and in the Renewes Head Formation, where sandstones replace sandstone/shale alternations.

Most discoidal holdfasts associated with fronds of Ediacara-type organisms are preserved in positive relief, but some of them, as well as some *Aspidella*, are preserved in negative relief, where a limonitic crust appears to have been associated with the moulding and casting.

The overall coarsening-up of the Fermeuse and Renewes Head Formations is interpreted as representing a delta front and slope deposit. There is evidence of waning storm deposition in the lower part of the Fermeuse Formation and general shoaling upwards to a deltaic sequence. The *Aspidella* facies were deposited near storm wave-base in delta front and slope environments.

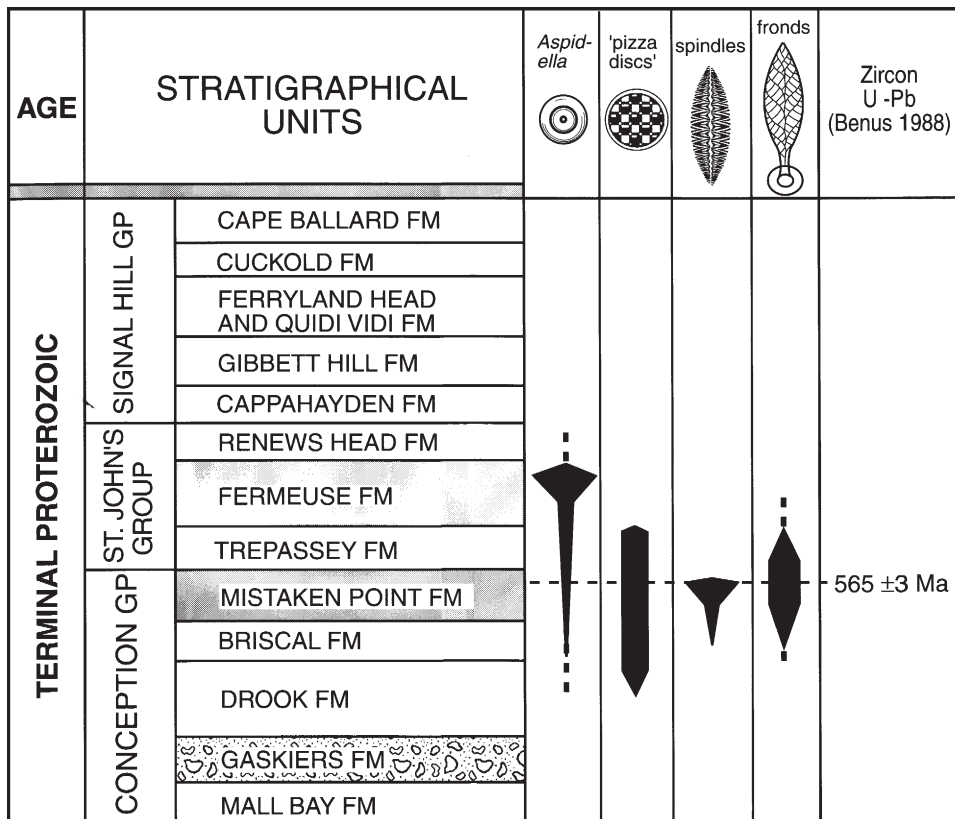


Fig. 69. Stratigraphical units of the Neoproterozoic above the Harbour Main group on the Avalon Peninsula, showing stratigraphical ranges and relative frequencies of *Aspidella* and other representative megafossil forms from the Mistaken Point assemblage. The age date is a U/Pb date on zircons from a volcanic ash layer on Bed E, Mistaken Point Formation (Benus, 1988) (after Gehling et al., 2000).

7.6.2. Fossil morphology

The type collection of Billing clearly shows radial and concentric markings. Three end-member ‘morphs’ were described by Gehling et al. (2000). They range from 5–110 mm diameter. The ‘type morph’ resembles the holotype (Fig. 70) with a sharp border in hyporelief surrounding a broader convex zone cut by radial grooves converging on a central slit or invagination. At the lower end of the size range (5–25 mm) each specimen consists of a central depression surrounded by a smooth, convex ring. The ‘flat morph’ is a flat, low-relief disc, with a central boss one quarter of the diameter of the disc (Fig. 70). The periphery is a sharply defined raised rim. Concentric or rarer radial markings occur between the boss and the rim. The size range is 30–100 mm. The ‘convex morph’ is rimmed by a low, flat flange rising sharply to a broad, convex disc with a prominent or slightly sunken central boss (Fig. 70), marked by grooves which tend to be concentrated at the edge of the boss. The size range is 5–110 mm. Size

appears to be a critical factor in the differentiation of the various morphs.

Density of discs on a surface may be high or patchy and local crowding in chains or clusters may be seen. Disc morphology is slightly but not exclusively facies controlled. The clear and sharp outlines of the discs preclude inorganic origin as products of gas/fluid escape in soft sediment.

Gehling et al. (2000) presented a triangular diagram relating *Aspidella* to the ‘medusoids’ *Ediacaria* and *Spriggia*. The progression from *Aspidella* to *Ediacaria* involves loss of invagination, increase in complexity and prominence of central boss: to *Spriggia* from *Ediacaria*, it involves increase in size, decrease in convexity and prominence of central boss; and from *Spriggia* back to *Aspidella*, it involves decrease in size and increase in invagination at the centre. The diagram illustrated possible intermediate forms in these progressions, and it was concluded that *Aspidella* does share certain key characteristics with

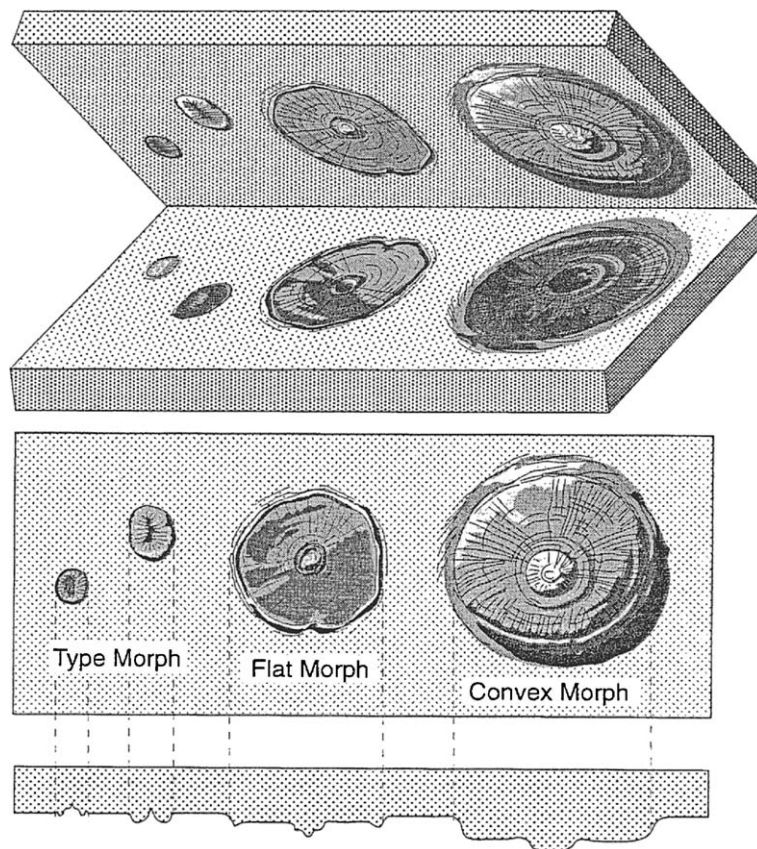


Fig. 70. Morphological end-members of *Aspidella*. In hyporelief the type-morph is flat to convex with radial grooves and ventral invagination; the flat morph has a raised marginal rim and central boss; the convex morph has a prominent central boss and both radial and concentric grooves: the diagrammatic cross-section shows profiles in hyporelief: the upper block diagram shows part and counterpart in opposite relief (after Gehling et al., 2000).

Table 13

Probable junior synonyms of *Aspidella terranovica* Billings, 1872 (after Gehling et al., 2000)

1933	<i>Paramedusium africanum</i> Gürich	Namibia	Flat morph
1947	<i>Ediacaria Flindersi</i> Sprigg	South Australia	Convex morph
1947	<i>Beltanella gilesi</i> Sprigg	South Australia	Convex morph
1947	<i>Cyclomedusa davidi</i> Sprigg	South Australia	Convex morph
1949	<i>Protodipleurosoma wardi</i> Sprigg	South Australia	Flat-type morph
1949	<i>Tateana inflata</i> Sprigg	South Australia	Convex morph
1949	<i>Cyclomedusa radiata</i> Sprigg	South Australia	Flat-convex morph
1949	<i>Cyclomedusa gigantea</i> Sprigg	South Australia	Convex morph
1949	<i>Madigania annulata</i> Sprigg	South Australia	Flat morph
1966	<i>Cyclomedusa plana</i> Glaessner and Wade	South Australia	Flat morph
1972	<i>Planamedusites patellaris</i> Sokolov	Ukraine	Flat morph
1972	<i>Medusinites patellaris</i> Sokolov	Ukraine	Flat morph
1976	<i>Tirasiana disciformis</i> Palij	Ukraine	Convex morph
1976	<i>Tirasiana coniformis</i> Palij	Ukraine	Convex morph
1977	<i>Tirasiana concentralis</i> Bekker	Russia, Ural Mts	Convex morph
1980b	<i>Paliella patelliformis</i> Fedonkin	Russia, White Sea	Flat morph
1980b	<i>Protodipleurosoma rugulosum</i> Fedonkin	Russia, White Sea	Type morph
1981	<i>Cyclomedusa minima</i> Fedonkin	Russia, White Sea	Type-convex morph
1981	<i>Cyclomedusa delicata</i> Fedonkin	Russia, White Sea	Flat-convex morph
1983	<i>Irridinitus multiradiatus</i> Fedonkin	Ukraine	Type morph
1986	<i>Spriggia wadea</i> Sun	South Australia	Flat morph
1987	<i>Vendella larini</i> Gureev	Ukraine	Type morph
1987	<i>Glaessneria imperfecta</i> Gureev	Ukraine	Flat morph
1988	<i>Jampolium wyrzhykoowskii</i> Gureev (in Ryabenko et al., 1988)	Ukraine	Flat morph

several discoid soft-bodied fossils from other continents, including also *Cyclomedusa*, *Tirasiana* and *Irridinitus*, from South Australia and the Ukraine. Taxonomically, there are probably many minor synonyms (Table 13).

Microbial mat textures ('elephant skin') occur on some fossiliferous surfaces, coated with iron oxide and carbonaceous material, possibly enhancing the chances of preservation (Gehling, 1999). Some rare individuals are preserved with a frond-like extension and may represent holdfast attachments of organisms of which the frond-like section is only rarely preserved.

7.6.3. Doubtful trace fossils

The rare supposed trace fossils *Palaeopascichnites*, *Intrites*, *Neonereites renarius* and *Yelovichnus*, which occur with *Aspidella*, were thought by Gehling et al. (2000) to be parts of body fossils, not trace fossils.

7.6.3.1. Other body fossils. A three-lobed body-fossil in positive relief, with rounded spatulate lobes radiating at equal angles to form a tripartite invagination or central rosette, occurs in the Fermeuse Formation at Ferryland. The margins of the lobes are smooth and slightly raised; the surfaces of the lobes are slightly raised and carry uneven costellae parallel to the lobe axis. Ten complete specimens are preserved in hyporelief, ranging from 20–26 mm long. There is no bifurcation of the lobes as in other Ediacara-type forms with three-fold symmetry. The fossil was named *Triforillonia costellae* gen. et sp. nov. (Fig. 71).

These authors concluded that there was no convincing inorganic explanation for the preserved suite of discoidal forms. Comparison with other fossil assemblages, associations with other fossil taxa, microbial mat textures and growth characteristics support this conclusion.

7.7. New discoveries

In 2004, a new discovery was reported from Spaniard's Bay (Narbonne, 2004) (Fig. 72). This is in a deep-water turbidite sequence of rocks dated at 575–560 Myr. More than 100 animal-like fossils were

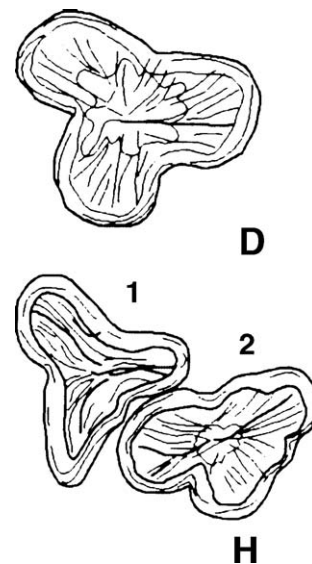


Fig. 71. *Triforillonia costellae* gen. et sp. nov. from the Fermeuse Formation, Ferryland coastal section. Sketch of two paratypes (after Gehling et al., 2000).

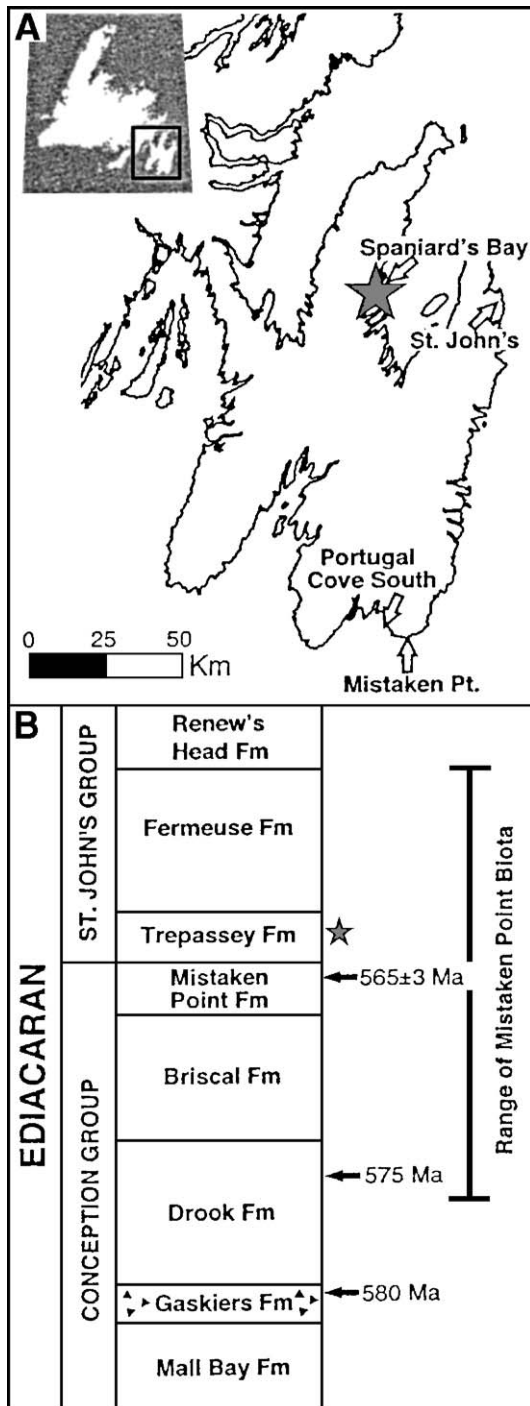


Fig. 72. The location of the new Spaniards Bay fossil site in the Trepassey Formation, St. Johns Group (reprinted with permission from Narbonne, 2004).

discovered, varying from centimeters to metres in size. They include plumose rangeomorph fractal-like branching patterns, bush-shaped and spindle-shaped rangeomorph constructions (Fig. 73). The deep ocean

environment probably protected these from storm waves and light, and they are excellently preserved even to microscopic features, including internal detail.

Clapham et al. (2004) reported the discovery of a new genus and species at Pigeon Cove near Mistaken Point (Fig. 74) Noting that the Mistaken Point fauna, although containing the Charnwood Forest taxa of *Charnia*, *Charniodiscus*, *Bradgatia* and *Ivesia*, was essentially endemic, containing as many as 20–30 taxa (albeit mostly as yet not formally named but just distinguished as ‘spindles’, pectinates, etc.), these authors described a most unusual form, previously referred to as “triangles”. They named it *Thectardis avalonensis*. It was found on two bedding plane surfaces which reveal ~200 specimens of the fauna. It has the form of an elongate cone, which lived as suspension-feeding ‘mat-sticker’ with the pointed base inserted in the sediment (Fig. 75). Individuals are up to 15 cm high. Incremental growth occurred at the distal end to the apex and it maintained the same length to width ratio as it grew.

7.8. Conclusion

The Newfoundland fossils are significantly different from those of any other global occurrence, although there is perhaps most similarity to Charnwood Forest, England. The Newfoundland occurrence is of critical importance in the understanding of the Ediacara-type biota and is now well age-constrained. The priority of the name *Aspidella*, although correctly claimed, should not, perhaps, initiate a flurry or taxonomic revisions, globally, considering that the taxonomic divisions of Ediacara-type biota have been erected in a climate of uncertainty about the relationships between individual forms, relationships to Phanerozoic biota and their functional activities in life.

8. Northwestern Canada

8.1. Introduction

Three separate occurrences have been recognised in Northwestern Canada, and comprise a major province of Vendian sequences.

8.2. Yukon

8.2.1. Mackenzie Mountains: Sekwi Brook

The first description of Ediacaran fossils from Laurentia (ancestral North America) was by Hofmann (1981), who collected body and trace fossils from the Sekwi Brook area in the Mackenzie Mountains. He

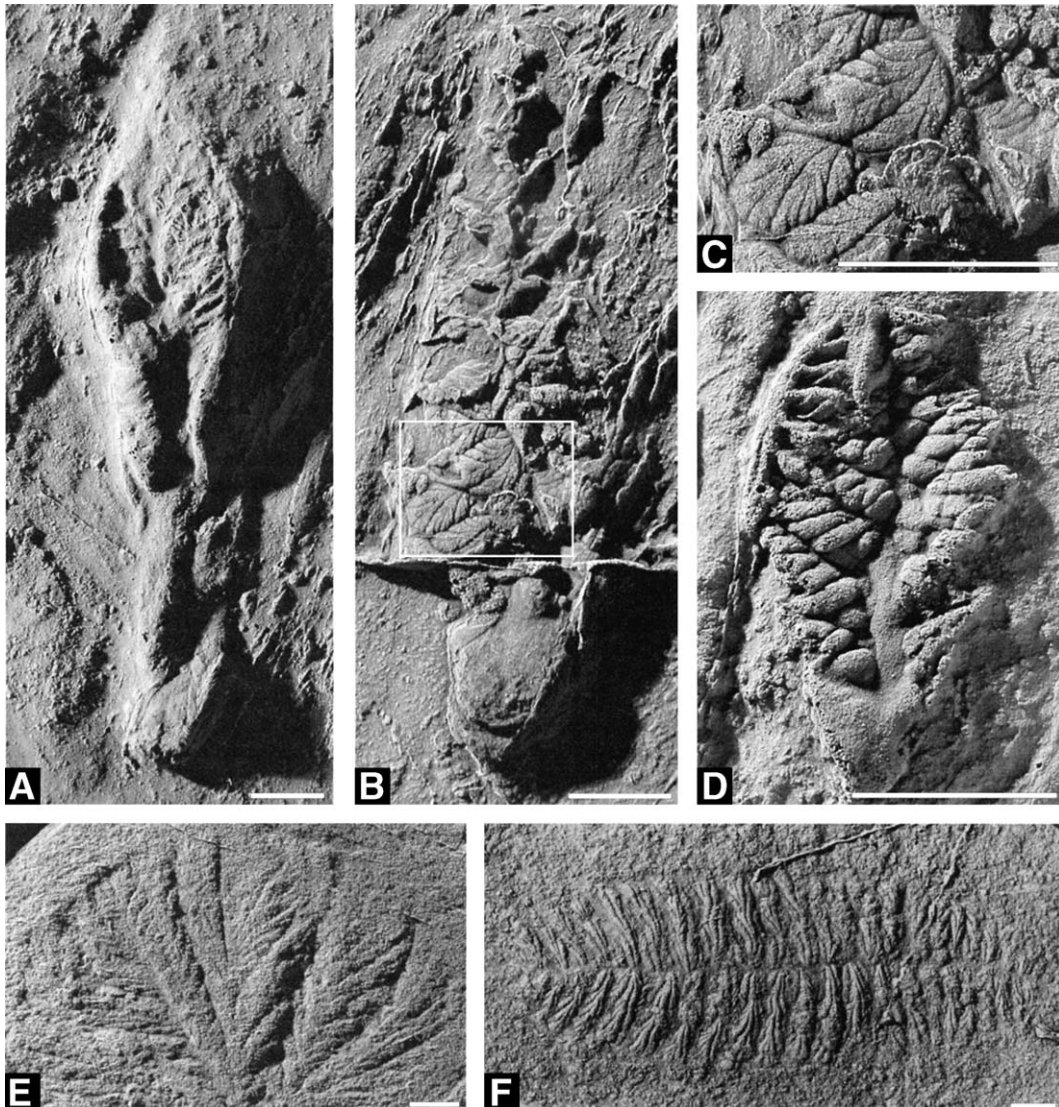


Fig. 73. Spaniards Bay rangeomorphs: (A) long stemmed frond with overlapping frondlets attached at their base to the central stalk; (B) short stemmed frond with leaf composed of pendant frondlets, hanging from a thin central stalk with side struts; (C) enlargement of part B; (D) *Charnia*-like frond with quilted array of major and minor branches overlying an internal organic skeleton. Mistaken Point rangeomorphs: (E) bush-shaped construction; (F) spindle-shaped construction (scale bar = 1 cm) (reprinted with permission from Narbonne, 2004).

reported the body fossils *Inkrylovia* sp. and *Sekwia excentrica*. A full description of this fauna was given by Narbonne and Aitken (1990) who found body and trace fossils through more than 1 km thickness of the Windermere Supergroup, which consists of four grand cycles of sediments.

The stratigraphy of the Windermere Supergroup is as follows:

- (4) Ingta Formation (230 m)
- (3) Blueflower (550 m) and Risky (150 m) Formations
- (2) Sheepbed (900 m) and Gametrail (300 m) Formations

- (1) Twitya (900 m) and Keele (500 m) Formations.

The site of the finds is shown in Fig. 76 and a sectional diagram in Fig. 77. The Ediacaran fossils are found in the upper part of the Sheepbed Formation and in the Blueflower Formation.

The Sheepbed formation has yielded the following fauna:

- Beltanella gilesi*
- Charniodiscus* sp.
- Cyclomedusa plana*

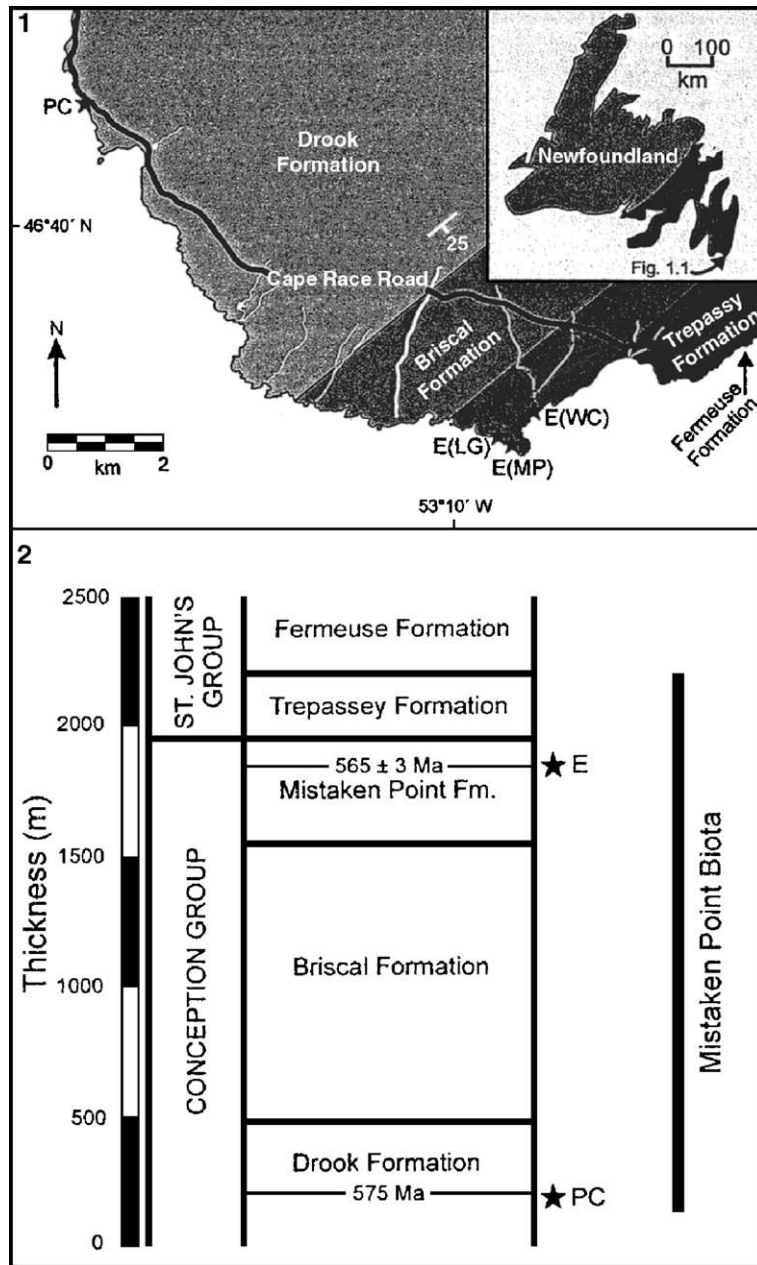


Fig. 74. Map showing the location of Mistaken Point and fossil surfaces with specimens of *Thectardis avalonis* n. gen and sp. PC is the Pigeon Cove surface, E(LG), E(MP), EWC are the E surfaces at Laurentian Gulch, Mistaken Point and Watern Cove, respectively. Below stratigraphic column showing the position of the fossiliferous surfaces and added ash beds from Benus (1988) (E) and Bowring et al., 2003 (PC) (after Clapham et al., 2004).

Euporpita

Kullingia sp.

Medusinites asteroides together with the trace fossil
Planolites montanus.

The Sheepbed Formation consists of coarse turbidite sandstones at the base together with fine turbidite

sandstones, and, in the upper fossiliferous part, laminated dolomitic siltstones and fine grained sandstones. The Gametrail Formation is dominated by ribbon-bedded carbonates together with debris flows and slide deposits. The upper Sheepbed and Gametrail deposits are interpreted as SW prograding slope deposits which buried axially prograding deep-

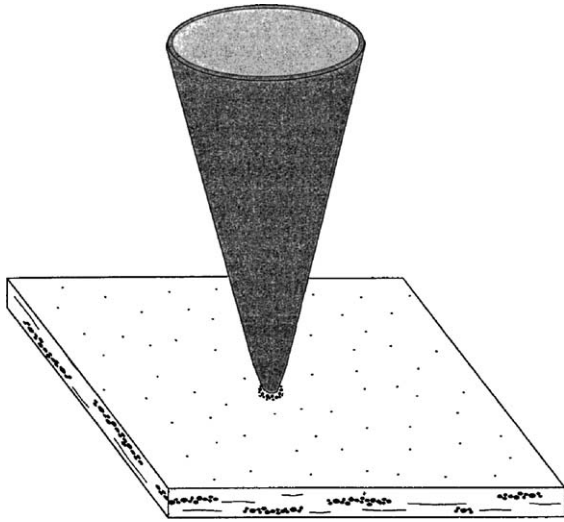


Fig. 75. Reconstruction diagram of *Thectardis avalonensis* in the interpreted life position (from Clapham et al., 2004).

sea fan channel deposits. The upper part accumulated below storm base.

The Blueflower Formation has yielded the following fauna:

Charniodiscus sp.
Inkrylovia sp.
Pteridinium sp.
Sekwia excentrica

Together with the trace fossils:

Aulichnites ichnosp.
Helminthoida ichnosp.
Helminthoidinites ichnosp.
Helminthopsis ichnosp.
Helminthopsis tenuis
Helminthopsis abeli
Helminthopsis irregularis
Terrowangea rosei
 and a knotted burrow.

The Blueflower Formation consists of shale, mudstone, turbidite sandstone, with limestone of turbiditic and grain flow origin. This is the lower part of a shoaling upwards pile which terminates in peritidal dolomites of the Risky Formation deposited in shallow water, re-establishing carbonate platform conditions. The Risky Formation of dolomites and thin bedded sandstones contains only simple trace fossils, *Palaeophycus tubularis* and *Planolites montanus*. The lower three quarters of the Blueflower Formation is interpreted as deposits of a slightly

channelled slope below storm wave base: it probably represents a depositional slope above a fan complex.

Deposits of the last Neoproterozoic glaciation directly underlie the Sheepbed Formation.

The Ingta Formation forming the uppermost cycle lacks typical Cambrian body or trace fossils and is taken to be Neoproterozoic. The unconformity above it (Fig. 77) separates it from correlatives of Backbone Range and Vampire Formations which contain small shelly fossils typical of the lowermost Cambrian stage and typical Early Cambrian trace fossils. Thus, the Sekwi Brook fauna is entirely Neoproterozoic (Vendian) in age. Baudet et al. (1989) studied acritarchs in this section and it was thus shown to be equivalent in age to the fossiliferous deposits of the Wernecke Mountains in Yukon, to the northwest (Fig. 76).

Narbonne and Aitken (1990) provided detailed descriptions of the individual body fossils, explaining their various attributions to taxa. They are listed in Fig. 78. Particular points of interest only are mentioned here. In the case of *Beltanella gilesi* they noted that it has traditionally been interpreted as a pelagic medusoid (Sprigg, 1947; Harrington and Moore, 1956), but was later interpreted as a benthic polyp attached to the sea bottom by a short stalk (Jenkins, 1988), a sea-pen type of attachment structure. The Sekwi Brook specimen (Fig. 79) exhibits a poorly preserved stalk extending outwards from the outer margin of the disc, implying that it was above rather than below the disc. One specimen of *Cyclomedusa plana* exhibits an uncompressed cone at its apex (Fig. 79), implying that it was buried in relatively cohesive mud while the flat outer ring rested on the seafloor. Of the specimens of *Cyclomedusa* sp., particularly interesting is the cluster of three discs which deform but do not cross-cut one another and evidence of increasing mutual deformation during growth (Fig. 79), supporting interpretation as a sessile benthic organism. It was suggested that the pelagic larva settled on the seafloor and dug a small pit for the attachment, the firm-bodied organism growing out concentrically in the shape of a cone. There is, however, no evidence of active burrowing except for the central tubercle. The organism was later buried by a sandy turbidite or storm bed and cast by sudden collapse of sand into the space which it formerly occupied. The suggestion is that *Cyclomedusa* and perhaps some other Ediacaran discs were sessile except in the larval stage.

With reference to *Kullingia* sp. (Fig. 80), it was noted that this genus had been likened by Foyn and Glaessner (1979) to a chondrophorian cnidarian, but that Seilacher (1984, 1989) had suggested that such chambered

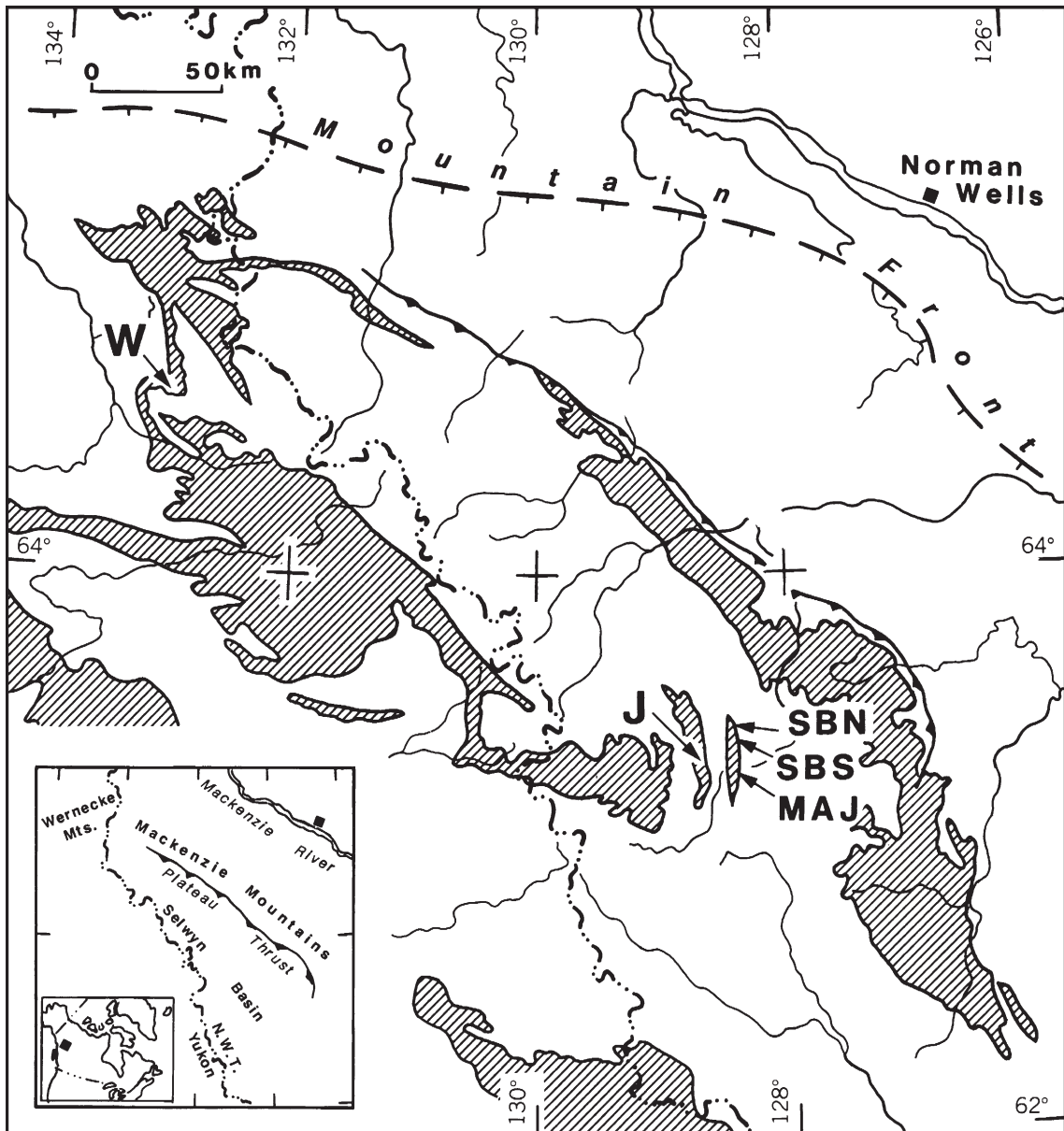


Fig. 76. Location of sections studied in the Mackenzie Mountains with the outcrop of the Windermere Supergroup shaded. S.B.N.=Sekwi Brook North, S.B.S.=Sekwi Brook South, M.A.J.=Majesty property. Other sections described elsewhere are in the June Lake Anticline (J) and Wernecke Mountains (W) (after Narbonne and Aitken, 1990).

Ediacaran discs were sedentary, benthic ‘quasiautotrophs’, segmented to facilitate metabolic processes. However, the close similarity between Ediacaran fossils of this type to Palaeozoic and modern chondrophorians supports the view that they are related (Stanley, 1986).

Six of the genera in the Sekwi Brook fauna are common to the shallow water facies of the Wernecke Mountains (*Beltanella*, *Charniodiscus*, *Cyclomedusa*, *Ediacaria*, *Kullingia*, and *Medusinites*). Six genera are reported

only from the Wernecke Mountains (*Beltanelliformis*, *Nadalina*, *Rugoconites?*, *Spriggia*, *Tirasiiana*, and *Vendotaenia*). Four genera are only found at Sekwi Brook (*Euporpita*, *Inkrylovia*, *Pteridinium*, and *Sekwia*). The authors believed that the apparent geographical and stratigraphical variation is due to a combination of original patchy distribution, palaeoenvironmental and preservational factors, rather than palaeogeography and evolution. They noted the problems of collecting in such

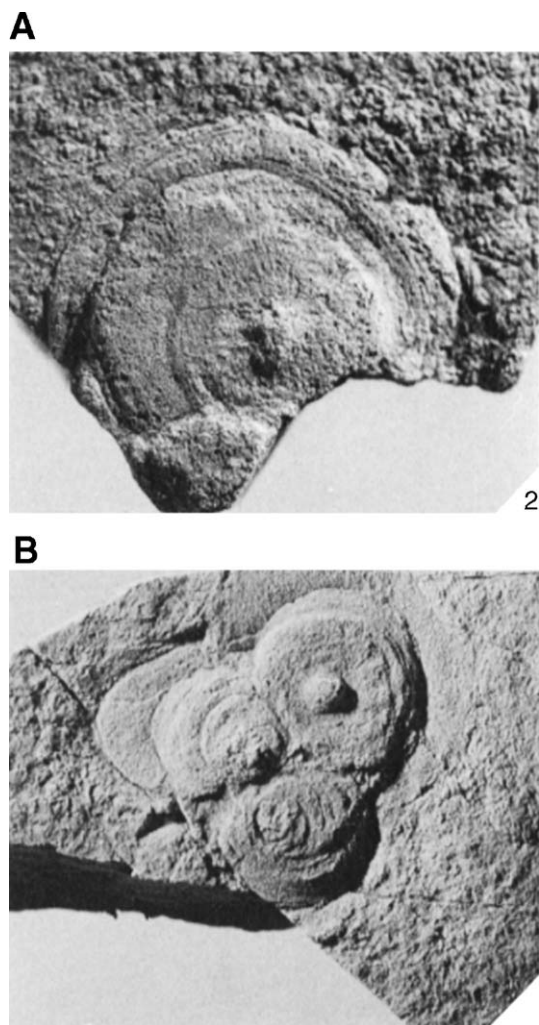


Fig. 79. Body fossils from Sekwi Brook South (SBS) and North (SBN) ($\times 1$); A) *Cyclomedusa* sp., hyporelief (SBN). B) *Cyclomedusa* sp., three specimens that interfered with each other during growth, indicating a sessile mode of life (SBS) ($\times 1$) (from Narbonne and Aitken, 1990).

remote regions. They believe the concept of a single Windermere Ediacaran (Vendian) fauna should be accepted.

They described the trace fossils in some detail. They are simple sub-horizontal burrows, directed meanders being common and patterned meanders rare to common (Fig. 81). They resemble the *Nereites* facies of Seilacher (1974), typical of Phanerozoic turbiditic slope deposits, but constitute a relatively simple version of it. Such meandering burrows apparently extended from the shallow-water shelf into the deeper water of the slope as early as Vendian times, but, with the development of complex branching, spreiten and deep vertical burrows in the Cambrian, were eliminated from shallow waters,

but persisted through the Phanerozoic in the deeper slope and fan environments.

The Sekwi Brook body and trace fossils are summarised in Fig. 78 from Narbonne and Aitken (1990) and global comparisons are summarised in Fig. 82 from the same source.

The Ediacaran fauna represents the rootstock from which all metazoans evolved, the oldest diverse assemblage of megascopic animals and trace fossils. At Sekwi Brook, the fauna occurs sporadically through 1 km of deep water strata (Upper Sheepbed Formation to top of Blueflower Formation) and there are 11 body fossils and 12 ichnospecies recognised. They are mainly sessile, benthic polypoid and frond-like organisms along with a possible pelagic (?) chondrophorian. Muddy slope deposits below storm wave-base is the environment indicated by the evidence and this is not consistent with the hypothesis that these taxa functioned exclusively as photoautotrophs. The fauna is broadly similar to those of the Wernecke Mountains, Flinders Ranges and Russian Platform, where the environment was shallow shelf. Thus the Ediacaran organisms had broad environmental ranges and these faunas can be correlated between different sedimentary environments.

8.2.2. Mackenzie Mountains: Bluefish Creek

Hofmann et al. (1990) described an Ediacara-type fauna from intertillite beds, a turbidite sequence within the Twitya Formation of the Windermere Group in the Mackenzie Mountains, northwestern Canada. They noted that the Ediacara fauna commonly occurs above the tillites of the Varanger glaciation (early Vendian), but here it occurs between tillites 2.5 km below the base of the Cambrian.

These finds were made within the Bluefish Creek area in the upper part of the Twitya Formation (Fig. 83). The locality is in the Sayunei Range, on a steep northwest-facing slope at 64.083°N; 128.833°W, and the fossils occur at four stratigraphic levels, in an interval 170–220 m below the top of the Twitya Formation, a 0.8 km thick sequence of siliciclastic turbidites. There is a deep-water diamictite above and diamictite of the Shezal Formation below (Fig. 83). Striated clasts and other features confirm the glacial origin of the latter. Dropstones, striated clasts, till pellets and relict ice-cemented boulders also show that the upper diamictite is of glacial origin. The Sheepbed and Blueflower formations of siliciclastic rocks above the Tepee Dolostone, both of Vendian age, carry Ediacara-type fossils in the Sekwi Brook/June Lake area to the south (Hofmann, 1981; Narbonne and

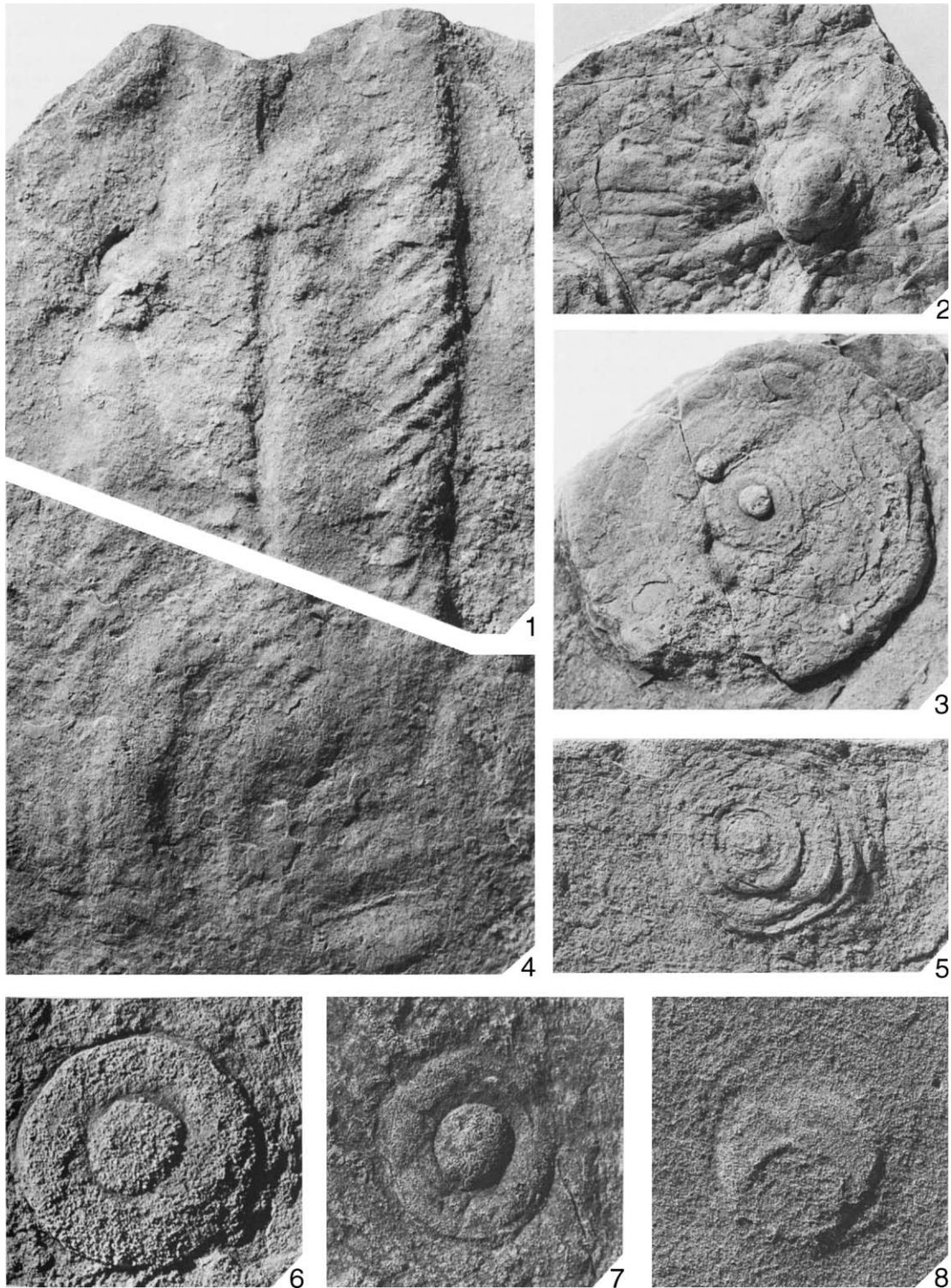


Fig. 80. Body fossils from Sekwi Brook South (SBS) and North (SBN). (1) *Pteridinium* sp. (SBS) ($\times 1$), (2) *Eoporpita* sp., hyporelief (SBN) ($\times 1$), (3, 5) *Cyclomedusa* sp. (SBN) ($\times 1$), (4) *Kullingia* ? sp., hyporelief (SBN) ($\times 1$), (6,7) *Medusinites asteroides* (Sprigg), hyporelief (SBN) ($\times 2$), (8) *Sekwia excentrica* Hofmann, hyporelief (SBS) ($\times 2$) (from Narbonne and Aitken, 1990).

TAXA	NORTHWESTERN CANADA		GLOBAL COMPARISONS											
	SHALLOW SHELF	BASIN SLOPE	SHALLOW SHELF						DEEP SLOPE/FAN					
	Wernecke Mtns.	Sekwi Brook	VENDIAN			EDIACARAN			OTHERS					
			Northern Europe	Podolia	Urals	Siberia	Flinders Ranges	Central Australia	Namibia	Central England	North Carolina			
BODY FOSSILS	<i>Beltanella</i>													
	<i>Beltanelliformis</i>	▬		□	□	□	□	○	○	○	□			
	<i>Charniodiscus?</i>			□				□	□	□		□		
	<i>Cyclomedusa</i>	▬		□			□		□			○		
	<i>Ediacaria</i>			□	□				□					
	<i>Eoporpita</i>			□					□					
	<i>Inkrylovia</i>			□					□					
	<i>Kullingia?</i>			□	□					○				
	<i>Medusinites</i>			□			○		□					
	<i>Nadalina</i>													
	<i>Pteridinium</i>			□	□						□			□
	<i>Rugoconites?</i>								□					
	<i>Sekwia</i>													
	<i>Spriggia</i>								□					
	<i>Tirasiana</i>				□	□						○		
<i>Vendotaenia?</i>			○	○		○								
ICHTHOFOSSILS	<i>Aulichnites</i>			□										
	<i>Helminthoida</i>			□					○					
	<i>Helminthoidichnites</i>			□	□				□					
	<i>Helminthopsis</i>													□
	<i>Lockeia</i>													□
	<i>Neonereites?</i>			□					○					□
	<i>Palaeophycus</i>				○									□
	<i>Planolites</i>			□	□				□	□				□
	<i>Torrowangea</i>			□	□									○

Fig. 81. Regional and global correlation of the Windermere Biota. Localities with less than two such taxa were omitted. Abundance symbols for northwestern Canada: narrow bar=rare (present in less than 10% of fossiliferous units); intermediate bar=common (present in 10–50% of fossiliferous units); broad bar=abundant (present in more than 50% of fossiliferous units). For global comparisons, same=square, similar=circle (after Narbonne and Aitken, 1990).

Aitken, 1990). The fauna in the Twitya Formation is by far the oldest Ediacara-type fauna reported from Laurentia and the first to be found below a glacial deposit in the Vendian. Eisbacher (1985) equated the upper tillite with the Varanger (Laplандian, Marinoan) glaciation and the older Shezal tillite has commonly been equated with the Sturtian glaciation, and this would indicate a latest Riphean age for the Twitya formation, which has not been dated by radiometric, palaeomagnetic or microfossil-based methods. However, Hofmann et al. (1990) note that these may represent two separate advances of the Varanger ice sheet, and such a division is recognised in the equivalent Laplandian Glaciation in parts of Russia (Sokolov and Fedonkin, 1985). The thickness of the

Vendian Strata above rules out the possibility of this fauna being any younger than the Varanger glaciation,

The fossils are preserved as very simple convex discoidal and annular reliefs on the lower surfaces of thin sandstone beds and as counterparts on the tops of the underlying shale beds. Three types are recognised (Fig. 84). The first type, common in the uppermost level 170 m below the top of the formation, comprises annular ridges in positive hyporelief, 10–35 mm across. The rings are slightly elongate and the central depressions are flat or slightly bumpy. The rings are very shallow features and may overlap slightly, indicating a shallow cup- or dish-like form. Comparison was made with *Nimbia oclusa* of the Valdai Series of the White Sea Region (Fendonkin, 1980c). Similarities were also noted

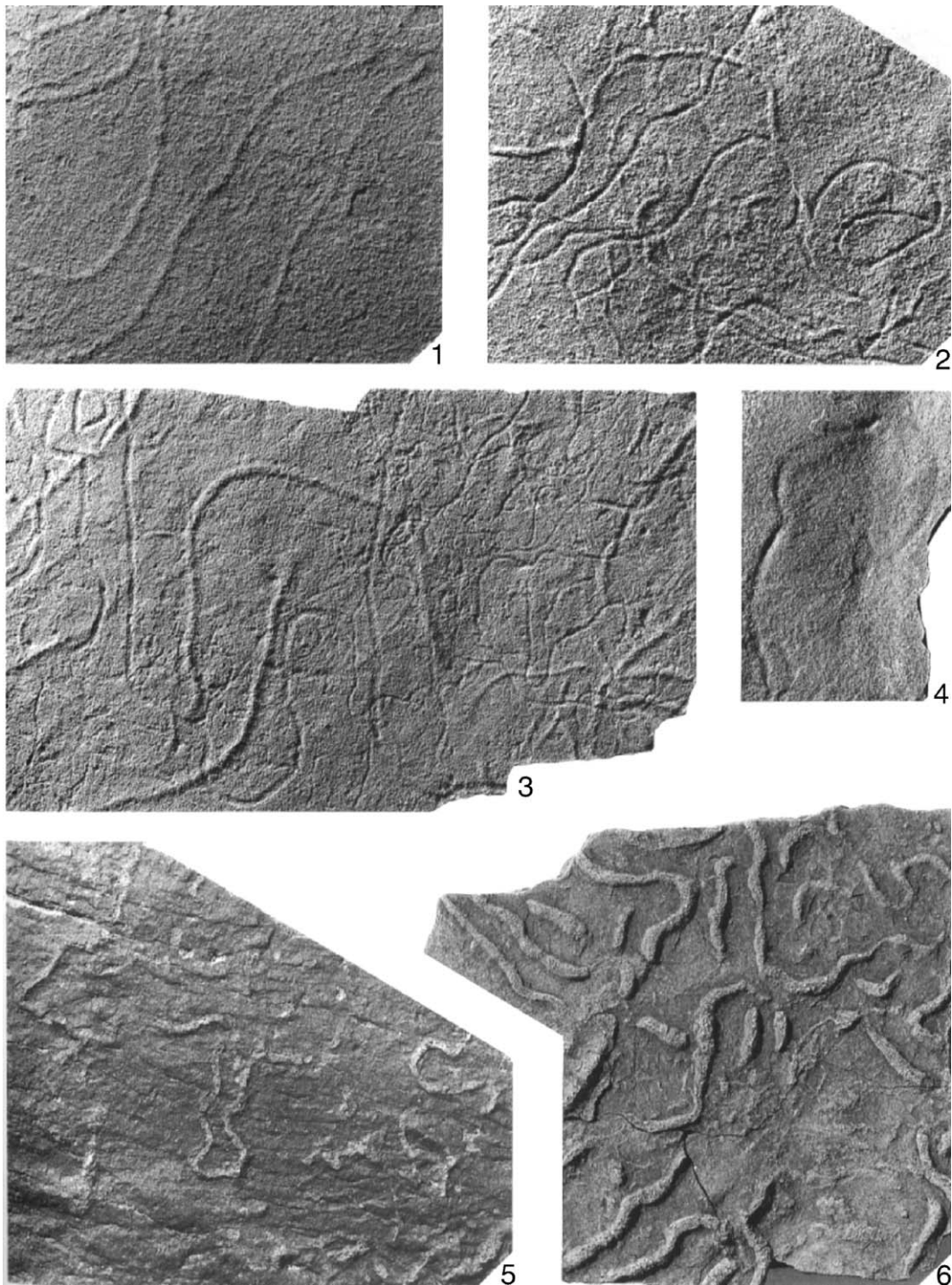


Fig. 82. Trace fossils from the Sekwi Brook South (SBS) and North (SBN). (1) *Helminthoidea* sp., hyporelief (SBN, SBS) ($\times 0.5$), (2, 3) *Helminthoidichnites tenuis* Fitch, epirelief (SBN) ($\times 0.5$), (4) *Helminthopsis* sp., epirelief (SBN) ($\times 0.5$), (5, 6) *Helminthopsis irregularis* (Schafthautl), hyporelief (SBS) ($\times 0.75$) (from Narbonne and Aitken, 1990).

to *Circulichnus montanus*, a species reported from the Ukraine (Gureev, 1986) as well as *Nimbia? gaojiashanensis* and *Annulusichnus regularis*, species reported

from Sha'anxi Province, China (Zhang, 1986), but these show great similarity in size and shape and may eventually be shown to be synonymous, so the first

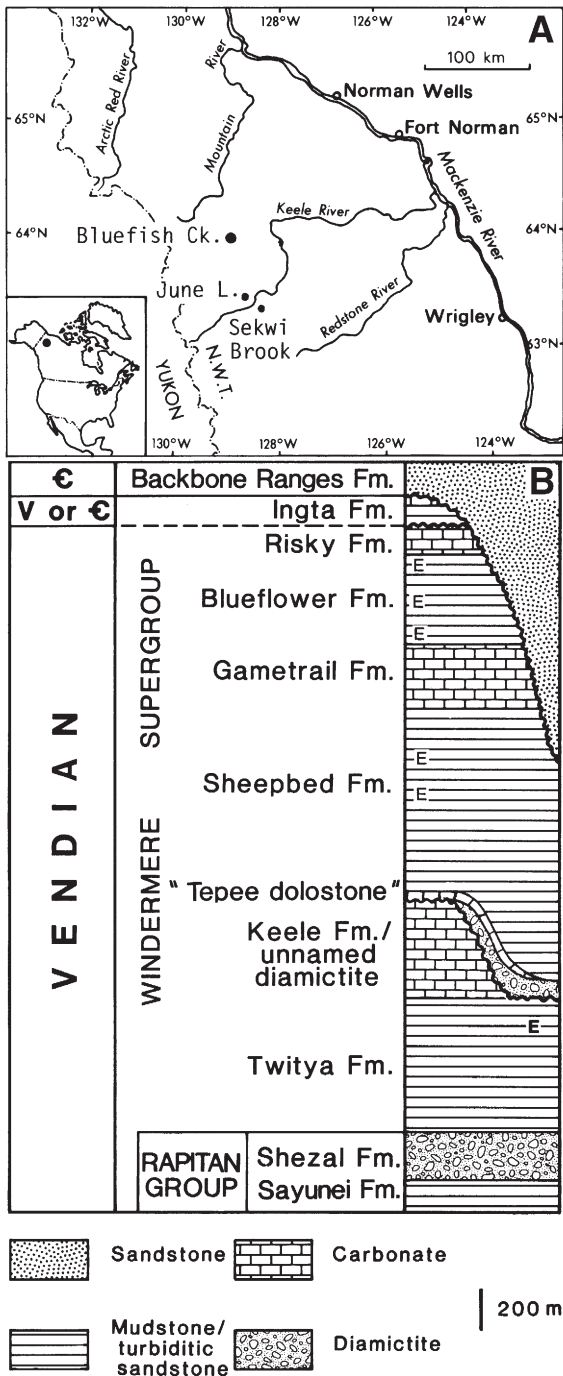


Fig. 83. Occurrence of Ediacara-type remains in the Twitya Formation, Mackenzie Mountains. (A) Location map, (B) composite stratigraphic section (left part of column for June Lake/Sekwi Brook Area; right part of column for Bluefish Creek Area. E=levels with Ediacara-type fossil remains (after Hofmann et al., 1990).

type is referred to the taxon *Nimbia oclusa*. The second type, preserved on the base of a parallel- to ripple-laminated sandstone bed 40 m below the uppermost

Nimbia layer, comprises rounded, closely crowded protuberances with 0.2–2.0 mm relief and 4.6–13.0 mm across. They may have central depressions and may form chains. These structures resemble the species *Vendella haelenicae* and *Vendella larini* recorded in the Vendian of the Ukraine (Gureev, 1987). Similarities were noted to *Beltanelloides simplex*, *Medusinoidea palij* and *Sekwia kaptarenkoe*, all species described by Ryabenko et al. (1988). However, despite the variability observed, Hofmann et al. (1990) believed that they are all variants of one taxon which they named *Vendella* sp. The third type occurs as a single specimen 200 m below the top of the formation, It has the form of a disc measuring 25 mm across, with a central turbercle. Although not unlike *Cyclomedusa*, they find closer similarity to *Irridinitus multiradiatus* from the Vendian of Podolia described by Fedonkin (1983b). The genus is described from elsewhere in Canada by Hofmann et al. (1985) and is probably the impression of a polyp. They named the taxon *Irridinitus?* sp.

These authors noted that this fauna has implications for models such as those of Glaessner (1984) and Sokolov and Fedonkin (1984) which relate the evolution Ediacara fauna to climate amelioration following the Varanger (Laplandian) glacial retreat.

8.2.2.1. Overall review. Narbonne and Aitken reviewed the Neoproterozoic of the Mackenzie Mountains, which they described as an arcuate range of 1 to 3 km high mountains located just south of the Arctic Circle (Fig. 85). They described the older Mackenzie Mountains Supergroup, an epicratonic succession of mainly shallow-water siliciclastic and carbonate sediments in which detrital zircons are dated at 1080 Ma and which is cut by dykes dated at 780–778 Ma. Above comes the Windermere Supergroup, with basal rift deposits and glacial diamictites, overlain by three “Grand Cycles” of siliciclastic and carbonate sediments. In the east, these sediments are of shallow water facies, whereas in the west they are of continental slope facies: the shelf margin prograded progressively southwestwards. The Cambrian boundary is located in the uppermost cycle, the Ingta Formation, being marked by an abrupt change from simple sub-horizontal burrow trace fossils to complex feeding burrows. The sub-trilobite Cambrian strata are c. 1.5 km thick.

Fossils are abundant, acritarchs, carbonaceous mega-fossils and microbial structures occurring throughout the entire succession, but are especially abundant in the Little Dal Group of the Mackenzie Mountains

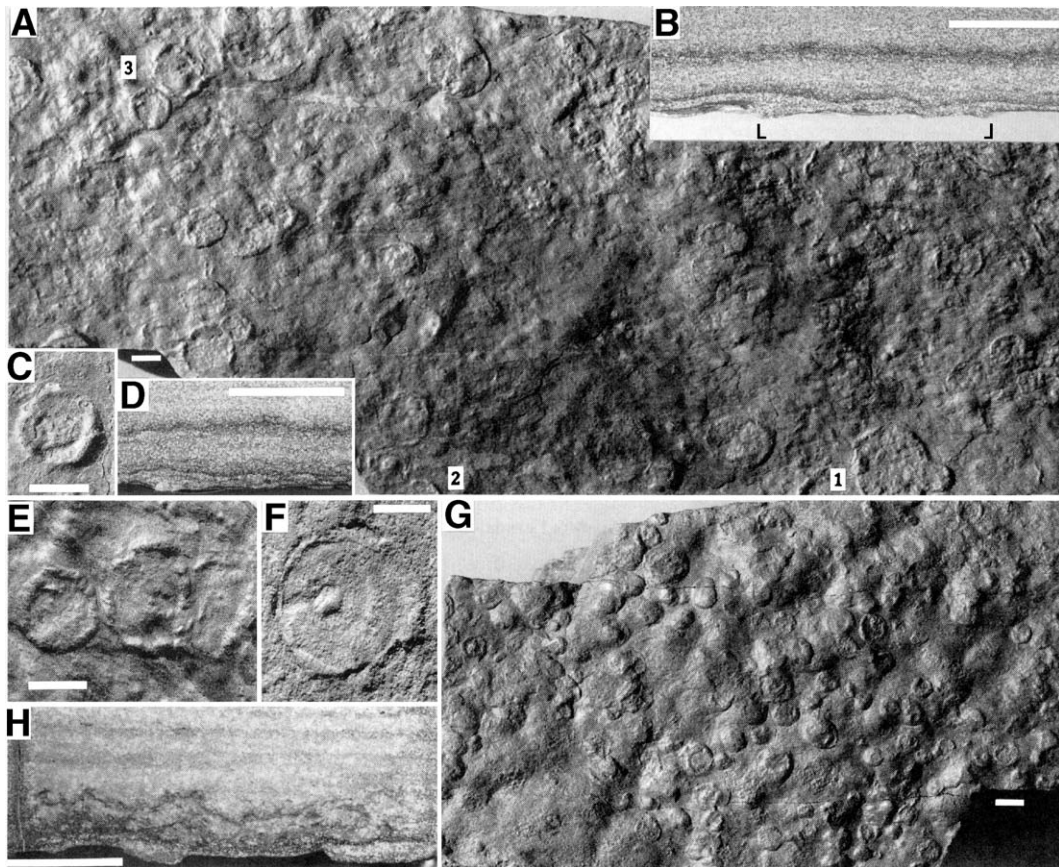


Fig. 84. Ediacara-type fossil remains, Twitya Formation (scale bar = 1 cm). (A) Lower bedding surface with *Nimbia occlusa* (170 m below the top of the Formation), (B) vertical section across specimen 1 in A, (C) lower bedding surface with *Nimbia occlusa* (170 m below the top of the Formation), (D) vertical section across specimen 2 in A, (E) enlarged view of specimen 3 and adjoining ones in A, (F) upper bedding surface with *Irridinitus?* sp. (200 m below the top of the Formation), (G) lower bedding surface with *Vendella?* sp. (170.4 m below the top of the Formation), (H) vertical section of two specimens of *Vendella?* sp., from near the upper left margin of G (from Hofmann et al., 1990).

Supergroup, and Ediacara-type fossils appear just below the second of the glacial units in the Windermere Supergroup and occur through 2.5 km of strata. These authors provided a comprehensive diagram covering the occurrence of microfossils, body fossils and trace fossils throughout the two Supergroups.

8.2.2.2. Chemostratigraphy and biostratigraphy: palaeomagnetism. Narbonne and Aitken noted the possibility of correlation of the two regional glacial diamictite horizons more widely and the fact that the palaeomagnetic record displays three hairpin curves which should be recognisable throughout the continents then attached to Laurentia. Carbonate interbeds typically show unaltered carbon isotope ratios: C and Sr chemostratigraphy shows marked excursions that should be globally correlatable. The last observation refers to the work of Narbonne et al. (1994) The C and Sr isotope abundances confirm that the simple disc-like

fossils in the Twitya Formation, below the upper diamictite horizon, predate all other known Ediacara-type faunas. A second negative $\delta^{13}\text{C}$ excursion occurs just below the palaeontologically (trace fossil) based lower boundary of the Cambrian. The Blueflower faunas correlate chemostratigraphically with faunas in Australia, Siberia, China and elsewhere, but the Sheepbed faunas correlate with those of Namibia, despite taxonomic difference. These results are encapsulated in Fig. 86.

8.2.3. Wernecke Mountains

Soft-bodied metazoan fossils of Ediacara-type were discovered in the Wernecke Mountains, Yukon, by Fritz et al. (1983) (Fig. 87). Both body and trace fossils were recorded by Hofmann et al. (1983), including *Cyclo-medusa davidi?* Sprigg and *Beltanelliformis brunsa*e Menner. Narbonne and Hofmann (1987) carried out further collections (Fig. 88).

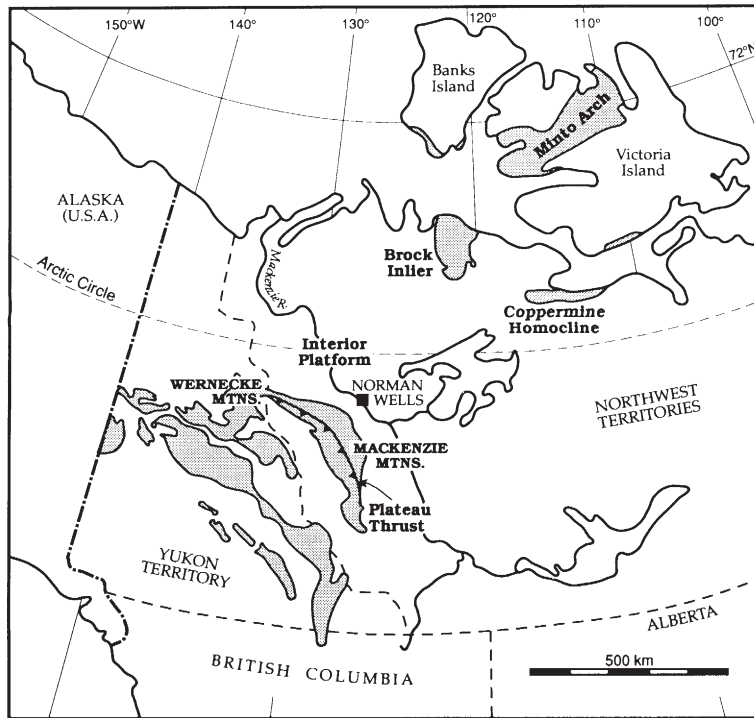


Fig. 85. Location map showing the distribution of Neoproterozoic strata in northwestern Canada (after Narbonne and Aitken, 1995).

The Wernecke Mountains are on the southern edge of the Yukon stable block, a site of mainly shallow water sedimentation throughout most of the late Proterozoic and early Palaeozoic. The strata pass southwards into deeper water shales and turbiditic conglomerates. They are equivalent to the upper part of the mainly clastic Windermere Supergroup, which can be traced through

the Canadian cordillera. The base of the Supergroup is younger than 770 Ma (Park and Aitken, 1986) and probably younger than 730 Ma (Evenchick et al., 1984).

Glaciomarine deposits occur in the lower part of the >2 km thick Windermere Supergroup. These deposits, mentioned above under the Mackenzie Mountains, are probably, according to these authors, equivalent to the

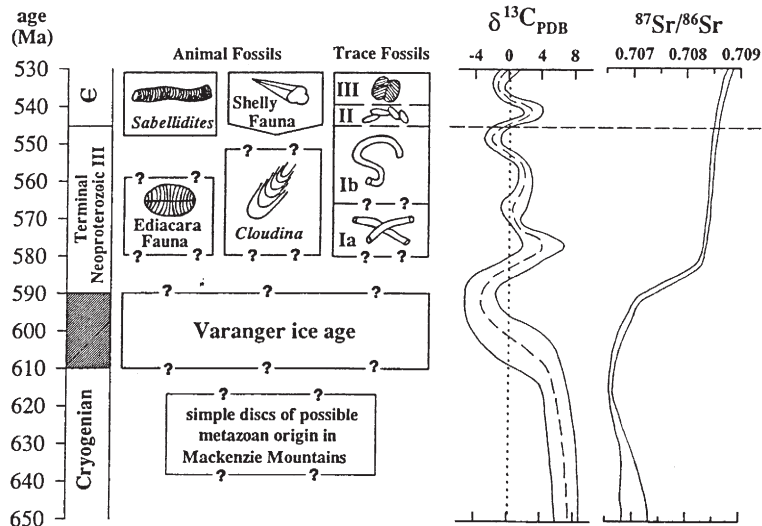


Fig. 86. Global composite of Neoproterozoic-subtrilobite Cambrian stratigraphy (after Knoll and Walter, 1992).

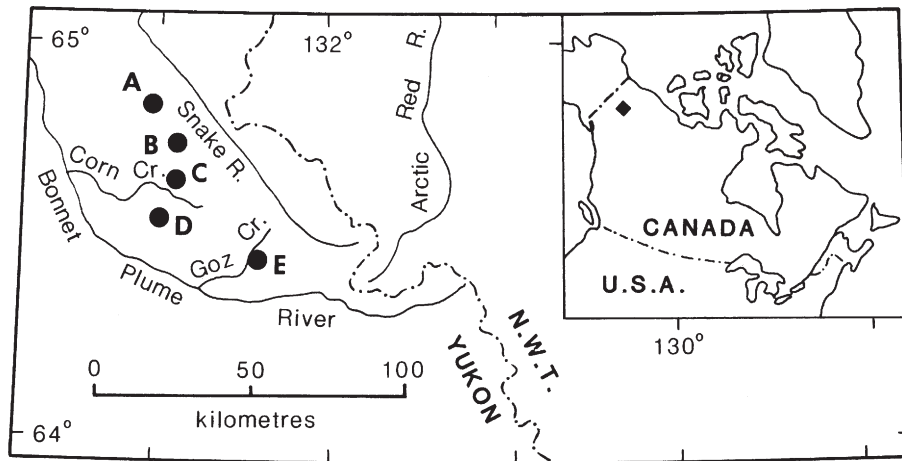


Fig. 87. Location of sections studied in the eastern Wernecke Mountains (after Narbonne and Hofmann, 1987).

Sturtian and Marinoan (Varangian, Laplandian) glaciations (though they could represent two stages of the Varangian glaciation). The Vampire Formation above contains small shelly fossils including *Anabarites trisulcatus* and *Protoherzina anabarica*, indicating probable equivalence to the *Anabarites–Circotheca–Protoherzina* Zone of SW China and the Nemakit-Daldyn Horizon of Siberia, both of which were likely to be placed just below the base of the Cambrian if the proposed base in Yunnan were to be accepted (Cowie, 1985). Trace fossils in the same beds contain arthropod burrows (*Rusophycus* and *Cruziana*), generally regarded as Cambrian or younger. The Vampire formation is conformably overlain by the Sekwi Formation, a carbonate unit containing trilobites of the *Fallotopsis* and *Nevadella* zones close to its base. Thus the Ediacaran fossiliferous strata occur between late Proterozoic glacial deposits and fossiliferous Cambrian strata and may be regarded as Vendian (Ediacaran) in age.

The fossiliferous strata comprise an alternation of carbonate and fine siliciclastic units, the soft-bodied fossils only occurring in the latter. The oldest of them is the 'Goz siltstone', which crops out in an isolated fault block at locality E in Fig. 87. It is lithologically similar to beds at locality D in this figure and also to the Sheepbed Formation of the Mackenzie Mountains. Thin- to medium-bedded siltstone with rare ripple marks and common load structures and channelling are indicative of a deeper water setting than elsewhere locally. Macrofossils occur on bedding planes in the siltstone. Siltstone unit 2 at location D consists of shale and siltstone, together with minor quartzose sandstone and dolostone. Sandstone beds are thin, graded, storm deposits (?). Cross-bedding and desiccation cracks occur in the upper part and these deposits are

interpreted as those of a wave or storm dominated shelf with sandbars. Carbonaceous remains of metaphytes occur in dark shales in the lower part of the unit, whereas metazoan and trace fossils occur as positive features on soles of thin storm-deposited sandstone beds near the top of the unit. Siltstone unit 1 crops out at localities A to D (Fig. 87); it includes more continuous sandstone beds. Sphaerolites are abundant but not desiccation cracks. Deposition probably occurred on a wave- or storm-dominated shelf. Macrofossils occur sporadically throughout the lower two-thirds of the unit, trace fossils are rare in the lower half but common in the upper half. Both occur mainly as positive features on the soles of thin, storm-deposited sandstone beds, but also rarely form negative features on the upper surfaces. No slabs exhibit both body and trace fossils. Shallow sub-littoral environments are indicated except for the fossils in the 'Goz siltstone', which lived in slightly deeper water.

These authors provided quite full descriptions of the fauna which includes 14 metazoan species, one metaphyte, 5 trace fossils and three dubiofossils. Of the body fossils, 11 can be allocated to 9 'medusoid' genera: there is a single pennate coelenterate (a possible attachment process). The gregarious species *Beltanelliformis brunsae* is dominant and of the ichnofossils *Planolites montanus* is common. The fauna is most similar to that of the Russian Platform (Fig. 88): it was suggested that intercontinental correlations of stages and even possibly zones might be achieved. The fauna is more diverse than that of the Mackenzie Mountains, although the strata are clearly equivalent.

Beltanella giles is a smooth disc with a narrow raised rim; two specimens preserved in hyporelief were 36 and 46 mm in diameter and 1.5–1.7 mm in maximum relief.

USSR STRATIGRAPHY		UNIT	WERNECKE MACROBIOTA
VENDIAN OR LOWER CAMBRIAN	lower Baltic 'Series'	Basal Vampire Fm.	Small shelly fossils - <i>Anabarites</i> , <i>Protohertzina</i> Arthropod trace fossils - <i>Rusophycus</i> , <i>Cruziana</i>
		(Hatched area)	
UPPER VENDIAN	Kotlin 'Series'	Risky Fm.	Simple trace fossils - <i>Palaeophycus</i> Simple trace fossils - <i>Planolites</i> , <i>Gordia</i> , <i>Neonereites?</i> Megafossils - <i>indet. medusoids</i>
		Siltstone unit 1	Simple trace fossils - <i>Gordia</i> Megafossils - <i>Beltanella</i> , <i>Beltanelliformis</i> , <i>Charniodiscus</i> , <i>Cyclomedusa</i> , <i>Ediacaria</i> , <i>Kullingia?</i> , <i>Medusinites</i> , <i>Nadalina</i> , <i>Rugoconites?</i> , <i>Spriggia</i> , <i>Tirasiana</i>
	Carbonate unit 1	No biota	
	Siltstone unit 2	Simple trace fossils - <i>Planolites</i> Megafossils - <i>Beltanelliformis</i> , <i>Medusinites</i> , <i>Rugoconites?</i> Vendotaenid algae - <i>Vendotaenia?</i>	
	?-?		

Fig. 88. Proposed correlation of the upper part of the Windermere Supergroup with the Vendian of the Russian Platform (after Narbonne and Hofmann, 1987).

Charniodiscus? sp. was represented by 19 specimens as convex epireliefs and concave hyporeliefs. Rough textured central discs are surrounded by smooth, flat outer rings. External diameters are 7.5–21.0 mm.

Cyclomedusa plana Glaessner and Wade, 1966 was represented by a single partial circular impression, an inner disc with a small bud-like concentric pattern superimposed in a third fold. The outer zone is smooth, with a narrow annulus of low relief at the margin. The diameter of the disc is 52 mm. Interestingly, the specimen figured also shows a sinuous trace fossil.

Cyclomedusa sp. has a distinct small central tubercle or pit. There are 15 specimens from the 'Goz siltstone' in epirelief. There is a scarcity of radial grooves in the Wernecke specimens which may simply indicate aboral surfaces of *Cyclomedusa davidi*. The diameters range from 17 to 76 mm.

Ediacara flinders Sprigg (1947) forms very large circular structures with tripartite organisation, three concentric discs. The largest of two specimens is 222 mm in diameter. This is the largest 'medusoid' known from the Ediacara type area and these two are at the upper end of the size range, and are most similar to a specimen from the White Sea coast described by Fedonkin (1985a).

Kullingia? sp. is represented by two specimens preserved as discoidal hyporeliefs, 54 and 60 mm in diameter, with about 1 mm of relief. The surface is smooth with faint closely spaced and regular concentric wrinkles. The larger size and more regular concentric ridges set them apart from *Beltanelliformis*.

Medusinites asteroides (Sprigg) Emend Glaessner and Wade, 1966 is represented by three specimens with subcircular convex hyporelief, composed of a smooth central disc separated by a subcircular groove from a broad, smooth outer ring, itself surrounded by a groove. Outer diameters 9.0, 20.5 and 25.6 mm, central disc diameter 4.3, 10.9 and 8.3 mm, relief respectively 0.8, 1.3 and 1.8 mm. The three specimens most closely resemble the holotype and two specimens described by Glaessner and Wade (1966).

Nadalina yukonensis sp. nov. is a new genus and species and the single whole specimen described is the type specimen. It is a discoidal structure of centimetric size with a large smooth inner disc, separated from the surrounding annular field with a narrow rim of small relief by a ring of numerous equally spaced millimetric pits: the width of the annulus is one half the radius of the inner disc. The type specimen, which is preserved in elliptical epirelief on medium grained sandstone,

measures 62×55 mm. There is a partial impression of a second specimen on the same slab.

Rugoconites? sp. is a single specimen poorly preserved as a hyporelief convex disc measuring 29×32 mm and with 2.7 mm maximum relief. There appear to be short radial bifurcating furrows suggestive of *Rugoconites*, a genus not reported until then from outside Australia.

Spriggia wadeae Sun 1986 is represented by a single disc preserved as convex hyporelief, 20 mm in diameter and with relief of 0.7 mm. Annular ridges increase in with outwards. Attached to one side of the disc is an irregular crescentic marking, with rough irregularities within it.

Trasiana sp. is represented by small discoidal hyporeliefs 10–18 mm in diameter and with a relief of 0.5–1.0 mm. They show tripartite organisation, a small central tubercle being surrounded by an inner disc that extends half way to the periphery and is surrounded by a broad outer disc. A circular groove separates inner and outer disc. There may be subsidiary circular wrinkles as well as indistinct radial markings.

Beltanelliformis brunsa Menner, in Keller et al. (1974) (Fig. 89) ranges in diameter from 2 to 3 mm to more than 30 mm, being smaller in siltstone unit 2 than in siltstone unit 1, i.e. it gets larger with age. Flat to button-shaped, circular to subcircular convex hyporeliefs, with some concave epireliefs, with less commonly concave hyporeliefs and full reliefs, measuring 2.2–33.1 mm across, have mean relief of 1.35 mm. Individuals are typically closely crowded together, with pronounced unimodal size distribution for specimens on individual bedding planes, indicating that each sample represents a population at the same stage of ontogenetic development, developed on a mud substrate before the arrival of storm-deposited sand. Specimens with high relief are smooth or have linear, curvilinear, bifurcating or star-shaped furrows. Those of low relief have narrow concentric peripheral folds or wrinkles and smooth central fields. Vertical sections of complete high-relief specimens show their lenticular nature with massive semicircular bottoms, deformed upper semicircle and involuted sides; internal sediment fill is laminated, graded, massive or exhibits slump structures. The hemispheres were passively filled with laminated or massive sediment.

The trace fossil descriptions of Narbonne and Hofmann (1987) are particularly lucid and more attention has been given to them here for this reason than to some other such detailed descriptions. *Gordia marina* Emmons, 1844, is preserved as convex epireliefs and concave hyporeliefs on thin beds of

fine-grained sandstone. The burrows are horizontal and irregularly meandering, lacking true branching but with some cross-overs. The burrows are smooth of c. 1 mm diameter, and the fill is the same as the host lithology. *Neonereites* sp. occurs in convex hyporelief on thinly bedded, fine-grained sandstone. Burrows are moderately sinuous, up to 90 mm long and consist of a uniserial string of sp 3–5 mm in diameter, spherical to slightly ellipsoidal pellets, some in contact but typically irregularly spaced. Pellets are composed of well-sorted sand. *Planolites montanus* occurs in convex hyporelief and convex epirelief on very thin beds of siltstone and fine-grained sandstone. Burrows are very sinuous and undulatory, occurring on bedding surfaces as small knobs and discontinuous, curved burrow segments. They are cylindrical with diameters ranging from 0.4 to 2 mm, and have a faint pinch and swell appearance. True branching and cross-overs are rare. The burrow fill is structureless and differs from the host lithology.

The single metaphyte recorded had the form of isolated, smooth carbonaceous ribbons, curved and bent, 0.4–2 mm wide and up to 30 mm long, with faint longitudinal striae. It was identified as *Vendotaenia* sp.

8.3. British Columbia

8.3.1. Rocky Mountains

Hofmann et al. (1985) described the discovery of metazoan fossils in the upper part of the Hadrynian Miette Group of the Windermere Supergroup in the Mount Robson Provincial park, British Columbia, close to the continental divide (Fig. 90). This find extended the geographical range of the cosmopolitan Ediacara-fauna to a new locality, in the upper part of the Miette Group, which crops out on both limbs of the broad Mount Robson Syncline. The fossil-bearing green siltstone is located on the west side of Mount Fitzwilliam, near the base of a carbonate unit draping a 12 m high stromatolite mound, one of similar mounds up to 30 m thick in a 100 m thick interval at the base of the carbonate unit. The carbonate unit is interpreted as a platform sequence and named the Yellowhead Platform; it is 400 m thick at this locality. It consists of stromatolite mounds and crinkly laminated dolostone in the lower part, followed by pisolitic, intraclastic peloidal dolostone. Underlying the platform are 120 m of poorly exposed, medium to dark grey and brown shales and siltstones containing lenses and beds of quartz sandstones. The remainder of the Miette Group, a 1000 m thick sequence of dark-grey to black fine grained clastics, is not exposed at this locality. The

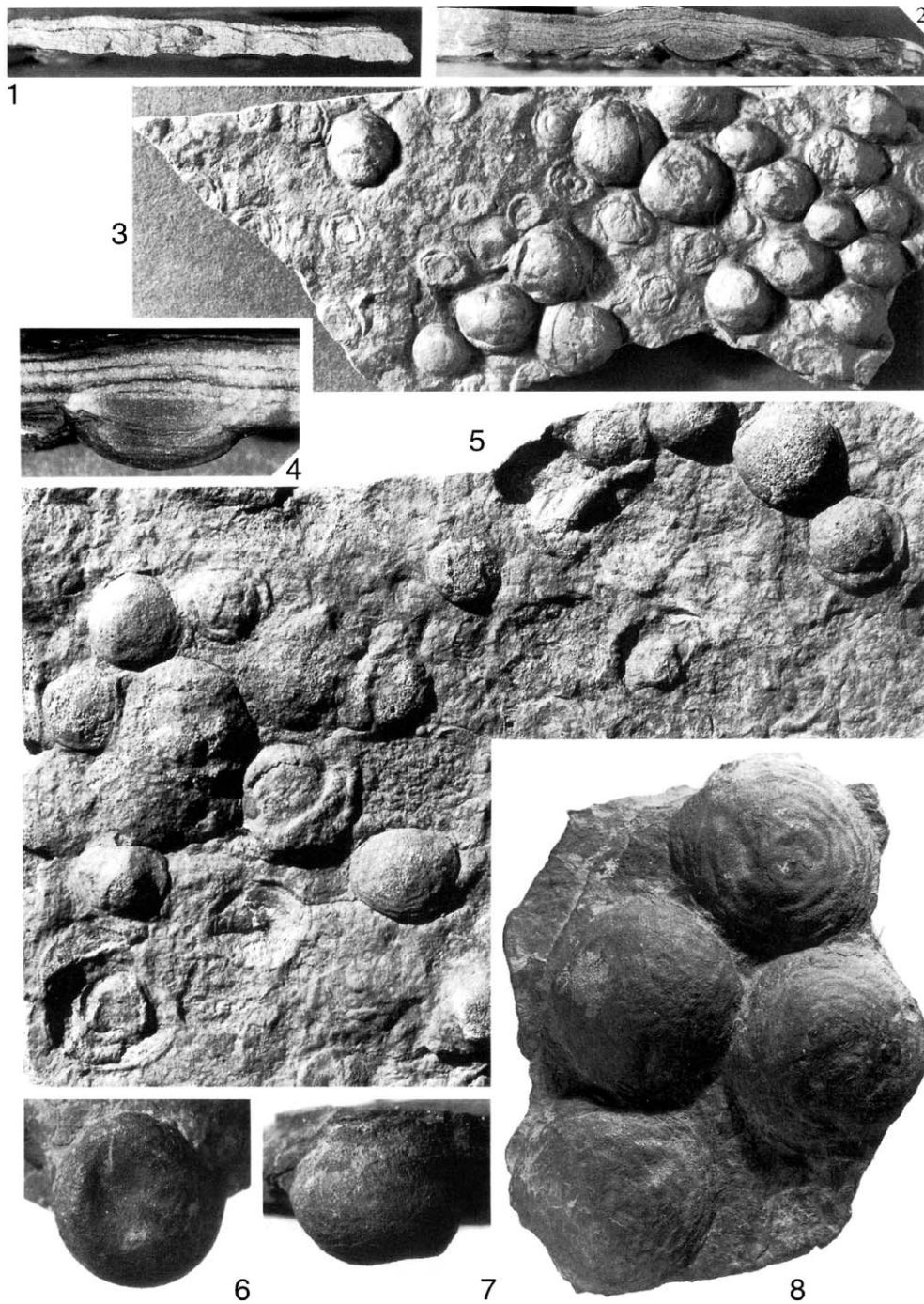


Fig. 89. Ediacara-type body fossils from the Wernecke Mountains. 1–8: *Beltanelliformis brunsae* Menner [(1) vertical section, left hand margin of 3; (2) vertical section along upper right hand margin of 3, showing draping of laminae over specimens ($\times 1$); (3) lower surface showing close association of high and low relief forms ($\times 1$); (4) vertical section showing laminated fill and slight draping of large specimen ($\times 1$); (5) cluster with specimens in both convex and concave hyporelief ($\times 0.7$); (6) bedding pane view of specimen preserved in full relief ($\times 2$); (7) side view of same ($\times 2$); (8) largest specimen observed in the Wernecke assemblage ($\times 1$)] (from Narbonne and Hofmann, 1987).

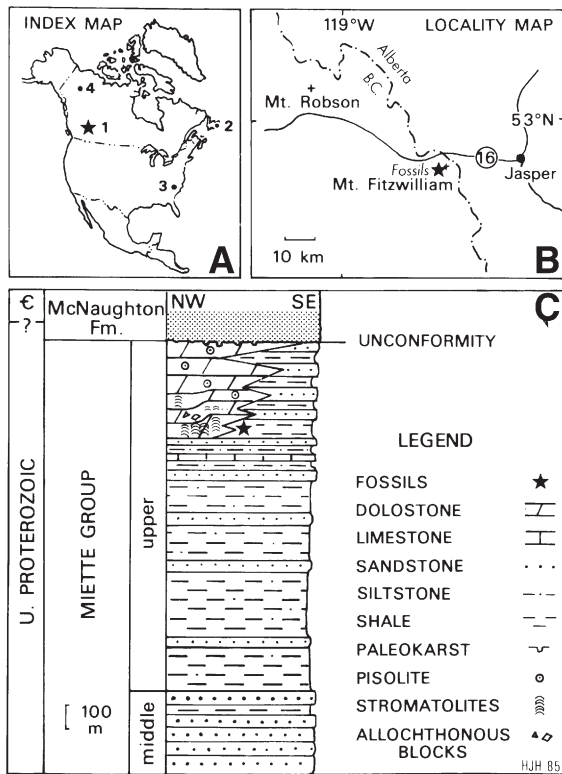


Fig. 90. Index map (A) showing the location of the Ediacara-type fossil finds in British Columbia (1) and previously reported occurrences in Canada and the United States (2–4); locality map for the Mt. Fitzwilliam area (B); stratigraphic section showing the position for the Ediacara-type fossils (C) (after Hofmann et al., 1985).

sandstones and conglomerates of the McNaughton Formation are separated from the carbonate unit below by a palaeokarst surface, and above this come the Mural Formation with trilobites of the *Nevadella* zone. The base of the Cambrian is undefined, but is taken to be close to the base of the McNaughton Formation, the Miette Group being upper Proterozoic (Vendian).

The fossils comprise 24 scattered, complete and partial elliptical impressions on the upper bedding plane surfaces of four slabs (Fig. 91). They range from 10 to 69 mm in maximum diameter. They are all interpreted as medusoid impressions and are tentatively assigned to three taxa, *Cyclomedusa davidi* Sprigg, the genus *Irridinitus* Fedonkin and the genus *Protodipleurosoma* (Sprigg, 1947). *Cyclomedusa* is the most widespread genus in the Ediacara type-area fauna, the second has only been definitely recorded from the White Sea fauna and the third has been described from the Ediacara type area and the White Sea. The last two were hitherto unknown in North America. Glaessner (1979c) considered *Protodipleurosoma* Sprigg to be synonymous with *Ediacaria* Sprigg; Fedonkin (1981a) described a species

Protodipleurosoma rugulosum from the White Sea. Hofmann et al. (1985) considered that this new find established the presence of the coelenterate-dominated Ediacara-type fauna in Canadian Cordillera, 1200 km south of the previously reported find in the Mackenzie Mountains (Hofmann et al., 1990). They suggested that more exposures of such a fauna were likely to be found in the Canadian Cordillera.

8.4. Conclusion

This major province of three separate occurrences in the Canadian Cordillera has been studied in considerable detail and has greatly extended our knowledge of the Vendian System and Ediacara-type soft-bodied faunas. It is the only one of the global occurrences in which soft-bodied organisms occur in interbeds separating tillites below the fossiliferous sequence (of Varanger, =Laplandian, =Marinoan) age; and, like the Newfoundland occurrences, includes fossils of soft-bodied organisms in sediments of quite deep-water, turbidite facies. In contrast to Newfoundland, where frond-like forms are

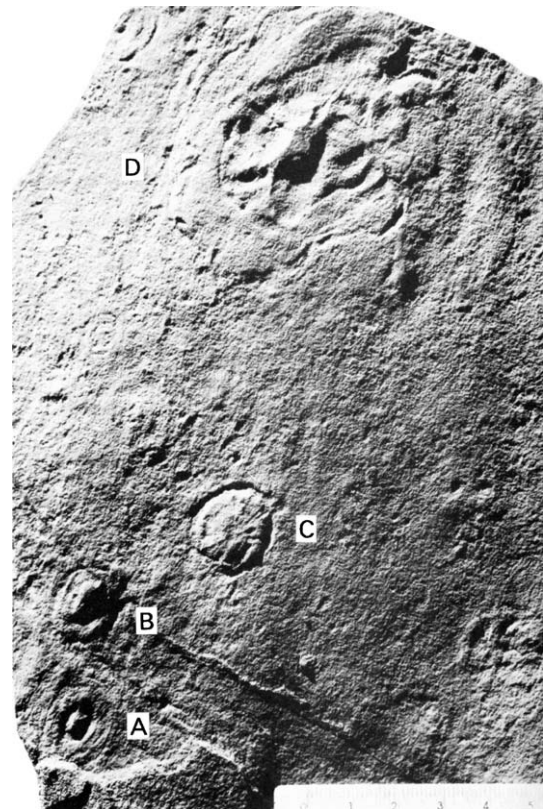


Fig. 91. Ediacara-type fossils from the upper part of the Miette Group. (A) *Cyclomedusa davidi*?, (B) *Irridinitus* sp., (C) *Protodipleurosoma* sp. (from Hofmann et al., 1985).

profuse, in this province, it is the discoidal fossils that predominate and frond-like fossils are rare.

The Cordillera continues southwards into the United States and the very north of Mexico. The occurrences there, for which the descriptions are less detailed, due either to a lack of diversity or less full publication, are described in Section 11.

9. Australia

9.1. Introduction

In Sections 9–13 other less well-researched occurrences are described. Besides the type-area for the development of Ediacara-type faunas in the Flinders Ranges of South Australia, there are three less significant developments in Australia:

Amadeus Basin, Northern Territory
Kimberleys, Western Australia
Stirling Range, Western Australia

9.2. Amadeus Basin, Northern Territory

9.2.1. Arumbera Sandstone

Glaessner and Walter (1975) reported the discovery of new Precambrian fossils from the Arumbera Sandstone in the Amadeus Basin, Northern Territory. The fossils were found at three localities, two 14 km SW of Alice Springs and the other 22 km WSW. Fossils were reported to be abundant at the stratigraphically higher of the first two localities and also at the latter locality, near Valley Dam on Laura Creek. The fossils were mostly found on sole surfaces of beds although some were found on upper surfaces. The hosts are 5–20 cm thick sandstone beds, with interbeds of siltstone and the bedding surfaces consist of irregular mounds and

hollows. Flute moulds are present and the fossils may be superimposed on ripple marks. Twenty-four rock slabs were collected.

The Arumbera Sandstone is about 500 m thick in the Laura Creek area and the lower part had been considered to be Precambrian since the discovery of a single fossil specimen named *Rangea* cf. *Longa* Glaessner and Wade, a component of the Ediacara soft-bodied fauna (Glaessner and Wade, 1966). The Arumbera Sandstone was divided into three units by Daily (1972) and units II and III contain the trace fossils. The fossils were discovered 85 m below a green siltstone at the base of Unit II. *Rusophycus*, *Diplichnites*, *Phycodes pedum* and *Didymaulichnus*, present in Unit II, are considered not to occur before the Early Cambrian. Unit I contains components of the Ediacara fauna and also *Hallidaya brueri* Wade, a component of the Mount Skinner fauna (Wade, 1969). The Olympic (upper tillite) member of the underlying Pertatataka Formation has yielded a radiometric age of c. 670 Ma (Walter, 1972b)

Fossils named *Arumberia banksi* gen. et sp. nov. were described as hollow, compressible ribbed bodies composed originally of flexible tissue, of conical to cylindrical shape and attached by a blunt apex (Fig. 92). Ribs are flat, 0.3–7.0 mm wide, divided by shallow grooves 0.05–0.7 mm wide. Ribs bifurcate in places and may incorporate finer ribs. Distal margin is indistinct. There is no trace of inner walls or septa.

The ribbing and grooving were interpreted as biogenic as it was considered that “they could not have been caused by mechanical forces”. The authors compared these bodies with *Namalia*, *Nasepia* and *Baikalia*, and concluded that despite similarities they could not be allocated to any systematic taxonomic position. Nevertheless, they concluded that they represented cup shaped animals and illustrated their conclusions with a diagram.

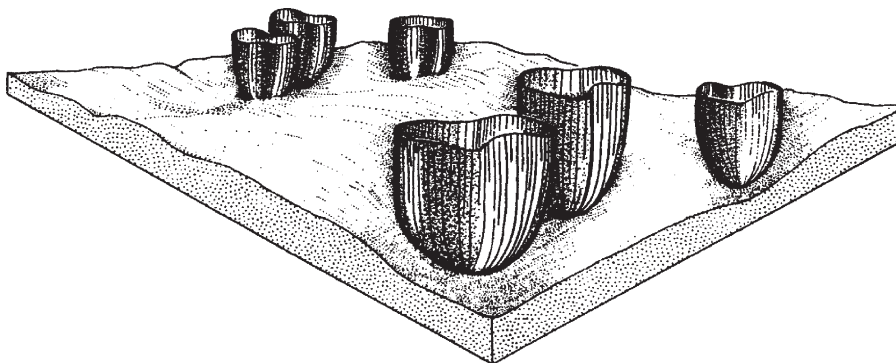


Fig. 92. Diagrammatic reconstruction of the appearance of *Arumberia banksi* during life. Each cup is 5–20 cm high. Only selected longitudinal ribs are shown (after Glaessner and Walter, 1975).

9.2.2. Further discoveries

McIlroy et al. (1997) studied the nature of the Precambrian–Cambrian transition within the Arumbera Sandstone in the northern Amadeus Basin in an attempt to determine whether evolution across this boundary was episodic or explosive. They could find no major facies differences between the unfossiliferous units I and II and the rich trace fossil bearing units III and IV (the subdivision system used divides Daily's unit I into two units, with two more above). The lowest sedimentary cycle of Arumbera III is devoid of trace fossils.

The sequence was revised by McIlroy et al. (1997). The transition to the Arumbera Sandstone at the base from carbonate sediments is abrupt. The sedimentary sequences within the Arumbera Sandstone generally commence with interbedded shales and poorly sorted sandstones that are bioturbated in the Cambrian part of the sequence. The sandstones may be turbiditic or indicative of a fluvial/deltaic regime locally. Sorting improves upwards, also the development of soft rock deformations.

McIlroy et al. (1997) provided sections of the sequence at Ross River Gorge, Cyclops Bore, Valley Dam, Hugh River and Wyeecha Springs. The Ross River section shows the appearance of trace fossils at the Cambrian boundary, at first few in number and then numerous, listing their taxonomic names. In the Valley Dam section (Fig. 93), the body fossil *Hallidaya brueri* occurs in the Neoproterozoic near the base or just above level A and *Kullingia* just below the erosive contact between levels A and D. Near Hugh River, they had found *Kullingia*, similar to that figured by Foyn and Glaessner (1979) from Norway. *Hallidaya* and a single specimen of *Kullingia/Ovatoscutum* sp. were also reported from Wyeecha Spring, the latter just below level C. These authors noted the occurrences of *Arumberia*, which they refer to as 'the flute-like pseudofossil'. They noted that a depauperate Ediacara-type fauna has been located previously at Valley Dam and Deep Well (Wade, 1969; Taylor, 1959) and that they had found further occurrences at Wyeecha Springs and near Hugh River. Trace fossils were recorded confidently from the Neoproterozoic part of the Arumbera sandstone for the first time. The changes in trace fossil diversity across the Precambrian–Cambrian transition show obvious parallels with the Flinders Ranges, and elsewhere in the world (Jenkins, 1995; Crimes, 1992).

The absence of trace fossils in Arumbera I compared with the Flinders Ranges was remarkable and these authors carried out many fruitless searches. It was concluded that the palaeoenvironment was unsuitable

for metazoan life or that taphonomic processes worked to destroy the usually very delicate Neoproterozoic trace fossils by current scouring before sandstone deposition. The latter answer was favoured.

A sharp lithostratigraphic change associated locally with channelling into the underlying Neoproterozoic sediments marks the Precambrian–Cambrian boundary on the northern margin of the Amadeus Basin, and coincides with a marked seismic reflector subsurface through strata between levels B and C (Kennard and Lindsay, 1991). Ediacara fauna, where developed are thus considered to be of Neoproterozoic age. In several sections, however, it is difficult to pick up the boundary on lithostratigraphic grounds or by an erosion surface. The lack of distinct traces in the oldest Cambrian beds did not help. It was concluded that a better stratigraphic correlation could be obtained by the use of strontium and carbon isotope based chemostratigraphy (as lately achieved in Siberia and Mongolia).

9.3. Western Australia: Kimberleys

This region in the extreme northeast of Western Australia was reconnoitred by Dr Wade in 1924 for hydrocarbons and the geology has been summarised by Grey and Griffin (1990). It is most probable that the only Ediacaran-type fossil discovered here by Wade comes from the Mount John Shale Member, a sequence of thinly black- and grey-laminated shales with interleaved cherty siltstone. The locality was however only given as "the Mount John Osmond Range".

This fossil occurrence was described by Sprigg (1949) together with some of his Ediacara finds from South Australia (Fig. 94). It was named *Protoniobia wadea* Sprigg gen. et sp. nov. It was described as a circular impression, 4.1 mm in diameter, with a few prominent annular undulations. Nodular structures in the centre are arranged in a polygonal pattern about a central depressed zone, the platform containing the nodular structures being slightly wider than the central zone and surrounded by a deep circular groove. Then come annular ridges separated by a second groove. There is a suggestion here of radial canals. Bud-like appendages occur opposite one another outside the circular structure, are incomplete hexagons and have concentric ridge and groove structures within them. He considered it to be a medusoid impression and compared it with the unique *Niobia dendrotentacula* (Mayer, 1900) of the Tortugas, Florida. Sprigg drew a comparison diagram (Fig. 94B). This is clearly a body fossil and resembles Ediacaran medusoids. The Kimberleys is a vast region and exposes great expanse of Proterozoic to

lower Palaeozoic rocks and there could well be further Ediacaran-type fossils recognised there in the future.

Although Sprigg recorded this occurrence as Cambrian, the age of the Mount John Shale Member as given by Grey and Griffin (1990) is 1128 Ma (± 110 Ma) citing Dow and Gemuts (1969). This would not equate with

the age of the Pound Quartzite of the Ediacara type area, being much older than the Vendian. However, age dating evidence in the Kimberleys is somewhat meager. Sprigg reported another occurrence of this fossil type in the Ediacara type area as somewhat smaller (20 mm) and with four daughter buds.

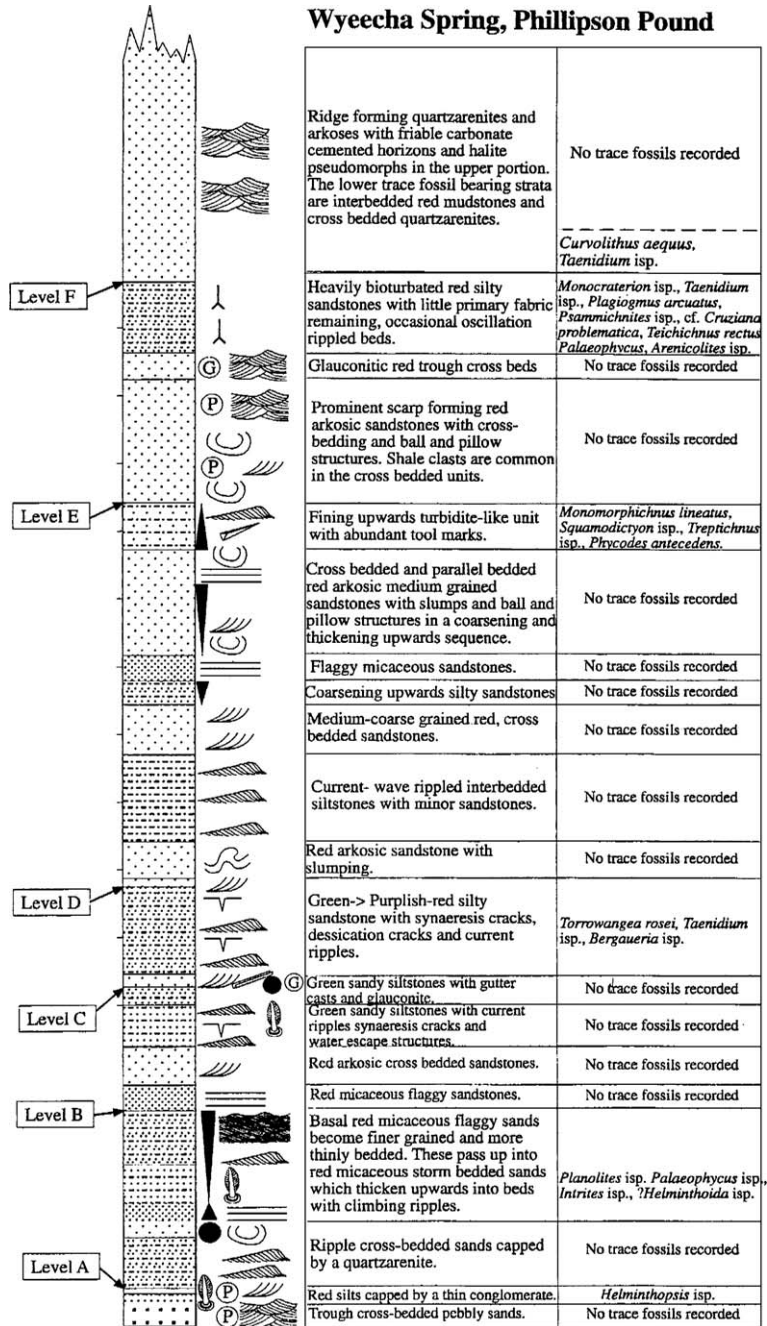


Fig. 93. Sectional diagram, the Neoproterozoic–Lower Cambrian succession of the Arumbera Sandstone at Valley Dam, Western Macdonnell ranges (after McIlroy et al., 1997).

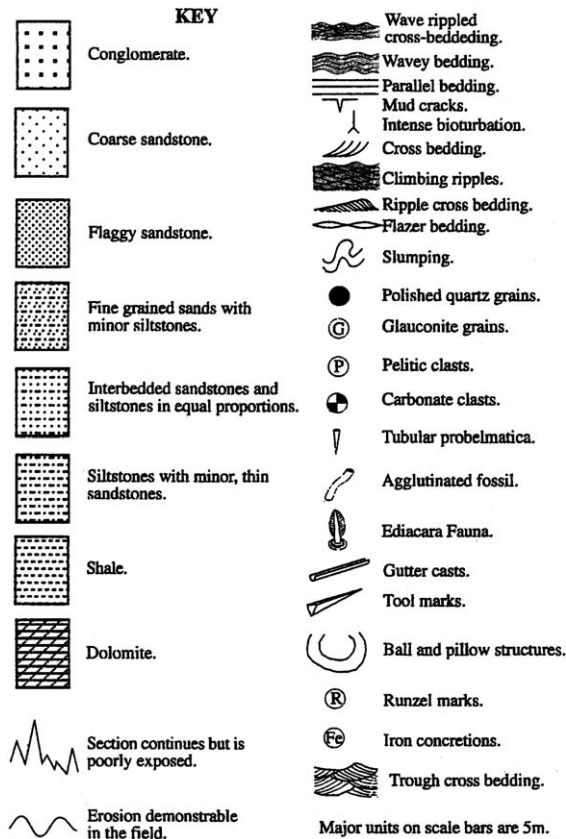


Fig. 93 (continued).

9.4. Western Australia, Stirling Range

Though in material terms the fossils so far recorded are slight, the discovery by Cruse et al. (1993) in the Stirling Range is of great interest because of the uncertainty about the age of these rocks.

The Stirling Range forms part of the Albany–Fraser Orogen (Myers, 1990) which includes large areas of gneiss and three tracts of sedimentary rocks, the Stirling Range Formation, the Mount Barren Group and the Woodline Beds, in isolated outcrop areas from west to east (Fig. 95). The Mount Barren beds vary from greenschist facies rocks to kyanite–sillimanite–staurolite–garnet bearing rocks, the Stirling Range rocks are of greenschist facies and the Woodline Beds, poorly exposed to the northeast of the Mount Barren outcrops, are probably similar. The Stirling Range beds have undergone two periods of folding and display fine crenulation cleavage. The sequence is monotonous and consists of alternating orthoquartzite and phyllite beds, deposited in a shallow, tidal marine environment. Despite the folding, metamorphism and cleavage, the quartzite display a wealth of sedimentary structures.

Possibly due to late faulting rejuvenating the topography, the Stirling Range forms a spectacular line of high peaks. Access to exposure is extremely difficult, except on well-worn foot tracks, and thus enormous areas of exposure have probably never been examined by geologists. Turek and Stephenson (1966) derived ages of 1340 and 1130 Ma by whole rock analysis Rb–Sr determination on five slate samples, and these beds have long been equated with the Mount Barren and Woodline occurrences to the east. The problem of age will be further discussed later.

Woolnough (1920) reported that “no trace of fossils has been detected despite an arduous search” and several other geologists reached the same conclusion. However, Cruse et al. (1993) reported discoid impressions measuring 8–40 mm, scattered on bedding top and bottom surfaces of medium-grained quartzite at two localities. Surfaces measuring 1 m² in area displayed many closely spaced imprints (Fig. 96). They are elliptical due to superimposed strain imposed during the folding process. The elliptical bodies are characterised by concentric annulations and radial structures. One larger imprint, measuring 30 mm in diameter (Fig. 97), is preserved in convex relief and is composed of three concentric zones; an inner 2.5 mm radius nodular zone; a 5 mm wide elevated zone with radial grooves; and an outer zone 5–6 mm wide consisting of three concentric rings. Faint parallel lines extend from the outer margin of the disc, suggesting that the disc is the buried attachment of a benthic metazoan such as *Charniodiscus*. Such discs attached to stalks are well-documented in Ediacaran assemblages. The smaller discs are on a fine to medium grained quartzite slab. They have depressed centres. Two closely spaced discs are on the trough and ridge of ripples formed in shallow water.

Cruse et al. (1993) believed that this unquestionable Ediacaran-type fossil occurrence indicated a revised age span of the Stirling Range Formation of 590–540 Ma, that of other analogous occurrences worldwide. If so, the Stirling Range Formation must be unconformable on the 1150–1190 Ma rocks of the Albany mobile belt gneiss. There is a very well-founded Rb–Sr age determination for the Mount Barren Group of 1077 Ma (Thom et al., 1980), so they suggested that the two sedimentary sequences are not of the same age and that the Turek and Stephenson age was that of detrital micas in the Stirling Range slates. However, although this inference may prove to be correct with further radiometric dating, it is perhaps dangerous to assume that all Ediacara-type fossils must be within such a narrow Neoproterozoic age span: and the argument

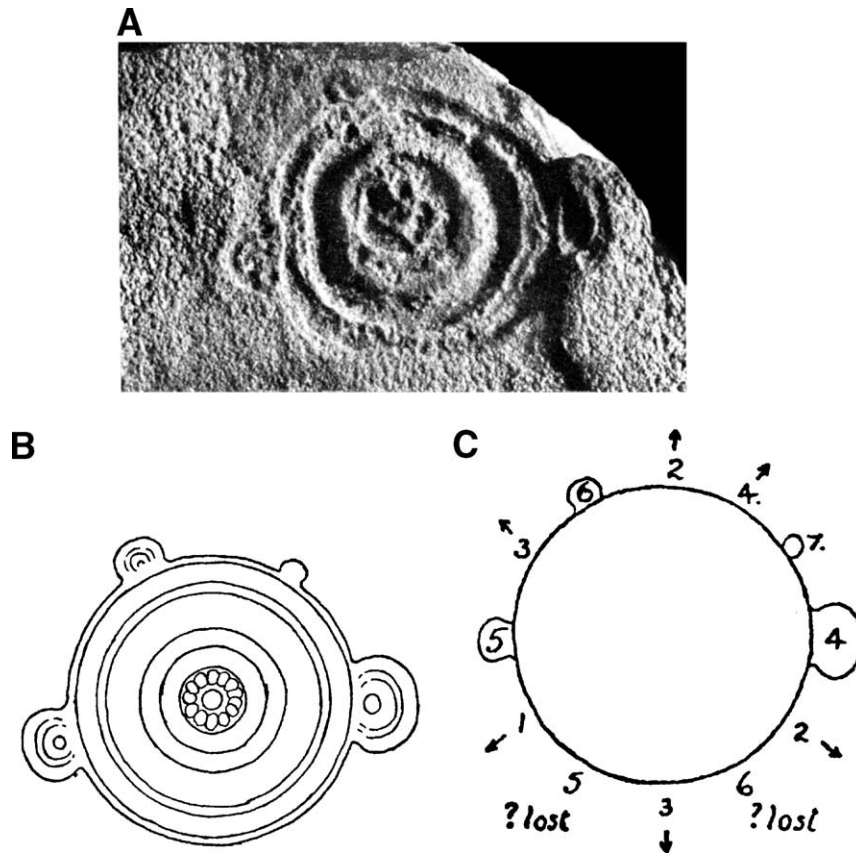


Fig. 94. (A) *Protoniobea wadea* Sprigg, holotype no. 102, Commonwealth Palaeontology Collection, Canberra A.C.T., collected by A.L. Wade from “lower Cambrian flags”, Mt. John Osmond Range, Kimberleys, Western Australia (from Sprigg, 1949). (B) Reg Sprigg’s drawing of the above (from Sprigg, 1949).

could be turned on its head, the conclusion being drawn that this represents an early development of Ediacaran type fossils in the late Mesoproterozoic. Palaeomagnetism could also provide valuable evidence.

Cruse and Harris (1994) mentioned the small discoid trace fossils (*I*) with central protuberances, which had been assigned to *Bergaueria*, and the larger discoidal impressions which they now compared closely with *Cyclomedusa* (Fig. 98). They again favoured a timespan of 590–540 Ma.

Rasmussen et al. (2002a,b) reported the results of U–Th–Pb geochronology on detrital zircon and monazite constraining the depositional age of the Stirling Range sequence to between 2016 Ma (± 6 Ma) and 1215 Ma (± 20 Ma), i.e. establishing a middle Proterozoic age. They also reported U-shaped trace fossils, apparently feeding trails produced by vermiform organisms with well-developed mucus producing capacity and capable of strong distortions of its body shape.

It is suggested that the Stirling Range Formation calls for both an extended search for further fossils (as

do the (?) greenschist-facies Woodline Beds) and their extension in the Queen Victoria Spring outcrops to the south.

The most recent word on this occurrence is in an abstract by Bengtson et al. (2002) who recorded trace fossils and discoid fossils in low-grade metamorphic sandstones. These had been identified as Ediacaran a decade before, although Rb–Sr whole-rock dating suggested a minimum age of 1.1 Ga. These authors did independent radiometric and palaeontological work on the fossil-bearing sequence and derived a range of 2.0–1.2 Ga, much older than the Ediacaran. Although the discoid fossils are of uncertain nature, the associated trace fossils indicate the presence of animal-like organisms. They are preserved in hyporelief on the sole of a thick bed of fine-grained sandstone. They consist of fine ridges, about 0.5–1.0 mm wide and high, forming parallel-sided pairs, 1.5–2.5 mm wide and up to more than 2 cm long. Ridge pairs may be straight but most curve more or less irregularly. A recurrent morphology is the ridges coming together at one end

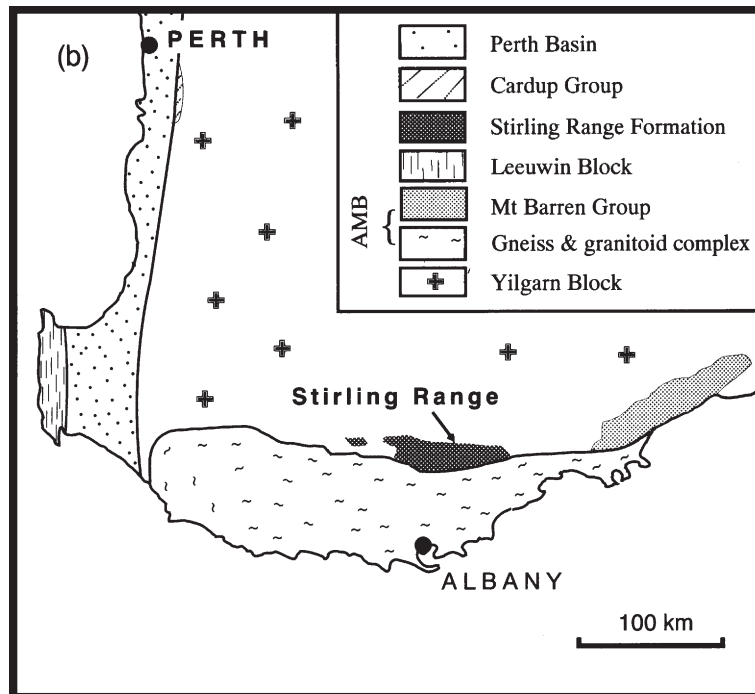


Fig. 95. Location of the Stirling Range and Mount Barren Formations (after Cruse et al., 1993, published with permission of the Geological Society of Australia).



Fig. 96. Small discolored impressions deformed to ellipses, identified at *Bergaueria* (from Cruse et al., 1993, published with permission of the Geological Society of Australia).

in a U-shape and at the other end flaring before terminating. The ridges are interpreted as natural moulds of mucus-reinforced sediment strings formed on the surface by a vermiform organism, with a well-developed mucus-producing capacity and probably a hydrostatic skeleton and musculature to allow it to change shape. In today's biota, this would be a description of an animal, but possibly the traces were made by an extinct multicellular or syncytial organism outside the crown-group metazoans. This offers a glimpse of the Mesoproterozoic (or even Palaeoproterozoic) biosphere which was apparently more complex than the singularly microbial algal world that is usually assumed.

10. Europe

10.1. Introduction

There are seven other occurrences of Ediacara-type faunas besides those in the Charnwood Forest, Russia and the Ukraine already described. These are in six different countries, there being two in Spain.

The countries are:

Wales
England



Fig. 97. Medusoid impression showing possible stalked structure (cf. *Charniodiscus*). These impressions were later compared with *Cyclomedusa* (photo supplied by K. Menamara).

Eire
Norway
Spain
Sardinia.

10.2. South Wales

During investigations of the geology of an area south of Carmarthen, South Wales, an isolated exposure of finely interlaminated mudstone and siltstone of possible volcanogenic origin was found to display disc-shaped impressions (Cope, 1977). The lithology was quite different to the Ordovician Arenig and Devonian Old Red Sandstone rocks nearby. Initially the material was

searched for microflora, but yielded none. The discoid impressions were at first identified as a trace fossil, *Astropolithon* by T. P. Crimes. This would have indicated an Early Cambrian age. Further searches yielded some 50 discoid specimens, their medusoid nature being apparent and confirmed by Crimes and R. J. F. Jenkins, an expert on the Ediacara fauna of South Australia. Cope listed at that time:

Cyclomedusa Sprigg (1947)
Medusinites Glaessner and Wade (1966).

Both these were illustrated in very well preserved specimens. Less well-preserved material was reported

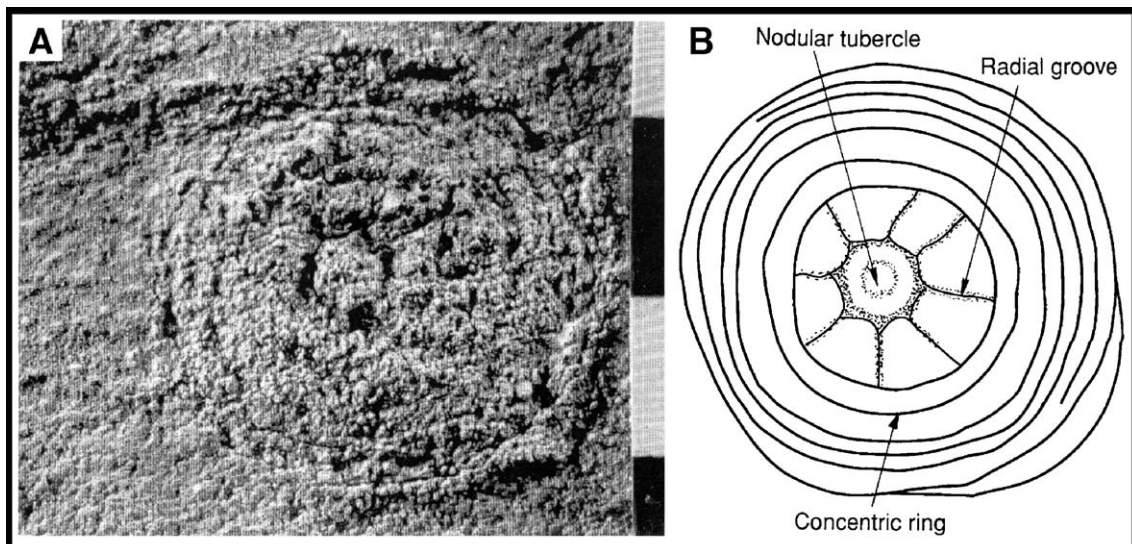


Fig. 98. Comparison drawing of the discoid impression in Fig. 97, now identified as *Cyclomedusa* (after Cruse and Harris, 1994).

to contain *Tribrachidium Glaessner* (1959). Previously the oldest rocks in this area had been taken to be Ordovician (Arenig), but Tremadoc rocks were now known to be represented. Cope accepted that this was an Ediacara-type fauna, but noted that, although it was likely to be Precambrian, a Cambrian age could not be ruled out.

Cope (1983) published a fuller account of these occurrences, providing a geological map (Fig. 99) in which the fossiliferous beds are marked as “?Lower Cambrian”. These and the rhyolites and tuffs beneath them were, however, considered to be quite possibly Precambrian. The fossiliferous sediments in question were reported to be interbedded in the uppermost rhyolites. The Ediacaran-type fauna is within a sequence of interlaminated siltstones and fine sandstones, separated by thin mudstone laminae. The undisturbed nature of these latter laminae indicates quiet water conditions, whereas climbing ripple lamination and flaser bedding indicate shallow water and periods of bedload transport

within a regime characterised by high suspension fall-out. There are indications that the material is largely volcanic ash which has settled directly in the water and in some cases been subjected to gentle current activity, separating the finer from the coarser material and producing thin graded beds, each the product of a single episode of volcanic activity, the ripples and the flaser bedding.

The fossils are preserved as casts on the under surfaces of the beds. The fossils occur only on the black manganese stained surfaces, representing thin mud laminae and it was assumed that the impressions were made in soft mud by the settling of the organism. They are exact counterpart moulds of the animal. In some cases, they are surrounded by a smooth zone, indicating shrinkage during desiccation. The main collecting area is a quarry from which specimens have been collected from at least five separate horizons within the 10 m section exposed. Feeding trails and medusoids only have been collected, no pennatulid, annelid, arthropod

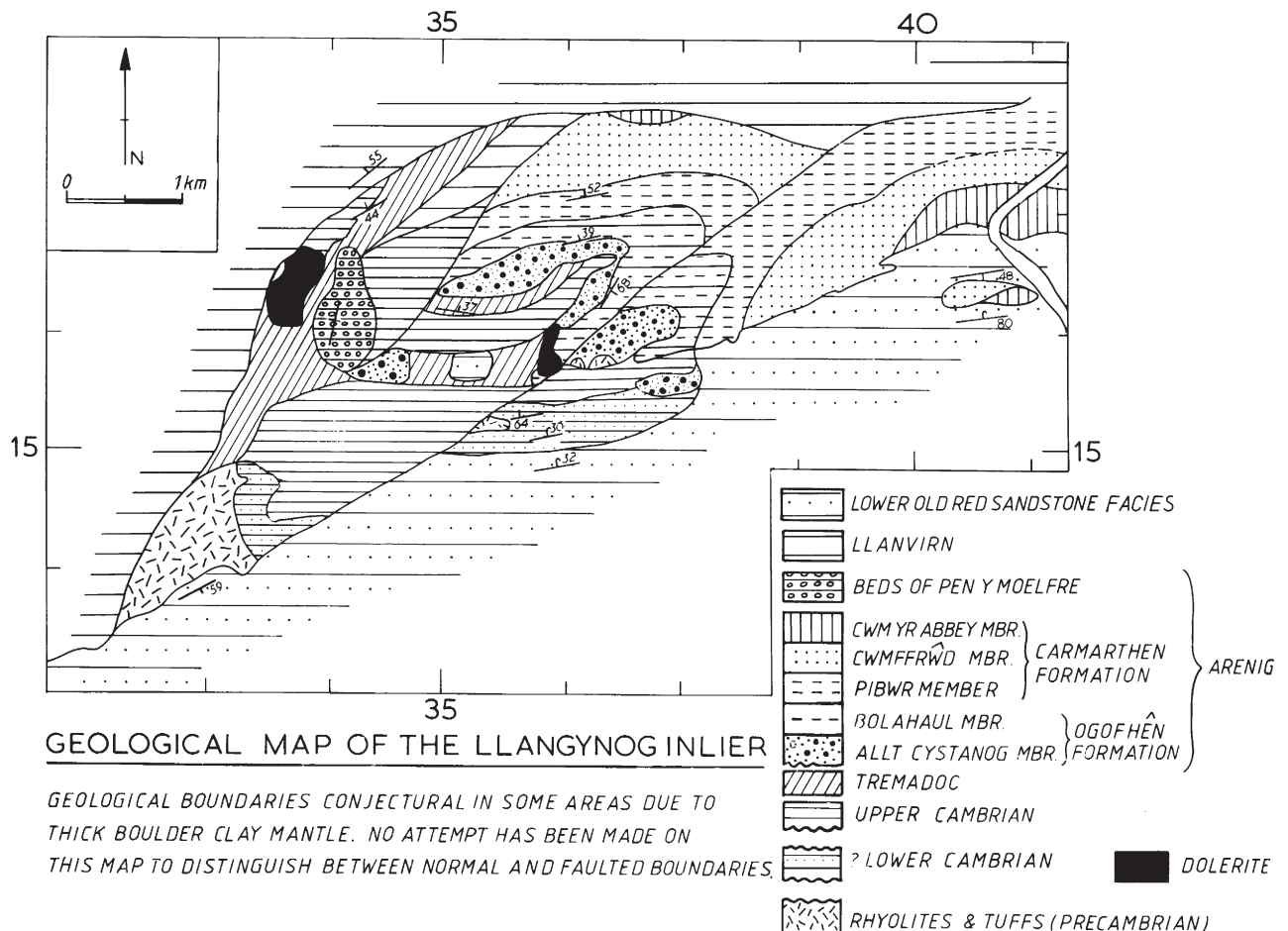


Fig. 99. Geological map of the Llangynog Inlier, near Carmathen, South Wales (after Cope, 1983).

or other fossils being recorded. The *Cyclomedusa davidi* specimens are generally 35–55 mm in diameter (with the largest 110 mm) and display concentric grooves and raised central knobs. The specimens of *Medusinides asteroides* Sprigg (1949) are the most common of the Carmarthen fossils, but are much smaller, measuring 3–15 mm in diameter. Cope illustrated specimens of both (Fig. 100). He also illustrated some shallow branching burrow system, possibly made by molluscs (although he notes that no molluscs are known from the Precambrian, we would not expect to find them unless they possessed hard parts). A worm track identified as *Cochlichmus* sp.

is also figured. Cope (in discussion, Fedonkin, 1985b) notes that, as in the case of the White Sea occurrences, there are shallow burrowing systems and surface feeding track traces, but there is no evidence of bioturbation and penetration of the sediments.

10.3. England, Longmynd

Bland (1984) published a review of the large impression fossil *Arumberia*, with special reference to the Longmyndian of England and Wales, on the border in Shropshire, which is probably of latest Precambrian

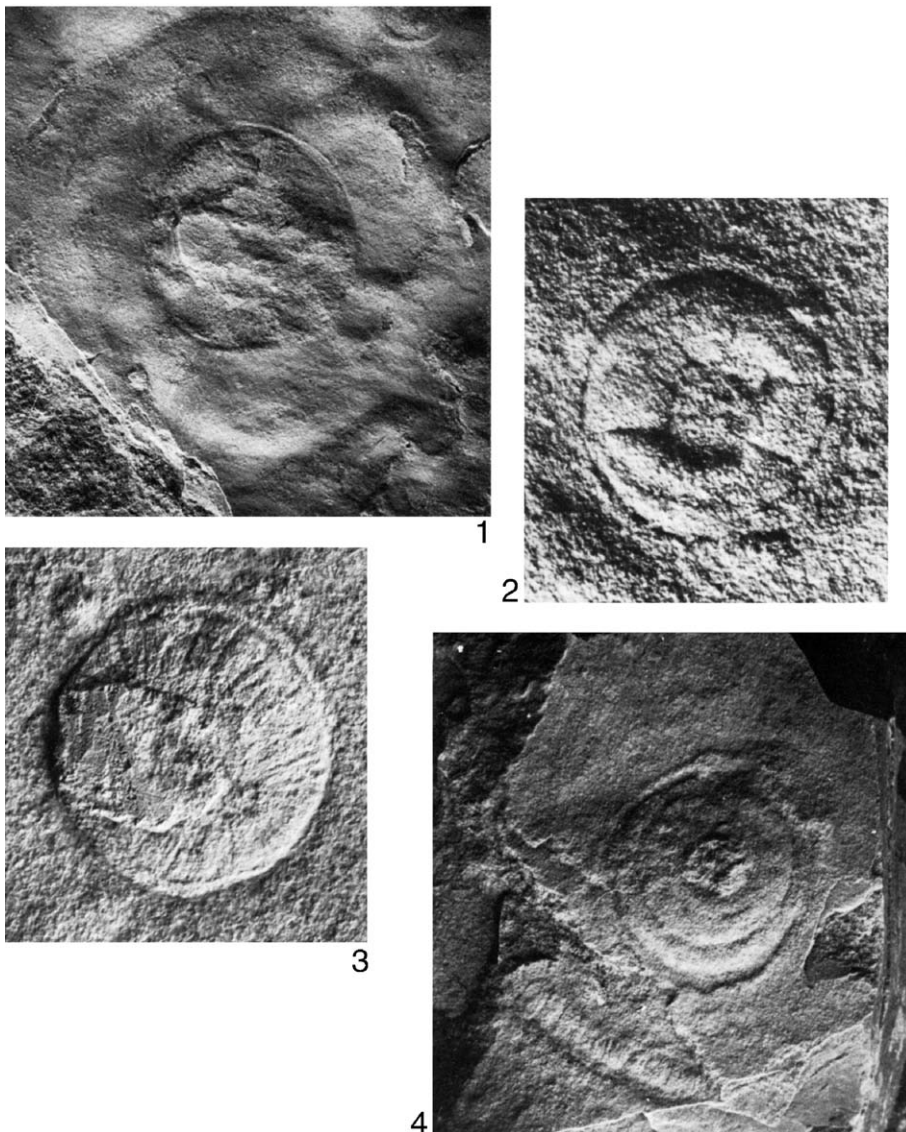


Fig. 100. Ediacaran fossils from the Llangynog Inlier, South Wales. (1) *Cyclomedusa* sp. ($\times 2$), (2) *Medusinides* sp. ($\times 3$), (3) *Medusinides* sp. ($\times 3$), (4) *Cyclomedusa* sp., possibly oral surface ($\times 2$) (from Cope, 1983).

(Vendian) age. This fossil was first described by Glaessner and Walter (1975) from the Arumbera Sandstone of Central Australia. The Longmynd occurrence was first described by Salter in 1856, but was wrongly assigned to *Arenicolites*. It occurs throughout the 6000 m thickness of shallow-water sediments above the Cardingmill Grit, through the Synalds, Lightfoot, Portway, Bayston-Oakwood and Bridges Groups. The beds containing *Arumberia* (Fig. 101) overlie 1500 m of deep-water turbidites of the Burway and Stretton Shale Groups. These may display positive epireliefs, possibly

related to *Cyclomedusa*. Further down in the Stretton Shale Group, there are impressions c. 2 cm in diameter resembling *Bronicella podolica* from Podolia, Ukraine, described by Palij et al. (1983). *Arumberia* occurs in the Longmyndian, as in the Avalon sequence of Newfoundland, in a regressive sequence transitional from marine to fluvial deposits above. There has been a lot of discussion whether *Arumberia* is organic but the fact that it is restricted to the late Precambrian and Early Cambrian supports an organic interpretation. Bland stated that detailed examination suggests that it forms

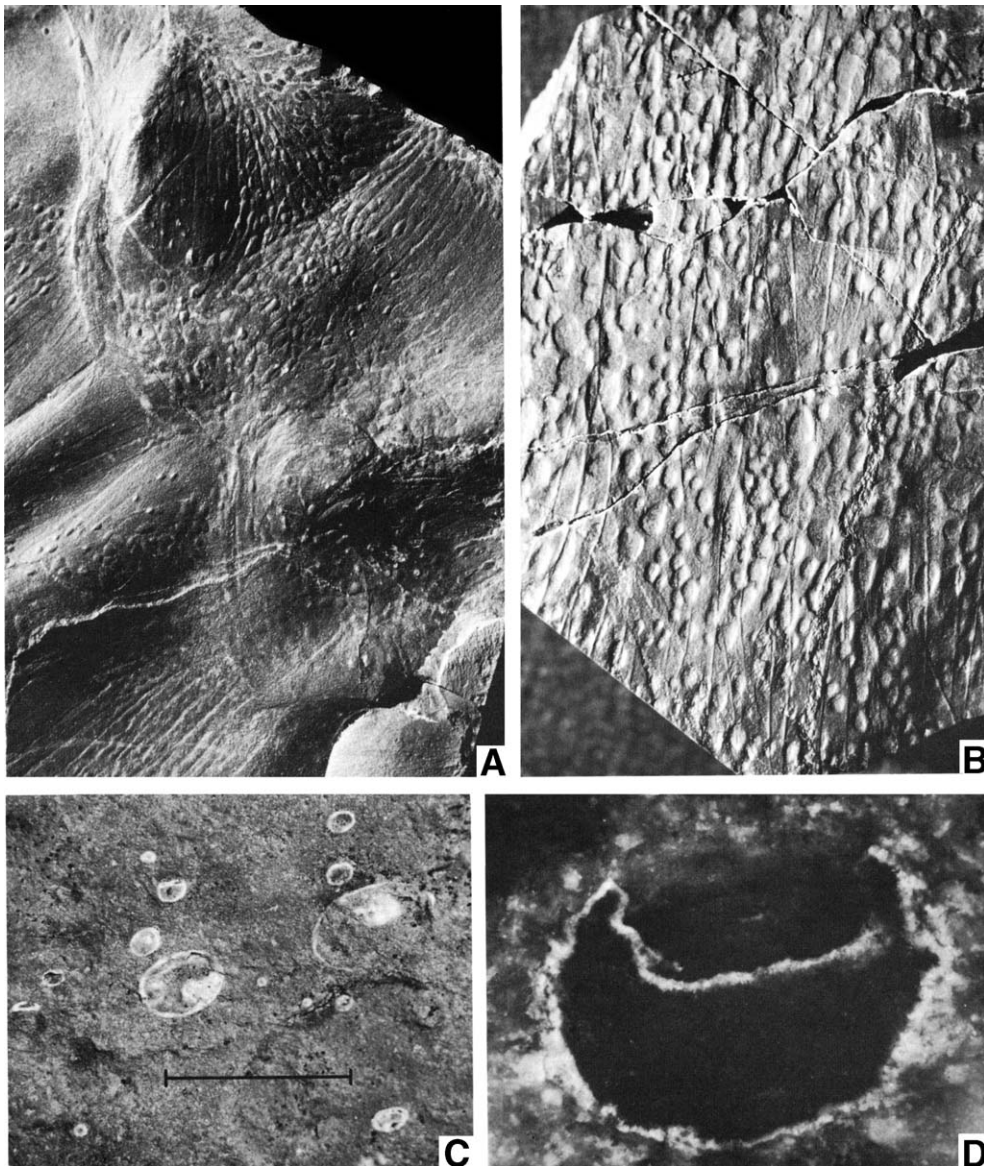


Fig. 101. *Arumberia*, from the Longmyndian? collected by Salter from the Synalds Group: from a probable upper surface, fine red and grey sandstone (width of field of view about 5 cm). (From Bland, 1984. Reprinted with permission of Cambridge University Press.)

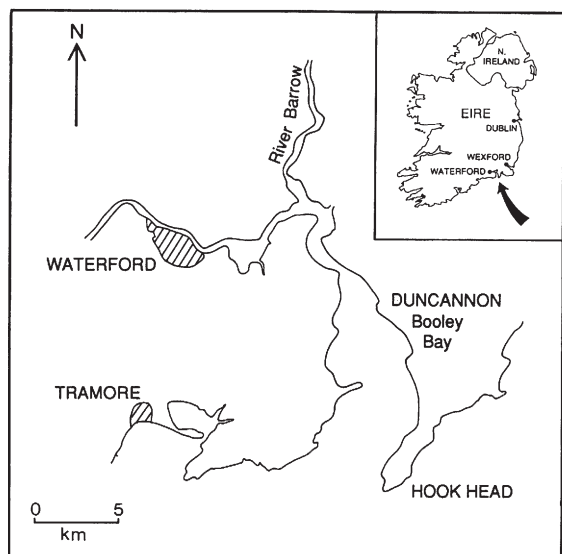


Fig. 102. Location of Booley Bay, Wexford, Eire (from Crimes et al., 1995. Reproduced with permission of John Wiley and Sons).

the underside of a relatively solid colonial organism growing closely applied to the mud surface; and consisting of thin-walled tabular elements, tubes of constant circumference throughout their length. He considered it to be close to *Chuarina*, but lacks organic mineral remains in the Longmyndian examples. He noted other occurrences in Australia, Namibia, Newfoundland and the Urals, and remarked that it also occurs in the 'series rouge normanno breton' of probable Early Cambrian age in northern France (Erquy and Brehec) and at the base of the Rozel Conglomerate in Jersey.

10.4. Eire, Wexford

An Ediacara-type fauna of two genera, one species of each, was described by Crimes et al. (1995) from Booley Bay, Wexford, Eire (Fig. 102). The type section of the Booley Bay formation was described by Gardiner (1978). Its age is likely to range from Middle Cambrian to Ordovician (Llanvirn). Macrofossils are absent, but microfossils from 1 km distant from Booley Bay support an Early to Middle Cambrian age in one case and a Middle Cambrian age in another (Gardiner and Vanguetaine, 1971). The strata on the south side of the bay are overturned and dip northwards, and consist of alternating grey sandstones, siltstones and shales, with minor pebbly mudstones. The sedimentary structures in the sandstones correspond to Bouma's (1964) turbidite facies model, and the very well developed sole structures (flute casts, groove casts and bounce marks)

also indicate a turbidite facies. The Booley Bay Formation and the Ribband Group which contains it, are considered to represent an initially deep-water basinal fills sequence of a major trough. The flow was by axial currents varying from easterly to westerly directions. In the upper part of the sequence are pebbly mudstones deposited by debris flows from a shelf area to the southeast (?), and there is evidence of progradation of the turbidites with time over massive black mudstones.

The new species *Ediacaria booleyi* (Fig. 103), which commonly has a diameter of 50 mm but may reach 200 mm, occurs on at least seven bedding planes, each usually with more than one specimen, whereas *Nimbia oclusa* may occur in isolation or as several hundred individuals to a bedding plane (Fig. 104).

Crimes et al. (1995) considered the possibility of inorganic origin, particularly noting some similarity to sand volcanoes as described by Walter (1972a), but rejected this origin on the grounds that *E. booleyi* has been exhumed from the ocean floor by turbidity currents, transported and deposited, to be preserved as

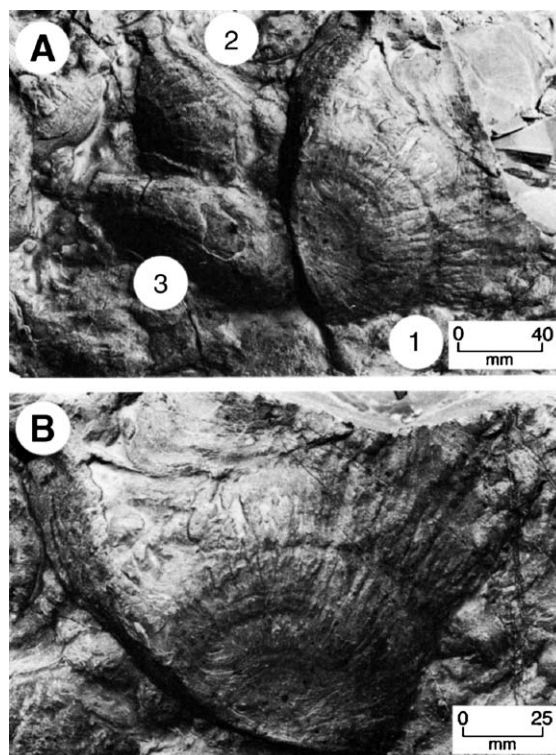


Fig. 103. (A) Examples of *E. booleyi* sp. nov. on the sole of turbidity current deposited sandstone. (B) An enlargement of specimen 1 above, comprising one side of the holotype (from Crimes et al., 1995. Reproduced with permission of John Wiley and Sons).

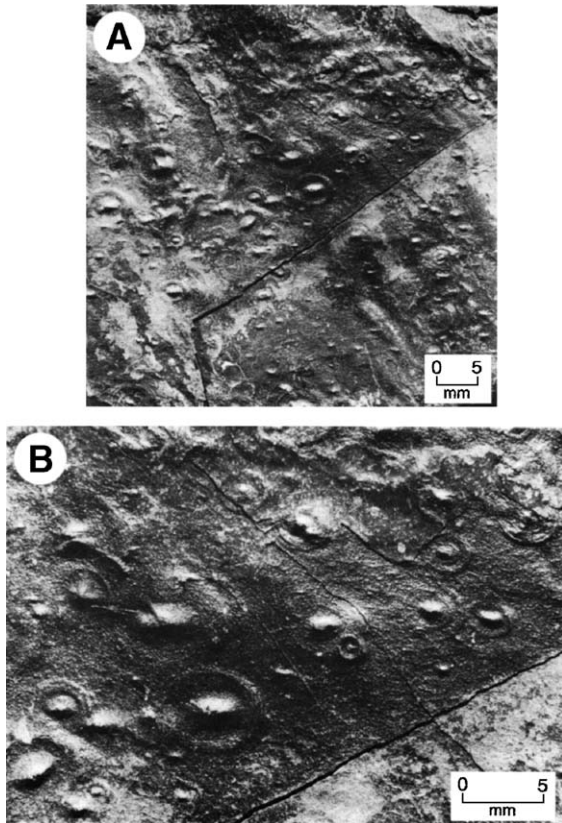


Fig. 104. (A) *Nimbia oclusa* Fedonkin 1980 on the sole of a turbidity current deposited fine sandstone, prominent central tubercle and outer ring clearly seen. (B) An enlargement of detail of part A (from Crimes et al., 1995).

casts. It is inconceivable that any inorganic sedimentary structure could be redeposited in this way and retain its shape: there is indeed no record of sand volcanoes being redeposited in this way. The structure is more complex than any known sedimentary structure and there is no central feeder tube, a requisite in the case of sand volcanoes. The concentration of *Nimbia*, up to 100 individuals, annular rings with a central tubercle, in an area of 50 cm², is likewise not consistent with sand volcano origin. Some *Nimbia* discs were deposited inclined to the bedding surface with the leading edge in the direction of the palaeocurrent. They also rejected concretionary origin. Restriction to the late Precambrian and Cambrian is also against inorganic origin, for if inorganic these forms should be found right through the geological column and they are not.

The question of the validity of Ediacara medusoid species was discussed by Crimes et al. (1995) with reference to *Ediacaria* and the three species of *Cyclomedusa* of Sprigg (1947, 1949). The twin example of *C. radiata* and *C. davidi* illustrated by Sun Weiguo

(1986a) was taken to illustrate that morphological features used in species differentiation could be due to the between exumbrellar and subumbrellar surfaces. They noted the doubt that *Cyclomedusa* was free swimming and the preference of Wade (1972a) for a benthic form with a central boss attachment to the substrate, an interpretation supported by Jenkins (1992). They mention the belief of Seilacher (1984, 1989, 1992) that none of the “medusae” of the Ediacara fauna can be interpreted with any certainty as jellyfish: that they were sedentary and not referable to any living phyla (and so he erected a new Kingdom, the Vendobionta).

Full systematic descriptions are given of *Ediacaria booleyi* and *Nimbia oclusa*, an interpretative diagram of the former, and a stratigraphic column diagram showing the levels at which they occur. *Ediacaria booleyi* is separated from the *Ediacaria flindersi* holotype by the nature of its radial structures. A diagram (Fig. 105) shows how *Ediacaria* individuals were impacted, carried a short distance (the excellent preservation rules out long distance transport) by turbidity currents and then redeposited. They consider that there is a requirement for them to have possessed a rigid outer wall, and consider that the evidence is against either genus having a mouth and two layered body as of a soft-bodied Coelenterate. They consider that the concept of an Ediacara fauna dominated by soft-bodied Coelenterates is erroneous.

The habitat of these organisms was considered. It was noted that Ediacara-type faunas have mostly been described from shallow water facies, although they have been described from Newfoundland (Misra, 1969; Anderson and Conway Morris, 1982; Jenkins, 1992) from deep water turbidites, all these examples being in situ: the Wexford occurrence is of a transported fauna. They believe that *Ediacaria* and *Nimbia* can only have been living together at the same source site. They suggest that in the Cambrian these benthic forms migrated into deep water where competition was less intense, and that this may be an early example of an onshore–offshore retreat.

Breandan MacGabhann (personal communication) rejects Crimes’ identification as an Ediacaran medusoid on three grounds: firstly, the shape and ornament is inconsistent with the type Ediacara material for that or any other genus: secondly, the proposed taphonomy, transport in a turbidity current, impaction on the seafloor and decay to form a cast infilled by sediment is not consistent with low-density organisms such as the Ediacaran organisms are envisaged to be. Such taphonomy requires the organism to be of similar density to the turbidity current (or it would not have stayed in the

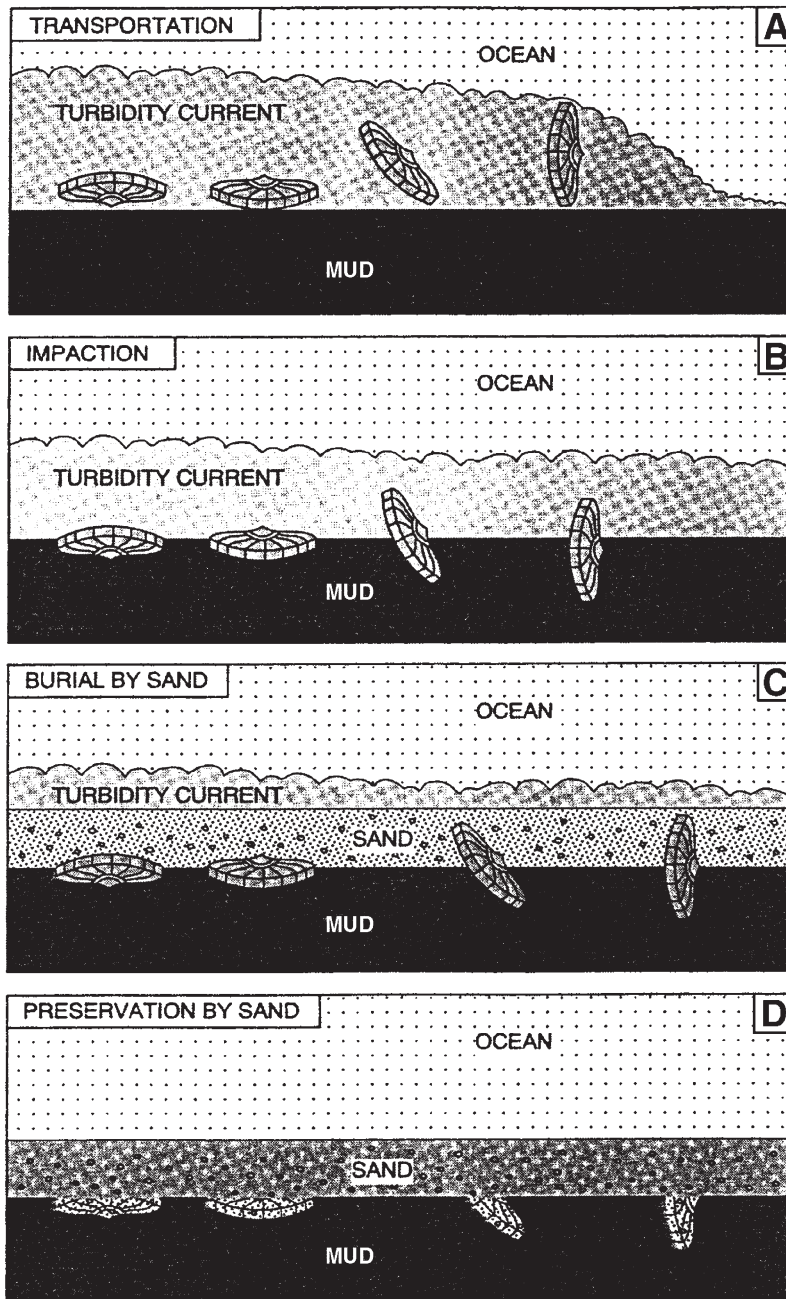


Fig. 105. Deposition and preservation of *E. booleyi* at Booley Bay. (A) Transportation by turbidity current, (B) impaction on muddy substratum, (C) burial by turbidity current deposited sand, (D) decay of the organism, leaving a mould in the mud and a casting by the turbidite sand (after Crimes et al., 1995).

current). Also none of the discs from Newfoundland, NW Canada, Australia or Russia show evidence of such transport. Thirdly, to survive such transport, it must have had a tough outer integument. He believes that none of the discs show evidence of such integument and it is against the feeding mechanism favoured for them, absorption of nutrients through the outer wall, not

through a mouth. The deep-water forms seem to rule out photosynthesis.

As a comment on the above objections, it may be noted that it is widely believed that many of the Ediacaran organisms were infilled by sand in a buried, sedentary position in life—this might negate his second objection?

10.5. Norway

Foyn and Glaessner (1979) described the occurrence of a medusoid fossil *Kullingia concentrica*, originally identified by Kulling (1964, 1972) as *Spriggia* Southcott. Sediments in eastern Finnmark range from Riphean through Vendian and Cambrian to Tremadocian, and two tillite formations occur there. The succession of sedimentary rocks on the Digermul Peninsula to the west of Tanafjorden (Fig. 106) has been deposited continuously with no stratigraphic break from the Upper Tillite horizon. About 700 m of sediments intervene between the tillites and the *Platysolenites* horizon where this primitive foraminifer first appears; above that horizon, the Cambrian beds are c. 1000 m thick. The Cambrian lower boundary is taken to be below the *Platysolenites* horizon at the base of the Breivik Formation, where the trace fossil *Phycodes pedum* Seilacher first appears.

The body fossil, now named *Kullingia concentrica* Glaessner nov. gen. nov. sp., occurs in three localities; on the northern slope of Mt. Luopakte, to the south of Lake

Tornetrask, where the fossil remains occur in the upper part of a 2 m thick sequence of grey, sandy, graded-bedded shales (Kulling, 1972); the second locality is 20 km south of Appartjako and to the south of Lake Rautasjaure, where fossils occur just above the contact with the Archaean basement (Kulling, 1964); the third locality is north of Tornetrask and about 7 km east of Vakkejokk, in sandy shale with cyclic sedimentation (Kulling, 1972). The fossil is a flat disc with a subcircular outline and concentric, fine, evenly spaced ribs around a usually low conical centre measuring about one sixth of the total diameter of the disc (Fig. 107). The distance between rib crests is c. 2 mm. The diameter was not given, but from the photograph it appears to be c. 7 cm. This fossil lacks the irregular spacing of the concentric ridges and furrows and the radial grooves of *Cyclomedusa*, which it otherwise resembles, and differs from *Ediacaria* Sprigg (as emended by Wade, 1972a) in the presence of regular concentric ribs near the centre of the disc. It resembles a single specimen collected from the Arumbera Sandstone, near Alice Springs, Australia, which Foyn and Glaessner (1979) figured, alongside a

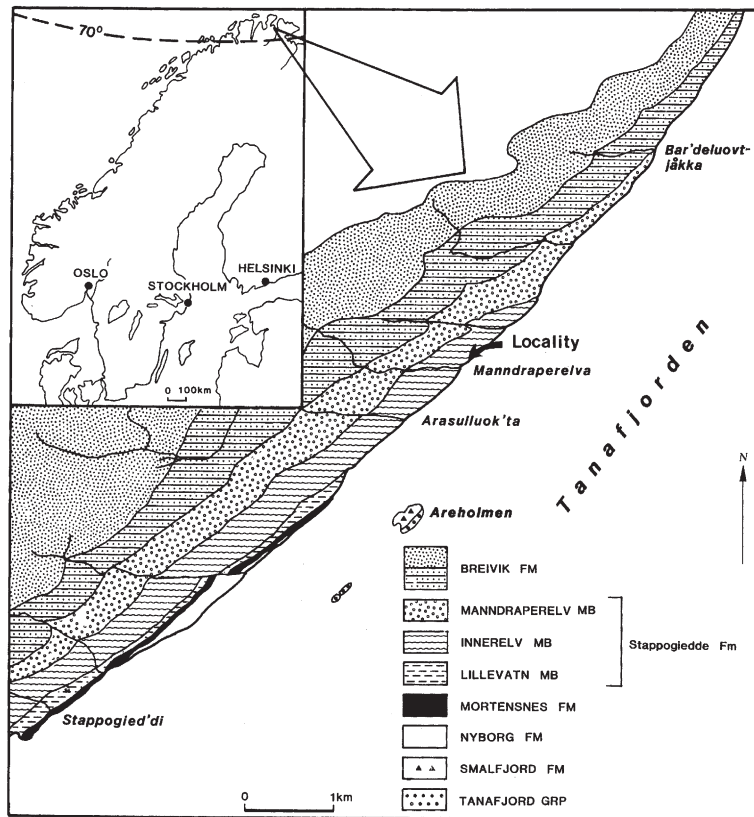


Fig. 106. Map of the Tanafjorden Region of northeastern Norway showing the location of coastal outcrops of late Proterozoic to lower Cambrian sequences along Digermul Peninsula (from Farmer et al., 1992. Reproduced with permission of Cambridge University Press).

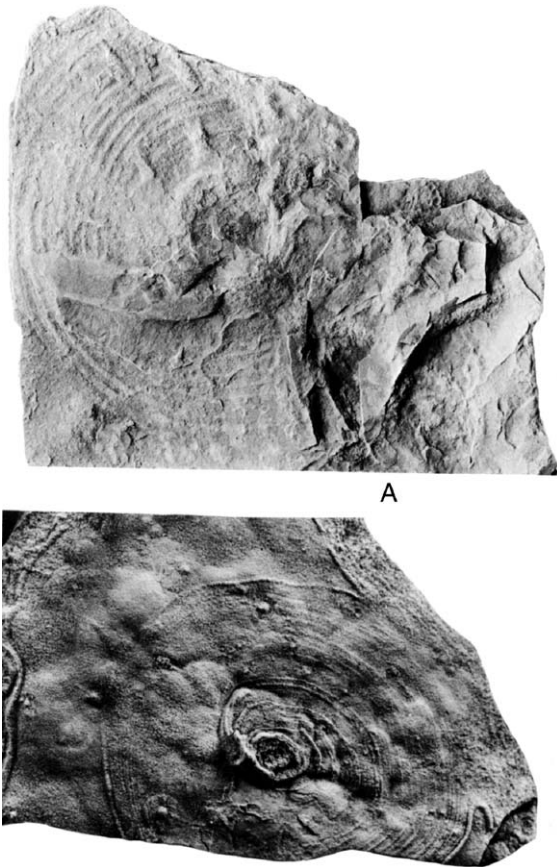


Fig. 107. *Kullingia concentrica*. The holotype from the NE slope of Luopakte Mountain, Tornetrask, compared with *Kullingia* aff. *concentrica* from the Arumbera Sandstone, east of Laura Creek, near Alice Springs, Central Australia ($\times 1$) (from Foyne and Glaessner, 1979).

fainter image of the Norwegian fossil. It was considered by them to be close to *Cyclomedusa* and might, as suggested by Wade (1972a), represent an early stage in the evolution of a hydrozoan (chondrophoran) float similar to that of the living *Porpita*. They added that it might, alternatively, have rested with its exumbrellar surface downwards on the seafloor.

Farmer et al. (1992) described further finds from the Tanafjorden Area of Finnmark on the Digermul Peninsula (Fig. 106). Their stratigraphic diagram shows two tillites, which are accepted as representing the Varanger (Laplandian) glaciation, both being assigned to the Vendian. The interglacial Nyborg Formation has yielded a date of 654 Ma (± 7 Ma). The upper tillite, the Mortensnes Formation, is overlain by the Lillevatn Member and then by the Innerelv Member, 275 m thick, which consists of sandstones and

shales forming two shallowing upwards sequences, each representing a transition from offshore marine (quiet basin, below wave base) to wave-influenced, shallow intertidal to subtidal deposition. These beds display prominent cleavage which tends to obscure sedimentary structures. The Innerelv Member is overlain by the Manndraperelv Member, a shallowing upwards turbidite sequence. The Proterozoic–Cambrian boundary appears not to be firmly fixed but is somewhere within the Breivik Formation above. The fossils are found in shoreline outcrops within the shallow-water facies of the Innerelv Formation, immediately north of Manndraperelv.

The fossil assemblage is comprised primarily of *Cyclomedusa* sp. Sprigg (1947), but also includes *Ediacaria* sp. Sprigg (1947), *Beltanella* Sprigg (1947), *Hiemalora* Fedonkin 1982 and *Nimbia?* Fedonkin 1982. The fossils occur within the upper portion of the lower of two successive coarsening upwards cycles, in fine-grained sandstones and siltstones. *Cyclomedusa* (c. 100 individuals) occurs on both upper and lower bedding plane surfaces. Faint radial ornamentation is rare, most individuals only show concentric ornamentation. Discs average 5 cm in diameter, but are slightly elliptical, a secondary feature? The other body fossils resemble the type specimens from elsewhere but the authors note that further detailed taxonomic study is needed.

Trace fossils are abundant on bedding surfaces of fine sandstones and siltstones of the Manndraperelv Member, but are unbranched surface trails and cylindrical burrows oriented parallel to bedding (*Planolites*-type). In the Lower Breivik Formation, about 5 m above its lower contact, a more diverse assemblage appears, dominated by larger forms [*Planolites*, *Cochlichmus*, *Gyrolithites* (a vertical spiral burrow) and *Phycodes*]. With them appear filamentous carbonaceous films (*Vendotaenia*) and carbonaceous annular tubes assigned to *Sabellidites*.

These authors suggested that whereas *Kullingia* is a quite separate form, chambered and probably pelagic, their “cyclomedusoids” were probably benthic. However, for stratigraphic purposes in northern Scandinavia, the lowest *Kullingia* zone as defined by Foyne and Glaessner (1979) should be broadened to include the common forms of the *Cyclomedusa* genus, as the ‘*Cyclomedusa*’ plexus.

These authors illustrated some small pillar structures which are clearly pseudofossils, but could easily be mistaken for body fossils or trace fossils.

10.5.1. Svalbard

The islands of Svalbard would appear to be likely sites of an extension of the Scandinavian and North

Russian (White Sea) fossiliferous Vendian. A brief note in Harland et al. (1997) defines the Late Vendian Scotia Group, but although microfossils and acritarchs confirm a Late Vendian age and these authors noted that Prins Karls Foreland contains the first recorded ‘Ediacaran biota’ in Svalbard, the Ediacaran metazoan body fossils have apparently not so far been found there. Svalbard must, however, be a promising site for further finds of such a fauna.

10.6. Spain

There are two localities in Spain where Ediacara-type fossils have been reported.

10.6.1. Galicia

Dozy (1984) described a fossil from Galicia, SE of Samos, has the form of fronds and resembles the Ediacaran frond-like organisms. The imprints are on the surface of fine silty laminated and thin bedded silty schists, with carbonate bed intercalations, belonging to the Candana Schist Formation, the Middle Division of the Candana Group. The environment was shallow marine or sublittoral, possibly extending into tidal flats, and the carbonate beds consist of algal mats and stromatolitic bioherms. The age is almost certainly latest Precambrian, comparable with the rocks of Charnwood Forest, England, as archaeocythids and the first trilobites appear in the overlying Vegadeo Group. The

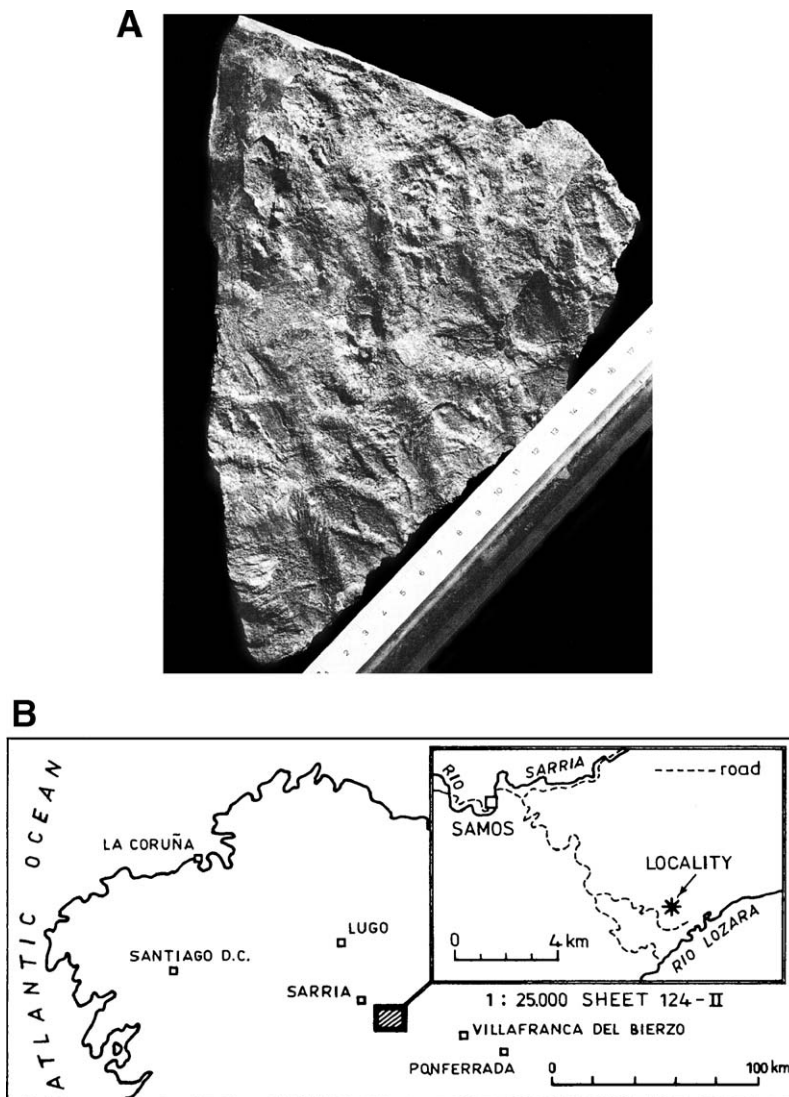


Fig. 108. Imprints of unknown origin from the late Precambrian, Lozara Valley, province of Lugo, Spain (from Dozy, 1984).

fossil imprints occur about 1000 m or more below the base of that group. It is on the sericitic surface of a silty schist. Dozy discussed possible origins, noting the lack of symmetry on either side of the axial line (Fig. 108). The possibilities are grazing traces, crawling trails burrows and body fossil imprints. The lack of symmetry (i.e. matching of the fronds) is a feature of Ediacaran frond-like imprints of body fossils. He notes that, if a single body imprint of an animal is the origin, it was 15 cm across and twice as long. He found similarities to fossils described by Richter (1955) from Namibia, by Glaessner and Wade (1966) from South Australia and by Anderson and Misra (1968) from Newfoundland, all referred to the sea-pens. He considered that it resembles *Arborea* (Glaessner and Wade, 1966), being larger than *Rangaea*. He also figured some puzzling reticulate imprints.

10.7. Central Spain

The second occurrence was described by Brasier and Hewitt (1979) from the Montes de Toledo in Central Spain. Whereas the occurrence described above was of only a single possible genus, but similar to a described Ediacaran genus, this record is of the genus *Chuarina* together with a number of trace fossils. Other characteristic Ediacaran fossils are absent and the Vendian age of the actual fossil-bearing beds is questionable.

These authors reported an unusual assemblage of body and trace fossils from, mainly, the Pusa Shales and Azorejo Sandstone exposed in the Valedelacasa Anticline of the Montes de Toledo in the Centroideric zone of the Iberian massif (Fig. 109). The pebbly mudstones of the Upper Alcludian in the figure have been variously interpreted as fluvio-glacial deposits, turbidites, marine fluvial and tidal with occasional fluvial influence. The Upper Alcludian also contains discontinuous beds of stromatolites and dolomite. Above, unconformably, come the Fuentes Olistostromes, local gravity slide breccias and conglomerates, with chaotic blocks of limestone, dolomite, shale, sandstone and conglomerate in an argillaceous matrix. However, at the same stratigraphic level as glaciogenic mixtites (Harland, 1974), they are of tectonic rather than glacial origin. Above come 700–2000 m of Pusa Shales with laminar bedding, flute marks, current lineations and slump horizons: the lower beds of which are proximal turbidites and the middle more distal turbidites. There is some evidence of bioturbation.

About 350–450 m above the base of the Pusa Shales, are megascopic carbonaceous discs, the compressed and

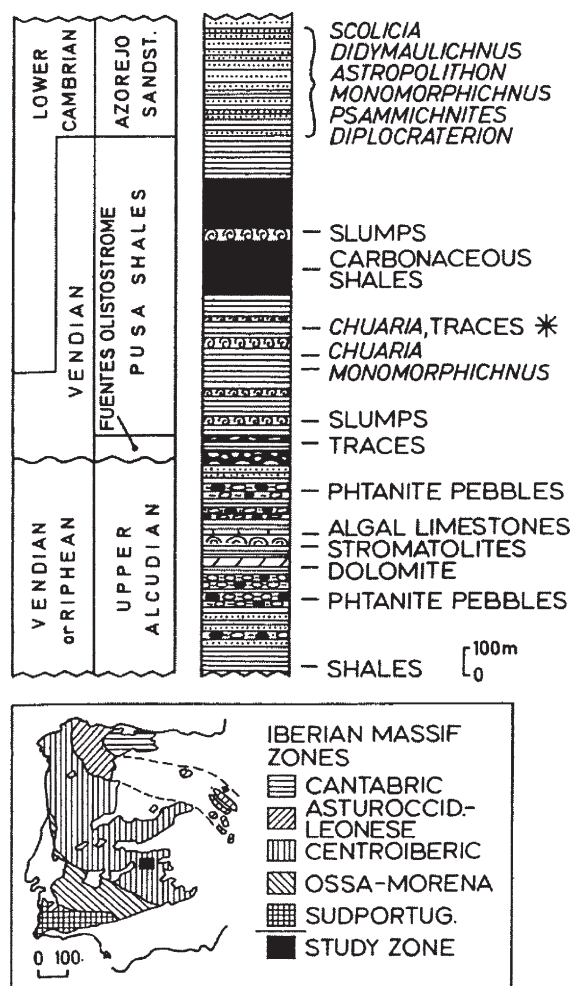


Fig. 109. Location and stratigraphic setting of the studies sequence in Central Spain. *The horizon which bears trace fossils (after Brasier et al., 1979).

stretched remains of organic bodies? They occur in three ways: touching or loosely clustered, without overlap and lacking evidence of coloniality; discrete bodies sparsely distributed (Fig. 110C); and long convoluted chains (Fig. 110A). The first larger forms have been compared with *Beltanelliformis sorichevae* Sokolov (1965, 1973), the smaller isolated discs with *Chuarina circularis* Walcott of Walcott (1899) and Ford and Breed (1973). The smaller forms have been reported from Upper Riphean and Vendian strata, whereas the larger type is only recorded from Vendian strata.

The distal turbidites of the Pusa Shales are succeeded by deposits of tidal sand bars and mud flats, at first as intercalations and then as the dominant facies. The lower 450 m of the Azorejo Sandstone above the Pusa Shales contains a trace fossil assemblage commonly found in coastal sand facies of presumed Early

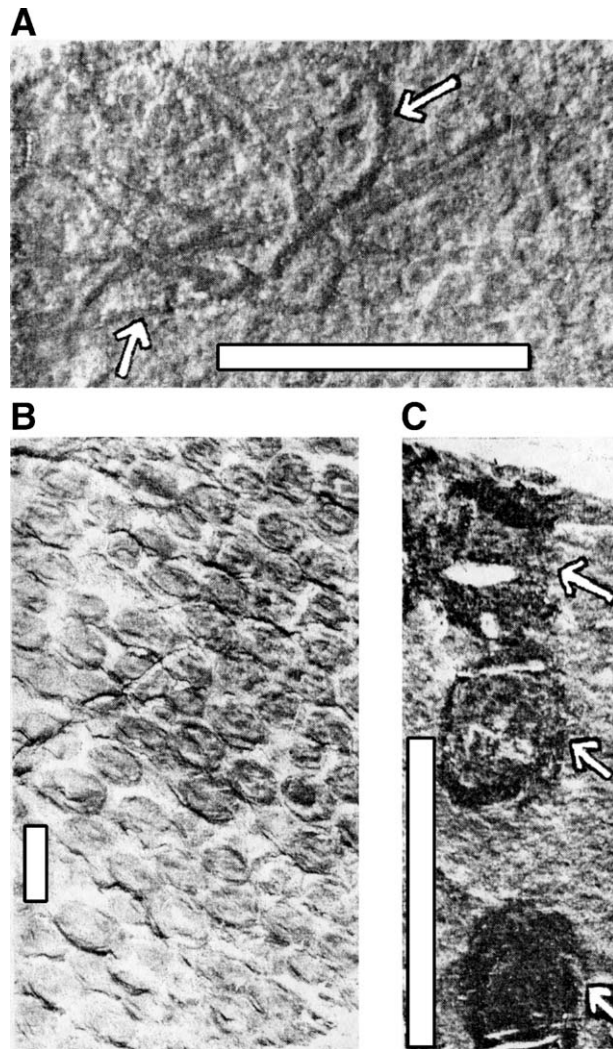


Fig. 110. Fossils from the Pusa Shales. (A) Convolute chain of carbonaceous discs. (B) Bedding plane covered with large carbonaceous discs resembling *Beltanelloides sorichevae*. (C) Three isolated carbonaceous discs. (Scale bar=10 mm) (from Brasier et al., 1979).

Cambrian age, and the limestone above it contains trilobites and *Archaeocyatha* of a late Early Cambrian age.

Chuarina has been the subject of a detailed analysis by Ford and Breed (1973). It has been variously referred to as an alga, a chitinous foraminiferid, a gastropod, a hyolithid operculum, a trilobite egg, an acritarch or as of inorganic origin. Those authors favour an origin as an unusually large algal sphaeromorphid acritarch. It has been reported widely and the genus *Fermoria* found in India (Sahni, 1936; Sahni and Srivastava, 1954) and Iran (Stocklin et al., 1964) is clearly synonymous. It appears not to be so certain that the larger *Beltanelliformis*-like forms and long chains described by Brasier et al. (1979) (Fig. 110A,B) are of the same origin. Brasier et al.

(1979) believed that the Pusa Shales are probably of Vendian age.

10.8. Sardinia

Debrenne and Naud (1981) reported the discovery of medusoid casts and traces in two levels of black shales within the “azoic” San Vito Formation in the Sarrabus area of Sardinia, to the northeast of Cagliari. The finds were within a 700 m thick series of grits, quartzites, silts and shales, yellow and green in colour. The San Vito formation is of uncertain stratigraphic age due to polyphase deformation, but these fossils suggest a late Precambrian age. The sequence is monotonous and rhythmic. The first fossiliferous

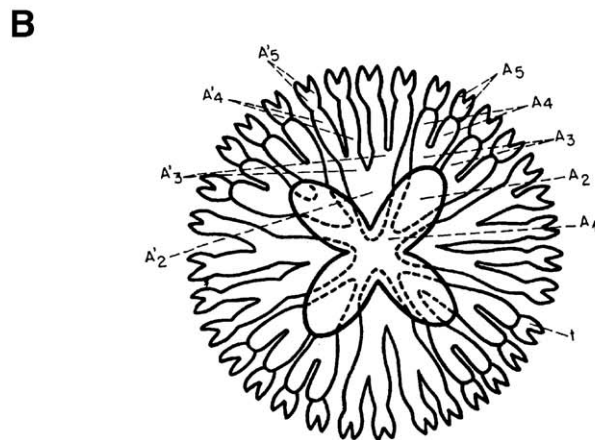


Fig. 111. Imprints in the San Vito Formation, Sarrabus area, Sardinia. (A) Holotype of *Ichnusa cocozzi*, (B) Hypothetical reconstruction of *Ichnusa* gen. nov. (from Debrenne and Naud, 1981).

horizon was above the second which had not yet been studied in detail.

There are numerous imprints of medusoid fossils. The moulds are circular or oval, the latter being attributed to deformation. They form a pellicle of fine silt, and are darker than the rest of the rock. Where the moulds are absent, they form an imprint on the surface below which is less clearly defined. The organisms were hemispherical or pyramidal, but they have been flattened due to the weight of the superincumbent strata and this makes interpretation difficult. There are lobes in the centre which do not have a regular form. The lobes subdivide in 2×4 lobes. It is difficult to determine if the gastrovascular system had 4 or 8 first-order lobes. The tentacles are only preserved on the holotype (Fig. 111A). The diameter is 2–3 cm. The organs of the medusoids have not been preserved, but it seems that there is only one species of which the tentacles have commonly been lost. This new genus and species, *Ichnusa cocozz*, was described and considered to resemble *Albumares* described by Fedonkin (1976) from the Valdai horizon on the Onega Peninsula and *Rugoconites* described by Wade (1972a, 1984). The symmetry would seem to be four or eightfold, and this suggests attribution to the Class Scyphozoa. The authors' drawing is reproduced in Fig. 111B.

There is an associated ichnofauna of *Planolites*, *Neonoxites*, *Neonereites* and *Helminthopsis* types, and a

number of circular impressions are of the right dimensions to be *Chuarina*, but may be of inorganic origin. Vendian traces are usually subhorizontal and shallow, and these traces are consistent with a Neoproterozoic (Vendian) age, which is also indicated by the presence of medusoids, but the exact age of the San Vito Formation must remain unresolved.

11. North America: United States and Mexico

11.1. Introduction

Besides the major occurrences in Newfoundland and Northwest Canada, there are four other occurrences of Ediacara-type faunas in North America:

United States (3)
Mexico (1).

11.2. United States: North Carolina

Gibson et al. (Gibson et al., 1984; Gibson, 1989) described the discovery of metazoan body fossils, comparable to those of the Ediacara fauna, in the Carolina Slate Belt in Stanly County, North Carolina. This discovery extended the palaeobiographic range of the Ediacara fauna to the southern Piedmont of the southeastern United States. The localities of the finds

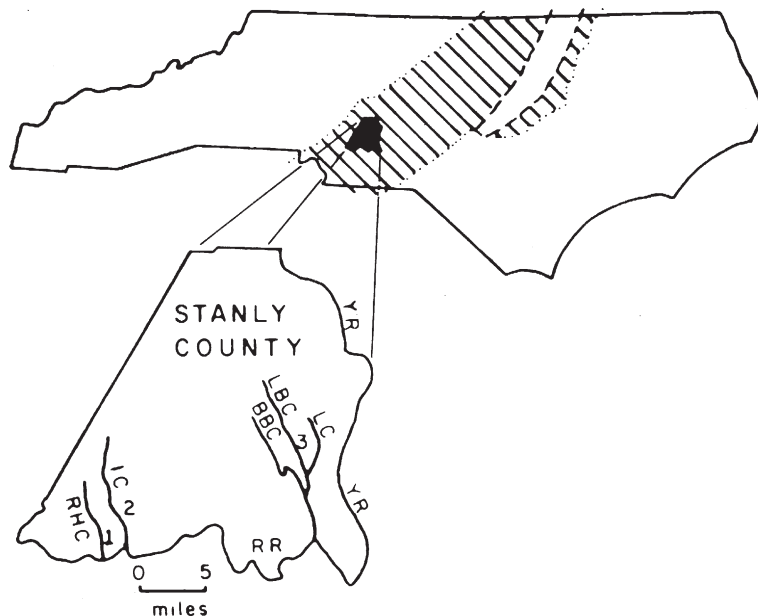


Fig. 112. Location map of Stanly County. Pattern indicates extent of Carolina slate belt. Fossil localities: RHC=Rock Hole Creek; IC=Island Creek; LBC=Little Bear Creek; LC=Long Creek; RR=Rocky River; YR=Yudkin River; 1, 2, 3=fossil localities; 2=location of fossils previously described as *? Paradoxides carolinensis* (after Gibson et al., 1984).

were Little Bear Creek and Rock Hole Creek (Fig. 112). The fossils were not found in place, but lithological comparison with the locally exposed bedrock shows that they were not transported far from their original position in outcrop. Previous descriptions of the occurrence at Island Creek, near Rock Hole Creek, of the trilobite *Paradoxides carolinaensis* (St Jean, 1973) have, as a result of re-examination, been identified as referring to an element of the late Precambrian Ediacara-type fauna.

The fossils were recovered from a narrow stratigraphic interval of the Albemarle Group in either the upper McManus Formation (Conley and Bain, 1965) or the upper Cid or lower Millingport Formations (Stromquist and Sundelius, 1969). The metazoan form collected along Little Bear Creek is about 9 cm long and 2.5 cm wide, and is a frond-like organism, consisting of 26 segments with a narrow axial region (Fig. 113), apparently a narrow ridge. Segments are curved posteriorly, terminate as spires and exhibit subdued linear ornamentation along each segment. The branches are separated by a well-defined groove. The specimens from Rock Hole Creek display a crude bilateral symmetry, but the median line has a zigzag trace, due to the alternation of the ends of the segments on either side. This is a well-known feature of the Ediacaran frond-like fossils. The grooves between the segments apparently bifurcate at the ends distal from the median furrow. There is a suggestion of a third wing or lateral appendages at the end of the segments.

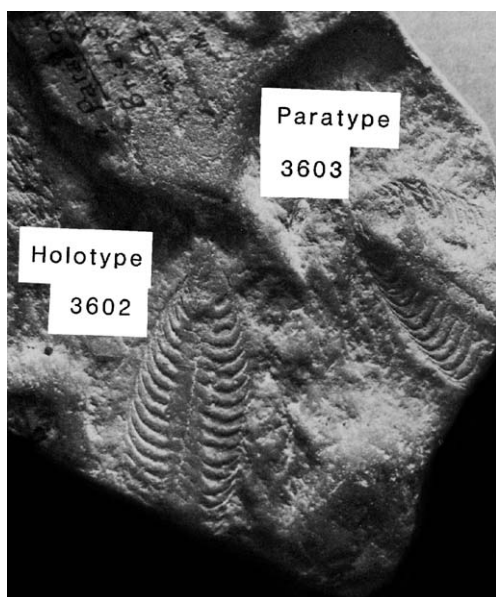


Fig. 113. Fossils from Island Creek previously described as ? *Paradoxides carolinaensis*, but now known to be *Pteridinium* (from Gibson et al., 1984).

Comparison was made with *Pteridinium* (Glaessner and Wade, 1966) from South Australia, South West Africa (Richter, 1955; Pflug, 1970a; Germs, 1972b) and the White Sea, Russia (Fedonkin, 1981a,b), as well as *Inkrylovia lata* Fedonkin and *Valdaina plumosa* Fedonkin from the Russian Vendian. It was concluded that the most similar taxa were *Pteridinium* cf. *simplex* described from the Flinders ranges, South Australia, or *P. nenoxa* described from Russia.

A late Precambrian (?Vendian) age is indicated for this part of the Slate Belt in southern North Carolina, as suggested by Cloud et al. (1976), when they described the trace fossil *Vermifora antiqua* Cloud from the Roxboro-Durham area. Their suggested age of 620 Ma was supported by U–Pb ages. However, this new evidence will require the re-examination of several anomalous radiometric age datings on Slate Belt rocks elsewhere.

The authors suggest that the organisms were transported from a shallow-water life site to their present host sediments (on the basis of what is known about the living environment of Ediacara faunas worldwide). They would have been fixed by a basal disc and had a stalk connection like *Charniodiscus*, and other “sea pens”, but there is no evidence of a holdfast.

11.3. California

The most important description of occurrences of Ediacara-type fossils in California is that of Hagadorn et al. (2000); there are also two brief abstracts mentioning occurrence in Nevada (Horodyski, 1991; Horodyski et al., 1994). McMenamin (1996) also provides a correlation diagram covering the Sonora, Mexico, occurrence, these occurrences and those in western Canada.

The Great Basin of the United States is well known for its thick, well-exposed Neoproterozoic to Precambrian sections, representing alluvial and marine facies. The first recognitions of Ediacara-type fossils in the Great Basin were made in Nevada (Horodyski, 1991) and in California by Hagadorn et al. (2000). Three sites in California have been recognised, Salt Spring in southern Death Valley, the southern Kelso Mountains in the Mojave Desert and White Mountains in eastern California. The regional stratigraphy, detailed stratigraphic context, palaeontological and chemostratigraphic information are summarised in Fig. 114.

In the Salt Spring locality, the fossil collection was made in the Wood Canyon Formation about 0.5 km north of Armargosa spring; and in the southern Kelso Mountains locality, from the same stratigraphic horizon

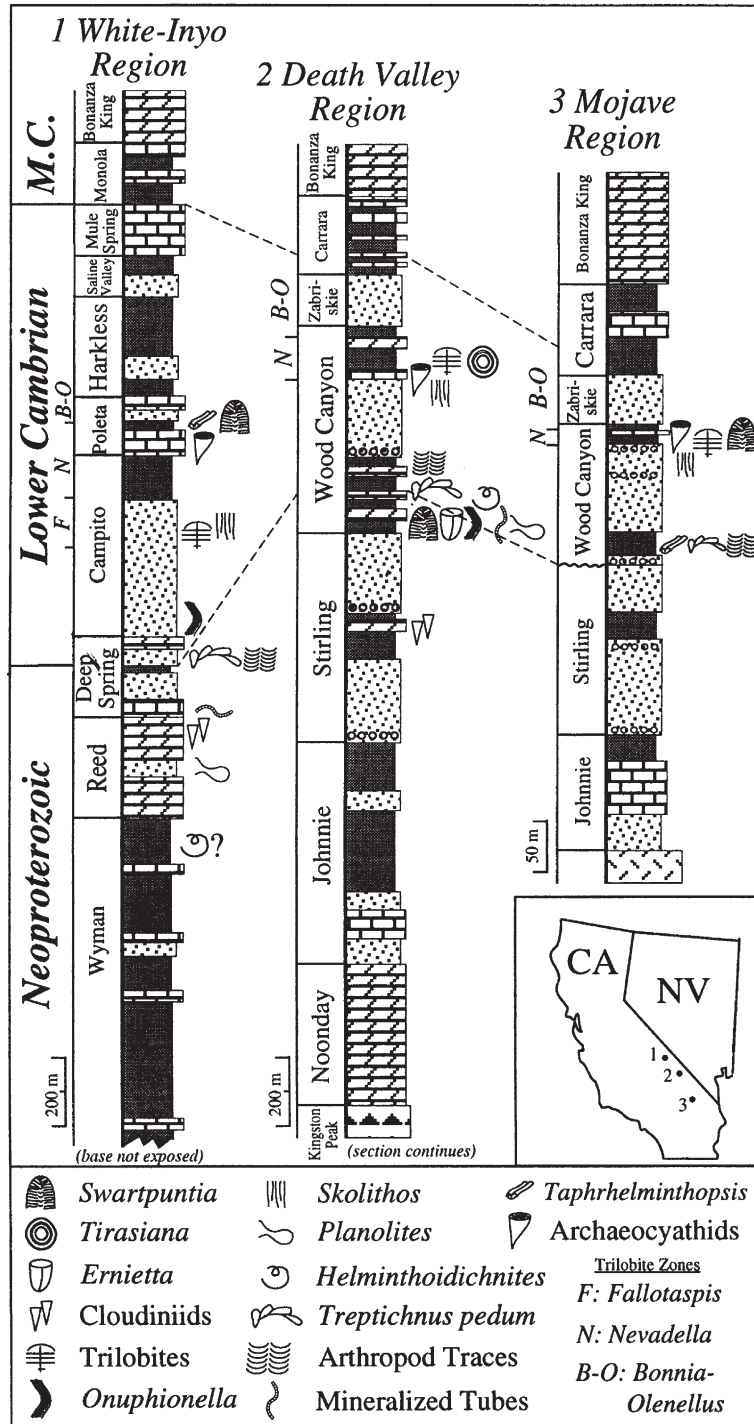


Fig. 114. Generalised litho- and biostratigraphic framework for the fossils from California presented; faunal symbols reflect confirmed first occurrences of body or trace fossils within each region and are positioned to the right of their corresponding section. Dashed lines=approximate position of the terminal Proterozoic–Cambrian boundary and Lower–Middle Cambrian boundary. The vertical scale for the Mojave region has been exaggerated ×3. Inset: sample locations within each of the three lithostratigraphic provinces (after Hagadorn et al., 2000).

about 4.5 km NW of Kelso Station. Both localities also yielded nevadiid trilobites and typical lower Palaeozoic trace fossils (including *Rusophycus*, *Skolithos*, *Trep-tichnus* and *Taphrhelminthopsis*) as well as body fossils and as cloudinid-like tubes. Carbon isotope studies are consistent with an Early Cambrian age.

The specimen of *Swartpuntia* from the White Mountains came from the Poleta Formation, which also carries archaeocyathids and similar trace fossils. Again carbon isotope studies support an Early Cambrian age.

These authors describe in detail a discoid form from Salt Springs (17 mm diameter and 0.5 mm vertical relief) comprising three concentric zones, the inner one raised (Fig. 115). After a lengthy discussion, they find it closest to *Tirasiana disciformis* from the central Ural Mountains, as described by Bekker in Sokolov and Iwanovski (1985). This specimen is preserved on the sole of a fine grained sandstone slab with a silt/claystone layer beneath. It is closely associated with the trace fossils *Cruziana*, *Diplichnites*, *Monocraterion*, *Palaeophycus*, *Planolites* and *Skolithos*. The environment of deposition is interpreted as mixed tidal and storm-swept shallow marine shelf.

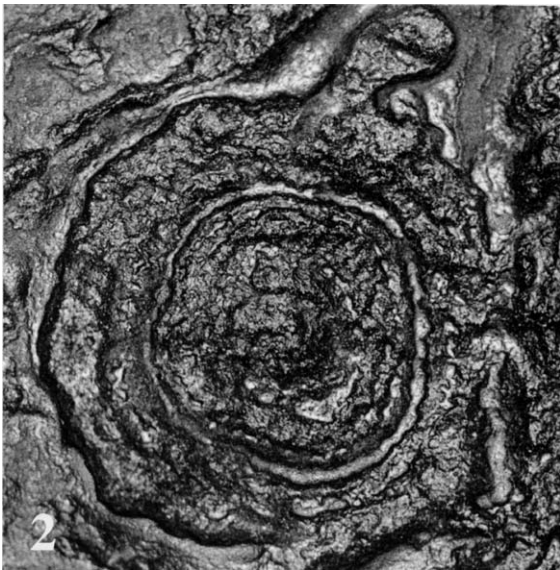


Fig. 115. (1) Sole of a bed from the upper member of the Wood Canyon Formation, Salt Springs Hills, California. A discoidal specimen of *Tirasiana disciformis* is at the centre of the slab amidst a variety of trace fossils, including an obliquely dipping *Planolites* burrow at upper margin ($\times 1.5$). (2) Close-up of *?Tirasiana disciformis*, illustrating two regions of circular rings surrounding a quasi-polygonal pointed and central region. The specimen is preserved in convex hyporelief ($\times 4$). (from Hagadorn et al., 2000).

The other form described in detail is a fragment of a frondose petaloid represented by specimens from Kelso Mountains and White Mountains. The specimen described measures 62×51 mm, consists of several petaloids and is part of a central stalk. There is evidence of superimposition of thin frond layers. The authors find closest resemblance to described specimens of *Swartpuntia gersmi* by Narbonne et al. (1997) from Namibia and their specimen is of about the same age as *Swartpuntia* described by Jensen et al. (1998) from Australia. They refer to it as *Swartpuntia* sp.

These authors noted in their discussion that although discoidal “medusoids” were known from Cambrian strata (Crimes et al., 1995), more complex Ediacaran forms such as *Swartpuntia* are rare in the Cambrian, possibly being only preserved under unique environments or taphonomic windows. These finds suggest that *Swartpuntia* may have an age range of about 25 Ma. The authors suggest that microbial blanketing of sediments may have allowed soft body preservation, also decreased oxygen, lack of vertical bioturbation, early diagenetic mineralisation and/or rapid burial.

11.4. Nevada

There are two abstracts (Horodyski, 1991; Horodyski et al., 1994) reporting the discovery of an Ediacara-type fauna in Nevada. The first report was of finds in sandstone near the contact between the Wood Canyon Formation and Stirling Quartzite, near Johnnie, just over the border in southern Nevada (Fig. 114). Some specimens are weathered and poorly preserved but others are well preserved. One of the latter resembles *Ernietta*, as reported from the lower Nama Group in Namibia, and like those specimens it is preserved in three dimensions, forming contiguous sand-filled structures like tubes. This was the first discovery of an Ediacara fauna in the western United States. Trilobites and Archaeocyathids occur in the upper part of the Wood Canyon Formation, indicating Early Cambrian age, and the new finds are below this; Horodyski suggested that they are below the Precambrian–Cambrian boundary, which must then be within the Formation.

Horodyski et al. (1994) amplified this aspect of the Nevada finds. They stated that the lower member of the Wood Canyon Formation is mainly a highstand systems tract that embraces the Precambrian–Cambrian boundary. They showed, by measured sections in the Chicago pass, Johnnie and at the Desert Range, that the base of the lower member is a thin transgressive sequence tract that interfingers with the Stirling Quartzite. Three

carbonate-topped parasequences constitute the overlying middle member of the Wood Canyon Formation in 200–250 m thick sections. The oldest of these contains the Vendian body fossil *Ernietta plateauensis* Pflug. The assemblage of the middle parasequence is of low diversity at Chicago pass and is similar to an assemblage found in the lower parasequence at Desert Range. Typical Cambrian trace fossils, including *Phycodes pedum*, are, however, found in the youngest sequence at both Chicago Pass and Desert Range. The authors concluded that as *Ernietta* occurs in the Vendian of Namibia and *Phycodes pedum* is an index fossil in the Early Cambrian in the Newfoundland boundary type-section (GSSP), the boundary must lie somewhere within the middle of the parasequence set. The carbonate carbon isotope values for the interval contain-

ing the Ediacara fauna match those of the interval in Namibia.

It may be noted here that the above deduction as to age is probably correct, but Ediacara-type faunas are now known to have survived into the Cambrian (in South Australia and Ireland, for example).

No full account of these important discoveries is known to the present author.

11.5. Mexico

McMenamin (1996) described an Ediacaran fauna of macroscopic animals and prototists, together with trace fossils, from the Clemente Formation, near Sonora, Mexico. He believed that this discovery extended downwards the time range of the Ediacaran

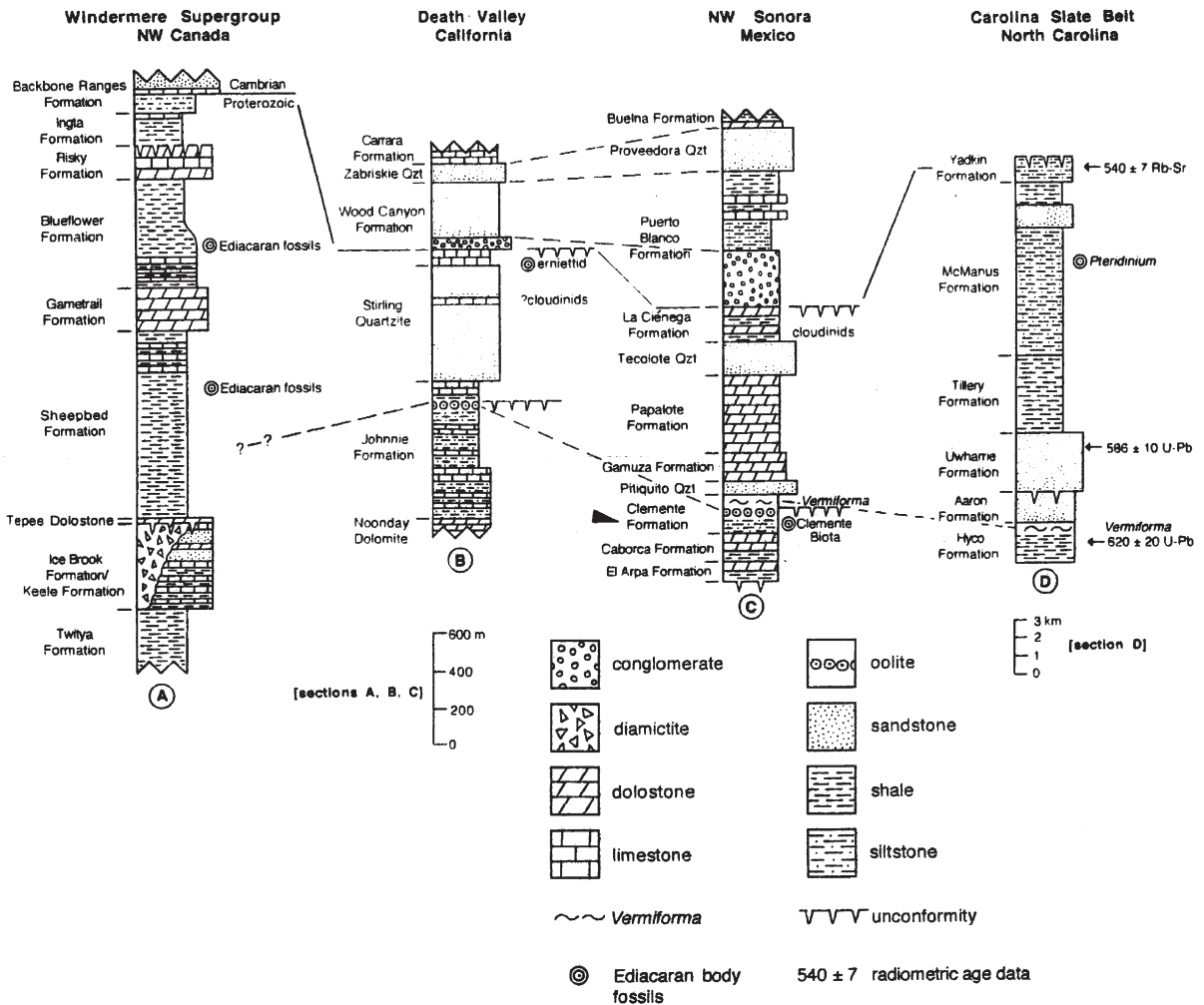


Fig. 116. Correlations between the Proterozoic strata of the Windermere Group in NW Canada (A), Death Valley, California (B), Sonora, Mexico (C) and the Carolina Slate belt, North Carolina (D). An arrow indicates the location of the new fossil find in the case of panel C. Radiometric dates are in myr (after McMenamin, 1996).

fauna, considering it to be the earliest example so far recorded. The finds were made in pre-Palaeozoic shallow marine strata in the Altar desert of the Caborca region. The Clemente Formation is a mixed siliciclastic/carbonate unit, the type section of which is in the Sierra el Rajon Range (Fig. 116). The most distinctive rocks are pale, tawny weathering oolite (unit 5 in the Formation). This can be correlated a bed near the base of the Rainstorm Member of the Johnnie Formation in Eastern California.

The fossils occur in a small regolith patch close to outcrop and are also present in beds up to 75 m below the oolite in the section. There are three types of body fossil, two trace fossils and several enigmatic forms which are known elsewhere also. The largest body fossil consists of rounded central cone in hyporelief, 2.1 cm across and 7 mm in height, featureless except for a slight wrinkle where it meets the essentially flat outer ring, which bears thin radial tubular structures. This fossil is compared with *Cyclomedusa plana*

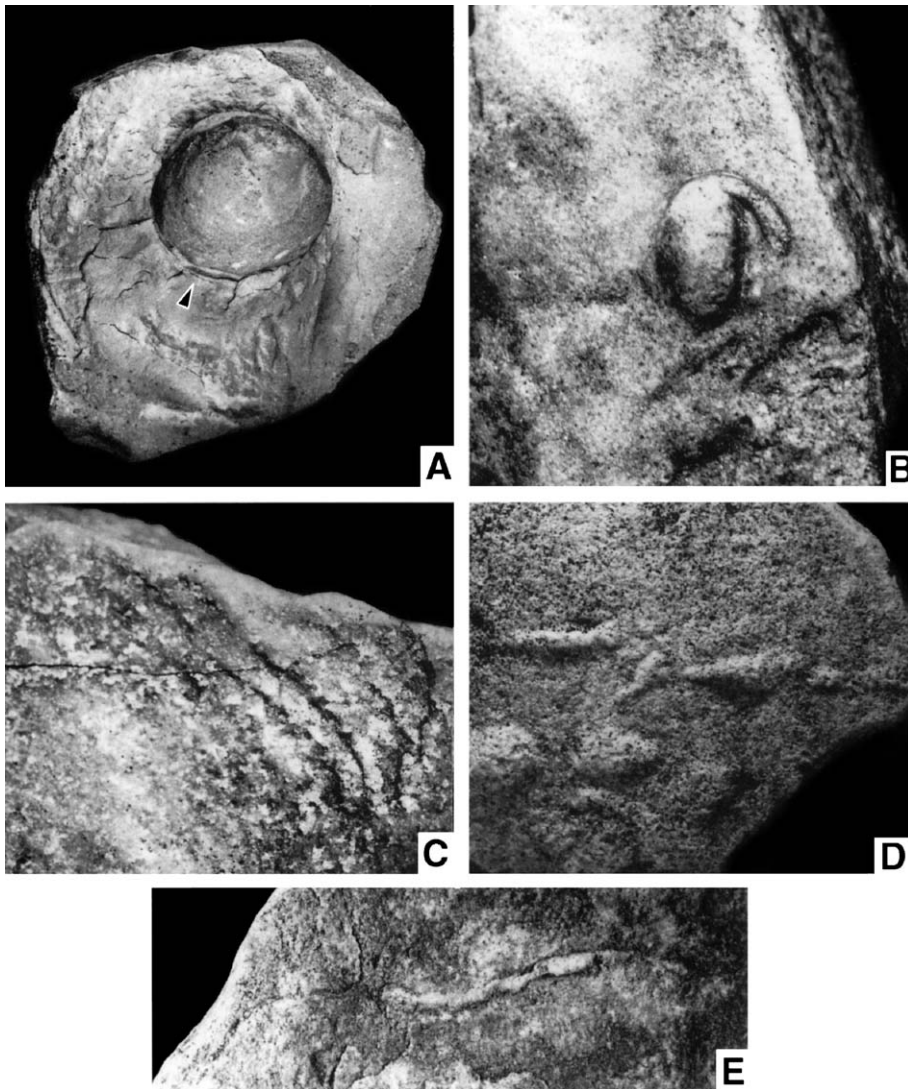


Fig. 117. Body and trace fossils from the Clemente Formation, Sonora, Mexico. (A) *Evandavia aureola*, a discoidal fossil preserved in hyporelief. Note the annular ridge at the margin of the central dome, arrowed (rock specimen is 6.0 cm across) (in Unit 1 of Clemente Formation). It was originally identified as *Cyclomedusa*, but this was revised in [McMenamin \(2005\)](#). (B) *Sekwia* sp. Note the crescentic indentation on the right side of the fossil (dimensions of fossil 1 cm diameter) (in Unit 4 of Clemente Formation). (C) Ernieetid fossil (width of rock specimen is 3 cm) (in Unit 4 of the Clemente Formation). (D) *Lockeia* ichnosp., preserved in hyporelief; eight specimens are visible (width of rock sample is 2.5 cm) (in Unit 4 of Clemente Formation). (E) *Palaeophycus tubularis* Hall, occurring in both convex and concave hyporelief (width of rock specimen is 6 cm) (in Unit 4 of the Clemente Formation) (after [McMenamin, 1996](#)).

Glaessner and Wade, recorded from the Sekwi Brook of the Mackenzie Mountains, northwest Canada (Narbonne and Aitken, 1990), and it is referred to that species, despite minor dissimilarity. A second specimen (Fig. 117B) is circular-to-elliptical in shape (1 cm diameter, 1.6 mm relief). It is a conical object, flattened and compressed by compaction of the enclosing sediment—this flattening imparts the crescentic fold diagnostic of the genus *Sekwia*. It is the fossil of a non-mineralised conical structure, which resembles the type species of *Sekwia excentrica*, described by Hofmann (1981). The third form is an incomplete specimen, a set of parallel tubular cylinders up to 2 mm wide, following a straight path and then curving together (Fig. 117C). They taper, separate and come to a terminal point. McMenamin saw similarities to Ernietids described from Namibia, and especially a not-yet-described-in-print example from the Wood Canyon Formation Nevada (Horodyski, 1991). The specimen was too incomplete to attempt a more detailed diagnosis. He noted that the first two resemble diploblastic animals such as Cnidarians, but believed that that does not mean that they are necessarily animal fossils. Despite the fact that trails unique to Protoctista are absent, Protoctista would have constituted at least part of the community because they are the evolutionary antecedents of animals. There are no traits unique to animals on the body fossils, and he believes that blanket references to Ediacara faunas as “multicellular animals” are incautious.

The trace fossils *Lockeia* and *Palaeophycus tubularis* Hall were described, the first low-relief teardrop-shaped convex hyporeliefs (Fig. 117D), the second sinuous horizontal tubular burrows lined with a thin clay layer (Fig. 117E). The organisms that produced them lived in a shallow marine habitat close to fair weather wave base.

McMenamin supported his statement that this is the earliest Ediacaran fauna with a columnar stratigraphic correlation diagram, which includes the Sonora section, Death Valley California, the Windermere Supergroup, NW Canada and the Carolina Slate Belt, North Carolina (Fig. 116). He gave his reasons for his correlations and noted that the Johnnie Formation of Death Valley and the Clemente Formation of Sonora were originally much closer, having been separated by sinistral movement on the Mojave–Sonora megashear. He argued that the Sonora occurrence was older than any Namibian occurrence and discounted the reported occurrence in tillites in NW Canada (Hofmann et al., 1990),

because they had since been demoted by Narbonne et al. (1994) to “possible metazoan origin”. He argued, based on indirect radiometric evidence, for a date close to or in excess of 600 Ma for the Sonora fauna.

McMenamin concluded his account of this important find with a statement that this discovery shows that the evolution of the Ediacaran biota occurred in shallow water. Although this is likely based on all the evidence, globally, finding the oldest Ediacaran biota in a shallow-water context surely does not necessarily mean finding where it evolved (the question of the chance of fossil preservation comes in here among others) and the statement that the biota evolved in North America appears naïve (it can be compared with some statements that Man evolved specifically in the Rift Valley of East Africa, when the fact is that the Rift Valley surely provides sites where the hominoid-bearing strata have been preserved from erosion and destruction)? His figure of 80 Myr for the time interval of the Ediacaran biota matches closely the figure estimated for the Vendian by Russian authorities, although a figure of c. 50 Myr is nowadays more widely favoured.

12. Africa, South America and Antarctica

12.1. Introduction

Northwest Africa and Central South America have been considered in a single chapter, because these areas were formerly close together prior to the opening of the Atlantic Ocean and because the descriptions are quite concise. A brief mention of Vendian rocks in Victoria Land, Antarctica, is also slotted in here.

12.2. Northwest Africa

12.2.1. Morocco

The first account of an Ediacara-type fauna from northwest Africa was of the discovery of ‘medusoids’ in the Basal Series of the terminal Precambrian Adoudouanian in the Anti-Atlas, Morocco (Houzay, 1979). These circular body fossils were discovered at Tafendra, near Irhem in lutite which forms the most part of the Serie de Base, the lowest of three divisions of the Adoudouanian. The series of detrital sediments (lutites and sandstones) and carbonates, 1500–2500 m thick, separates rhyolites and andesites of Precambrian III and sediments of Early Cambrian age carrying archaeocyathids and trilobites (Fig. 118). There is another occurrence of circular body fossils near Ouaremdaz village 6 km to the SSE of

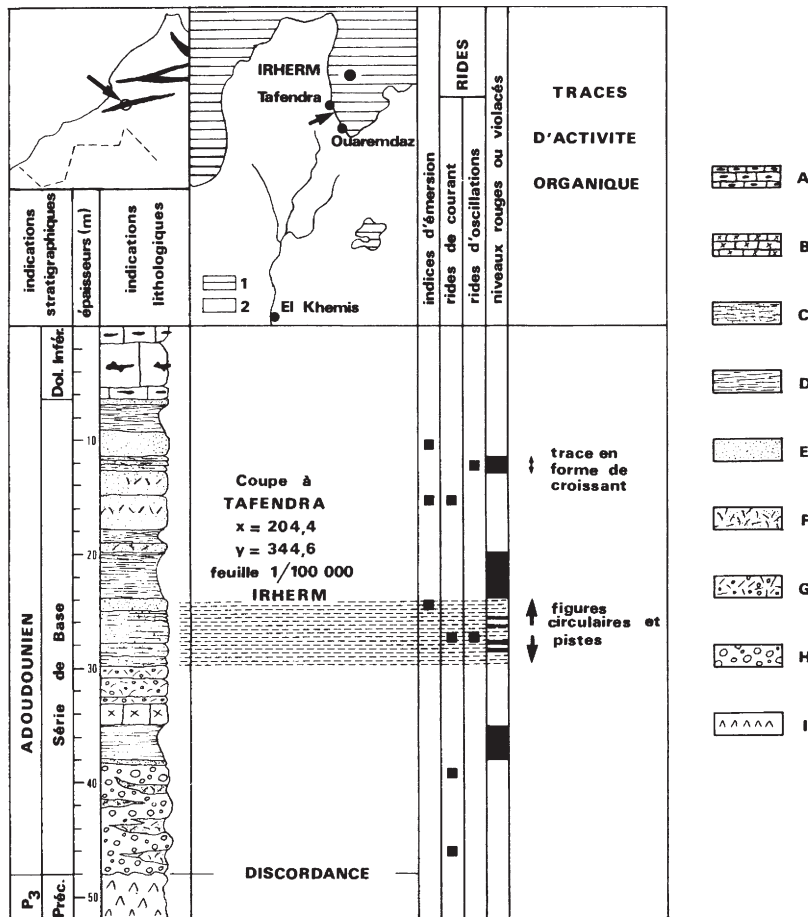


Fig. 118. Location diagram and stratigraphic column for the occurrences at Tafendra, Morocco. The horizontally dashed ornamented band in the section show the circular impressions have been found. 1=Precambrian outcrop, 2=Younger rocks. (A, B) Dolomites, (C, D) Lutites, (E, F) Grits, arkoses, (G, H) Microconglomerates, conglomerates, (I) Rhyolite (after Houzay, 1979).

Tafendra (Fig. 118). There lutites have a total thickness of 6 m of similar material to that at Tafendra and the individual beds are tens of centimetres thick, hard and of a dark violet colour. The beds are generally flat but are rarely undulose surfaced, with symmetrical or asymmetrical ripples. The upper lutite surfaces display desiccation polygons. The circular structures only occur on flat surfaces, are sparse and isolated. There is no carbonate at all in the lutite. This was a rhythmic deposit of very calm water and the sedimentary structures are consistent with an intertidal setting bordering a continent subject to very feeble erosion.

The circular structures are mostly elliptical and have a central swelling (of up to 5 mm) surrounded by a number of annular ridges and furrows. In section, they are seen to displace several thin laminations in the host sediments upwards and downwards.

Houzay considered diagenetic and other inorganic origins but favoured impressions of primitive animals,

drawing comparisons with medusoids described from Australia (Sprigg, 1947, 1949; Glaessner and Wade, 1966), from Newfoundland (Misra, 1969) and from England (Ford, 1958; Boynton, 1978). He noted that carbonate, not elsewhere present in the lutite, is present at the apex of the circular structures and favoured jellyfish as the fossilised animal, but with some imposed diagenesis. He found the greatest similarity to the genus *Cyclomedusa* (Sprigg, 1947).

12.2.2. Algeria

Bertrand-Sarfati et al. (1995) described further developments of Ediacara-type fossils in two outcrops in the northeastern part of the Taoudenni basin, Algeria (Fig. 119A), southeast of Chenachane. The Cheikhia Group, bounded by two major unconformities, is partially preserved in large synclines (Fig. 119B). It is a thick siliciclastic sequence truncated by an erosional surface, produced in tilting and faulting of the craton

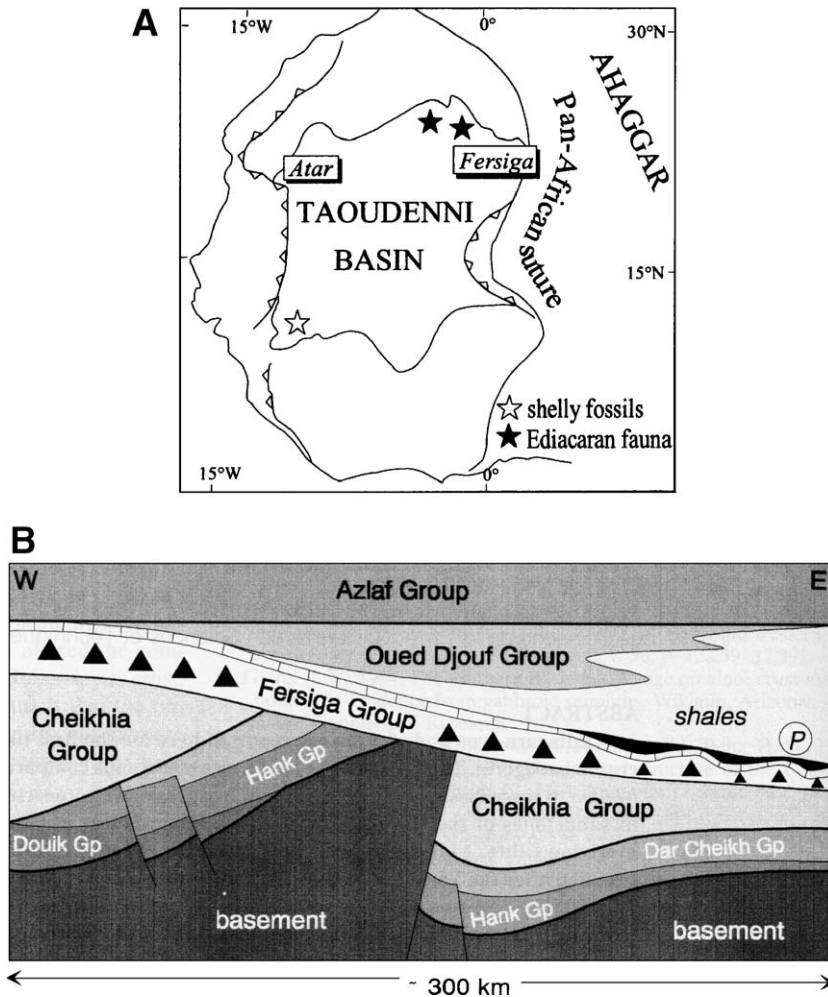


Fig. 119. (A) Location diagram, Taoudenni Basin, Algeria. (B) Sectional diagram showing the geological relationships in the NE Taoudenni Basin, Algeria (vertical scale exaggerated) (after Bertrand-Sarfati et al., 1995).

during the Pan-African tectonic event. The specimens are preserved as sandstone casts on the upper bedding surfaces of thin sandy layers, and in thin section the cast is separated from the underlying sandy layer by a darker line, enriched as are other discontinuity surfaces in iron oxide. There is evidence of some transport of these bodies while floating by water movement. Some bodies were folded and truncated before burial, now being non-discoidal. The typical form, seen in 16 specimens, is slightly elliptical, bipartite discs, 1.5 mm thick with an outer smooth ring and a central raised disk. There are three protuberances on the inner disc of one specimen. A few discs in negative relief may be counterparts. The outer discs have diameters of 6–12 mm and the inner discs 2–6 mm.

The fossils are small and simple. There are no complex forms as in some other Ediacara-type faunas.

Comparisons were drawn with *Medusinites* (Glaessner and Wade, 1966) and *Nimbia*.

In the NE Taoudenni Basin the Cheikhia Group, which contains these fossils, is unconformably overlain by continental tillites, glaciolacustrine, fluvioglacial and aeolian deposits of the Fersiga Group. These are beneath a thin veneer of layered carbonate mudstones overlain by stromatolitic phosphorite with *Renalcis*-like microfossils, shales and ash beds. Above again comes a transgressive sedimentary wedge. This sequence records glaciation and deglaciation.

The Ediacara-type fauna described cannot be precisely allocated to the post-Varanger (<580 Ma) or pre-Varanger (>610 Ma) faunas. However, the biostratigraphic constraints indicate that the host deposits date from between 620 and 580 Ma, contemporary with the Pan-African orogeny and were

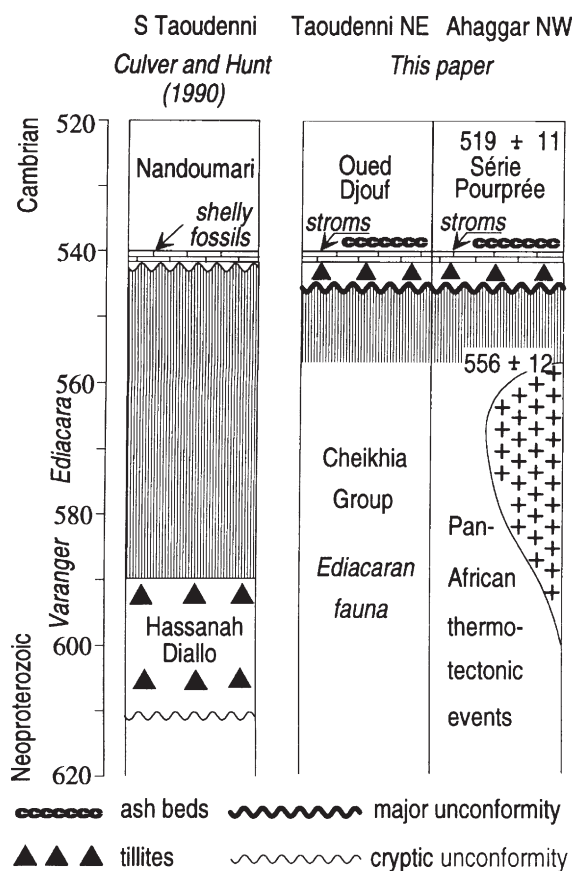


Fig. 120. Correlations of the late Neoproterozoic to Cambrian strata in NE Taoudenni basin and NW Ahaggar, also with comparison with the stratigraphic interpretation proposed by Culver and Hunt (1990) in the S Taoudenni basin (after Bertrand-Sarfati et al., 1995).

later folded, faulted and eroded. In Ahaggar, glacial sediments everywhere overlie an unconformity and the carbonate cap carries the Early Cambrian small shelly fauna, the unconformity being dated at 556 Ma (± 12 Ma). Thus, the authors concluded that the glacial deposits of northwest Africa are Early Cambrian in age, not of Varanger age, the Varanger glaciation being apparently absent in western Africa. The subject of the age of the glaciation is further covered in a later paper by Trompette (1996), discussed below. Bertrand-Sarfati et al. do not attempt to date the Ediacara-type fauna, but it is clearly older than the glaciation represented in the Taoudenni Basin. They illustrate their interpretation of the time sequence in Fig. 120, contrasting it with that derived by Culver and Hunt (1990) for the southern Taoudenni Basin.

Trompette (1996) noted that cratonisation favours glaciation because cratons are ideal cradles for the

development of continental ice caps. He considered that the widespread continental glaciation in Western Africa, developed near the Proterozoic–Cambrian boundary, could no longer be referred to the Vendian. The discovery of an Early Cambrian small shelly fauna in eastern Senegal (Villeneuve, 1984) extends the glaciation to Atdabanian time. The age of its beginning cannot be determined accurately and it may be Vendian or Early Cambrian. Trompette also discussed the Paraguay fold belt of South America (Brasil) and concluded that it was probably Vendian in age and restricted to the shoulders of rifted basins, local highlands, which initiated the short-lived Pan-African–Brasiliano cycle that extended from c. 600 Ma to 520 Ma. There it affected middle latitudes (60°). The Late Vendian (?) to Early Cambrian ice cap of Western Africa also represents a glaciation affecting middle latitudes (50° – 30°). This research is important because there have been many attributions of the Ediacaran explosion of primitive Metazoa to the legacy of the Varanger (Laplандian, Maranoan) glaciation, for a wide variety of reasons. In Western Africa, there appears to be no evidence of a glaciation preceding the Ediacara-type faunas, but there is of one closely following them, which extended into the Cambrian and had its beginning at an uncertain date. The Ediacara-type fauna of Morocco is ascribed to the terminal Precambrian (Vendian), whereas that of the Taoudenni Basin is probably of Vendian, but could conceivably be of earliest Cambrian age.

12.3. South America

12.3.1. Argentina

Acenolaza and Durand (1986) described an Upper Precambrian–Lower Cambrian biota from NW Argentina. The discovery included impressions of body fossils and trace fossils. These finds were made in a NW–SE aligned sedimentary basin which probably originated as a rift on the old South American Precambrian platform which separated the Arequipa Massif from the Brazilian cratonic area of Rio de La Plata. Within the basin, flysch-like elements are intercalated with volcanic rocks. The host rocks are the Puncoviscana and Suncho Formations (Fig. 121), both of which carry trace fossils and soft-bodied impressions. The Puncoviscana Formation consists of turbiditic sandstones and shales, limestones and conglomerates. The Suncho Formation consists of greywackes, slates rhythmically interstratified. Both formations are deformed and stratigraphic resolution is difficult.

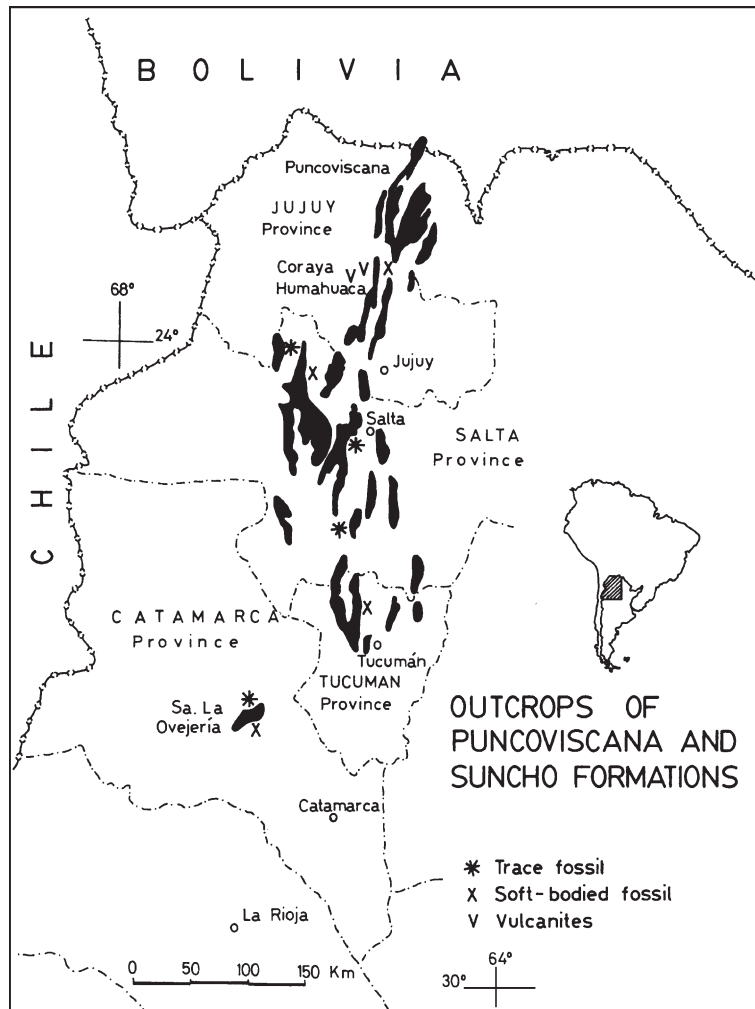


Fig. 121. Geographical distribution of the Upper Precambrian–Lower Cambrian units in Argentina (sedimentary and very low grade metamorphic rocks with fossils) (from Acenolaza and Durand (1986). Reproduced with permission of Cambridge University Press).

The impressions of soft-bodied organisms on bedding planes were found near Munano (Salta), Humahuaca (Jujuy), Sierra de La Ovejería (Catamarca) and Choromoro (Tucumán). ‘Medusoids’ were present at all these localities, including *Beltanelliformis* and *Sekwia*. The first are discoidal, subcircular to circular, 5–10 mm in diameter with central protuberances. They are crowded together (‘gregarious’) almost covering the surface. The largest individuals were found at Sierra de La Ovejería. *Sekwia*, described by Hofmann (1981), has a peripheral border and longitudinal crest, probably due to flattening (Fig. 122).

Trace fossils identified comprise three types:

Creeping or tube-shaped traces: *Cochlichnus*, *Helminthopsis*, *Nereites*, *Gordia*, *Torrowangea*, *Phycodes*, *Palaeophycus*, and *Planolites*.

Appendicular sharp traces: *Asaphoidichnus*, *Diplichnites*, *Dimorphichnus*, *Monomorphichnus*, *Oldhamia*, *Protichnites*, *Protovirgularia*, *Tasmanadia*.
Bilobate trace: *Didimaulichnus*.

Nereites saltensis, *Oldhamia radiata*, *Oldhamia flabella* and *Oldhamia antiqua* nowhere occur at the same horizons as the other traces, something that may be a function of bathymetry. The biota and traces cannot be integrated into a normal stratigraphic section due to tectonic complications. The relative ages of the trace fossils are thus difficult to determine. However, two groups, one of impressions of soft bodies and one of sharp appendages can be separated; where there are abundant soft body impressions, as at Choromoro, and Tucumán, the rocks are believed to be exclusively of late Precambrian age. Those with sharp traces, as at San

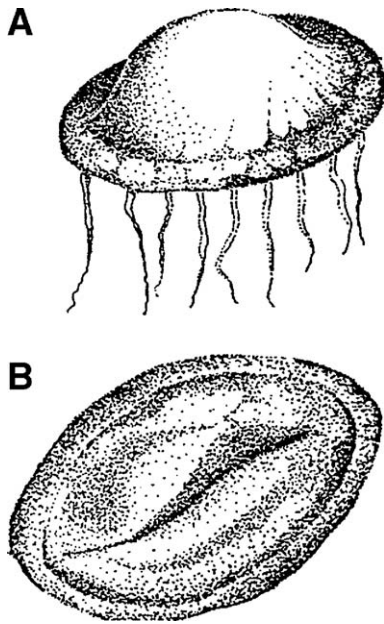


Fig. 122. Schematic reconstruction drawing of *Sekwia* from outcrops at Coraya, Jujuy (see Fig. 121) (from Acenolaza and Durand (1986). Reproduced with permission of Cambridge University Press).

Antonio de Los Cobres, Munano, are taken to be of Early Cambrian age. The Puncoviscana trace fossils and microbial mats were later reinterpreted by Buatois and Mangano (2003).

A correlation diagram with other Gondwana occurrences of Ediacara-type faunas and North American occurrences was provided by Acenolaza and Durand, and also a palaeogeographic reconstruction of Gondwanaland and North America.

12.3.2. Brasil

In the Paraguay River Basin of Brasil, Paraguay and Bolivia, there are also Upper Precambrian rocks, and these have glacial tillites at the base (the Jangada and Puga Formations); the tillites are overlain by marine limestones containing stromatolites (*Collenia*, *Aulophycus*, etc.). These are probable correlatives of the upper Proterozoic of Argentina, although not necessarily deposited in the same basin.

The Upper Paraguay River basin has been mentioned by Trompette (1996) in connection with Northwest Africa; and also by Acenolaza and Durand (1986) in connection with the occurrences in Argentina. Neoproterozoic fossils were reported from there by Hahn et al.

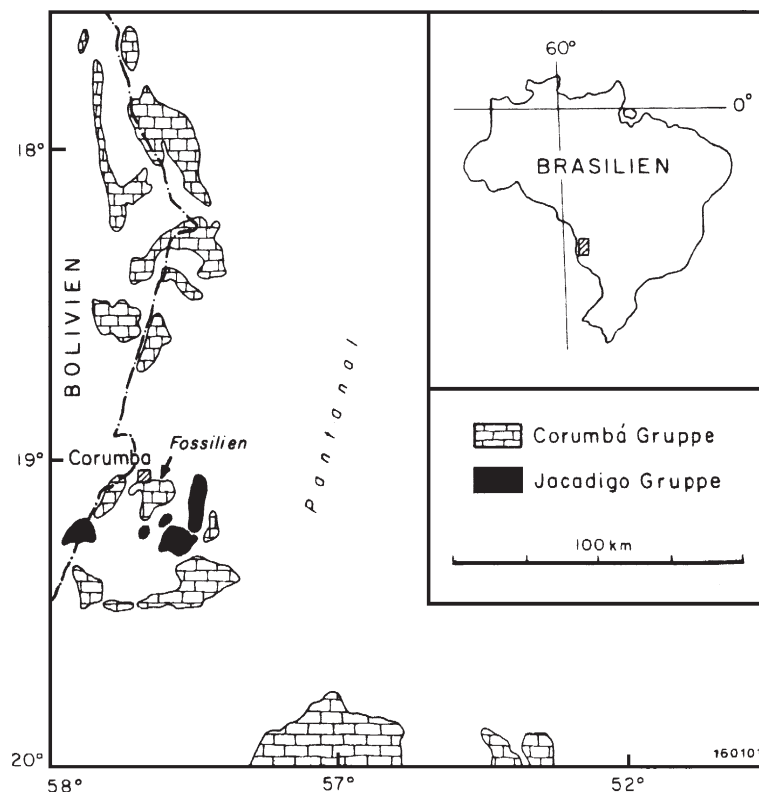


Fig. 123. Location diagram, site of find of *Corumbella* (after Hahn et al., 1982).

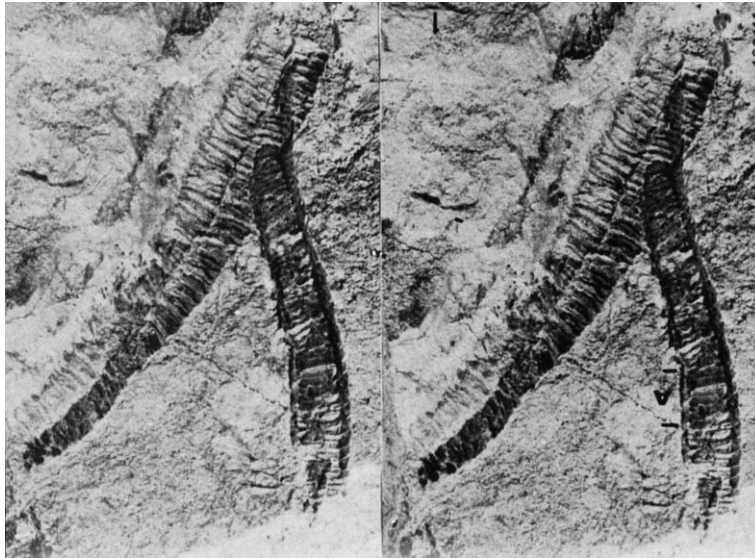


Fig. 124. Photograph of *Corumbella weneri*, $\times 3.58$ (from Hahn et al., 1982).

(1982) from a limestone quarry at Corumba–Ladario in the Matto Grosso Province of SW (Fig. 123). They occur in shale of the Corumba Group which has been determined by Rb/Sr age dating as ca. 600 Ma old, i.e. Vendian. The fossils are preserved in three-dimensional condition by virtue of their chitinous periderm. There are several specimens but they are all of a single organism, which has been named *Corumbella weneri* n. gen and n. spec. nov (Fig. 124). This is of frond-like

form and there is some resemblance to the genus *Charnia* of the Vendian and also to recent Pennatularia (sea-pens), but there are significant differences:

- (1) A chitinous periderm.
- (2) The unbranched primary polypar (stalk) consists of ring-shaped segments which contain four ‘sclero-septa’ in the interior.
- (3) Above it is branched into secondary ‘polypars’ which are biserially arranged, each with its own periderm tube. There are at least three layers of secondary ‘polypars’ on each side and many sets outwards towards the distal end.

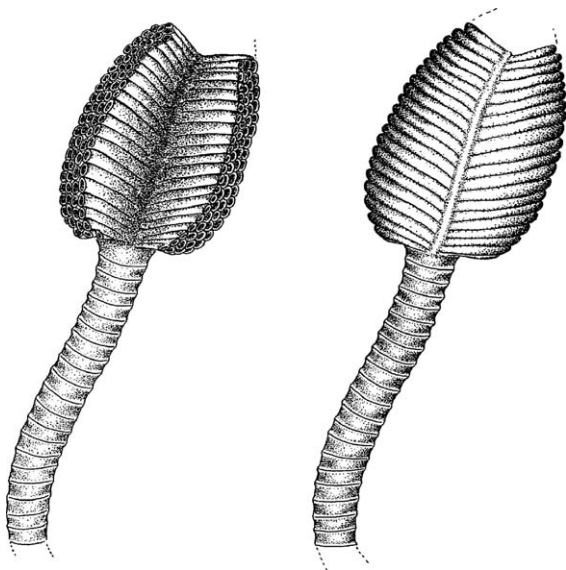


Fig. 125. Reconstruction drawing of *Corumbella weneri* (after Hahn et al., 1982).

A reconstruction drawing by Hahn and Pflug is shown in Fig. 125. The stalk resembles that of the living Scyphozoan genus *Stephanoscyphus* Allman 1874, and this was taken by these authors to show that the Neoproterozoic organism was a Scyphozoan. However, it was admitted that such biserially arranged secondary ‘polypars’ are not found in Scyphozoans. It was suggested that *Corumbella weneri* represented an early side-branch of Scyphozoan evolution and a new sub-class of the Scyphozoa named Corumbellata subclass was erected. This metazoan is significantly different from the commonly found ‘medusoid’, frond-like and other members of the Ediacara-type fauna, and must be regarded as an unique Vendian fossil—that it is Vendian there is no doubt, on account of the age dating and the fact that glacial tillites precede the appearance of it and *Cloudina* in Brasil. The structure

of the secondary fronds does resemble the ‘mattress’-like structure of Vendian fossils recognised by Seilacher (1989).

Zaine and Fairchild (1985) described fossil metazoans and microfossils from the Corumba Group (Tamengo Formation) in SW Brasil, reclassifying *Aulophycus luciano* Beurlen and Sommer 1957 as *Cloudina luciano* (Beurlen and Sommer), and recognising the microfossils *Bavlinella faveolata* (Shepeleva) and, questionably, the acritarch *Vanadalosphaeridium* sp. Despite Hahn et al. (1982)’s attribution of this fauna to the Ediacaran, these authors doubted if the palaeontological evidence was adequate to permit definite conclusions in this respect.

Hahn and Pflug (1985) described ‘*Cloudina*-like’ calcareous tubes from this formation as well as Argentina and Namibia. They erected a new family of worm-like animals with two genera *Cloudina* Germs 1972 (from Namibia) and *Acuticloudina* n.g. from

Argentina. *Cloudina waldei* from the Tamengo Formation, Brasil differs from *Cloudina hartmannae* and *Cloudina riemkeae* of Germs (1972a,b) by the length of the single tubes, their breadth and diameter of the walls. The tubes are composed of several smaller single tubes which are set one in another as are the parts of a telescope, being open distally and proximally—only the first of them is closed at the bottom. The tubes are of organic material but with cones of calcium carbonate inserted. Unlike the Serpulidae, the organism was unable to secrete a calcareous ring, but could only produce calcareous cones which are limited to one side of each single tube. They illustrated this with drawings (Fig. 126). If Cloudinids are annelids, they are more primitive than Serpulids; however, slender evidence from elsewhere of budding asexually is against this and they do not favour a relationship to the Cribricyatha, despite some resemblance in the structure.

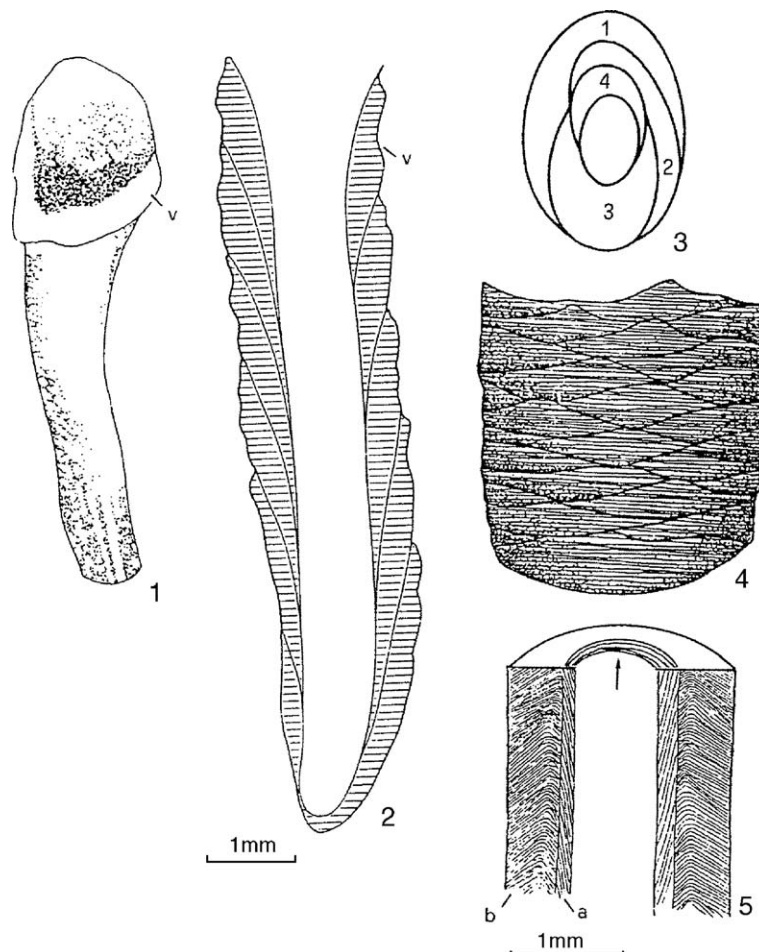


Fig. 126. Reconstruction drawing of *Cloudina waldei* from the Tamengo Formation, Brazil (after Hahn et al., 1982).

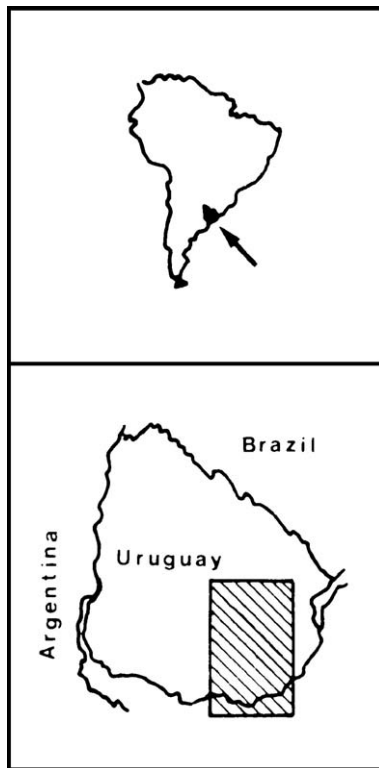


Fig. 127. Geographic distribution of the Arroyo del Soldado Group, Uruguay (stippled). Letters A–E indicate fossil sites with Vendian skeletal fauna (after Gaucher and Sprechmann, 1999).

12.3.3. Uruguay

Gaucher and Sprechmann (1999) described an upper Vendian skeletal fauna from the Yerbal Formation of the Arroyo del Soldado Group in Uruguay (Fig. 127). A stratigraphic section is shown in Fig. 128. The upper Vendian age is determined on the basis of biostratigraphy, radiochronological datings and field relationships. The host sequence represents a transgression from supratidal and intertidal to subtidal depositional environments and the fossils are all in siltstones. The Yerbal Formation was deposited in cold climatic conditions whereas the overlying Polanco Formation was deposited in tropical conditions. No Ediacara-type soft-bodied fossils have been recorded there, but the shelly fauna is claimed to be the oldest diverse shelly fauna known. It consists of *Cloudina riemkae* Germs and three new genera and species, all less than 5 mm in diameter:

Titanotheca coimbrae
Waltheria marbergensis
Soldadotubulus siderophoba

Titanotheca coimbrae is interpreted as an agglutinated foraminifer (Fig. 129), extending the range of the group back into the Neoproterozoic. *Waltheria marbergensis*, with a phosphatic shell, lacks a foramen and is not a foraminifer. It has a multilayered shell and branching, unknown in other mentioned fossils. *Soldadotubulus siderophoba* occurs exclusively in iron oxide-poor laminae in ferruginous siltstones. It occurs at only a single locality and only 12 examples, not well preserved, have been found in thin section. The taxonomy of this organism remains uncertain. The fauna consists of these four forms with mineralised exoskeletons and two other possible forms.

Undetermined vase-shaped and discoidal fossils and microfossils including *Bavlinella faveolata* and *Leiosphaeriodia* cf. *Leiosphaeriodia tenuissima* accompany this skeletal fauna.

The authors advance arguments that skeletalisation was a response to onset of predation. *Cloudina* and sponge spicules from Mongolia provided the only evidence of skeletalisation up to now. It is clear that agglutination and phosphatic tests had been acquired as adaptations already in the late Precambrian (upper Vendian) and this evidence implies that diversification of a skeletal fauna occurred even earlier in the Neoproterozoic.

12.4. Antarctica

Whereas no Vendian Metazoan fossils have been discovered in Antarctica, there are sediments in Northern Victoria Land (Cooper et al., 1982) which carry fossils of Vendian age. These were mapped as the Robertson Bay Group and range up to the Late Cambrian or Ordovician. The Acritarchs and other microfossils include *Chuarina circularis* Walcott?, *Protophaeridium*, and *Bavlinella faveolata* (Shepeleva) Vidal; the assemblage in the Molar Formation (equivalent to the Robertson Bay Group, is, in particular, characteristically Vendian, and there are strong indications that the sequence extends down into the Vendian. There are also Vendian rocks in the Shackleton Mountains, in Antarctica, southwest of the Ross Sea.

13. Asia

13.1. Introduction

Of the countries dealt within this section, China is particularly important; however, literature search concerning China is difficult because one has to rely

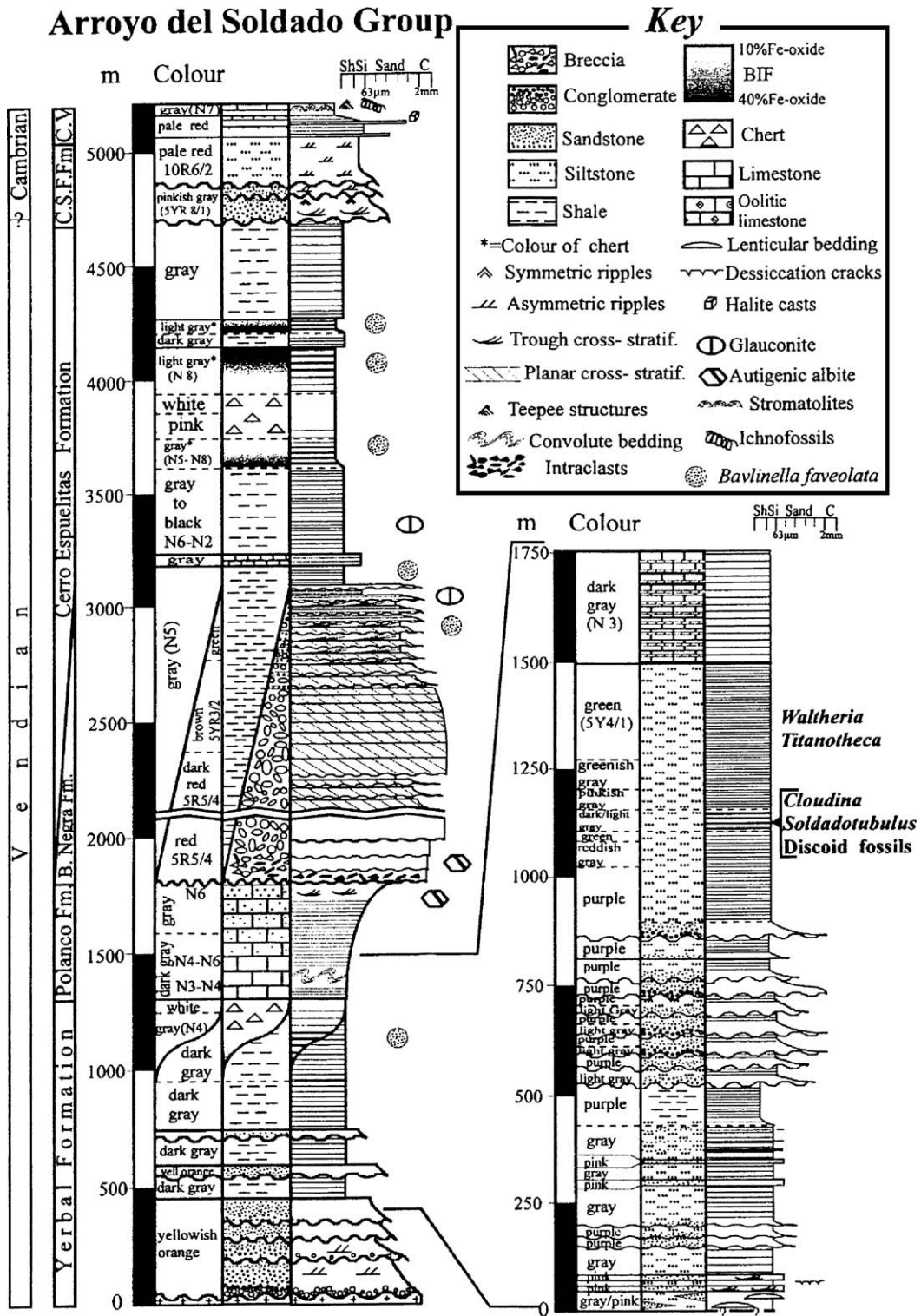


Fig. 128. Generalised stratigraphic column of the Arroyo del Soldado Group, Uruguay, and detail of the Yerba Formation at the stratotype (Point A in Fig. 127), showing the occurrence of fossils. (after Gaucher and Sprechmann, 1999).

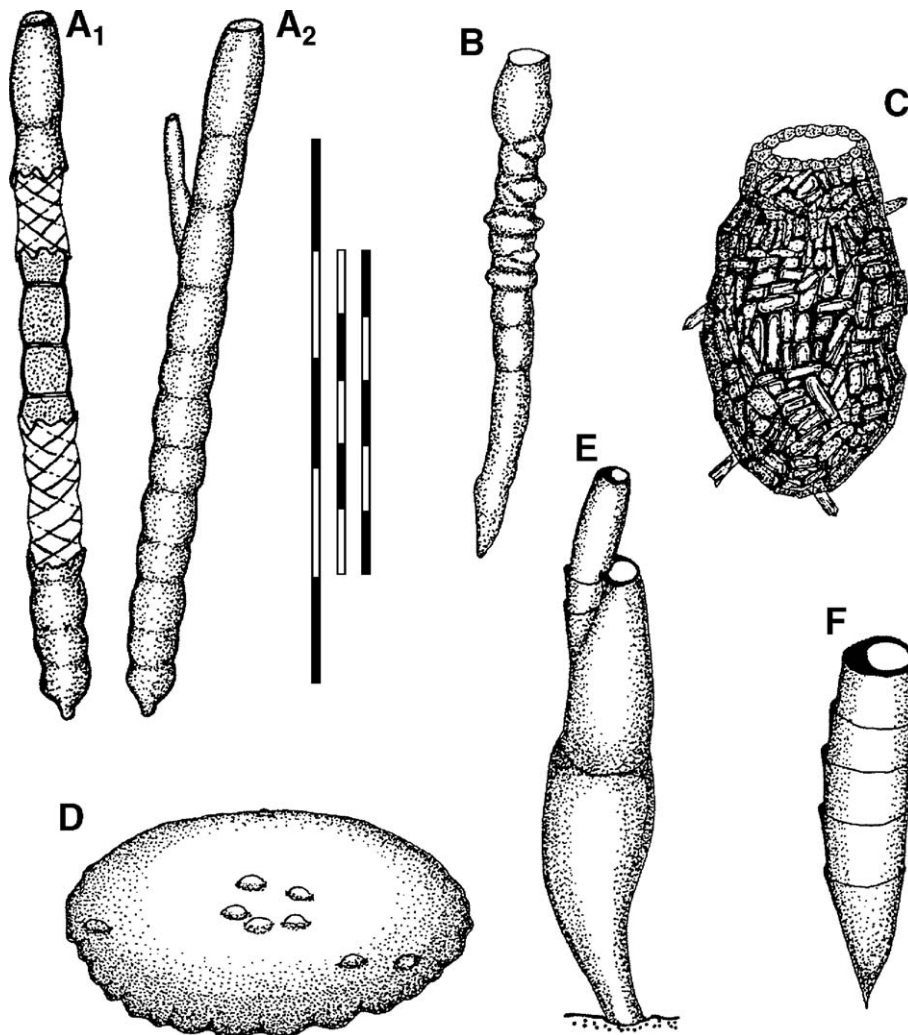


Fig. 129. Reconstruction of different skeletal fossils of the Arroyo del Soldado fauna. (A1, A2) *Waltheria marburgensis*, structure of shell and inferred external appearance. (B) *Soldadotubulus siderophoba*. (C) *Titanotheca coimbrae*. (D) Discoid fossils. (E) *Cloudina riemkae* Germs 1972, forma beta. (F) *Cloudina riemkae* Germs 1972, forma alpha. (Simple scale bar represents 0.5 mm for b, 1.0 mm for C; double scale bar represents 1 mm for A and 3 mm for E–F) (after Gaucher and Sprechmann, 1999).

on short English language summaries accompanying Chinese language publications, for the most part. Chinese language publications tend to be brief and not well illustrated. Therefore, although there are a handful of relevant English-language publications, China has been considered here alongside other Asian occurrences, rather than being afforded a separate section.

13.2. Iran

Stocklin (1968) drew attention to the fact that the Infracambrian of northern Iran has yielded stromatolites and problematic fossils. A distinct shale marker, traceable from the Central Alborz Mountains to Azerbaijan contains small disc-like objects which

closely resemble *Fermoria* sp. from the Precambrian–Cambrian Vindhyan “System” of India (Sahni and Srivastava, 1954) or *Beltanella gilesi* Sprigg (?) of the Upper Valdai Series of the Russian Platform, just below the boundary of the Lower Cambrian (Keller, 1963). The exact location of the find was not given. He also noted the occurrence of *Dickinsonia*, *Spriggina* and *Medusinites asteroides*, discovered by geologists of the Rio Tinto Company in the ‘Rizu Series’, east of Yazd in central Iran. A determination based on lead isotopes from a sedimentary ore deposit in the ‘Rizu Series’ beds above the fossiliferous horizon gave an age of 595–760 Ma (± 120)—not a very useful determination considering the latitude of error. Glaessner (1984) briefly mentioned the existence of an Ediacara-type fauna in Central Iran,

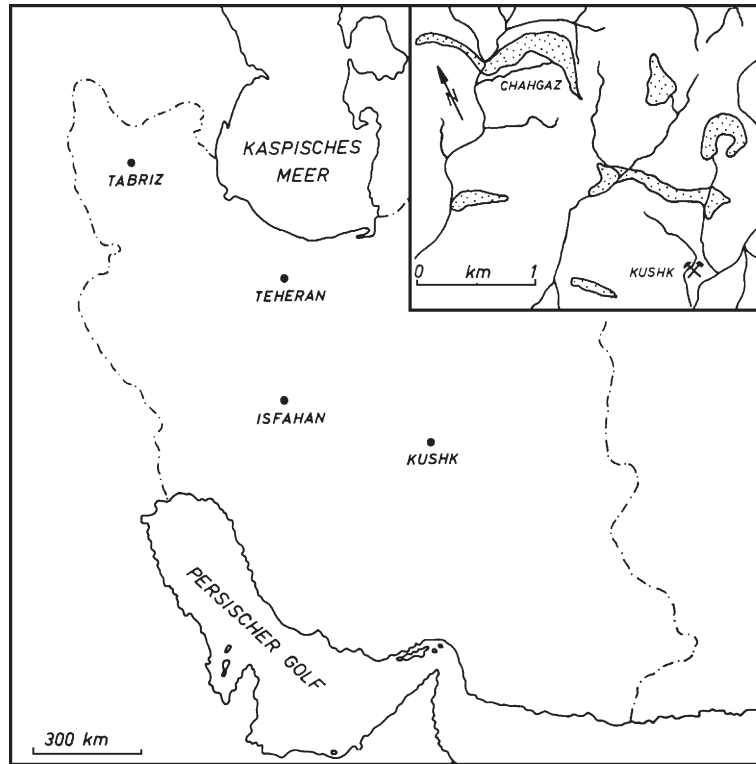


Fig. 130. Location map, Ediacara-type biotas discovered in Iran (after Hahn and Pflug, 1980).

near Kushk, bear Bafq, but specimens sent to him were rejected as Ediacara-type fossils except for a *Chuaria*-like specimen. He later identified among further specimens sent to him a new jellyfish, described by Hahn and Pflug (1980) as *Persimedesites chahgazensis* nov. gen., n. sp. from the late Precambrian Esfordi Formation at Chahtagaz, near Kushk, Yazd Province, Central Iran (Fig. 130).

This is clearly Stocklin's second locality. The holotype shows the subumbrella face in detail, in a

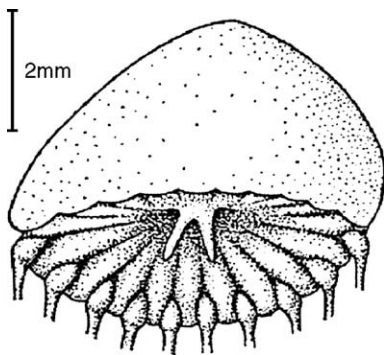


Fig. 131. Reconstruction diagram of *Persimedesites chahgazensis* showing some of the four (?) oral tentacles and the marginal tentacles (after Hahn and Pflug, 1980).

nearly three-dimensional preservation. Another specimen shows the exumbrella face in positive relief. The oral region is somewhat raised and occupied by several, probably four, tentacles, of which the remains of some are visible on one specimen. The subumbrella face is divided into c. 22 radial lobes, separated by deep furrows. They begin at the oral region and continue to the periphery. There is some distortion but no branching. In the marginal region of the subumbrella, there are marginal lobes alternating with the radial lobes, oriented vertically and with a round scar on the tip. A drawing by Hahn and Pflug is reproduced in Fig. 131 and photographs in Fig. 132. The exumbrella shape is preserved only in depressed form, but it was probably inflated in life. The swollen condition of the tentacle bases was considered to be a specific feature of *Persimedesites*. Taxonomically, they referred it to the subclass Scyphomedusida and to the Saemaeostomatida, and considered it to be most like *Eulithota* Haeckel 1969 from the Upper Jurassic (Harrington and Moore, 1956). Some resemblance to *Rugoconites enigmaticus* Glaessner and Wade (1966) was also noted.

Hamdi (1989,1990) described the regular biological evolution of the late Precambrian–Cambrian Soltanyeh

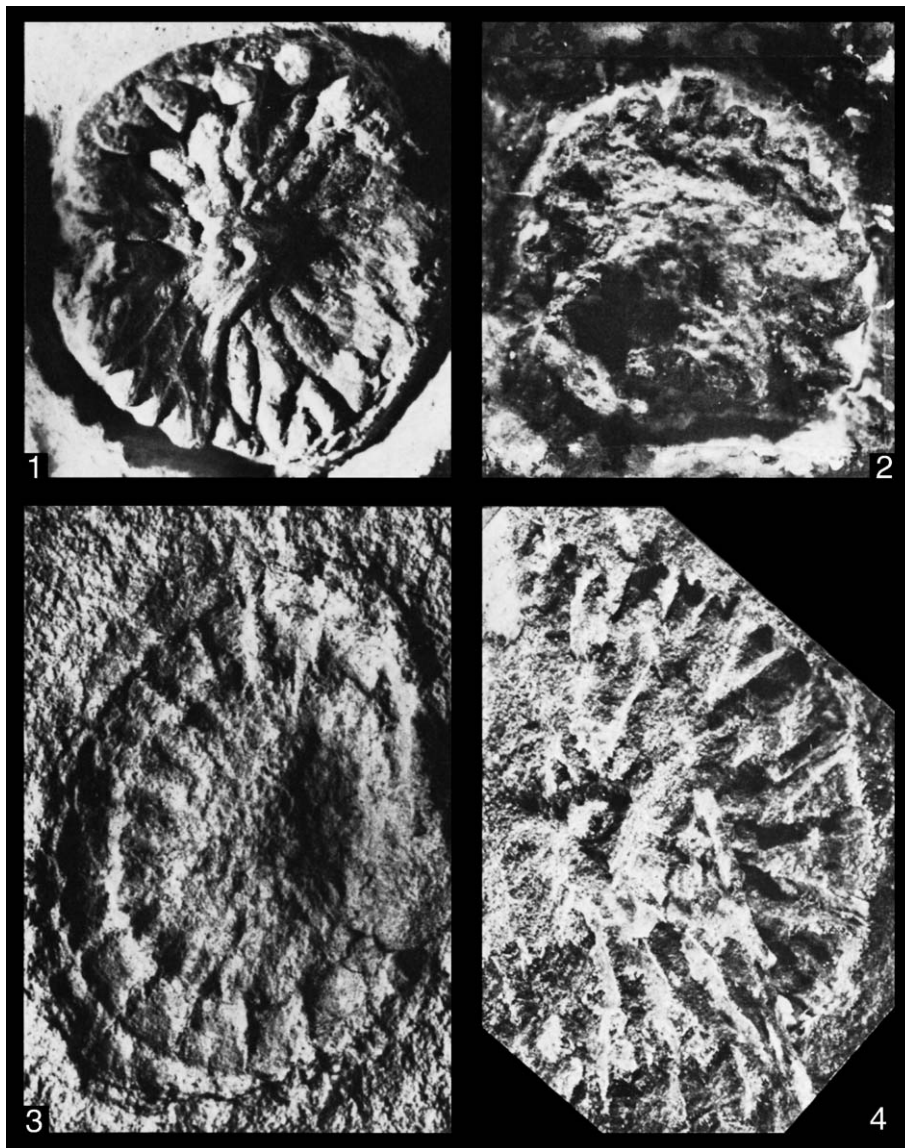


Fig. 132. Four views of *Persimedesites chahgazensis* (holotype and three paratypes) ($\times 5.7$, $\times 7.5$, $\times 5.8$, $\times 2.7$) (from Hahn and Pflug, 1980).

Formation in the Dalir and Valiabad area of the Alborz Range, Northern Iran). The two lower zones were of Vendian age. The *Rugatathea–Tubulella* Zone is restricted to the Lower Dolomite member and contains the oldest small shelly fossils of the Soltanyeh Formation, and also contains *Hyolithellus*-like fossils, *Spirellus* and *Olivoides multisculcatus*. The *Chuar*ia Zone, contains, restricted to the Lower Shale Member, *Chuar*ia *circularis*, the trace fossil *Planolites* and acritarchs *Protosphaeridium*, *Orygmosphaeridium* cf. *Rubiginosum*, *Protoleiosphaeridium nervatum*, *Leioligotritetum compactum*, *Botryoligotritetum*, *Laminarites*, and *Caryosphaeroides*. It is apparent that there is an

extensive development of Vendian sediments beneath the Cambrian in Northern Iran, which does not appear to have been researched in detail.

Hamdi (1989,1990) reported on late Precambrian–Early Cambrian microfossils from Central Iran. Fossils from three locations (the Chabedoc section, Chah-shur section, and Deh-medhi section) were listed and it was noted that there were a great number of Lower Cambrian small shelly fossils at the latter location. A fourth section was described, the Kushk section to the north of the Kushk Mine, where the Kushk Shales overlie the Rizu Formation. Here a siphogonuchitid and *Spirellus* sp. were recorded, also the Vendian metazoan fossils,

Charnia sp., *Spriggina* sp., *Rangea* sp. and *Persimedites chahgazensis*.

Hamdi noted that the base of the Cambrian was placed at the base of the Middle Dolomite (3rd) member of the Soltanyeh Formation in Northern Iran. The fossils recovered in Central Iran would provide a firm basis for stratigraphic correlation between the northern and central sequences. Whereas the lower two members in the Soltanyeh Formation sequence corresponded to the Vendian of Russia, members 2–5 corresponded to the Meishucunian of China and in part to the Tommotian of Siberia. The biota of Central Iran corresponds closely with that of Northern Iran and China.

13.3. Oman

There are Neoproterozoic sediments in the Huqf Group of the Oman (Gorin et al., 1982; Burns et al.,

1994) gave an age range of ~560–~540 Ma for this group. Carbonate rocks at the top of the group contain *Cloudina*, which is commonly associated with Ediacara-type faunas. The thick sequence below, above the basement, must be a likely subject for discovery of further developments of Ediacara-type fossils.

Conway Morris et al., 1990 described the occurrence of *Cloudina* cf. *hartmanni* from south-central the Ara Group Oman of the Huqf Formation (Figs. 133 and 134) and illustrated it (Fig. 135). It occurs in biohermal algal mounds only a few metres high, which separated restricted platform or lagoonal deposits, in which finely laminated stromatolites were abundant, from an open platform with higher energy conditions. Radiometric determinations indicated an age of 550 Ma (± 10 Ma) for the Ara Formation. These authors mentioned the two taxonomic camps, one favouring relation to the cribrocyathans and the other with polychaete annelids. Neither

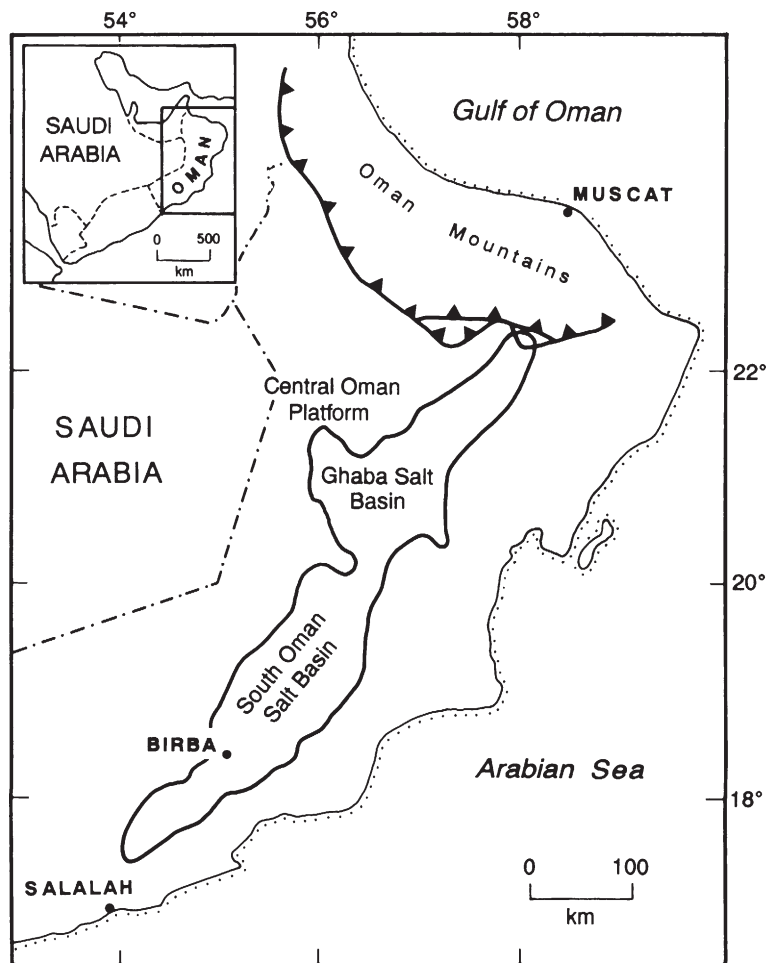


Fig. 133. Locality map for southeastern Arabia showing the principal salt basins of Oman and the Birba borehole from which the cloudinid specimens come (after Conway Morris et al., 1990, reprinted with permission of American Journal of Science).

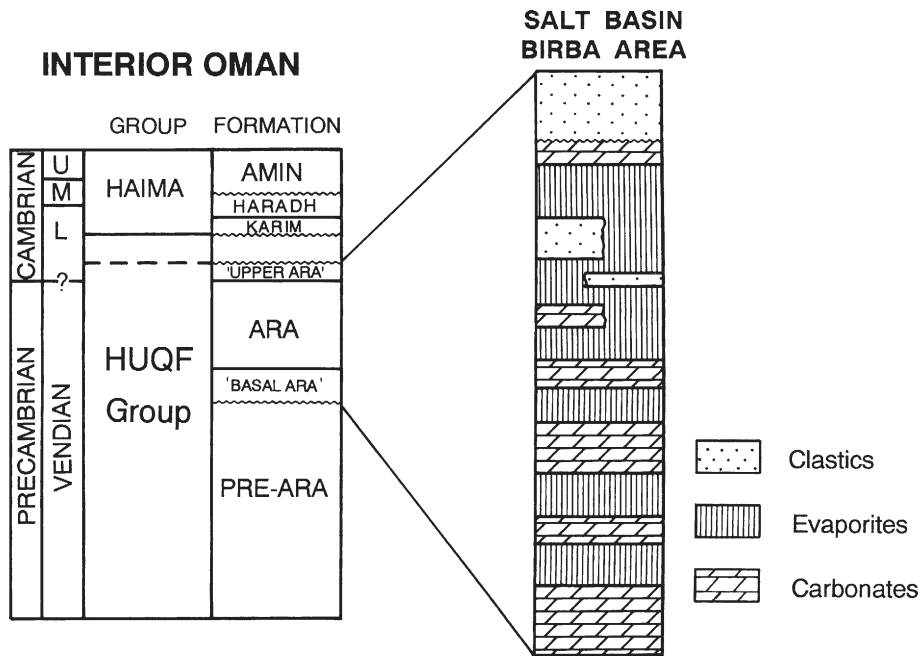


Fig. 134. Stratigraphic section for the Precambrian–Cambrian boundary sequence of southern Oman, including Birba: also the internal sequence of the Ara Formation of the Birba area (after Conway Morris et al., 1990, reprinted with permission of American Journal of Science).

answer, they considered, was convincing. *Cloudina* was a distinctive element of late Proterozoic faunas, possibly extending into the Cambrian, and has been found widely over the globe (they provided a map of known occurrences at the time, but others are now known). The appearance of the biomineraliser, with calcified walls, close to the Precambrian–Cambrian boundary, could have ecological significance. It appears to be limited to quite a short time interval prior to the Cambrian.

The biohermal reefs of Oman are interbedded with evaporitic salt deposits, unlike the reefs of Namibia. They could well provide an important resource for further research on these mineralised fossils, although much of the occurrence appears to be subsurface and not in outcrop, and samples have been obtained by hydrocarbon exploration drilling.

13.4. Mongolia

Brasier et al. (1997) recorded Ediacaran sponge spicule clusters in sediments containing Anabarites of the lowest skeletal-fossil-containing limestone horizon in southwestern Mongolia (Fig. 136). The spicules are in the upper Tsagaan Gol Formation and are above Sturtian diamictites, post-Sturtian limestones and Ediacaran dolostones containing the Stromatolite *Boxonia gromulosa*: they are beneath limestones yielding increasingly diverse Nemakit-Daldyn to Tommotian type skeletal

faunas (Fig. 137). The spicules are small (<0.1 mm long and <0.02 mm thick) and abundantly preserved in translucent brown iron oxides within layers of spongiform cherts (Fig. 138). All spicules can be referred to the Cambrian to Recent glass sponges of Class Hexactinellidae. These spicules provide the earliest clear evidence for the existence at this time of organisms that can be assigned without question to an extant metazoan phylum. There is evidence to suggest that the earliest sponge fauna of Mongolia may be contemporary with the acme of Ediacara-type fauna development elsewhere. This discovery indicates that hexactinellid sponges achieved skeletal diversity by the latest Precambrian, earlier than previously supposed. The delayed appearance of sponge spicules in the fossil record was related not only to biological evolution, but also to the delayed and tectonically controlled appearance of suitable biofacies and taphofacies.

These Mongolian occurrences also suggest that detailed studies may reveal Ediacara-type faunas in this region of Central Asia.

13.5. India

13.5.1. Krol Formation, Lesser Himalayas

The first descriptions of an Ediacara-type fauna from India are contained in two papers by Mathur and Shanker

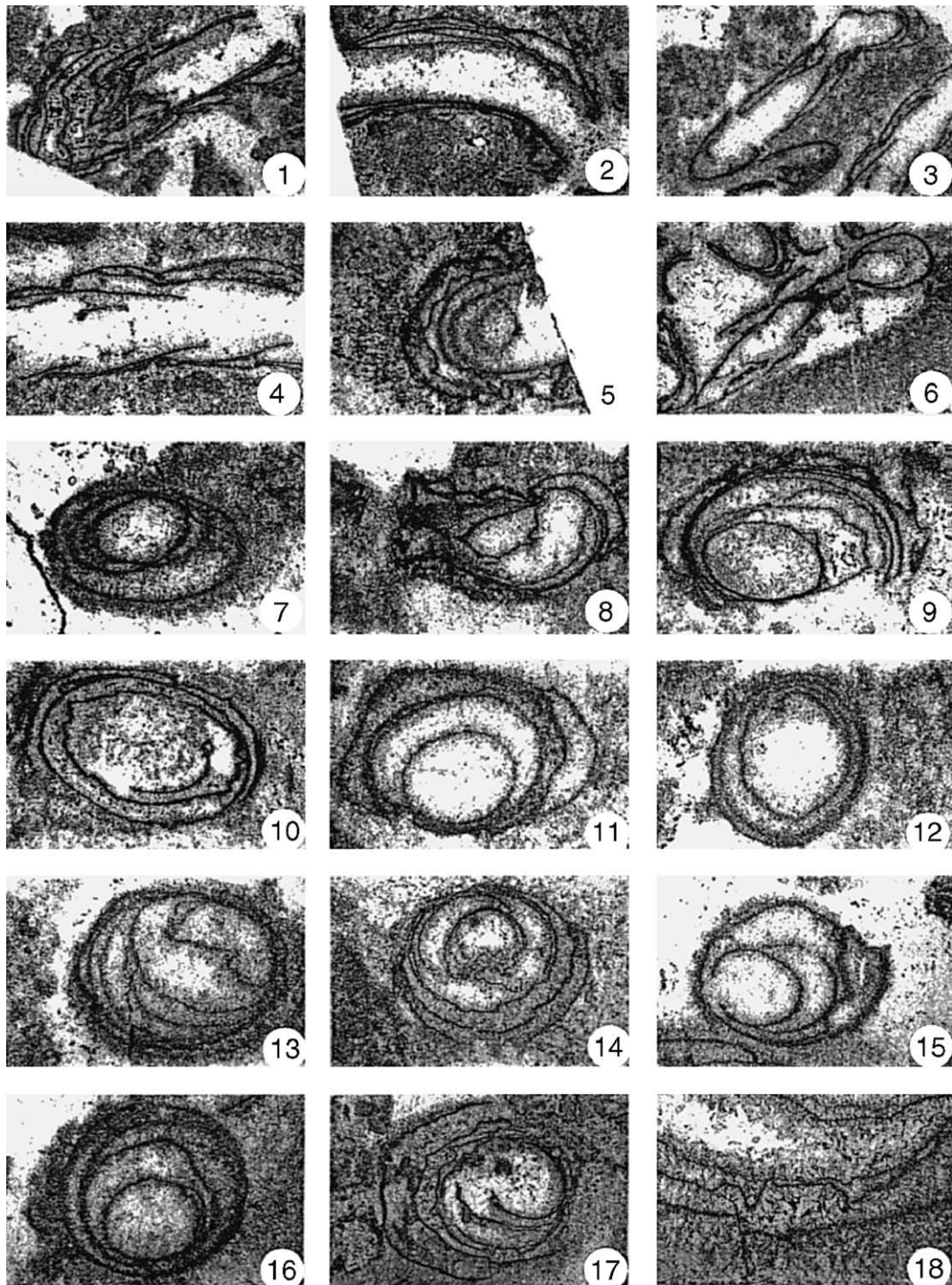


Fig. 135. Representative examples of *Cloudina hartmannae* from the Ara section, subsurface Oman, in oblique (first six) and transverse sections (remainder). Scale range from $\times 6$ to $\times 23$ (from Conway Morris et al., 1990, reprinted with permission of American Journal of Science).

(1989, 1990). The finds were made in the southern limb of the Naini Tal Syncline in the Lesser Himalayas, about 750 m South-southeast of Narayan Nagar, on the Naini

Tal–Khurpa Tal road, Uttar Pradesh. Distinctive soft-bodied fossils and simple trace fossils were recorded, similar to Ediacaran fossils from South Australia

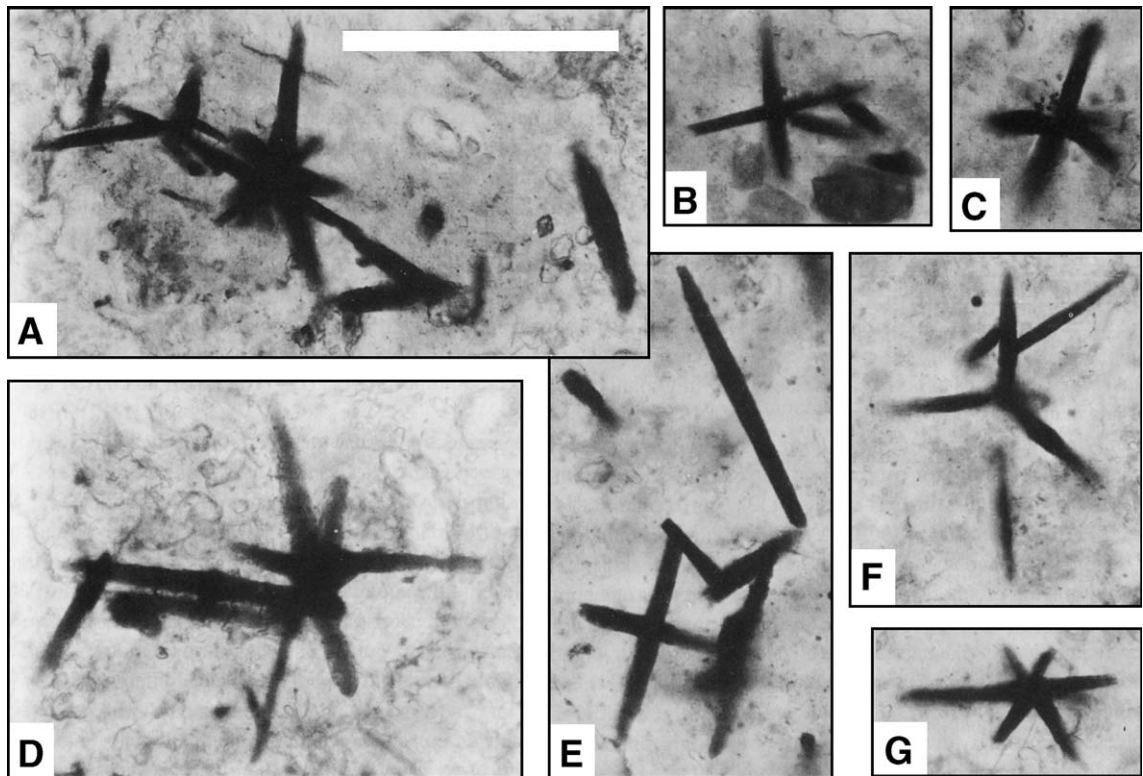


Fig. 136. Clusters of Ediacaran hexactinellid sponge spicules from southwestern Mongolia; preserved in iron oxide with early diagenetic chert concretions. The clusters can preserve original skeletal architecture (scale bar=0.1 mm) (from [Brasier et al., 1997](#)).

described by [Glaessner \(1984\)](#). These fossils occur in the upper part of the Krol Formation, in thinly bedded greyish-black shales interbedded with ferruginous and calcareous siltstones, 80 m from the top of the Krol Formation. The fossils include, as impressions on bedding planes, the soft-bodied metazoans *Beltanelliformis* sp. cf. *Beltanelliformis brunsa* Menner and *Pteridinium* sp. cf. *Pteridinium simplex* (Gurich), as well as the trace fossil *Gordia* sp. cf. *Gordia arina* Emmons, the crawling feeding burrow of a worm-like organism.

[Mathur and Shanker \(1990\)](#) added to this description. The medusoid coelenterates *Tirasiana* sp., *Medusinites* sp. and *Beltanella* sp. were present as impressions on bedding planes. Two specimens of *Tirasiana* were described, one as 7 mm diameter discoidal in epirelief (1 mm), with a small central pit within a narrow inner disc, separated by a prominent circular furrow from a broad outer disc. The second specimen was in convex hyporelief; there was central tubercle and the outer disc carried indistinct radial markings. A single specimen of *Medusinites* was described as subcircular ± 8 mm diameter) with a convex hyporelief, a smooth central disc separated, half way out, by a circular furrow from a broad smooth outer ring, again with indistinct radial

markings. Three impressions of *Beltanella* were described, smooth discs, 16 mm in diameter and 1.5 mm in hyporelief, surrounded by a flange about 7 mm wide. All three resemble specimens described from the Yukon, Canada ([Narbonne and Hofmann, 1987](#)).

[Shanker and Mathur \(1992\)](#) reported more fully on the discovery of an Ediacara-type fauna in the Precambrian–Cambrian sequence of the Krol belt in the Lesser Himalayas. This belt forms several lenticular developments extending from Solan, through Mussoorie and Dehra Dun to Naini Tal in the southeast ([Fig. 137](#)). It is believed that these separate lenses represent a single sedimentary basin with a northerly to northeasterly dip. There are three sequences, here on the northern edge of the Indian Shield, the oldest being the Blaini Formation, the middle being the Krol Formation and the upper the Tal Formation ([Fig. 138](#)). The latter has yielded brachiopods, trilobites, small shelly fossils and trace fossils of the *Phycodes* facies, all of which indicate that it is largely of Cambrian age. Small shelly fossils also occur with the Ediacara-type fauna in the upper Krol Formation, but these rocks are attributed to the late Vendian, the boundary with the Cambrian being placed between the

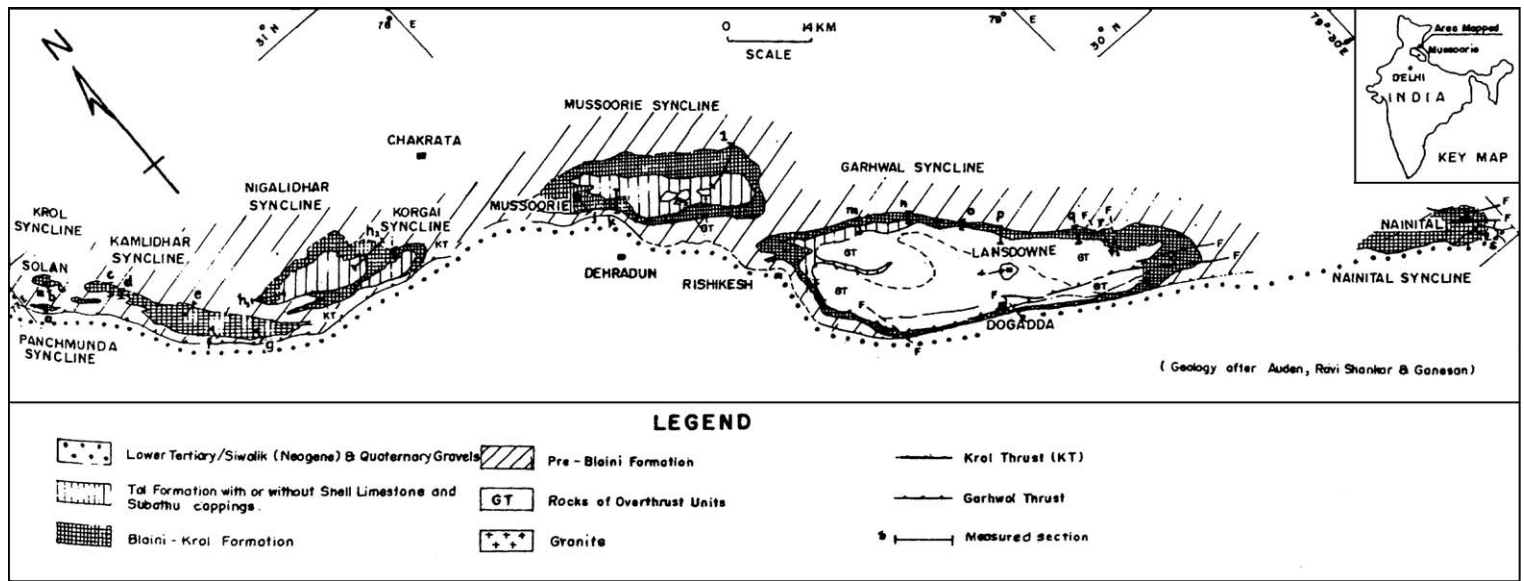
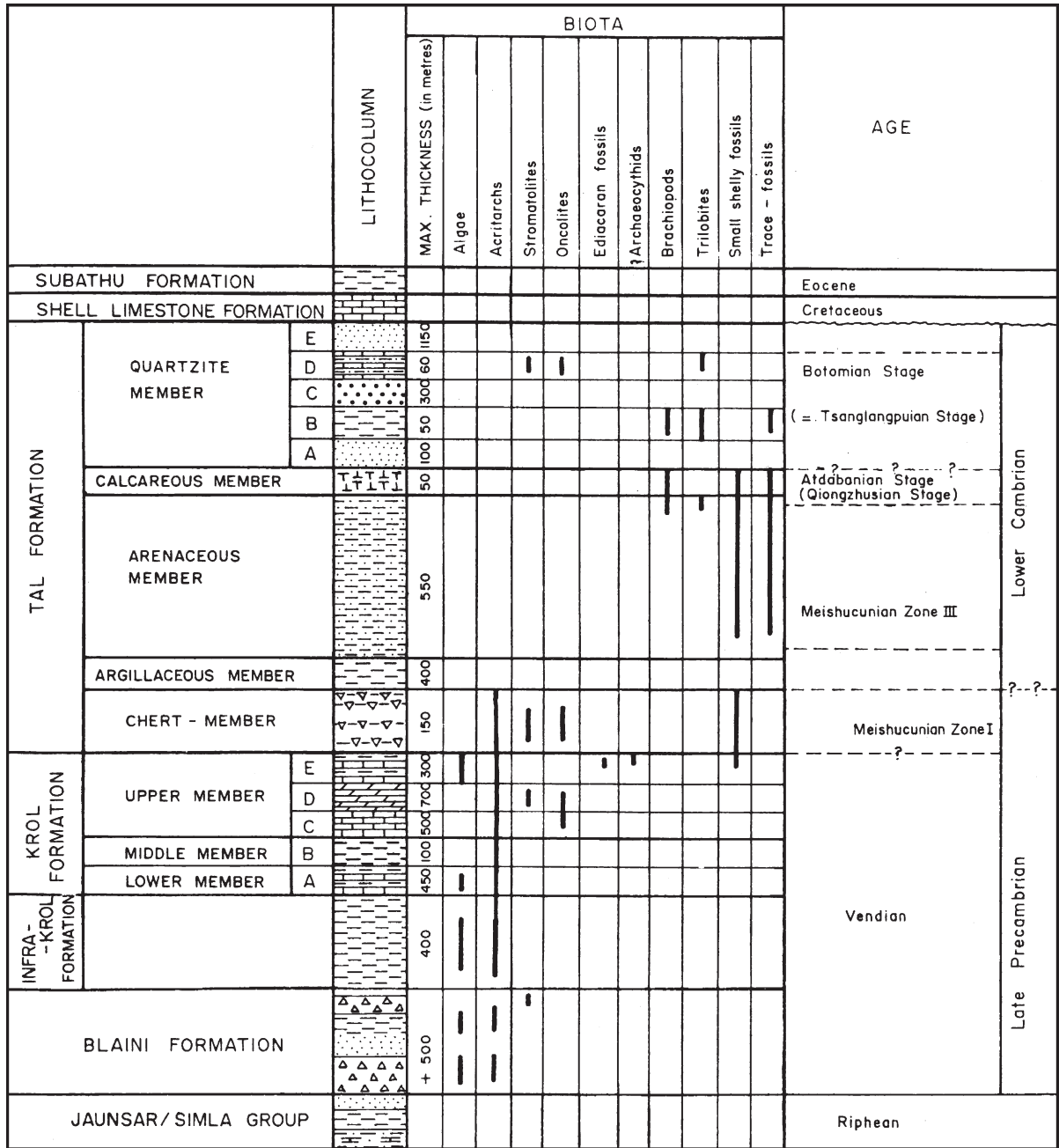


Fig. 137. Geological map of the Blaini-Krol-Tal Basin, Lesser Himalayas (after Shanker and Mathur, 1992).



● Not to Scale

LEGEND










- | | | |
|---|---|--|
|  Limestone |  Purple & greenish shale |  Felspathic arenite |
|  Dolomite |  Siltstone / Calc. siltstone |  Chert - phosphorite |
|  Shale / Slate |  Quartz arenite |  Diamictite |

Fig. 138. General stratigraphic column of the Late Precambrian–Early Cambrian of the Blaini-Krol-Tal succession, showing the distribution of fossils (after Shanker and Mathur, 1992).

lower Chert and Upper Arenaceous divisions of the Tal Formation. The Krol Formation also contains algae, acritarchs and stromatolites.

The Krol Formation includes sandstones (quartz arenites and quartzitic sandstones), limestones and dolomites, but the Ediacara-type fossils occur as

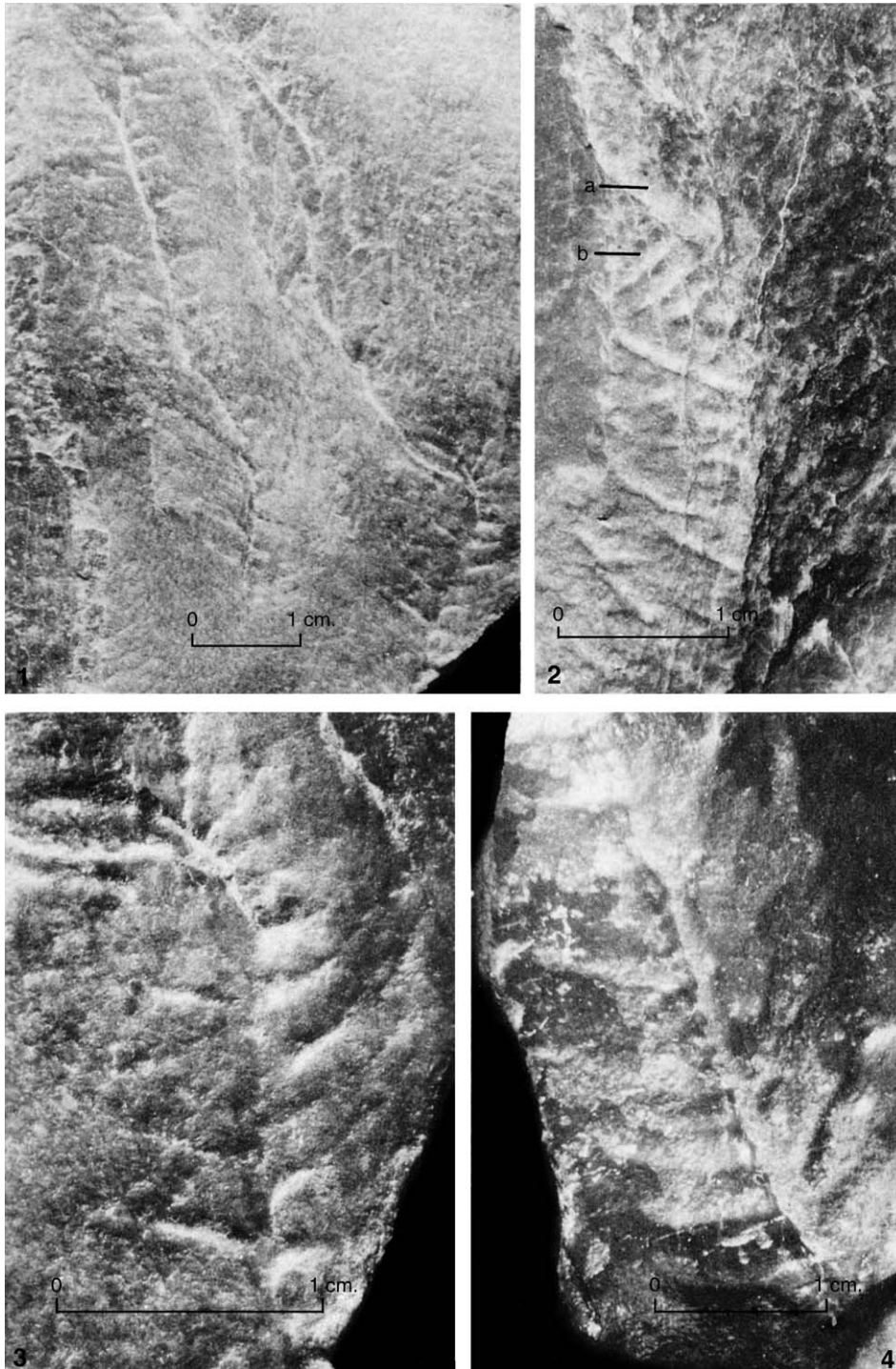


Fig. 139. *Charniodiscus* sp. cf. *Charniodiscus arboreus* (Glaessner). This shows the primary and secondary furrows (from Shanker and Mathur, 1992).

impressions on the bedding planes of thinly bedded greyish-black shales interbedded with ferruginous siltstones. The sequence is marked by rhythmites and lenticular bedding. It is interpreted as the deposits of well-developed tidal flats (intertidal or subtidal). There are no mudcracks but micro- and meso-scale ripple marks are present as well as loadcasts.

Shanker and Mathur described *Charniodiscus arboreus* (Fig. 139), which they compared with specimens described from South Australia (Glaessner and Wade, 1966). Several broken specimens were collected, 25–80 mm long and 12–20 mm wide. The primary fronds are arranged alternately on either side of the central stem. *Sekwia excentrica* is represented by eight specimens, circular to subcircular with a marginal groove and several eccentric coarse wrinkles. They range from 2.5–3.5 mm in diameter and have a relief of less than 1 mm. They resemble specimens described by Hofmann (1981) and Acenolaza and Durand (1986) from the Argentine. *Irridinitus* sp. is represented by five specimens, subcircular to elliptical and with concave epirelief (the subumbrellar surface). The dimensions are 1.5 mm × 2.5 mm and there are radial markings (canals?) which emanate from the small concentric groove in the centre (mouth?) and run out to the narrow marginal ridge. The specimens resemble those described by Hofmann et al. (1985). *Kimberella quadrata* is represented by two specimens, elongate slender bell-shaped forms, tapering more to a presumably open end, with the opposite termination presumably open-ended. Four pinched gonads were described attached to radial canals. The specimens are flattened and distorted. The Ediacara forms from South Australia by Glaessner and Wade (1966) were attributed to medusoid affinities.

Further specimens discovered 145–840 m below the Tal Formation boundary in the Garhwal, Mussoorie and Nigalidhar Synclines were mentioned briefly by these authors as a late addition and figured. They include *Cyclomedusa davidi*, *Cyclomedusa* sp., *Charniodiscus holdfast*, and *Zolotsya biserialis*.

Bhatt (1990) disputed the Ediacaran attribution of Mathur and Shanker (1990), suggesting that none of the criteria of Rozanov (1989) was met. Although it is true that there can be no certainty that the Krol fauna is Vendian rather than Cambrian, because the extension of the Ediacara fauna into the Early Cambrian are well established (in South Australia and Ireland, for example), this argument appears to be unimportant. Whatever its age, the Krol fauna is manifestly an Ediacaran-type soft-bodied fauna. Bhatt and Mathur (1990) recorded shelly microfossils of Meishucunian type from 100 m

below the Krol medusoids, which might well indicate an Early Cambrian age for the soft-bodied fauna, but Shankur and Mathur suggest that the first appearance of these shelly microfossils may have been in the Vendian. Bhatt's other argument that the 'medusoids' are loosely grouped with cnidarian jellyfish remains, although none shows diagnostic characters, repeats the objections of Seilacher (1989); Mathur and Shanker countered this with the view that the attribution to the cnidaria is based on many morphological comparisons.

Rai (1998) reviewed the palaeobiology and evolutionary evidences of the terminal Proterozoic sequences of Himalaya and Peninsular India. He noted that the Krol Belt contains an exceptionally well-preserved shallow marine sequence, the Krol and Tal Formations being developed above the Blaini Formation, which is equivalent to the Varanger Glaciation, and demarcates the base of the terminal Proterozoic (Vendian/Ediacaran) timespan. The Krol/Tal succession contains two specific microbial communities: (1) Acritarchs: (2) Cyanobacterial/algal. The Krol formation is characterised by large and highly ornamented Acanthomorph acritarch genera (*Asterocapsoides*, *Appendisphaera*, *Cavaspina*, *Cymatiosphaeroides*, and *Ericiasphaera*) including many new taxa, whereas the small-sized acritarchs, which are confined to the lowermost units of the Tal Formation, include *Baltisphaeridium* and *Michrystidium* which appear at the end of Precambrian time. The assemblage closely resembles those from the Pertatataka Formation of the Amadeus Basin, central Australia, the Dushuantuo Formation of the Yangtse Gorge, China and the Miroyedikha Formation of Siberia. Rai also described the cyanobacterial fossil community of the Krol Formation, which comprises filamentous, coccoidal and bizarre forms.

13.5.2. Neemuch District, Central India

The Vindhyan of the Neemuch District, Indore State, Central India, contains a problematic fossil named *Fermoria* by Chapman (1935). It long-baffled palaeontologists and palaeobotanists alike. There are various mentions in Records of the Geological Survey of India (v.38, p. 66; v. 60, p. 18; v.61, pp. 21–22). In 1909, it was likened to *Chuarina circularis* described by Walcott from Arizona, but was later thought to be a brachiopod by Walcott and Resser (1927), was thought to be blue green algae on the basis of incineration tests, and again thought to be brachiopod by Chapman (1935). In 1952, Misra (Sahni and Srivastava, 1954) thought them to be ostracods, but it was later suggested that they were inorganic. Sahni and Srivastava (1954) examined some very good specimens and noted that

the *Chuar*-like carbonaceous ovoids are on the end of broad filaments, which may be clustered in a divergent pattern with the discs at the divergence end. The discs are on the broad end of some filaments that have a funnel shape. There can be no doubt now that they are organic. They are clearly closely related to *Chuar*, and the association with filaments contrasts with the simple ovoid pattern in the case of the Spanish occurrences.

Rai (1998) mentions the important Proterozoic successions of Peninsular India (Bhima, Kaladgi, Kurnool, Vindhayan and Trans-Aravalli Vindhayan basins, which, although now widely separated may represent continuity of sedimentation, represented by sequences 5000–6000 m thick, in a mega basin). The important megafossils are *Grypania*, *Chuar*, *Tawuia*, *Sinosabellidites*, *Protoarenicola* and *Pararenicola* besides stromatolites and trace fossils. These basins must constitute a substantial subject for future research both on the Vendian but also on the evidence of life forms in the preceding Proterozoic. Rai suggests that the Varanger glaciation should be taken with coeval glacials as the base of the terminal Proterozoic system.

13.5.3. Bhandar Group, Vindhyan Supergroup, Central India

De (2003) reported the discovery of medusoid genera resembling *Ediacaria* and *Hiemalora* in a shale horizon at the base of the Bhandar Group, the uppermost of the Vindhyan Supergroup in Central India (Figs. 140 and 141). These fossils are within shales just below the Lakheri Limestone formation which includes stromatolites. An age of 550–543 Ma is suggested for the Lakheri unit containing these fossils, but it is only inferred from comparisons with Namibia. A continental shelf environment above storm wave base is suggested for these fossils.

13.6. China

There are five regions of China where Neoproterozoic megafossils have been reported. These are (Fig. 142):

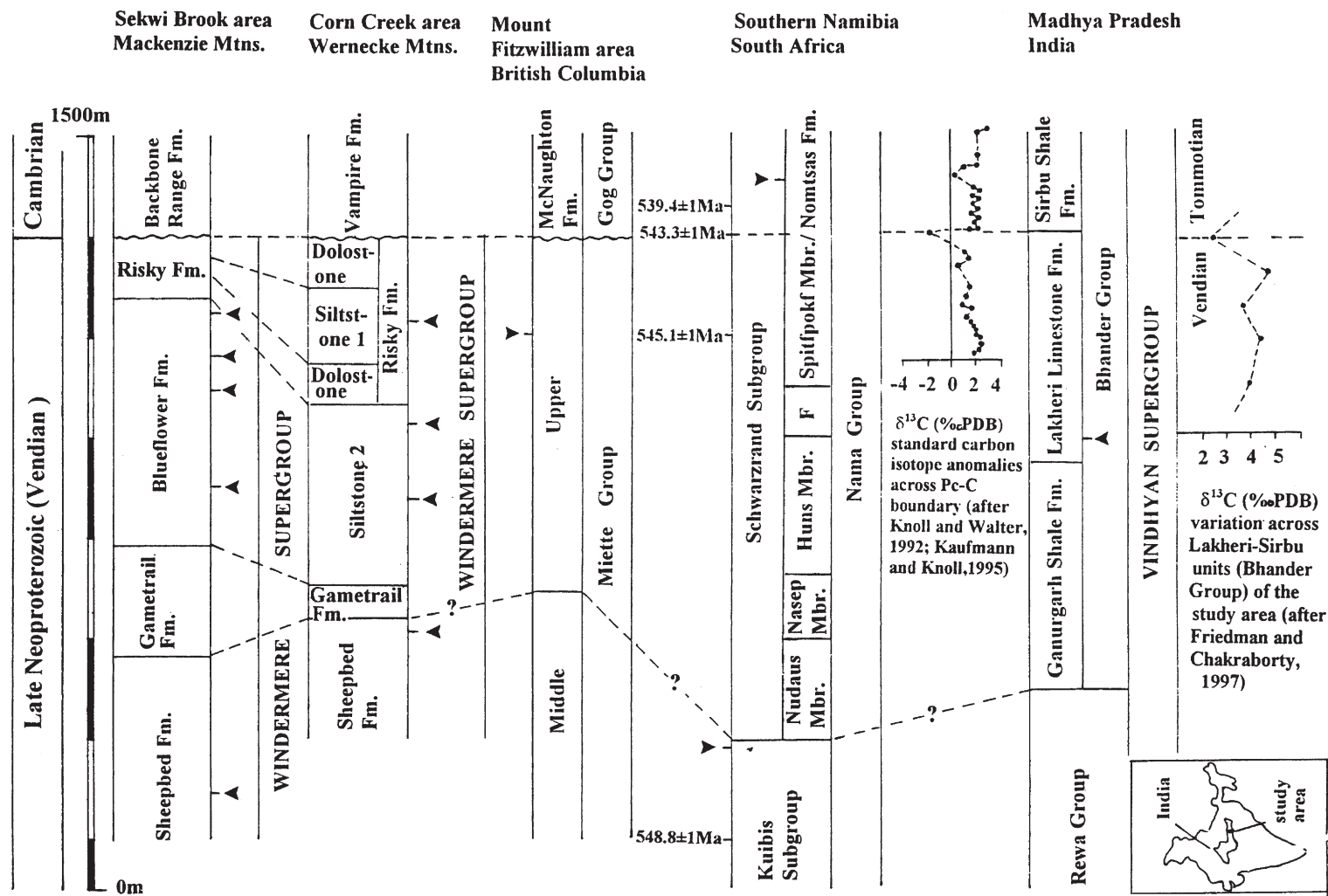
The Yangtse Gorges, Hubei and neighbouring Shaa'nxī Province
Weng'an, to the south in Guizhou Province
Liaoning Province, on the Liaodong Peninsula, in the north
Anhui Province, near Huainian
Heilongjiang Province in the north

13.6.1. Pennatulids from the Yangtse Gorges

Sun Weiguo (1986a) reported late Precambrian pennatulids (sea-pens) from the Shibantan Member, Dengying Formation, of the Sinian System, east Yangtse Gorge (Fig. 143) in Hubei Province, the first genuine discovery of Ediacara-type metazoan fossils in China. Although initially referred to *Charnia* Ford (1958) and described as *Charnia dengyingensis* by Ding and Chen (1981), it was concluded by Sun Weiguo that it was a new genus, *Paracharnia* gen. nov. The fossil occurrence is within the stratigraphic section midway between the Nantuo tillite below and the appearance of small shelly fossils of Meishucunian type. It is thus equivalent to Vendian age.

The frond is feather-like and elongate, uniformly wide throughout two-thirds of its length; and the median stem is wide and naked. The polyp 'leaves' are freestanding and small, fusiform in shape, closely spaced on either side of the stem, and each polyp is joined to the stem by a distinct leaf stalk, forming an angle of 50°–80° to the axis of the frond. Secondary branches are evident on the edge of individual polyp leaves. There are more than 60 polyp leaves on either side and the positions of leaf stalks alternate, there being up to 13 secondary branches on a single polyp leaf. The genus differs from *Charnia* in having a wide, naked stem in stead of a zigzag axial trace. The species has been named *Paracharnia dengyingensis* (Ding and Chen) emend. A drawing from Sun Weiguo (1986a) is reproduced in Fig. 144. This occurrence appears to be a convincing example of an Ediacara-type fossil, albeit of a unique genus. It is closely associated with *Vendotaenia* sp., which suggests correlation with the Kotlin Formation of the Valday Group in Russia. The Tranzhusan Member of the Dengying Formation above (Fig. 143) contains the small shelly fossils *Circotheca*, *Anabarites* and *Protoherzina* and was ascribed by Sun to the basal Cambrian.

Sun Weiguo provided some radiometric ages which relate the Nantuo glaciation to the Sturtian glaciation and put the Cambrian lower boundary much older than recent radiometric determination has indicated. More modern radiometric determination has in fact placed the Doushuanto Formation (see below) in the Vendian at 570 Ma (± 20 Ma) (Xiao et al., 1998) and the probability is that the Dengying Formation is also Vendian within an age between this and the base of the Cambrian (543 Ma). It contains *Cloudina*, *Namapoikia* and *Namacalathus* (Xiao, 2005). The Doushantuo diversification of complex acritarchs was ephemeral and most disappeared when the Ediacaran animals began to diversify at c. 575 Myr ago (Xiao, 2005).



(Narbonne and Aitken, 1990;
Narbonne and Hofmann, 1987)

(Hofmann et al. 1991)

(Grotzinger et al. 1995)

Fig. 140. Location of the Babupur Sections of the Bhandar group, Central India (after De, 2003).

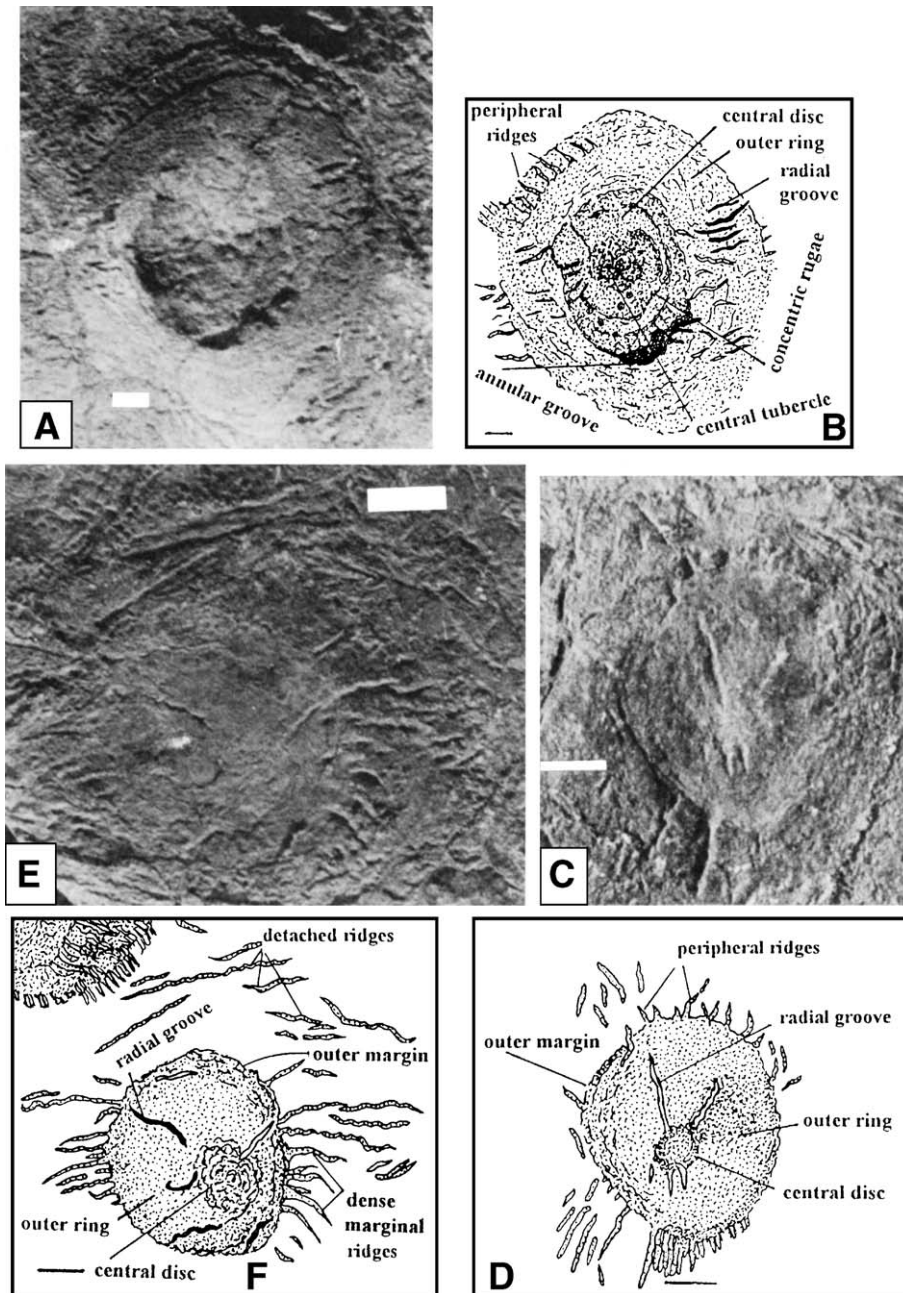


Fig. 141. Medusoid fossils from the Bhandar Group, Vindhyan Supergroup, Central India (from De, 2003).

13.6.2. Primitive medusoids or dubiofossils from Liaoning Province

Sun Weiguo (1986b) discussed the many reports of Ediacara-type medusoid fossils from southern Liaoning Province (Xing Yusheng, 1976; Xing and Liu, 1979). These were referred to eight species of *Cyclomedusa*, to *Planomedusites*, to two species of *Medusinites* and to a new genus, *Liaoningia*. However, Glaessner (1984) and Sun Weiguo (1986b) rejected them as body fossils and

considered them to be dubiofossils, gas-escape structures. Despite this, they had been repeatedly cited in papers (e.g. Wang et al., 1980; Chen et al., 1981) and even in textbooks. Sun Weiguo illustrated them and cross-sectioned specimens and stated that they are similar to gas escape structures found in modern beach sands, confirming the prior rejection. He also reported that the formation is Riphean (age c. 850 Ma), not Vendian.

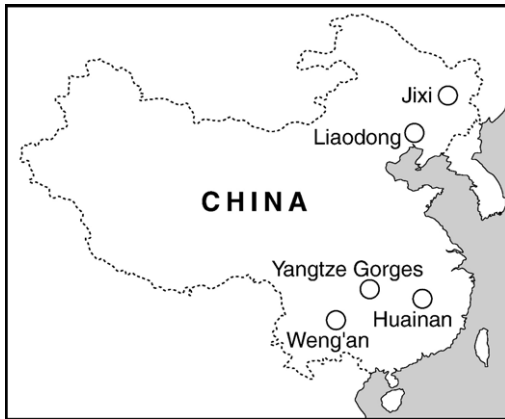


Fig. 142. Location map of important sites of Neoproterozoic fossil recoveries in China.

Sun Weiguo (1998) did, however, later accepted the validity of primitive Ediacara-type fossils from the late Proterozoic Xinmingcun Formation of Jinzhou District, Dalian, and Liaoning Province. He reported that the fossil *Liaoningella discoida* gen. et sp. nov. emend now has to be interpreted as such. The specimens were small circular to sub-circular discs with a complete margin and a few concentric ridges and grooves on an otherwise smooth surface. They were non-skeletal, preserved as three-dimensional body casts and external moulds. Some specimens at low angles to the bedding showed evidence of thin form, and tough and rigid character. There was no evidence of digestive system or locomotive apparatus. They probably lived by surface diffusion and internal absorption. Most were solitary but some were twins with a clear separation between, suggesting asexual reproduction. Although megascopic, their body configuration and inferred living style was more like that of unicellular organisms. This observation may throw new light on the Ediacara-type organisms, which may represent a primitive stage in metazoan evolution and specified adaptation to the low oxygen environment then prevailing.

Zhang-Xingliang and Shu-Degan (2002) reported again on discoid structures from the Xinmingcun formation in the Dalian area of the southern Liaoning Province. These had previously been compared with Ediacara fossils based on concentric rings. More recently they had been interpreted as primitive forms of Ediacaran body configurations and attributed a life-style more like unicellular organisms. More than 300 specimens had recently been collected. They occur in mudstones, not sandstones, lack radial structures and are generally smaller than Ediacaran individual fossils, ranging from 5 to 40 μ . Some appear to be holdfasts, but

no frondose remains at all have been found. The rings are helical rather than concentric and larger individuals show more cycles than smaller ones. They are different to the Ediacara-fossils and it is difficult to assign them to any known taxa.

13.6.3. *Dickinsonia* from the Huainian Group, Anhui Province

Niu-Shaowu (1997) described the discovery of *Dickinsonia costata* Sprigg (1947) in the Liulaobei Formation of the Huainian Group (Fig. 145) in Shouxian County, Anhui Province. Grey-green shales and fine-grained sandstones are intercalated with thin, silty limestones containing megascopic algae with *Chuarina circularis* as well as *Tawuia sinensis* and *Tawuia dalensis*. *Dickinsonia* is elliptical in outline, 1.8 cm long and 1.2 cm wide, and has c. 60 segments. It has a small triangular pygidium. It is quite similar to the holotype from South Australia and specimens from the Russian White Sea fauna. It was reported that the isotopic age of the Huainian Group is 840 Ma, which, if correct, would mean that this is an occurrence of a Vendian (Ediacara-type) fossil in a Riphean formation.

Fu-Jun-Hui (1989) also ascribed a Riphean age to the Huainian biota, suggesting an age range of 850–750 Ma. He believed that it was the oldest late Precambrian biota, characterised by Megaacritarchs, Cyphomegaacritarchs and Metazoan fossils.

Sun Weiguo (1986c) had suggested 850–740 Ma for the Liulaobei Formation (Fig. 145), and noted that of the worm-like fossil organisms in it, *Sinosabellidites* Wang, had only a superficial resemblance to the late Vendian–Early Cambrian true Sabellidites, and had much in common with the accompanying macroscopic algal remains of *Tawuia* Hofmann. In the Jiuliquao Formation of the older Fengyang Group (Fig. 145), representatives of primitive worm-like animals were recognised (*Pararenicola*, *Protorenicola*), macroscopic in size, with elongate cylindrical bodies, anterior aperture, prominent elastic annulations; features characteristic of metazoan origin, although definite relationship to any kind of living worm, cannot be demonstrated. They were claimed as the oldest multicellular animals in the geological record.

13.6.4. Algae and animal embryos in Neoproterozoic phosphorites from Weng'an

Zhang (1997) stated that the Doushantuo algal fossils from Weng'an possess structures morphologically comparable to male and female reproductive organs of some modern rhodophytes. The thallus forms imply a possible evolutionary transition from colonial to complex tissual

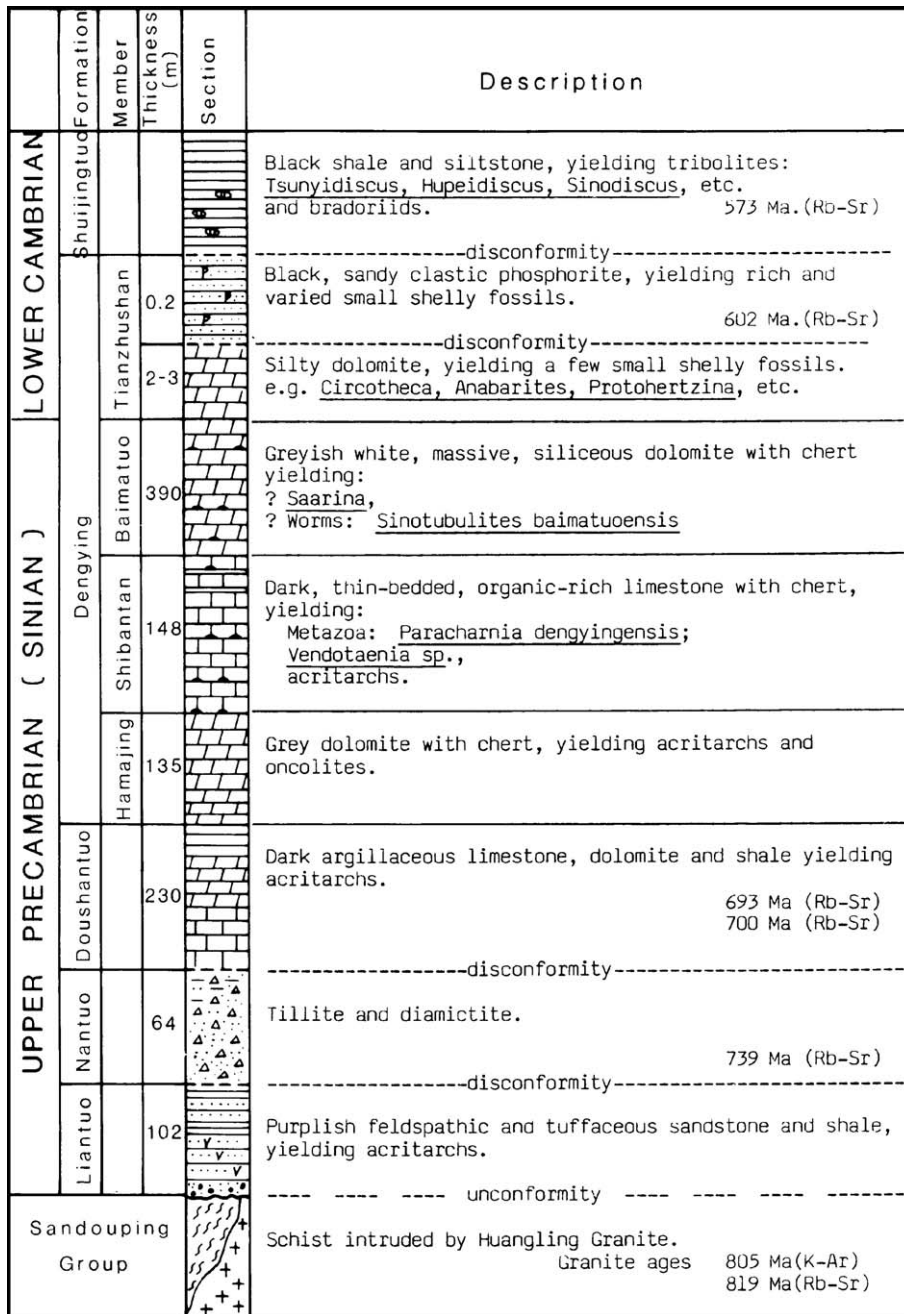


Fig. 143. Diagrammatic section of the Late Proterozoic (Sinian) sequence in the eastern Yangste Gorge area, Western Hubei Province, China (after Sun Weiguo, 1986a).

organisations among the Neoproterozoic algae; and there is evidence of both sexuality and multicellularity.

In a more detailed account, Xiao et al. (1998) reported that phosphorites, which can be dated at 570 Ma (± 20 Ma), occur near Weng'an in Guizhou Province, and contain algal thalli preserving many of the reproductive processes of modern marine flora, as

well as embryos preserved in early cleavage stages which indicate that divergence of lineages leading to bilaterian metazoans may have occurred well before their macroscopic traces or body fossils occur in the fossil record. The host rocks of the Doushantuo Formation (Fig. 146) are slightly older than those bearing Ediacara-type fossils.

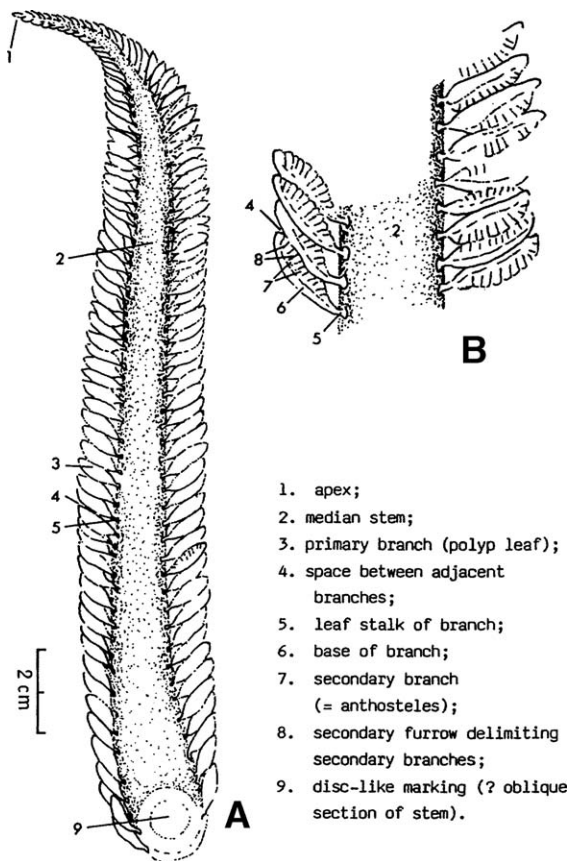


Fig. 144. Diagrammatic reconstruction and terminology of *Paracharnia denyngensis* based on re-examination of the holotype. (A) General appearance showing major structures of the frond. (B) Details of polyp leaves, enlarged from panel A. The once flexible upper portions of the polyp leaves were in some cases folded downwards because of flattening (after Sun Weiguo, 1986a).

Xiao et al. (2000) ascribed an age to these fossils of 555 Ma (± 3 Ma) and confirmed that they are older than the Redkino Formation of Russia which contains Ediacara-type fossils. However, they could not confirm that they are older than the Newfoundland occurrences, the remains there being dated at 565 Ma (± 3 Ma). The eggs and egg cases are accompanied by small fossils containing spicules, possibly recording the presence of sponges. Supposed gastrulae of cnidarian or bilaterian metazoans could be alternatively interpreted, but there are microscopic tubes which display tabulation and apical budding characteristic of some cnidarians, especially extinct tabulates. These small benthic colonial fossils may, like some Ediacarian remains, represent stem-group eumetazoans or stem-group cnidarians that lived in the late Proterozoic ocean.

The embryos are illustrated in Fig. 147 and the Doushantuo thalli are compared with modern algae in

Fig. 148. Xiao (2005) states that it is not possible to say to which animal clade the embryos belong—crown group sponges, cnidarians or bilaterians.

13.6.5. A diverse fossil assemblage from Shaa'nxi Province

Zhang (1986) reported a diverse biota in South Shaa'nxi Province from the Gaojiashan Member of the Upper Sinian Dengying Formation (equivalent to the Shibantan member in the Yangtse Gorges) (Fig. 142). He regarded this as Ediacaran, but gave the age as about 650 Ma—too great an age as the underlying Doushantuo Formation, which contains Ediacara-type fossils, has been accurately dated, at a much lesser age. Only *Nimbria*, questionably recognised, is an Ediacara-type soft-bodied fossil. Pyritisation is responsible for its preservation.

He listed:

Worms of uncertain taxonomic definition:

- Conotubus hemiannulatus*
- Conotubus gaojiashanensis*
- Conotubus mimicus*
- Conotubus impolitus*
- Conotubus humatus* sp.nov.
- Conotubus cepholatus* sp.nov.
- Conotubus adpressus* sp. nov.
- Conotubus* sp.
- Gaojiashania cyclus*
- Gaojiashania zonatus* sp. nov.
- Ninggiantella shaannanensis* gen. et. sp. nov.

Globomorphs:

- Olivoooides papillatus* sp. nov.

Coelenterates:

- Nimbria?* *gaojiashanensis* sp. nov.

Trace fossils:

- Planolites annulari*
- Planolites* cf. *beverleyensis*
- Planolites* ichnosp.
- Pelecypodichnus?* Ichnosp.
- Bucusichnus gaojiashanensis* ichnigen. et ichnosp. nov.
- Sellaulichnus meishucunensis*
- Torrowangea* ichnosp.
- Longshanichnus changpingensis*
- Neonereites* ichnosp.
- Annulusichnus regularis* ichnogen. et ichnosp. nov.
- Skolithos isolatis* ichnosp. nov.
- Intrites* cf. *punctatus*
- Shaa'nxilithes ninggiangensis*
- Shaa'nxilithes erodus* ichnosp. nov.

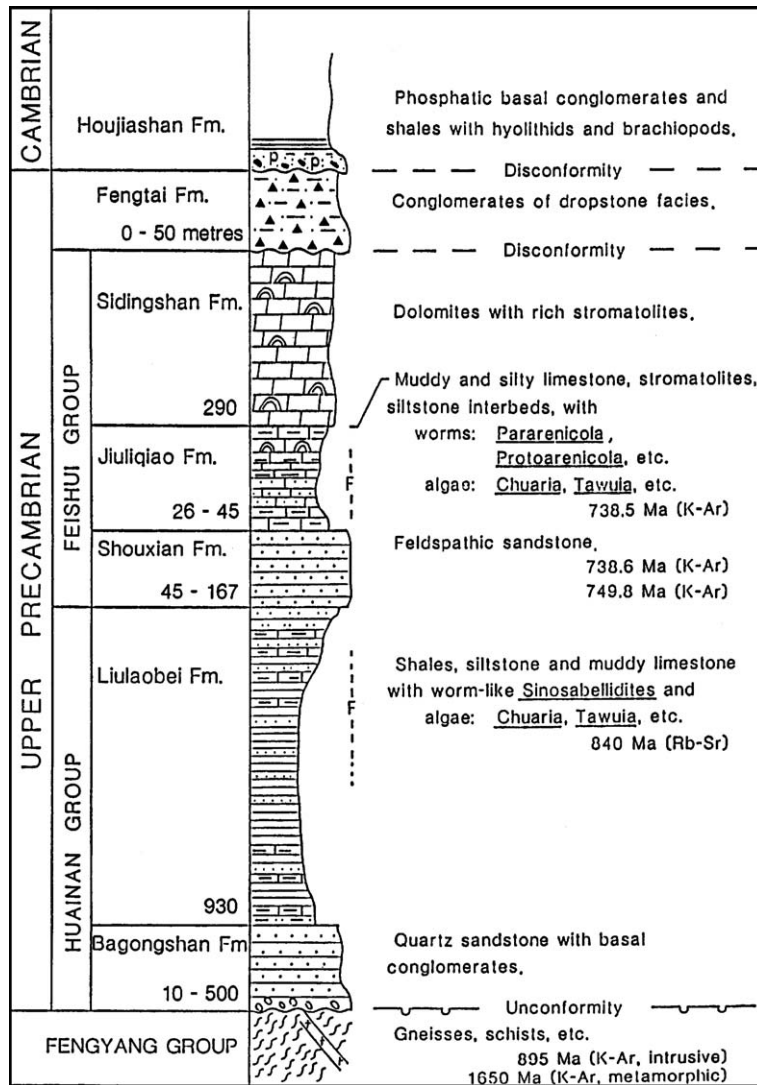


Fig. 145. Generalised stratigraphic column of the upper Precambrian in the Huinian District, Anhui Province, China. The levels of occurrence of macroscopic fossils are marked by 'F's and vertical lines showing the extent of the occurrence (after Sun Weiguo, 1986c).

Helminthopsis

Algal microfossils:

Chuarua? sp.

Vendotaenia antiqua

and others.

This list was divided into three assemblages:

- III. *Torrowangea*–*Planolites*–*Annulusichnus* assemblage (upper part)
- II. *Conotubus*–*Gojiashania* –?*Vendotaenia* assemblage (middle part)
- I. *Shaanxilithes*–*Helminthopsis* assemblage (lower part)

13.6.6. New information concerning the Dengying Formation

Hua Hong et al. (2002) reported on a diverse fossil assemblage from the latest Neoproterozoic Dengying Formation in southern Shaanxi Province, to the south of the Yangtze Gorges (Fig. 142). This is dated at 550 Ma, overlying the Doushantuo Formation. The occurrences are near Kuanchuanpu and Hujiba, in two sections. The fossils in the first occur in light grey dolomites of the upper part of the Gaojiashan Member (the same Member as was described above by Zhang Liu), immediately below are the chert and limestone interbeds which contain the small shelly Cambrian-type fossils. In the latter section, they occur in siltstone and

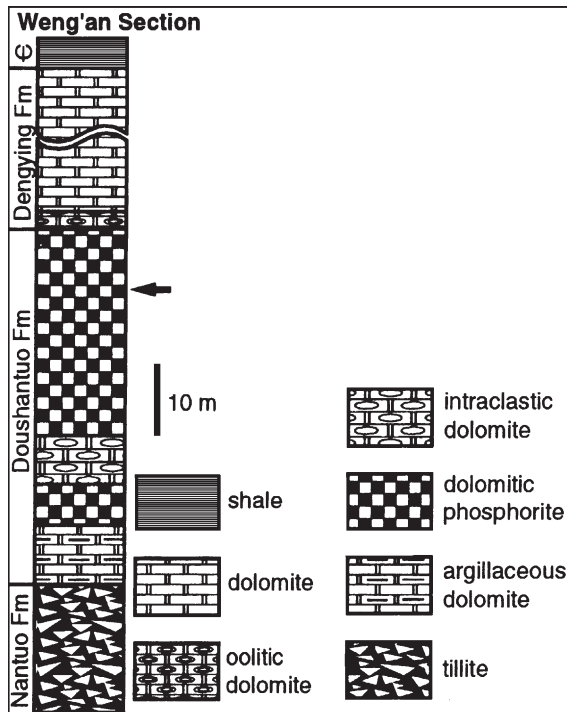


Fig. 146. Generalised stratigraphy of the fossiliferous Weng'an section of Guizhou Province, South China. The arrow indicates the level in the Doushantuo Formation containing phosphatised algae and embryos (after Xiao et al., 1998).

carbonate rocks of the same Member, overlain by 300 m of dolostones before calcarenites containing the small shelly fossils appear. Fossils are commonly pyritised, preserving some soft tissues. Phosphatised fossils can be chemically extracted. The assemblage includes:

Mineralised skeletal fossils

Tubular fossils: single layered tubular shells (*Chenella*) or multi-layered columnar structures (*Sinotubulites*, *Qinella*).

Conotubular fossils: include *Cloudina* and *Conotubus*.

Vase-shaped microfossils: 1.5–2.5 mm in diameter, calcareous wall, rigid deformation.

Globular fossils: spherical or elliptical, 0.05–1 mm diameter, single or multi-layered wall occurring in isolation or strings.

Cup-like fossils: cup- or bowl-shaped, with irregular dentate walls.

Problematica: branched or anastomosing tubular fossils, may be calcareous algae;

spherical (filled or hollow) and calcified cake-like structures; many bizarre structures.

Worm-like fossils

Including macro-carbonaceous film coated varieties such as *Sabellidites*, *Paleolina* and *Tawuia*. They are characteristically body fossils not moulds and range up to 10 mm in diameter and 100 mm in length. Those from siltstones are generally pyritised and carbonised and those from carbonate rocks calcified. They have not been fully interpreted as yet.

Trace fossils

12 ichnogenera and 15 ichnospecies are recognised, including grazing traces of worm-like animals but also vertical burrows such as *Skolithos* and *Intrites*. The presence of the vertical burrows is contrary to the general view that such traces are absent from Vendian rocks (for instance, see Fedonkin and Runnegar, 1992).

Carbonaceous megafossils

Three types occur in siltstones: circular or elliptical carbonaceous films; straight or curved ribbon-like structures with tiny branches; and foliated structures with longitudinal lines. They have distinct morphologies and are easy to recognise.

Members of this assemblage are illustrated in Fig. 149. This assemblage is obviously only described in preliminary fashion and will in future be further studied in detail. The vase-shaped fossils are probably testate amoebae (Xiao, 2005).

Conway Morris et al. (1990) recorded a “Claudina-like” mineralized tube from the uppermost dolomites of the Gaojiashan Formation at Kuanchuanpu, Shaan'xi (Fig. 150). These tubes are more or less circular.

13.6.7. Heilongjiang Province

Liu Xiaoliang (1981) described Ediacara-type medusoids from near Jixi, Heilongjiang Province, in the Northeastern of China. These were in the Shichang Member, Liunao Formation of the Mashan Group of the fold belts there. Four genera and six species were described, of which two general and five species were new. The list is:

Arumberia banksi Glaessner and Walter
Jixiella capistratus gen. et. sp. nov
Glaessnerina sp.
Mashania longshanensis gen. et sp. nov
Mashania augusta gen. et sp. nov

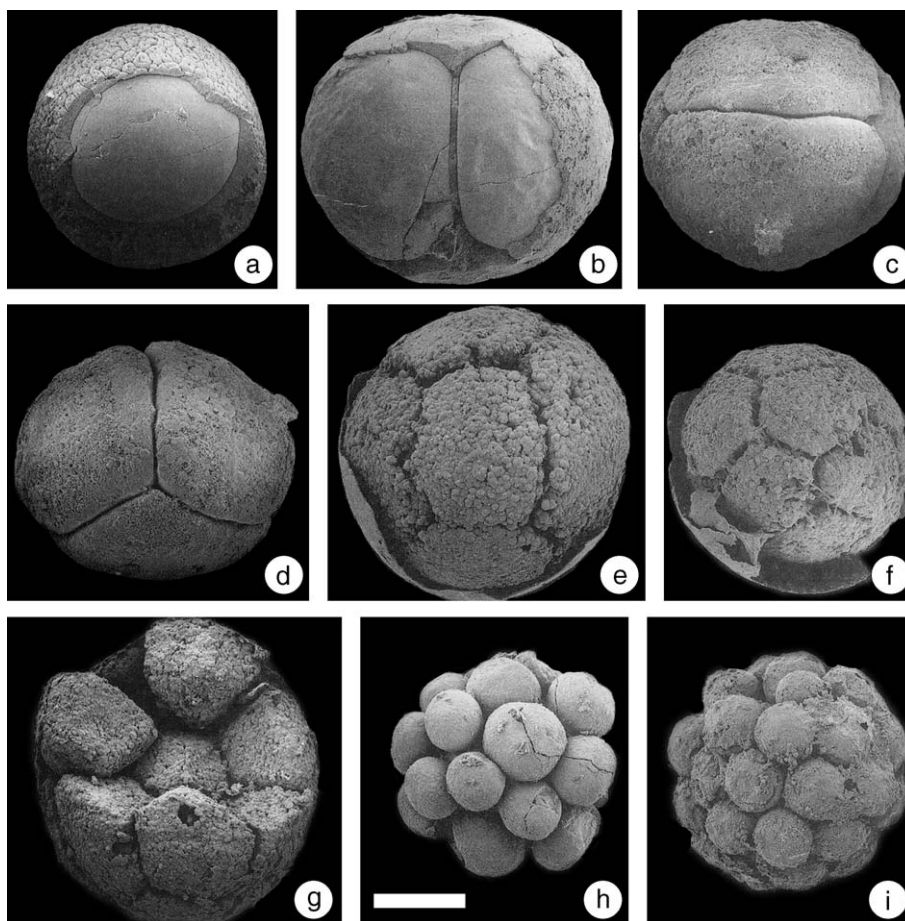


Fig. 147. Fossil embryos preserving different stages of cleavage from the Doushantuo Formation. (a) Fertilised egg with thick membrane. (b) Two-cell stage. (c, d) Four-cell stage. (e) Eight-cell stage. (f, g) Later cleavage stages showing faceted cell geometry; and in (g) three-dimensional distribution of cells. (h, i) Multicellular structures, in (h) as especially possible for colonial protists. (scale bar=200 μ m for a, e, f, g, h, i: 150 μ m for b: and 240 μ m for c, d) (from Xiao et al., 1998).

Mashania deformata gen. et sp. nov

Mashania annulata gen. et sp. nov

Mashania closely resembles *Pteridinium*, but the primary branches are radiate in the anterior part and the free body is of different shape, although it appears to be bended and warped. The host sediments are considered to be of late Precambrian age and equivalent to the Xidong Group of the Sinian System in South China, the Vendian in Russia and the Wilpena Group of South Australia.

14. Trace fossils

14.1. Introduction

Crimes (1992) discussed the record of trace fossils across the Proterozoic–Cambrian boundary in a

comprehensive treatment which is an ideal reference text, with the proviso that new finds and revisions are likely to have been made in the decade since it was published; and the further proviso that it nowhere considers the trace fossil record of the Sturtian and the earlier pre-Vendian record. He considered the record from the Laplandian/Varanger/Marinoan glaciation onwards.

The dramatic increase in abundance and diversity of trace fossils at about the time of the lower boundary of the Cambrian had been described by many authors (Seilacher, 1956; Alpert, 1975; Daily, 1972; Crimes, 1975, 1987; Fedonkin, 1980a,b; Brasier, 1982; Urbanek and Rozanov, 1983; Crimes and Anderson, 1985; Fritz and Crimes, 1985; Nowlan et al., 1985; Paczesna, 1986; Narbonne et al., 1987). The use of trace fossils to define the Neoproterozoic (Vendian)/Cambrian boundary precisely has been considered earlier by a number of

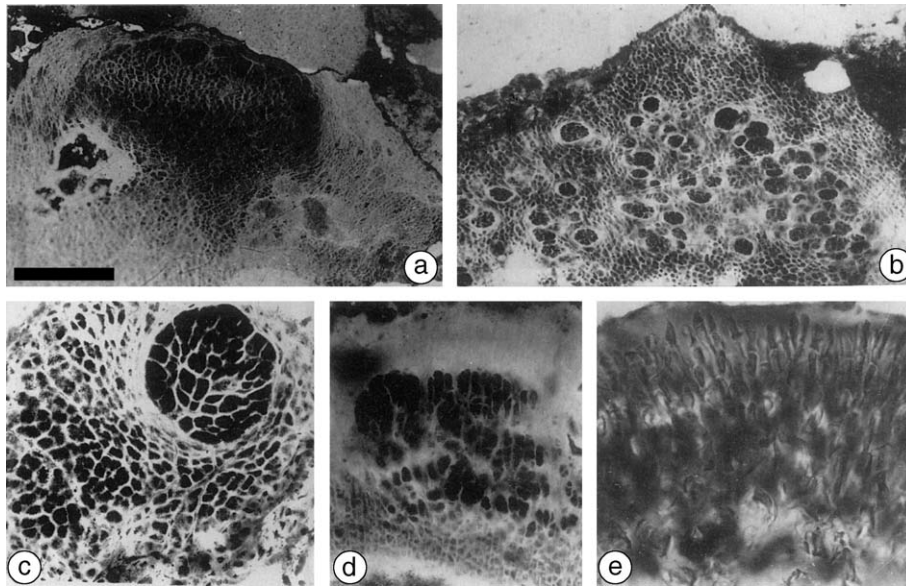


Fig. 148. Reproductive structures in Doushantuo thalli compared with those of a modern red alga. (a–d) Doushantuo thalli—(a) clusters of dark cells (carpospores) arising from filaments or supporting cells; (b) packets of dark cells preserved in an anatomically preserved thallus; (c) higher magnification of carpospores within surrounding vegetative tissue; (d) linearly arranged dark cells interpreted as possible spermatangia; (e) spermatangial sori of the modern florideophyte red alga *Gracilaria* sp. (scale bar in a; for a, b, d=100 μ ; for c=50 μ ; for e=30 μ) (from Xiao et al., 1998).

authorities (e.g. Daily, 1972; Alpert, 1977; Fedonkin, 1980a; Crimes, 1987; Narbonne et al., 1987): and this has actually been implemented in the GSSP section for the boundary on the Burin Peninsula, in Newfoundland.

Trace fossils are produced by animals moving on or within sediment and have a specific form related to the size, shape and behaviour of the animal. They may even reproduce the shape of the producer animal as with trilobite resting traces (*Rusophycus*) and some echinoid resting traces, but this is rare. Most do not do this. It is important to realise that evidence an increase in traces and increase in animal diversity need to be considered quite separately.

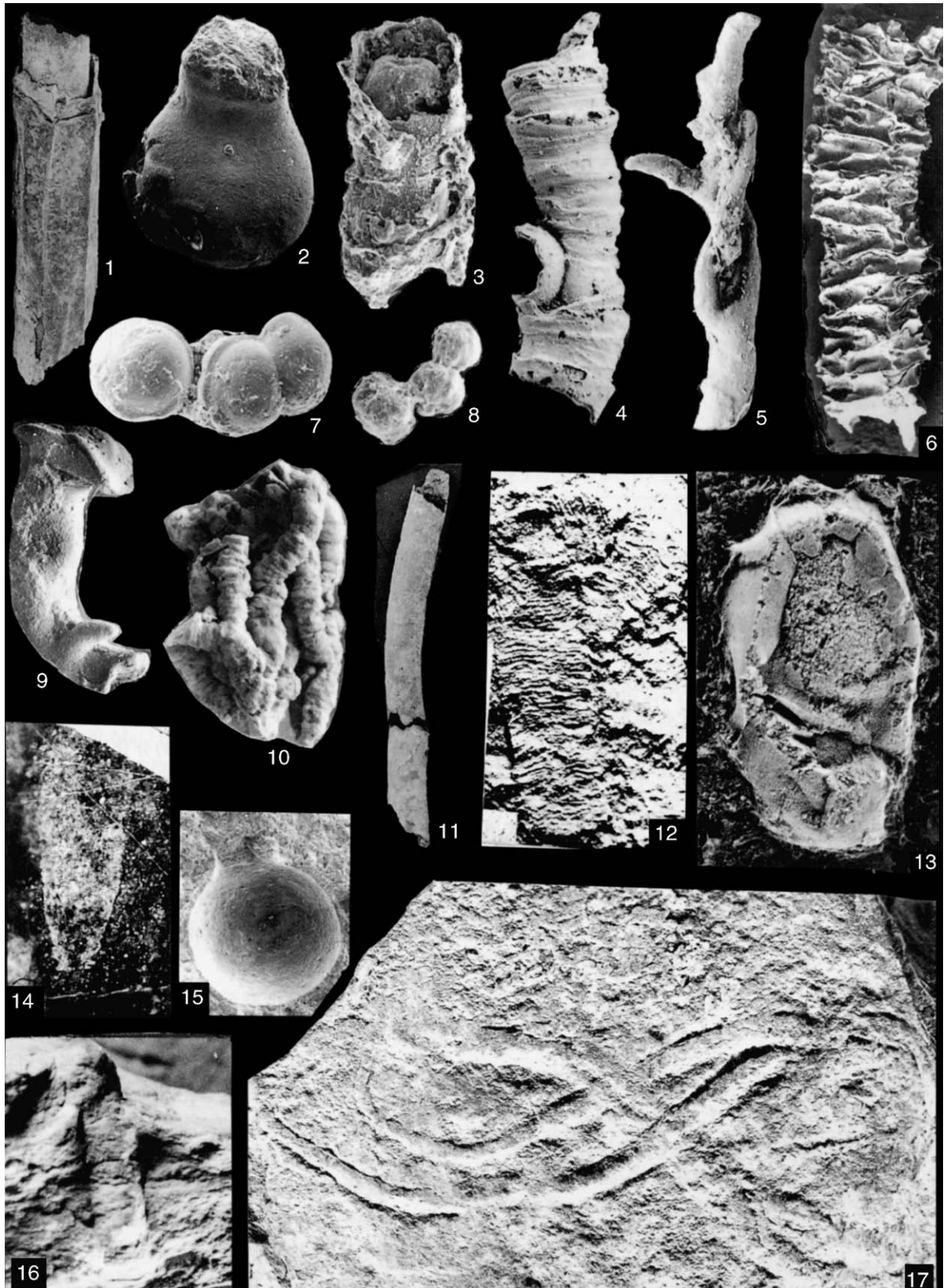
Seilacher (1956) suggested that there was an increase in abundance and diversity from Precambrian (rare) to Cambrian (abundant): this was based on studies of the Grand Canyon, USA, and Salt Range, Pakistan. He believed that it reflected explosive evolution at the end of Precambrian time. Crimes (1992) listed the genera recorded in the Vendian, and Tommotian and Atdabanian Stages of the Lower Cambrian (Table 14). He also published a diagram

illustrating this change (Fig. 151) and another diagram illustrating the ichnogenic diversity from Precambrian to Tertiary, separating shallow water, bathymetrically independent and deep water genera. In Table 14, there are six genera restricted to the Vendian and most of these are rather different to the long ranging Palaeozoic types. The Precambrian trace fossils are all shallow water or facies crossing types. Deep-water forms were rare in the Cambrian, increased significantly in the Ordovician and again in the Cretaceous.

According to Crimes, this evidence shows that (benthic) animal life first developed in shallow waters and only gradually colonised the deep waters. Prior to the Vendian life, it was mainly planktonic and microscopic but there were some megascopic organisms, among the dominant carbonaceous filamentous algae, microphytes and acritarchs. The critical question is, of course, whether there were megascopic benthic animals in the pre-Vendian (Ediacaran) periods. This is considered below.

The shallow-water niches filled up rapidly because the areal extent of muddy niches was low and this in the

Fig. 149. Fossils from South Shaanxi Province. The following are identified: (1) *Qinella levis* Zhang, Li and Dong ($\times 10$). (2) *Protolagena gaojiashanensis* Zhang and Li. (3) *Cloudina* sp. ($\times 58$). (4) *Cloudina lijigouensis* Zhang, Li and Dong ($\times 45$). (6) *Sinotubulites cienegensis* McMenamini ($\times 15$). (11) *Chenella regularis* Zhang and Hua ($\times 16$). (12) *Shaanxilithes ningqiangensis* Xing, Yue, and Zhang ($\times 12$). (15) *Protolagena limbata* Zhang ($\times 23$). (16) *Skolithos isolatus* Zhang ($\times 7$). (17) *Bucerusichnus octoideus* Zhang and Dong ($\times 1$). (From Hua Hong et al., 2002).



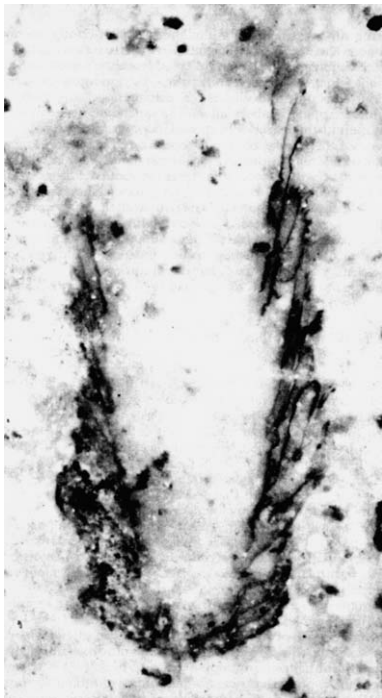


Fig. 150. Cloudinid-like tube from the Gaojiasshan Formation, Kuanchuanpu, Shaanxi, China ($\times 20$) (after Conway Morris et al., 1990, reprinted with permission of American Journal of Science).

first instance caused the rapid development about the time of the Cambrian boundary of meandering and other complex paths. Similar pressures also caused colonisation of deep-sea niches to commence in the Cambrian although this only became widespread in the Ordovician.

Crimes then considered the evidence from four key areas, the White-Inyo Mountains, Cassiar Mountains, Burin Peninsula (Newfoundland), the site of the GSSP, and Tanafjord, Finnmark, Norway. In the case of the first, the lowest two units yielded only unbranched, tubular burrows of *Planolites*-type: the diversity increase to more complex forms comes in rather late (late Tommotian–Atdabanian), but this may be due to extensive limestone and dolomite lithologies in the lower two units, rock types that rarely yield trace fossils. In the Cassiar Mountains, the lowest investigated part yielded only *Planolites* and *Gordia*; *Chondrites* and *Helminthopsis* appeared 37 m above, and about 200 m above, in strata supposed to be about the Vendian–Tommotian boundary, *Didymaulichnus*, *Neonereites*, *Skolithos* and *Taphrhelminthopsis* appeared. It was suggested that the Precambrian/Cambrian boundary had here been placed too high. The Burin Peninsula yielded the most extensive suite of trace fossils of any sequence covering this boundary. Member 1 of the Chapel Island Formation, considered to be Vendian, yielded *Butho-*

Table 14

Trace fossil genera recorded in the Vendian and Early Cambrian

Geological period or stage	List of genera
Vendian	<i>Arenicolites</i> , <i>Bergueria</i> , <i>Bilinichnus</i> , <i>Broksella</i> , <i>Buthotrephis</i> , <i>Cochlichnus</i> , <i>Curvolithus</i> , <i>Didymaulichnus</i> , <i>Gordia</i> , <i>Harlaniella</i> , <i>Intrites</i> , <i>Nenoxites</i> , <i>Neonereites</i> , <i>Nereites</i> , <i>Palaeopascichnus</i> , <i>Planolites</i> , <i>Scolicia</i> , <i>Skolithos</i> , <i>Torrowangea</i> , <i>Vendichnus</i> , <i>Vimenites</i>
Early Cambrian	<i>Arenicolites</i> , <i>Bergueria</i> , <i>Bilinichnus</i> , <i>Broksella</i> ,
Lower Tommotian	<i>Buthotrephis</i> , <i>Chondrites</i> , <i>Cochlichnus</i> , <i>Conichnus</i> , <i>Curvolithus</i> , <i>Didymaulichnus</i> , <i>Gordia</i> , <i>Gyrolithes</i> , <i>Monomorphichnus</i> , <i>Muensteria</i> , <i>Neonereites</i> , <i>Nereites</i> , <i>Phycodes</i> , <i>Planolites</i> , <i>Protopaleoductyon</i> , <i>Scolicia</i> , <i>Skolithos</i> , <i>Teichnichnus</i> , <i>Torrowangea</i> , <i>Treptichnus</i>
Upper Tommotian	<i>Arenicolites</i> , <i>Astropolichnus</i> , <i>Belorhapse</i> , <i>Bergueria</i> , <i>Brooksella</i> , <i>Buthotrephis</i> , <i>Chondrites</i> , <i>Cochlichnus</i> , <i>Conichnus</i> , <i>Cosmorhapse</i> , <i>Curvolithus</i> , <i>Didymaulichnus</i> , <i>Diplichnites</i> , <i>Diplocraterion</i> , <i>Gordia</i> , <i>Gyrolithes</i> , <i>Helminthoida</i> , <i>Helminthopsis</i> , <i>Hormosiroidea</i> , <i>Mammilichnis</i> , <i>Monocraterion</i> , <i>Monomorphichnus</i> , <i>Muensteria</i> , <i>Neonereites</i> , <i>Nereites</i> , <i>Phycodes</i> , <i>Plagiogmus</i> , <i>Planolites</i> , <i>Protopaleodictyon</i> , <i>Rhizocorallium</i> , <i>Rusophycus</i> , <i>Scolicia</i> , <i>Skolithos</i> , <i>Taphrhelminthopsis</i> , <i>Teichichnus</i> , <i>Torrowangea</i> , <i>Treptichnus</i>
Atdabanian	<i>Archaeonassa</i> , <i>Arenicolites</i> , <i>Arthropycus</i> , <i>Asteriacites</i> , <i>Astropolichnus</i> , <i>Belorhapse</i> , <i>Bergueria</i> , <i>Brooksella</i> , <i>Buthotrephis</i> , <i>Chondrites</i> , <i>Cochlichnus</i> , <i>Conichnus</i> , <i>Cosmorhapse</i> , <i>Cruziana</i> , <i>Curvolithus</i> , <i>Dactyloidites</i> , <i>Dictyodora</i> , <i>Didymaulichnus</i> , <i>Diplichnites</i> , <i>Diplocraterion</i> , <i>Dolopichnus</i> , <i>Gordia</i> , <i>Gyrolithes</i> , <i>Halopoa</i> , <i>Helminthoida</i> , <i>Helminthopsis</i> , <i>Hormosiroidea</i> , <i>Isopodichnus</i> , <i>Laevicyclus</i> , <i>Mammilichnis</i> , <i>Monocraterion</i> , <i>Monomorphichnus</i> , <i>Muensteria</i> , <i>Neonereites</i> , <i>Nereites</i> , <i>Paleodictyon</i> , <i>Phycodes</i> , <i>Planolites</i> , <i>Protichnites</i> , <i>Protopaleodictyon</i> , <i>Rhizocorallium</i> , <i>Rosselia</i> , <i>Rusophycus</i> , <i>Scolicia</i> , <i>Skolithos</i> , <i>Squamodictyon</i> , <i>Syringomorpha</i> , <i>Taphrhelminthopsis</i> , <i>teichichnus</i> , <i>Torrowangea</i> , <i>Treptichnus</i> , <i>Zoophycos</i>

Bold=those restricted to the Vendian. Note that the base of the Tommotian Stage is here taken as the Cambrian boundary. Since this list was published by Crimes (1992), an additional Manykian Stage (=Rovno, Nemakit-Daldyn) has been added the base of which corresponds to the appearance of *Phycodes pedum*: the base of the Cambrian remains as shown above.

trepis, *Gordia*, *Harlaniella*, *Planolites* and *Torrowangea*, whereas there is a dramatic increase in diversity in Member 2 A, *Didymaulichnus*, *Phycodes* and 17 other more complex forms appearing. The Vendian–Tommotian was placed at or a few metres above the base of

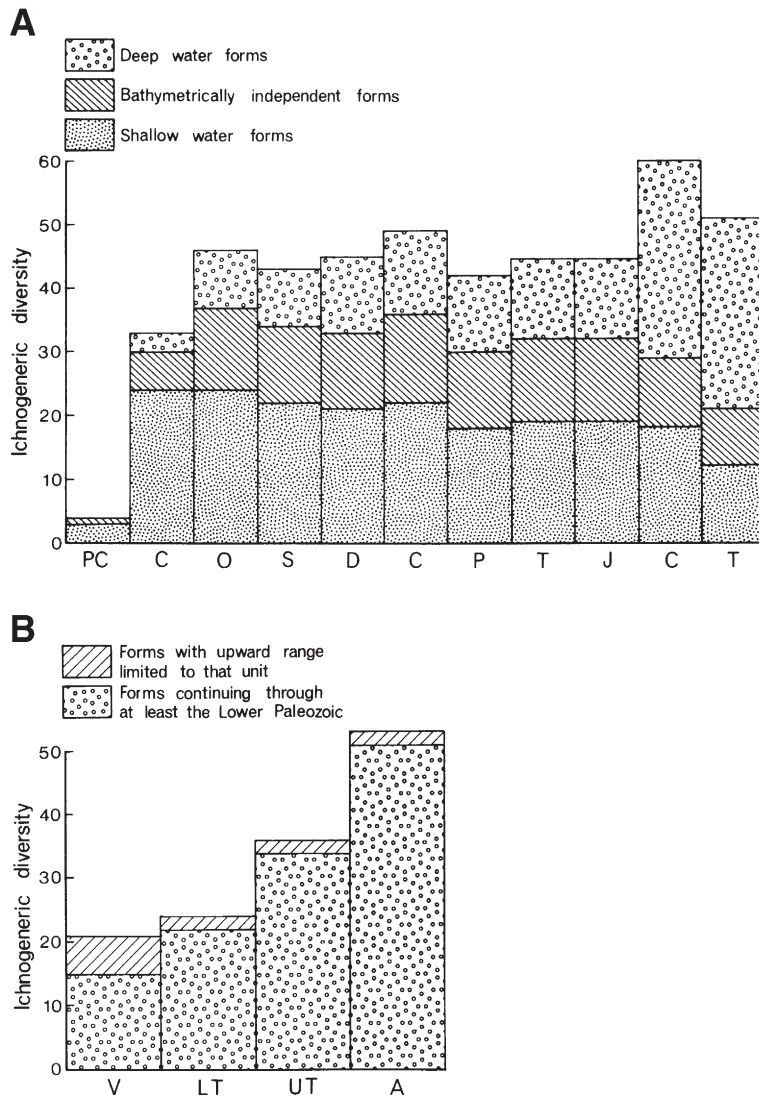


Fig. 151. Ichnogenic diversity from the Precambrian to the Tertiary (after Crimes, 1992).

Member 2A and this dramatic increase occurs at this boundary, which in the GSSP here was marked by the entry of *Phycodes pedum*.

Diversity continues to increase steadily through the section. The excellently exposed section at Tanafjord is known through the work of Banks (1970). *Arenicolites* and *Skolithos* appear 200 m above the Vendian tillite in the middle of the Innerelv Member (which has yielded Ediacara-type fossils). The overlying Manndraperev member also has *Curvolithos* and *Planolites*, whereas the Lower Breivik member above it has yielded *Phycodes*, *Treptichnus* and *Rusophycus*. Further increase in diversity marks the Upper Breivik Member.

Considering the case for explosive evolution at this boundary, Crimes notes that three of the sections

indicate a steady increase across the Vendian–Cambrian boundary, whereas there is a dramatic increase in the Burin peninsula section at or below the likely base of the Tommotian (Crimes takes the Tommotian to be the lowest stage of the Cambrian whereas later an additional stage, the Manykai Stage was added: this does not seem to affect his arguments but the Tommotian as shown by him would probably nowadays be divided into the Manykay and Tommotian, the former representing the Rovno or Nemakit-Daldyn formerly considered to be Vendian). Crimes suggested a climatic explanation for the difference between the sections (Newfoundland was then in a tropical position: Cassiar Mountains on the equator) and concluded that the available evidence suggests that the most rapid









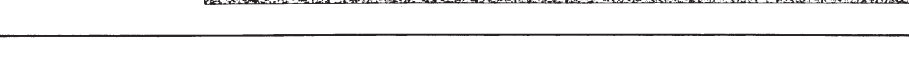

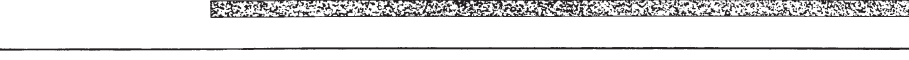






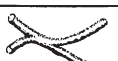
			Simple filled burrows
			Pelleted traces
			Bilobed burrows
			Vertical burrows
			Coelenterate resting traces
			Arthropod traces
			Radiating traces
			Branching burrows
			Spreite traces
V E N D I A N		T O M M O T I A N	
P R E C A M B R I A N		E A R L Y C A M B R I A N	
		A T D A B A N I A N	

Fig. 152. Evolutionary development of the main trace fossil lineages across the Precambrian–Cambrian boundary interval (after Crimes, 1992).

diversity increase did occur in Newfoundland early in the Cambrian and that these organisms later migrated to other regions.

Crimes illustrated the development of the main Phanerozoic trace fossil lineages across the Precambrian/Cambrian boundary (Fig. 152) and the evolutionary development of simple sediment-filled burrows, branching burrows, stuffed and spreite burrows, trails and resting traces across this boundary (Figs. 153–156). He described all these types in some detail. Ethological changes across this boundary were then discussed. The subdivision into feeding, dwelling, resting, crawling and grazing traces are shown in Table 15 and the changes from the Vendian through to the Atdabanian are shown in Table 16 (both based on Crimes, 1992). He noted that the attributions in Table 15 had been reached with some difficulty.

He concluded that the main trace fossil lineages were initiated in the Vendian and Early Cambrian. The Vendian traces were mostly restricted to very simple unbranched burrows, pelletal traces and bilobed burrows.

Trace fossils have a very important role both in stratigraphy and in understanding the nature of the biota, and this is especially true of the Vendian.

14.2. Zonation

The first zonal scheme for Proterozoic–Cambrian boundary interval trace fossils was made by Jiang et al. (1982) for the Meishucun section, China. However, the two lower zones were based on non-diagnostic and/or poorly preserved specimens and neither of the proposed indicators *Sellaulichnus* and *Cavaulichnus* have been recognised outside China. Even if they are locally significant, they cannot be used in a global system of zonation (Narbonne and Myrow, 1988). Crimes (1987) proposed a truly global zonation (Table 17).

Narbonne and Myrow (1988) supported the global significance of this system, but, in a largely simultaneous, bed by bed study of the Chapel Island Formation, derived a slightly different zonation system, again of three zones but the lower zone only corresponding to the upper half of Crimes's lower zone. Their system is shown in Table 18 and Fig. 157. The lower zone in this system corresponds approximately to the Kotlin Interval of Russia and the Ukraine and the second to the Rovno Interval and Nemakit-Daldyn Interval of Siberia. The precise correlation of their upper *Rusophycus avalonensis*

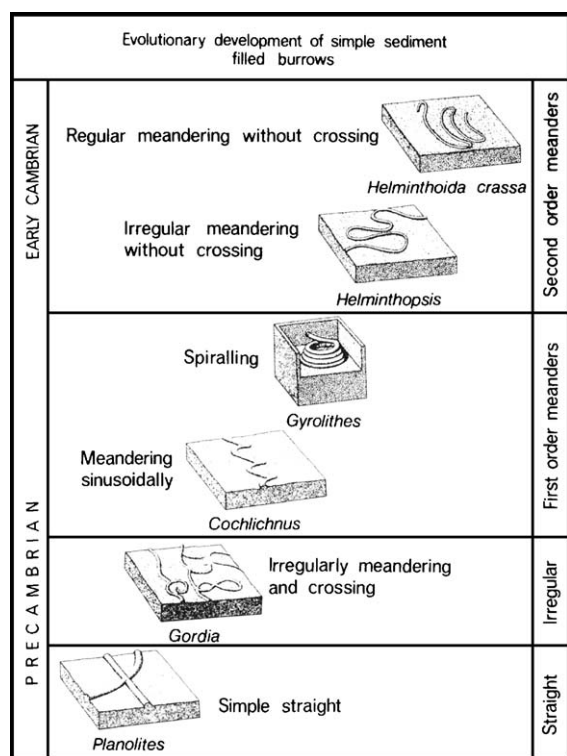


Fig. 153. Evolutionary development of simple sediment-filled burrows across the Precambrian–Cambrian boundary interval (after Crimes, 1992).

zone with the Lower Cambrian shelly fossil stages remains uncertain. Nowlan et al. (1985) observed *Rusophycus avalonensis* in association with an *Anabarites*–*Protohertzina* shelly fossil assemblage which they correlated with the Nemakit-Daldyn (Manakay), whereas Crimes (1987) regarded the base of this zone as late Tommotian in age. The appearance of *Rusophycus avalonensis* 450 m below the lowest Tommotian small shelly fossils in Newfoundland (Narbonne et al., 1987) implies an older age for its appearance, at least mid-Tommotian according to Narbonne and Myrow (1988).

McIlroy (2003) questioned the validity of Crimes's zonation system in a study of the Finnmark, Norway occurrences. The Manndrapereiv Formation, equivalent to the *Harlanella podolica* zone, contains 11 ichnospecies, including many diagnostically Neoproterozoic taxa as well as *Belorhaphé* and *Helicolithus* genera normally expected in the Atdabanian. Other genera were:

Cochlichnus
Curvolithus
Gordia
Helminthoida

Intrites
Monomorphichnus
Palaeopaschichnus
Planolites
Suzmites

Squamodictyon was also possibly present.

It was argued that whereas *Phycodes pedum* is a good stratigraphic marker, being found in all facies from mudstone to arenite and abundant in siliciclastic mid-shelf environments, it was of patchy occurrence. The conclusion reached states that a number of complex trace fossils have their first appearance in the Neoproterozoic of Norway, including *Belorhaphé*, *Helicolithus*, *Monomorphichnus*, *Spirorhaphé*, *Suzmites* and *Hormosiroidea*. A similar situation was recorded from the White Sea region where *Olenichnus* and *Monomorphichnus* were recognised (Fedonkin, 1985d; Jenkins, 1995). The initiation of the Cambrian explosion seems to have occurred in the Neoproterozoic, because such complex forms occur even in the beds containing the Ediacara-type body-fossils. The subdivision of the Lower Cambrian and definition of the lower boundary based on trace fossils appeared to be questionable, being not founded on sound ethological criteria. Facies variations need to be taken into account. It needs reassessment because ethological diversity was clearly established earlier than hitherto supposed.

It must be agreed with McIlroy that, although the establishment of ichnospecies-based zones represented a great advance in our ability to correlate Vendian–Early Cambrian sequences, there is an obvious need for some further refining of the system including the equivalence of shelly fossil- and acritarch-based systems.

Some further developments since Crimes published his findings, include the finding of borings in the shells of *Cloudina* in sediments of the Gaojia-shan Member of the Denying Formation just south of Xi'an in Shaanxi Province, China (Hua Hong et al., 2003). One-fifth of the samples studied was bored. The identity of the borer is not known, although a mollusk has been suggested. This indicates the existence of predation in the Vendian, just below the Cambrian boundary and the probable existence of a mollusk. The predation (the earliest so far recorded) was selective as associated *Sinotubulites* were not affected.

Brasier and McIlroy (1994) reported *Neonereites uniserialis* (a chain of ovate pellets) just above the Portaskaig tillite in Islay, Scotland, rocks with a minimum age of 600 Ma. They consider this the earliest putative evidence for coelomates or pseudocoelomates.

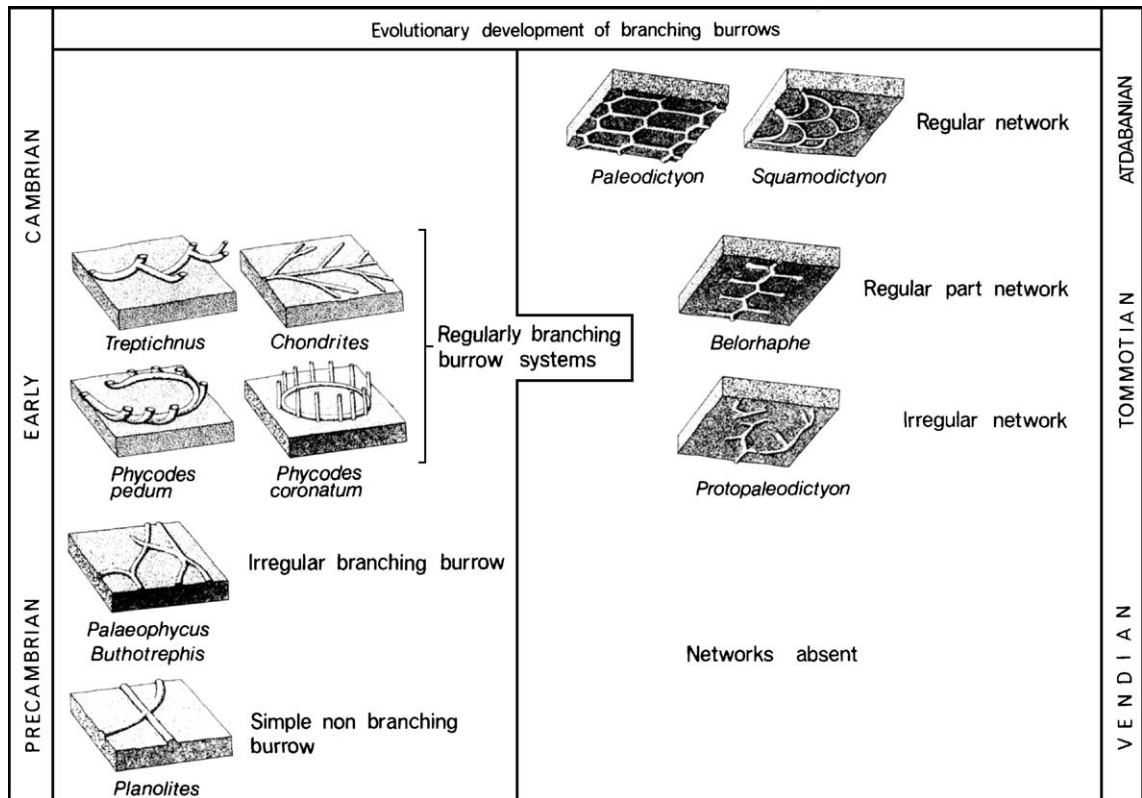


Fig. 154. Evolutionary development of branching burrows across the Precambrian–Cambrian boundary interval (after Crimes, 1992).

Valentine (2004) generally accepts Crimes' findings, reproducing his diagram, but considers the scanty evidence of bioturbation in Vendian sediments to be important. Though there is some evidence of penetration burrows, they are short, small and rare. The lack of mixing by animal activity allows a greater chance of preservation of late Neoproterozoic traces.

14.3. Pre-Vendian trace fossils?

Also important is the question of trace fossil representation in pre-Vendian sequences.

Kauffman and Steidtmann (1981) claimed to have possibly found the oldest metazoan trace fossils in the early Proterozoic Medicine Peak Quartzite in Wyoming, of age of deposition more than 2000 Ma. They stressed the possible importance of this find, for which they admittedly could not present unequivocal evidence of biological origin, because the mode of origin and early evolution of metazoans remains the greatest question in Precambrian biology.

The pre-Vendian record of trace fossils is a very grey area. Those from Wyoming mentioned above

have the right shape but the authors admitted they are questionable: Clemmey (1976) found burrows in 1000 Ma rocks in Zambia, which Cloud (1978) regarded as later introductions onto a laterite profile although Clemmey (1978), in reply still maintained their ancient age of formation. His Fig. 4 in the original paper is quite convincing. The most comprehensive treatment of the topic that the author could find was by Gong (1999), unfortunately in the Chinese language with some English language explanations. Gong suggested in his Fig. 1 and Table 2 that many of the common trace fossil genera have been found in Proterozoic rocks ranging from 600 to 1000 Ma old. The list includes *Planolites*, *Skolithos*, *Cochlichnus*, *Nimbria*, *Didymaulichnus*, *Helicoichnus*, *Spirodesmos*, *Scolicia*, *Paleodictyon*, *Squamodictyon*, and *Chondrites*. Some of the references are given in English, but the reference list is incomplete. He has delineated quite complex forms in 1000 Ma rocks (including *Phycodes*) but the forms figured from even older rocks are quite simple. It is quite impossible to evaluate the weight that should be given to this publication—it would require a full translation from the Chinese language and then a check on all the references (many

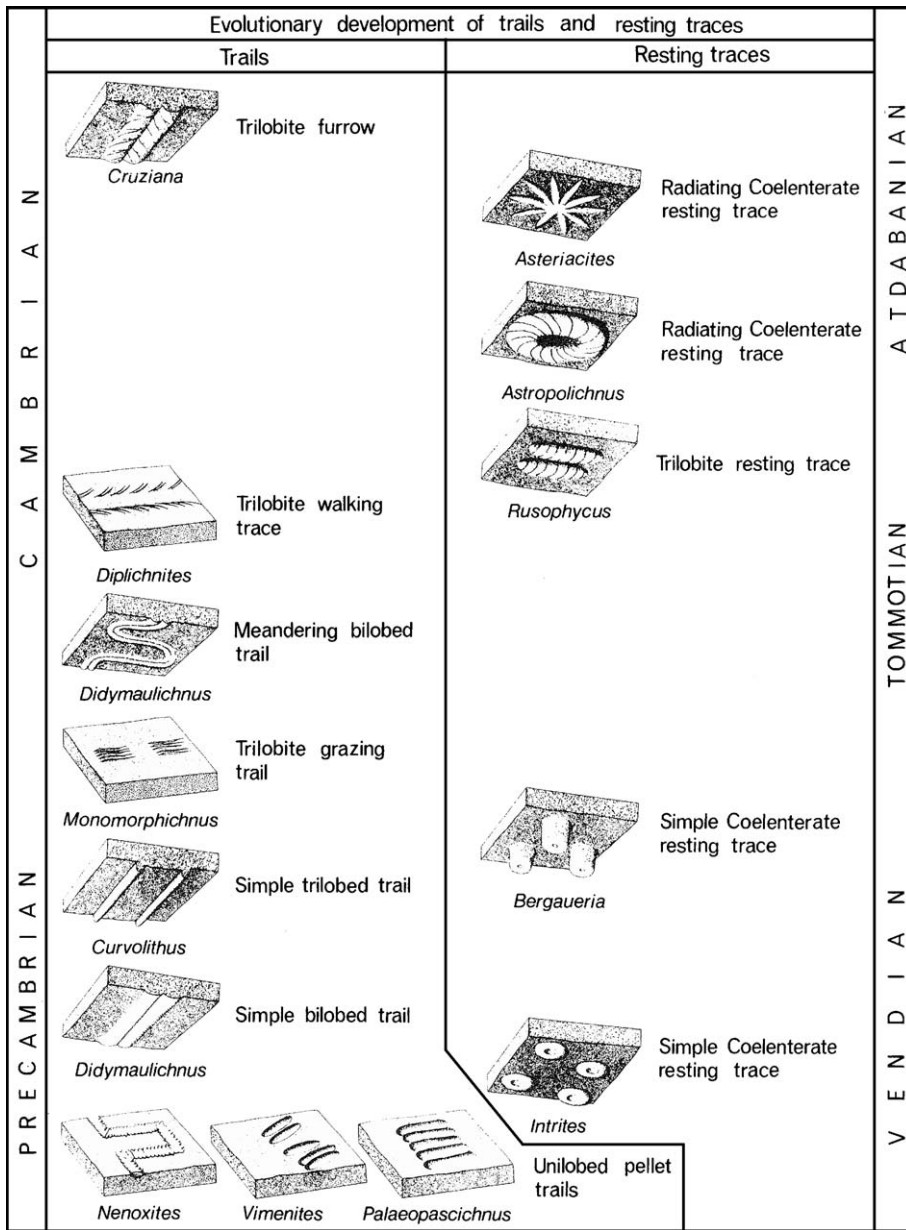


Fig. 156. Evolutionary development of trails and resting traces across the Precambrian–Cambrian boundary interval (after Crimes, 1992).

Signor and Lipps (1992) argued emphatically that the evidence is unequivocal that the diversification of trace fossils paralleled but did not precede the diversification of shelly fossils (Byers, 1982; Crimes, 1987, 1989, 1992). No trace fossils are known, they said, that support the contention that metazoans existed prior to the Vendian. Simple traces appear at about the same time as the first Ediacara-type fossils and arthropod-grade traces just above the Precambrian/Cambrian boundary and just before the first trilobites. The absence of any incontrovertible traces

in any ancient environments indicates an absence of coelomates prior to the Vendian and possibly other metazoan life.

Seilacher et al. (1998) reported the trace made by a triploblastic animal form rocks more than 1 Myr old in India.

The older traces that have been reported (by Clemmey, Kauffman and Steidtmann, and Gong, as mentioned above, and by a number of others) have not been generally accepted (e.g. Bergstrom, 1990; Crimes, 1992; Fedonkin and Runnegar, 1992). Simple

Table 15
Types of traces (after Crimes, 1992)

Type of trace	Genera
Feeding	<i>Achaeonassa</i> , <i>Arthropycus</i> , <i>Belorhaphé</i> , <i>Brooksella</i> , <i>Buthotrephis</i> , <i>Chondrites</i> , <i>Cochlichnus</i> , <i>Dictyodora</i> , <i>Gyrolithes</i> , <i>Halopoa</i> , <i>Harlaniella</i> , <i>Hormosiroidea</i> , <i>Muensteria</i> , <i>Neonereites</i> , <i>Nereites</i> , <i>Palaeopascichnus</i> , <i>Phycodes</i> , <i>Plagiogmus</i> , <i>Protopalaeodictyon</i> , <i>Teichnichnus</i> , <i>Torrowangea</i> , <i>Treptichnus</i> , <i>Zoophycus</i>
Dwelling	<i>Arenicolites</i> , <i>Diplocraterion</i> , <i>Dolopichnus</i> , <i>Laevicyclus</i> , <i>Rhizocorallium</i> , <i>Rosselia</i> , <i>Skolithos</i>
Resting	<i>Asteriacites</i> , <i>Astropolichnus</i> , <i>Bergueria</i> , <i>Conichnus</i> , <i>Dactyloidites</i> , <i>Intrites</i> , <i>Isopodichnus</i> , <i>Mammillichnus</i> , <i>Rusophycus</i> , <i>Vendichnus</i>
Crawling	<i>Bilichnus</i> , <i>Cruziana</i> , <i>Curvolithus</i> , <i>Didymaulichnus</i> , <i>Diplichnites</i> , <i>Protichnites</i> , <i>Scolicia</i>
Grazing	<i>Cosmorhaphé</i> , <i>Dimorphichnus</i> , <i>Gordia</i> , <i>Helminthoidea</i> , <i>Helminthopsis</i> , <i>Monomorphichnus</i> , <i>Nenoxites</i> , <i>Paleodictyon</i> , <i>Squamodictyon</i> , <i>Syringomorpha</i> , <i>Tarphhelminthopsis</i>

burrowing traces imply the presence of coelomate grade metazoans some time up into the Vendian (=Ediacaran) period but not earlier. Bioturbation related to the slightly later appearance of vertically burrowing organisms and their traces could have been responsible for erasing Ediacara-type organism largely from the post-Vendian fossil record, recycling carbon from the disturbed sediments and returning it to the carbon cycle (Fischer, 1984). If the evidence from trace fossils does provide little or no support for a “Hidden Evolution” as favoured by Durham (1978) and Runnegar (1982c), it still leaves open the possibility of small flatworm-like animals roaming the sediment surfaces, interstitial sand and firm substrates, without leaving any record. The precursors might have been small and left no trace or traces easily overlooked. Metazoa may have originated in a meiofauna. The above possibilities are suggested by Signor and Lipps (1992); however, there remains another interesting possibility, more likely than the meiofauna answer considering the size of the Ediacara-type soft-

Table 16
Distribution of ethological groups across the Precambrian–Early Cambrian boundary (after Crimes, 1992)

Ethological group	Vendian (%)	Cambrian (L. Tommotian) (%)	(U. Tommotian) (%)	(Atdabanian) (%)
Feeding	52	57	47	40
Dwelling	10	9	11	15
Resting	14	9	14	15
Crawling	14	17	11	11
Grazing	10	9	17	19

Table 17
The zonation system of Crimes (1987)

Zone	Description
III Lower Cambrian	First appearance of arthropod burrows (e.g. <i>Rusophycus</i> , <i>Cruziana</i> and spreiten dwelling burrows (e.g. <i>Diplocraterion</i>). Approx. 45 ichnogenera known
II Basal Cambrian	First appearance of complex feeding burrows (e.g. <i>Phycodes</i> , <i>Teichnichnus</i> , <i>Treptichnus</i>). Approx. 45 ichnogenera known.
I Vendian	Simple, subhorizontal traces. A few ichnogenera apparently restricted to this zone (e.g. <i>Harlaniella</i> , <i>Palaeopascichnus</i> , <i>Neonoxites</i>). Approx. 15 ichnogenera known.

Table 18
Summary of the zonation system based on trace fossils from the Chapel Island Formation, Burin Peninsula, Newfoundland (after Narbonne and Myrow, 1988)

Zone	Description
<i>Rusophycus avalonensis</i>	Remainder of Chapel Island Formation and overlying Random Formation. A concurrent range zone, it is characterised by the first appearance of <i>R. avalonensis</i> , <i>Tarphhelminthopsis circularis</i> and several other taxa (Fig. 157): its top is placed at the first appearance of trilobites. The zonal assemblage contains at least 40 species, most of which first appear in it. New forms include arthropod burrows, spreiten burrows, complex feeding burrows and graphoglyptids. Most species range upwards into younger trilobite-bearing strata, but <i>R. avalonensis</i> and <i>T. circularis</i> are apparently restricted to this zone. Equivalent to Crimes’s Ichnofossil zone III
<i>Phycodes pedum</i>	Lower part of member 2 of the Chapel Island Formation. The base is characterised by the first appearance of <i>P. pedum</i> . No ichnospecies are restricted to this zone. 13 ichnospecies comprise the zonal assemblage (Fig. 157), including complex feeding burrows, vertical dwelling burrows, a vertical, helical burrow <i>Gyrolithes</i> and anemone burrows (<i>Bergueria</i> , <i>Conichnus</i>). Most of the new ichnospecies first appear in the basal 3 m of the zone. Equivalent to Crimes’s Ichnofossil zone II (approximately equivalent to Rovno “Horizon” of the Baltic Series and Nemakit-Daldyn of Siberia.
<i>Harlaniella podolica</i>	Member 1 and the lower 2.4 m of member 2 of the Chapel Island Formation. Defined by the range zone of <i>H. podolica</i> and also represents the upper half of the age range of <i>Palaeopascichnus delicatus</i> . Characterised by low diversity, less than 10 ichnospecies; simple, sub-horizontal trails and burrows constructed at or near the sediment/water interface. Equivalent to the upper half of Crimes’s Ichnofossil zone I (approximately equivalent to the Kotlin “Horizon” of the Valdai Series of the East European Platform.

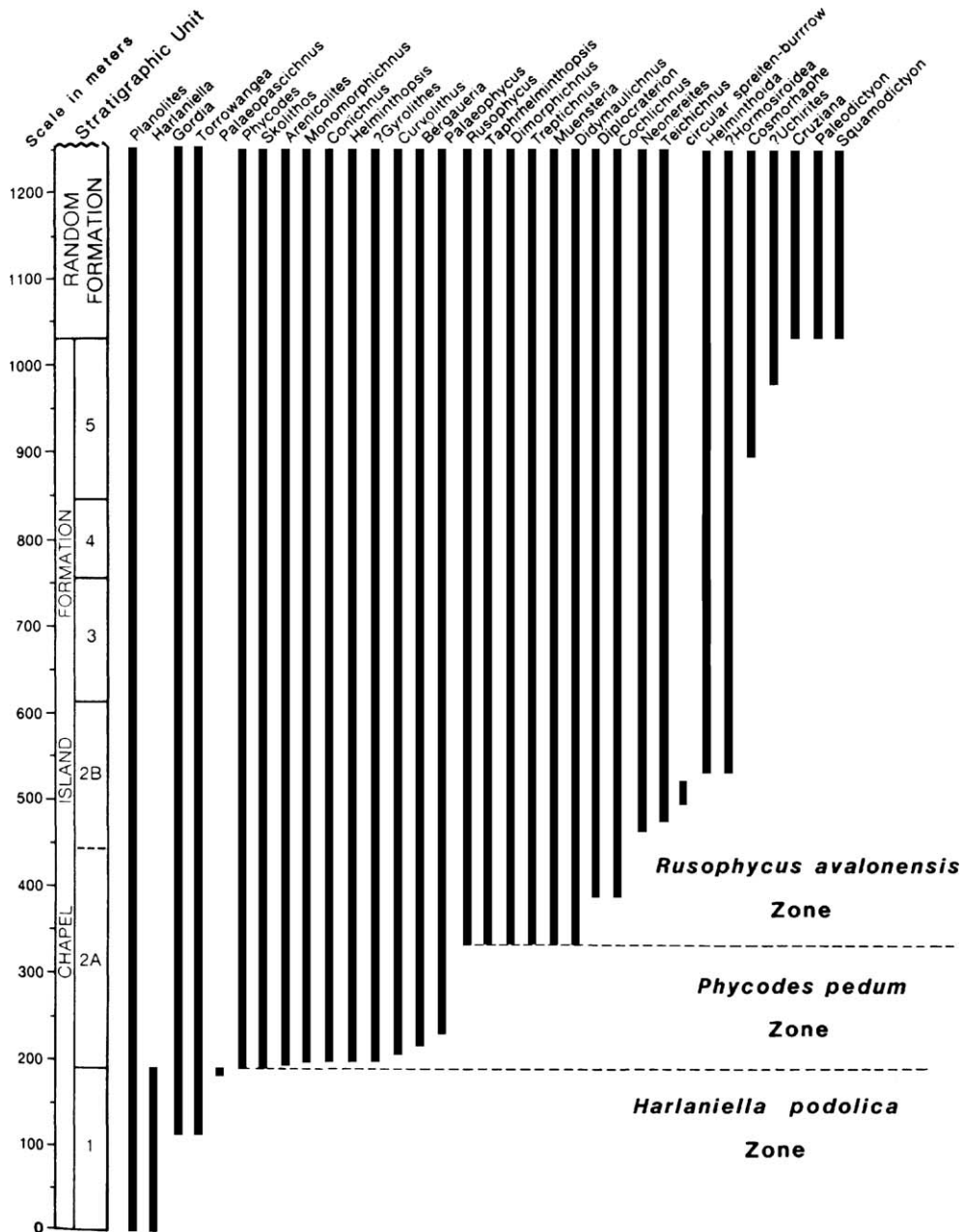


Fig. 157. Generalised trace fossil range chart for the Chapel Island and Random Formations, Newfoundland, Canada (data from Crimes and Anderson, 1985; Narbonne et al., 1987); (after Narbonne and Myrow, 1988).

bodied organisms—that the precursors may have been quite large but entirely planktonic, and thus leaving no traces.

Although the list of proposed pre-Vendian trace fossils of Gong (1999) may be chimeric, as most authorities seem to imply, it might be worthwhile instituting a systematic search for trace fossils in unmetamorphosed or very low metamorphic grade sedimentary rocks of pre-

Vendian Proterozoic age widely. For it is conceivable, that a trace might be found that matched one from the Vendian and later rocks; and could be matched with a known coelomate metazoan.

After the above text was written, the author read a new account of trace fossils in the Stirling Range Formation, Western Australia (Rasmussen et al., 2002a,b). As reported in Section 9, this occurrence is in rocks now

firmly radiometrically dated as older than 1200 Ma. The attribution to feeding traces of mucus-secreting annelids is difficult to dispute.

15. Geochronology

15.1. Introduction

Geochronology is the discipline in which ages of rocks are estimated (Knoll and Walter, 1992)—on which review much of this section is based. Geologists in the 19th Century had only methods based on fossils to determine order of superposition, i.e. the sequence of geological events; they could make no determination of how old they were in years—absolute ages. This changed with the development of radiometric methods of age determination on minerals and whole rocks, through the first 40 yrs of the twentieth century (Lewis, 2000). Thus estimates of age can now be made in the chronometric scale, the basis of which is the year; this is based on the decay of radiogenic isotopes (e.g. of U, Rb, K, C). In practice, this method establishes a series of reference points in rock sequences. Stratigraphy permits an estimation of age to be inserted into the Global Stratigraphic Scale (the familiar Geological Column), in which the beginning of each division is defined by a Global Stratotype Section and Point (GSSP) (referred colloquially as the “Global Spike”), and selected by convention to define the boundary between this division and the one beneath it (in the case of the Vendian/Cambrian boundary the GSSP is located in the Burin Peninsula, Newfoundland).

Chronostratigraphic age can be known with certainty in the Global Stratotype Section, but the ages of all other sections elsewhere on the globe are determined by correlation, using physical, chemical or biological features of the rocks. Such correlation includes methods based on the overall lithological characteristics of the rocks (lithostratigraphy); specific geometric relationships of packages of sedimentary rocks, commonly utilising geoseismic profiles (sequence stratigraphy); fossils and trace fossils (biostratigraphy); magnetic features—palaeomagnetism can be used in a stratigraphic sense, based on reversals of polarity, as well as for determining palaeogeographic latitudes: e.g. in studies of the breakup of Rodinia and the Vendian glaciation mentioned below—(magnetostatigraphy); and secular variations in certain chemical element ion ratios related to palaeoenvironments, especially climatic (chemostratigraphy), a quite new entry in the list of methods, and very applicable to the Neoproterozoic.

Problems do arise because many biostratigraphical and climatological signatures from place to place over the globe are slightly diachronous, not entirely synchronous and this can be a problem when high stratigraphic resolution is required. Radiometric determinations also have their problems such as determination of constants (Rb–Sr), loss of gas (K–Ar), inability to collect completely fresh rock or mineral samples or complete absence of suitable material for analysis, superimposed later geological heating or metamorphism. Better methods such as Ar–Ar and the ion probe determination of U–Pb ratios in zircons have recently greatly improved accuracy, but even with the latter there are problems of being sure what one is measuring, i.e. because zircons tend to build on older cores, individual crystals may go through more than one sedimentological cycle.

15.2. The Neoproterozoic

Knoll and Walter (1992) remarked that of the long history of the Proterozoic eon, c. 2000 Myr, only in the final 40 Myr (the post-glacial part of the Vendian) is there a record of unequivocal metazoans. Most of the eucoelomate phyla that populated the Phanerozoic have no record in the Proterozoic. The end of the eon was a period of remarkable evolutionary innovation. The events at that time in geological history are rooted in a broad framework of geotectonic, biogeochemical and climatic change, which radically altered the Earth's surface and ushered in the Phanerozoic world.

The idea that drastic environmental and evolutionary developments are related is not new, but its importance is emphasised in the case of the Neoproterozoic/Cambrian timespan because there are special problems facing stratigraphy in the case of the Proterozoic. Fossils are rare and microfossils predominate. It is very difficult to establish synchronicity between events recorded in Neoproterozoic sections separated by large distances across the globe, yet obtaining fine-tuned chronostratigraphic correlations is critical to understanding the very important evolutionary events of the late Proterozoic.

There are thick sedimentary rock sections beneath the Cambrian lower boundary at many localities across the globe. These have so far been conventionally correlated based on glaciogenic developments and Ediacara-type animal remains. The Laplandian (Varanger, Marinoan) glaciation, at 610–590 Ma, the most widespread and intensive Neoproterozoic event (and possibly of all glaciation events), was formerly taken to be the basal Vendian, and both in Russia and in Canada appears to have been included in the Vendian. However, the Ediacaran, which now replaces the Vendian, is now

defined with its base the cap-carbonate above the glacial section (see for instance [Brakel, 2004](#)). The highly localised glaciations close to the Cambrian boundary recorded in Central Asia (Baikonurian), China, north-east Africa and South America are of little use in this respect. Ediacara-type faunas are unsatisfactory because of doubts of their taxonomic relationships, and because, although they were originally found in a discrete interval of the Vendian above the glaciogenic sediments and not in the top (=Kotlin) part, they were later found in unequivocal Early Cambrian sediments (e.g. South Australia). Some occurrences, which have been questioned, have also been recorded from Varangian/Laplandian interglacial sediments in northwest Canada (and these should now be assigned to the pre-Ediacaran?). The Ediacaran fossils can also only define broad stratigraphic bands. Recent age dating has shown that the various fossil assemblages across the globe are not strictly co-eval and distinct soft-bodied fossil-based biozones have not so far been established.

Other problems facing any attempt to obtain a finer correlation system based on these fossils are taphonomic (non or selective preservation as fossils), biogeographical (variations in the nature of populations from say, Newfoundland to South Australia), and palaeoenvironmental (difference between shallow-water and deep-water populations).

Considering the other possible bases for correlation, trace fossils, which are valuable for providing largely independent evidence of animal evolutions, can also be used to delineate a coarse zonal pattern of 3 zones in the upper Vendian and Early Cambrian (see Section 14), but this is based on siliciclastic sediments and they are not useful in this respect for carbonate sediments such as predominate in the important Siberian (Olenek) sequences. The system also needs revision, as noted in Section 14, because facies variations do not seem to have been adequately considered.

The small (“Meishucunian”) shelly fossils, which appear about the lower boundary of the Cambrian, were at one time considered to usher in the Cambrian but such fossils seem to have overlapped this boundary and they do not seem likely to provide a fine correlation basis for the Vendian; there is also a problem of lithology here, i.e. they appear to be restricted to certain lithologies and not widespread in the lithologies bearing soft-bodied fossils. Likewise, chitinous sabellidites also appear at or just below the boundary, but do not appear to offer a basis for fine correlation. Stromatolites, which are trace fossils left behind by microbial communities, have a rather coarse pattern of temporal change, although they might be of use in providing an auxiliary system of correlation.

[Knoll and Walter \(1992\)](#) concluded that there was a need for new systems capable of fine correlation and described emergent methods based on protists (vendotaenids, acritarchs) and on isotope geochemistry. Vendotaenids, problematic organic ribbons, have so far yielded a system only capable of coarse correlation in broad stratigraphic bands, the boundaries of which remain uncertain. Acritarchs, organic-walled microfossils of phytoplanktonic protists, are more promising. Acanthomorphic and other morphologically complex acritarchs are useful in correlating Phanerozoic sequences and more than 24 assemblages of complex acritarchs had been described from the Neoproterozoic by the time Knoll and Walter were writing in 1992. Several biozones can be recognised, Varanger and immediately post-Varanger acritarchs are distinctive; most species of large, morphologically complex acritarchs appeared about the time of the Ediacara radiation and the latest Proterozoic assemblages are characteristically simple and low in diversity. Several distinctive taxa appeared at the end of the Proterozoic and there was a major radiation at the beginning of the Cambrian. These microfossil assemblages appear to be capable of providing an independent framework for stratigraphic correlation even when no megafossils are present in the Neoproterozoic and Early Cambrian sequences.

[Grey \(1998\)](#) reported application of these methods to the Centralian Superbasin and Adelaide Rift Complex in Australia. Five assemblage zones and two palynofloras were recognised. The zones are identifiable despite taphonomic and palaeoenvironmental complications, and are independent of lithology, lithostratigraphy and sequence stratigraphy. Although the proposed Ediacaran stratotype in the Adelaide Rift Complex is too thermally mature for the preservation of acritarchs, this system is useful for correlation elsewhere in this region: Global extension of the scheme has not so far been possible because only a few of the species are known from elsewhere, but further research could make such extension possible in the future (this research is mentioned further in Section 17).

Secular variations in the isotopic composition of seawater have been useful in correlations of Phanerozoic sequences. C and Sr isotope ratios in carbonates and the S isotopic ratios in sulphates exhibit stratigraphically useful patterns. Despite previous doubts, it has been found that C and Sr isotope signatures in micritic carbonates and oolites bound by sedimentary carbonate cement are retained in Proterozoic rocks. Such signatures varied markedly through Neoproterozoic time,

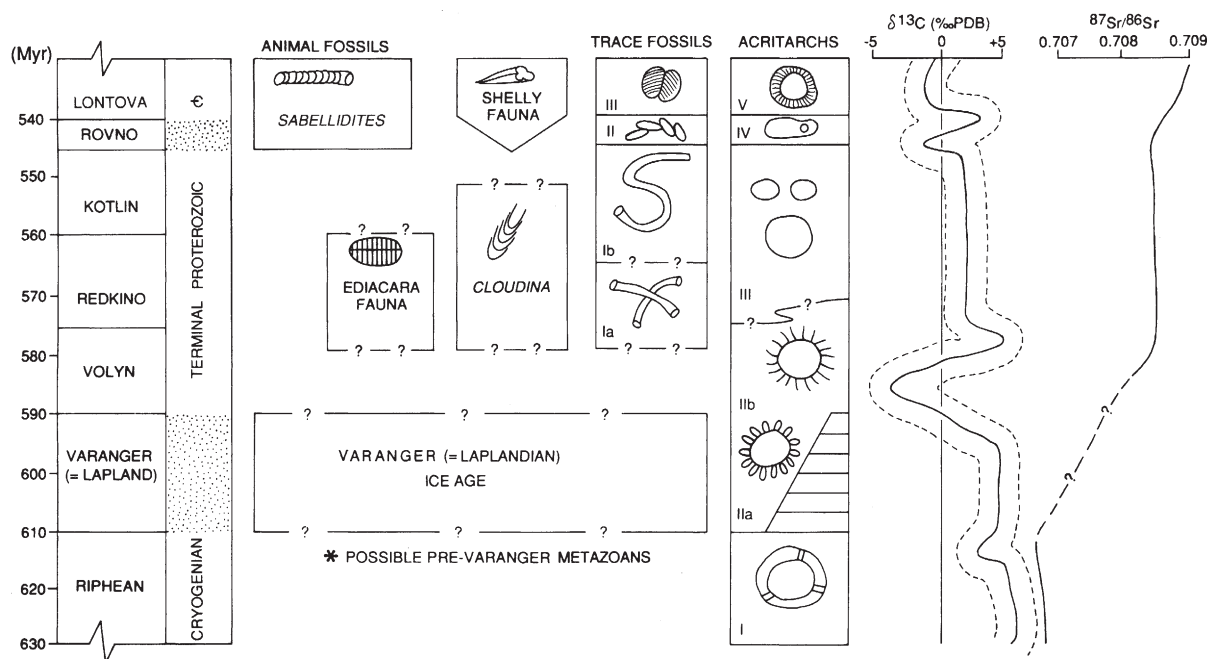


Fig. 158. Summary of the terminal Proterozoic biostratigraphy and chemostratigraphy. Showing the position of the Varanger (Laplandian) ice age. The shaded areas between periods indicate that the GSSP's had yet to be ratified by the International Union of Geological Sciences. Geochronological estimates are subject to change as data improve. The numbered vertical sequences of trace fossils and acritarchs indicate biostratigraphic zones that can be used for intercontinental correlation of sedimentary sections. C and Sr isotope curves are based on analyses of carbonate rocks (after Knoll, 2000).

providing secular patterns of strong stratigraphic potential (Fig. 158). Detailed isotopic curves have been constructed from analyses of a number of rock samples from various key sections globally, with sedimentological and petrographic control, and the results are most satisfactory.

The isotopes of carbonate and organic matter found in seawater reflect both degree of isotopic fractionation by photoautotrophs and carbon fluxes in and out of the ocean; rates of organic carbon burial exert a primary influence on these rates, with higher δC indicating greater burial. Ocean mixing can also be a significant factor. There was a plunge in the δC at the close of the basal Ediacaran (Marinoan) ice age affecting both carbonate and organic carbon. This was followed by a positive excursion with a short-lived peak and then a period of stability at a value of about +2%. Profiles in Siberia and elsewhere indicate another rapid shift to negative values followed by a strongly positive excursion just below the Cambrian lower boundary (Fig. 158).

Fewer pre-Varanger/Laplandian glaciation profiles have been examined but there are again distinctive patterns of secular variation evident in Svalbard, E. Greenland, NW Canada and Namibia. Many carbonates

in rocks ranging from 850 to 610 Ma in age contain carbon that is isotopically heavy with values of about 5% and matched by correspondingly heavy values for organic carbon. Periods with such values are punctuated by shorter intervals of low values. Although it has been suggested that these related to low sea level stands or are of diagenetic origin, several falls in value occur at or near the tops of glaciogenic horizons and are believed rather to be primary, marking changes in the world oceans.

Knoll and Walter (1992) concluded that these signals are useful for stratigraphic correlation, but that to obtain their full potential need to be coupled with other stratigraphic tools, and all such determination material needs to be assessed for possible diagenetic alteration.

Strontium isotope composition of seawater reflects relative contributions of continental erosion and hydrothermal input. The secular variation curve is shown in Fig. 158. The stratigraphic sensitivity is particularly fine close to the Varanger glaciation and the Vendian/Cambrian boundary. Sulphur isotope variation, although marked in Neoproterozoic rocks, relates to local sulphur availability and has no simple relationship to seawater composition.

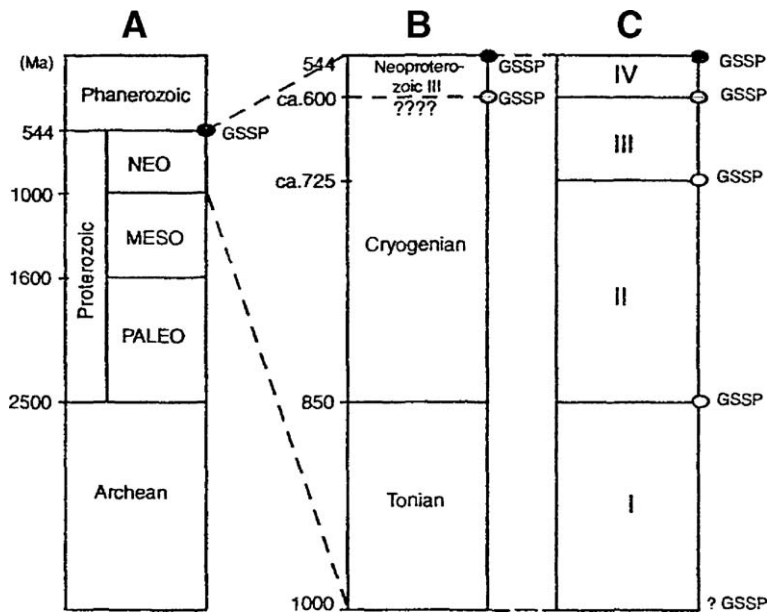


Fig. 159. The geologic time scale with emphasis on the Neoproterozoic: (A and B) the scale as it currently exists, (C) how it might look in the future. Black ovals=boundaries defined by a GSSP, grey ovals=boundaries with a GSSP currently under consideration, unfilled ovals=boundaries potentially definable by a GSSP (after Knoll, 2000).

Knoll and Walter mention sequence stratigraphy, which is related to transgression/regression and unconformities, as a possible basis for global correlations; however, although it can display synchronicity on a regional scale, not enough research has been carried out to show whether it has any potential for global correlation. There is also the complication that many important Proterozoic sequences formed in intracratonic settings in which depositional space was available only intermittently, resulting in very incomplete sequences.

15.3. Update on Neoproterozoic geochronology

Knoll (2000) noted the problem of connecting the biostratigraphically conceived and chronostratigraphically defined Phanerozoic time scale to Proterozoic scales was sphinx-like in its boundary difficulties. The Neoproterozoic Era has been divided, informally, into three Periods Vendian, Cryogenian and Tonian (Jackson, 1997: Fig. 159)—the Cryogenian is synonymous with the Sturtian period of Harland et al. (1989). The Vendian (=Ediacaran) is defined at the top by the basal Cambrian GSSP, but the GSSP at the bottom has not been chosen yet. Knoll believed that the emerging picture justified extending the chronostratigraphic time scale to embrace this interval and that the various methods (ice ages, Ediacaran fossils, acritarchs, isotopes

and an increasing number of radiometric dates) are adequate for this. Carbon isotope signals have been demonstrated to be global in nature and produce sharply defined correlations, strontium isotope methods are useful but achieve a less sharp chronostratigraphic definition. Methods based on biostratigraphy (acritachs, Ediacaran fossils) show promise of usefulness for global correlations. The terminal Proterozoic period is coming into sharp focus and it was recommended that the initial boundary GSSP be placed at the base of or within the cap carbonate that lies above the Varangian/Laplandian/Marinoan-aged tillites (see Section 17)—this has now been done (see Section 15.5). The common sharp boundaries of tillites and the lithological and geochemically distinct cap carbonates, which represent the rapid if not catastrophic end to the glaciation, are probably synchronous within thousands, not Myr.

Knoll (2000) published two chronostratigraphic diagrams, for, respectively, the Vendian and the upper part of the Cryogenian (Figs. 159 and 160). He concluded, using his analogy with depicting the sphinx, that blending the Phanerozoic with the Precambrian was best done by taking the entire Neoproterozoic, which contains a rich record of biological and environmental events, and blending it as a transition zone between the Phanerozoic and the remainder of the Precambrian which, from the mid-Mesoproterozoic era onwards, is not susceptible to sharp correlation using

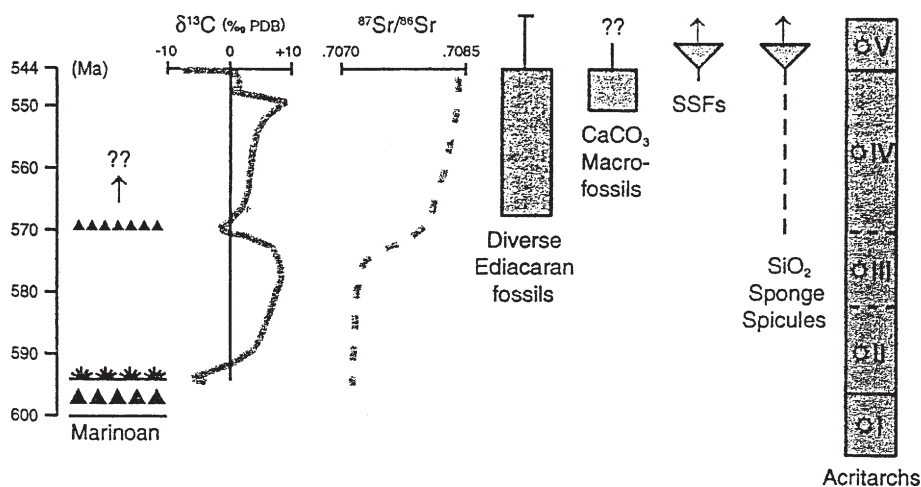


Fig. 160. Chronostratigraphy of the Ediacaran period showing the Marinoan and later minor glaciation, the carbon and strontium isotopic curves, the range of the diverse Ediacaran fossils, the range of the carbonate skeletalised macrofossils; also the range of small shelly fossils (SSFs), siliceous sponge spicules and the zones of acritarchs (after Knoll, 2000).

fossils or isotopes as tools. So far, this has not been done.

15.4. Recent advances

It is now accepted that the Ediacaran Period extended from about 600 Ma to 543 Ma (for example see McMenamin, 2005). With more age determinations on the various provinces of Ediacaran development, it has become clear that the main development of the characteristic soft-bodied fauna in the principal geographical provinces was widely different. The Newfoundland development at Mistaken Point is dated at 575–565 Ma (Clapham et al., 2004); the Ediacaran animals began to diversify in the Doushantuo Province of China at 575 Ma (Xiao, 2005); the White Sea fauna is constrained by U–Pb zircon dates of 558 and 555 Ma; the South Australian fauna appears to be contemporary with that of the White Sea at c. 555 Ma (Xiao, 2005); the Namibian fauna is probably the youngest ranging through only 6 Myr (550–543 Ma) before the Cambrian boundary and extending tenuously into the Cambrian. The Charnwood Forest fauna appears to be older than any of these: McIlroy et al. (1998) note that an age date of 603 Ma (± 2 Ma) for the South Charnwood Diorites sets a minimum for the fauna, but that this needs substantiation.

15.5. Formalisation of the Ediacaran Period

The International Commission on Stratigraphy in 2005 at Florence (see for example Brakel, 2004) defined the base of the Ediacaran Period as “the base of the

Marinoan cap carbonate/(Nuccaleena Formation) in the Enorama Creek section of the Central Flinders Range, Adelaide Rift Complex, South Australia”. Coordinates were given. The principal observed correlation events are (1) the rapid decay of Marinoan ice sheets and onset of distinct cap carbonates throughout the World; and (2) the beginning of a distinctive pattern of secular changes in carbon isotopes. This terminal Proterozoic period shall be known as the Ediacaran Period in recognition of its transcendent characteristic, the Ediacaran biota.

15.6. The Stirling Range biota

The evidence for the existence of possible discoid fossils resembling the Ediacaran fossils in the Stirling Range, Western Australia, in rocks no younger than Mesoproterozoic is mentioned in Section 19.

15.7. Conclusion

At the time of writing, the upper boundary of the Ediacaran Period, the lower boundary of the Manykayan stage of the Cambrian, is precisely determined chronostratigraphically at 543.7 Ma. However, there are some doubts about the reliability of the lithostratigraphic benchmark afforded by the GSSP in the Burin Peninsula, Newfoundland, because of doubts about the validity of the trace fossil markers there utilised. The lower boundary of the Ediacaran is defined as stated in Section 15.5—time will tell whether the definition of the base of the Ediacaran Period is really workable, in view of the controversy over the glaciation prior to the commencement of the Period (see Section 17).

Over the next decades, there will undoubtedly be new developments, particularly in indirect methods of stratigraphic correlation filling in the gaps between radiometrically derived values, and there will also be additions of more accurate “bench-marked” points in the various global key sections of the Ediacaran, utilising highly accurate methods.

16. Geotectonics

16.1. The breakup of Rodinia

Powell and Meert (2001) noted that the idea of a Mesoproterozoic supercontinent is entrenched in the literature, although configurations remain controversial. Rodinia is the most widely used name of several applied to it, the associated global ocean being named Mirovoi. Rodinia gave birth to all subsequent continents. Rodinia was formed in a series of Mesoproterozoic and early Neoproterozoic collisions (lumped together as “Grenvillian”) and broke up in the early Neoproterozoic forming a number of rifts and passive margins. There may have been a second, short-lived supercontinent, referred to as Pannotia (Powell, 1995).

The continental shelves of Rodinia have been suggested to be “the cradle of all animals” and its death “heralded the advent of modern biota” (McMenamin and McMenamin, 1990). Certainly, the Ediacara-type soft-bodied benthic fauna flourished on the widespread shallow shelf seas formed in its break up. However, two glaciations, the Sturtian and the Marinoan/Varanger/Laplandian, intervened before these organisms appeared and, according to Kirschvink (1992), the supercontinent’s death led to a series of ice-house events that, if proven to be synchronous, could represent a unique climatological period in the Earth’s history. Dinely (2000) suggested that the Grenvillian orogeny produced a supercontinent extending from about 60°N to the south polar region, but southward migration rotated the greater part of the land mass into southern latitudes, whereupon a long and very intense continental glaciation occurred: however, the evidence seems rather to suggest that two major periods of glaciation occurred, separated by c. 100 Myr, and advocates of the Snowball Earth hypothesis would extend the freeze-up to the oceans. It is also suggested (Powell and Meert, 2001) that the break up may have triggered extremely rapid continental motion or true polar wander.

A very recent reconstruction of Rodinia is illustrated in Fig. 161. In Fig. 162, the age ranges of good palaeomagnetic control for the various component

blocks of Rodinia are shown. This indicates a weakness of the palaeomagnetic control over the Sturtian and early Vendian.

A critical question is whether the two extreme glaciations of the Neoproterozoic were causally related to the break up of Rodinia. It is interesting to note that Evans et al. (2001) suggested the existence of a late Archaean–early Proterozoic supercontinent (“Kenorland”) from c. 2.7 to c. 2.2 Ga and its breakup would coincide with the three early Proterozoic glaciations (Cobalt, Quirke Lake, and Hough Lake) recorded by Harland et al. (1989). A causal relationship between supercontinent breakup and the Proterozoic glaciations would appear to be more consistent with the climatic origin suggested for the Snowball Earth model, rather than with either the Phanerozoic-plus or increased obliquity models (see Section 17).

Signor and Lipps (1992) noted that the appearance and radiation of animals had been related to the break up of a late Proterozoic supercontinent (Valentine and Moores, 1972), but the causative link between the rifting event and evolution of animals was not explicit and seemed dubious. There also remains the problem whether the appearance of the Ediacara-type animals in the form of fossils represents the actual development of the first Metazoa, or whether, as now seems more likely, there was a previous hidden evolution (the major question considered in Section 18).

The breakup of Rodinia may have had a causal relationship to the extreme Neoproterozoic glaciations and may have provided ideal conditions for the initial evolutionary diversification of animals; however, although both these connections appear to be quite likely on the available evidence, neither is established.

McMenamin (2005) published an up-to-date summary of the geotectonic setting of the Vendian world, the amalgamation of the Rodinian supercontinent composed of all the large continental elements of the planet occurring at c. 1000 Ma in the collisional Grenville Orogenic Event. At about 750 Ma, Rodinia split up by rifting, a drawn out process not completed until the beginning of the Cambrian. The succeeding supercontinent of Gondwana was amalgamated at this time. As the fragments of Rodinia went their separate ways, they set in motion the drowning of almost all the continental margins. Marine transgression initiated the Palaeozoic era. The initiation of the breakup of Rodinia was followed by at least two glaciations which were approximately synchronous globally, and these punctuated the overall transgressional regime by glaciation-related falls in sea level. The base of the Vendian is defined in many places by a cap carbonate, marking

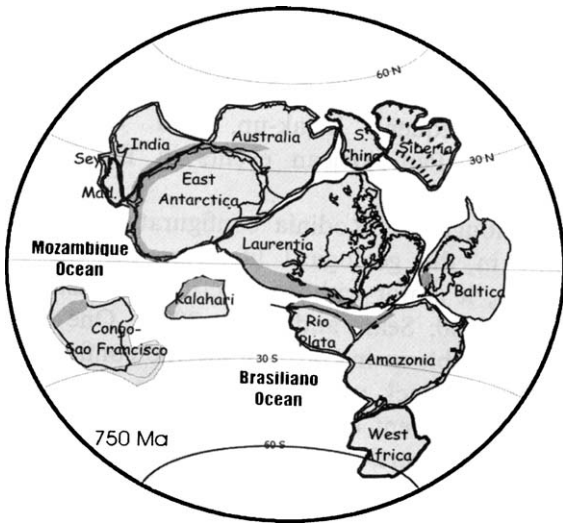


Fig. 161. The supercontinent Rodinia at 750 Ma modelled from various sources. Dark grey shading is the Grenvillian belts, aged 1300–900 Ma, within the supercontinent (after Powell and Meert, 2001).

the end of the Maranoan/Laplandian glaciation, and after this was deposited the transgression resumed, and the many Vendian sedimentary sections record this. These sections, which include the characteristic Ediacaran fossiliferous intervals, have been globally correlated by a combination of radiometric dating, lithostratigraphy, biostratigraphy and carbon/strontium isotope stratigraphy.

17. Glaciation

17.1. Introduction

Major glaciation occurred at the beginning of the Vendian period and there was a minor localised glaciation about the time of the Cambrian lower boundary. Harland et al. (1989), on their Geologic Time Scale chart, show the first as two triangles, one above the other, labelled “Mortesnes” above and “Smalfjord” below: the latter is indicated by a triangle

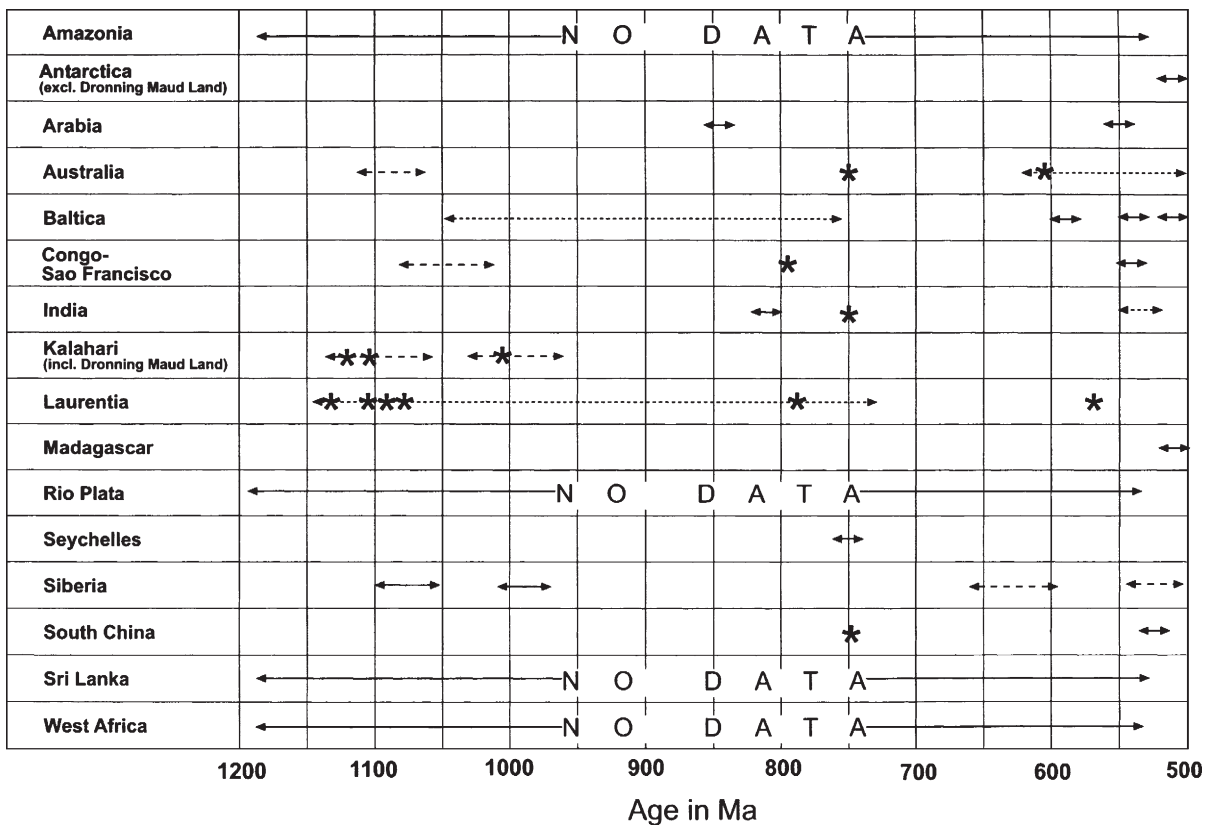


Fig. 162. Cratonic blocks of Rodinia and the age ranges of good palaeomagnetic control. Solid lines with arrows=individual poles. Fine dashed lines=time spans with nearly continuous palaeomagnetic control. Coarser dashed lines=time spans with intermittent palaeomagnetic control. Asterisks=positions of most reliable palaeopoles. Data taken from the 2000 edition of the global palaeomagnetic database or information in Precambrian Research, Volume 110 (after Powell and Meert, 2001).

labelled “?Late Sinian”. This latter apparently represents a localised glaciation known from tillites/diamictites in NW Africa and South America and referred to as the Baikunur Glaciation in Central Asia. The two earlier glaciations represent the globally widespread glaciation that heralded the Vendian and is more commonly referred to as Laplandian or Varanger (Northern Hemisphere) and Marinoan (Southern Hemisphere). This glaciation is of critical importance in this text, because it is widely considered to have commenced about 610–600 Ma and lasted about 10 or 20 Ma, and closely preceded the appearance of the Ediacara-type fauna. Harland et al. (1989) also indicated a Sturtian glaciation; this was indicated by two triangles at c. 750 and 700 Ma: the later one is labelled Sturtian, having been recognised in Australia; the earlier one is unlabelled. No further glaciations are indicated for the Proterozoic except for 3 around 2200–2300 Ma.

There does not appear to be as much detailed publication on the Sturtian glaciation as on the basal Vendian glaciation, which has been very widely recorded based on tillites/diamictites in many sequences studied in many parts of the globe. In some regions, there are two glacial stages separated by an interglacial stage, in others there is but a single stage.

Because the Ediacara-type soft-bodied faunas appeared just after this glaciation, it has frequently been considered to have a relationship to this radiation. However, word of caution here, because the sudden appearance of these fossils could be due to taphonomic, fossil preservation causes not an evolutionary radiation—they might have existed previously but not been preserved. If this was a radiation, various reasons for the outburst of life, mainly benthic, have been suggested. Glaessner (1984) suggested that the presence of wide areas of tidal waters at this time provided food for this outburst, Fedonkin (in Sokolov and Fedonkin, 1985) simply suggested that the post-glacial palaeogeography provided living space for a vast number of benthic organisms, whereas most writers on the subject in the 1990s have focused on the likelihood of an almost complete snuffing out or severe impoverishment of the pre-existing biota during a uniquely widespread and intensive glaciation. This brings us to the “Snowball Earth” concept.

17.2. The “Snowball Earth: paradigm

17.2.1. Historic origins

The initiators of this appear to have been Harland and Rudwick (1964), when they recognised “The Great Infracambrian Ice Age”, which they placed at 600 Ma

(±50 Ma) (although they did not coin the term “Snowball Earth”). They illustrated glacial striae from Norway, a tillite and the global position of tillites on the closely assembled continental masses; and pointed out that glacial deposits of this age occurred on virtually every continent. They suspected that, from palaeomagnetic evidence, the continents had clustered together, due to plate movements, near the equator. This idea was received skeptically by some scientists (according to Hoffman and Schrag, 2000), because of doubts about the reliability of the palaeomagnetic evidence, but it is now widely accepted. Doubts as to identification of glacial deposits and geochronological reliability have also been expressed.

Harland and Rudwick (1964) mentioned the Ediacara soft-bodied fauna and suggested that only a very few of the metazoans existing before the Cambrian were preserved as fossils. They also suggested that only a few of the organisms then existing were megascopic organisms. There must, they believed, have been some trigger mechanism setting off the evolutionary event represented by these fossils. The adverse conditions for life during the ice age, the change in climate after it, the drop in sea-level during the ice age also removing favourable life habitats, the return of the sea-level providing optimum conditions but with the biota now impoverished—empty environments suitable for an outburst of new life—were important factors relating the biota to the glaciation. These authors tended to lump the appearance of the soft-bodied Ediacara fauna and the Cambrian explosion in one evolutionary event, whereas scientists nowadays tend to separate in time the early soft-bodied Vendian radiation from the Cambrian explosion of skeletalised organisms, but this does not affect the validity of these pioneer arguments.

Harland and Rudwick (1964) believed that there was no better explanation of equatorial glaciation than changes in radiation from the sun.

17.2.2. Further development

In the 1960s, a Russian scientist, Michael Bodyko of Leningrad Geophysical Observatory, was researching the effect of solar radiation of atmospheric particles in studies of the effects of a “nuclear winter” and found a way to explain tropical glaciations, using equations that describe the way that solar radiation interacts with the Earth’s surface and atmosphere to control climate (Hoffman and Schrag, 2000; Fairchild, 2001). Reflectance of solar energy is increased in some geographical surfaces more than in others. This is quantified as “albedo”. Snow reflects most, seawater least and land

surfaces are intermediate in albedo (but vary with the type of vegetation or rock surface). The more reflection, the cooler the temperature. Snow and ice, in fact, stabilise their own existence, the process being known as “albedo feedback”. This effect causes polar ice sheets to grow. The feedback process can theoretically run out of control at latitudes below 30° N and S because sunlight is striking a larger surface per degree of latitude in this equatorial zone. This mechanism once triggered could cause the entire planet to freeze over. Nevertheless, Bodyko did not believe in a complete global runaway freeze in the past, for two reasons: firstly, because it would extinguish all life, yet the evidence of microscopic life in the older Proterozoic rocks showed that there was a continuum of life through Neoproterozoic glaciations. The second reason was that, there was no known means of escape from a runaway global freeze over that is a reversal.

These two objections are nowadays not valid. In the late 1970s, studies in Antarctica showed that communities of microorganisms could survive in the extreme cold and dry conditions of the Antarctic dry valleys and in dust particles within floating ice. The key to the resolution of the second objection is carbon

dioxide, which is a major gas emission from volcanoes. In normal climatic conditions, the continual build-up of this gas, which would cause a greenhouse (“hot-house”) climate, is countered by the chemical breakdown of silicate rocks during erosion, the carbon dioxide being converted to bicarbonate which is washed into the oceans, where it combines with Ca and Mg to produce carbonate sediments. Kirschvink (1992) showed that volcanoes would continue activity through a global runaway freeze over, but there would be no water to erode rocks (it would all be trapped in ice), so the carbon dioxide emitted would have nowhere to go and would build up to incredibly high levels. Thus a global “ice house” regime would inevitably be followed by a global “hot house” regime. Calculations in 1992 showed that the global freeze over would, assuming the present scale of volcanic activity globally, last for up to tens of millions of years: it would produce the longest lasting and most intense glaciation in Earth history.

The possibility of a global freeze over is enhanced by the fact that the Neoproterozoic glacial deposits are immediately overlain, for example in Namibia, by cap carbonate rocks formed in tropical conditions, consistent

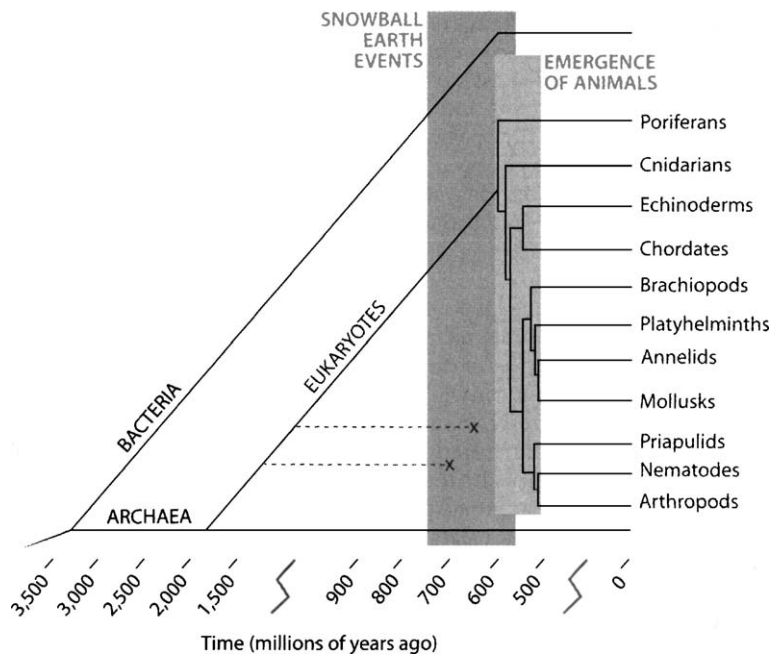


Fig. 163. According to Hoffman and Schrag (2000), “all animals descended from the first eukaryotes, cells with a membrane-bound nucleus which appeared about 2 billion years ago. By the time of the first of the hypothesised snowball Earth episodes more than 1 billion years ago, eukaryotes had not developed beyond unicellular protozoa and filamentous algae. Despite the extreme climate which may have “pruned” the eukaryote tree (dashed lines), all animal phyla ever to inhabit the Earth emerged within a narrow window of time in the aftermath of the last snowball event. The prolonged genetic isolation and selective pressure intrinsic to a snowball Earth could be responsible for the explosion of new life forms”.

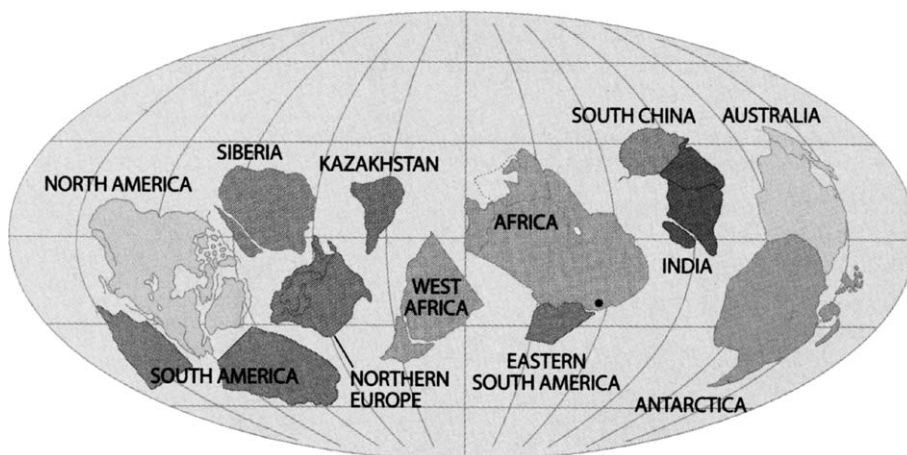


Fig. 164. Earth's landmasses were considered to be most likely clustered near the equator during the global glaciations that took place about 600 Ma ago. Configuration illustrated by Hoffman and Schrag (2000).

with a sudden culminating hot climate. The evidence suggests that the cap carbonate accumulated rapidly, perhaps in a period of thousands of years (Pierrehumbert quoted by Hoffman and Schrag, 2000). A number of processes then combine to reduce the carbon dioxide build up. The cap carbonate in Namibia has unusually low Carbon 13/Carbon 12 ratios, typical of periods of extinction in the Phanerozoic record but lasting longer. This is consistent with the expected extinction of much of the pre-existing life in a global freeze-over.

Hoffman and Schrag (2000) concluded that the "Snowball Earth" concept explained a number of extraordinary features of the Neoproterozoic geological record and that it shed light on the early evolution of life. Nevertheless, many authorities do not accept its validity or suggest that it is only partly true—for example, advocating the alternative "Slushball Earth" concept, with the globe only partly freezing over in the part in which continents were congregated. Some of these viewpoints will be briefly summarised later, but it is important to remember that, in this study, we are really concerned with the role the basal Vendian glaciation exerted in the radiation of soft-bodied organisms that occurred immediately after it.

Harland and Rudwick (1964) as early as 1964 related this great ice age to the explosion of animal life after it. Hoffman and Schrag (2000) suggest that prior to this event the most complex organisms that had been evolved were filamentous algae and unicellular protists. One (or even possibly a series of such events, if one includes the less well-known Sturtian glaciation) would have 'acted as a filter' on the evolution of life. All subsequent animal life would stem from eukaryotes surviving from the pre-glaciation(s) biota, which was

'pruned' during the glaciation(s). Repopulation after each glaciation would occur under new and rapidly changing selective pressures, quite different from prior to the glaciation(s), and a biologically emptied environment would favour emergence of new forms (Fig. 163). This proposal will be discussed again, later in this text.

These authors lastly turned to possible causes of 'these calamities' and why the world was later spared such intense glaciation. They considered a weakened sun (−6% in the Neoproterozoic): this could explain both the events and the lack of such an event in the Phanerozoic; however, if so, why no evidence in the hundreds of million years before the event (the Huronian–Sturtian record of more than 1000 Myr displays no glaciations). They preferred an explanation related to the clustering of continents in low latitudes (Fig. 164), arguing that a delayed freeze over there would have continued the burial of carbon unchecked and the "safety switch" would fail. The publication of Hoffman and Schrag has been drawn on extensively here because it is a clearly written account by the 'advocates for the Snowball Earth concept'. In the following text, a few developments of the concept and opposing views are summarised.

17.2.3. Concise summary of recent arguments

Fairchild (2001) published a concise summary of the arguments and counter-arguments. He mentioned the fact that sea ice thickness may not have been so great as to preclude transmission of light through the ice and photosynthesis by organisms in the water below. Hyde et al. (2000) alternatively suggested that there was a varying amount of ice free conditions (the "Soft

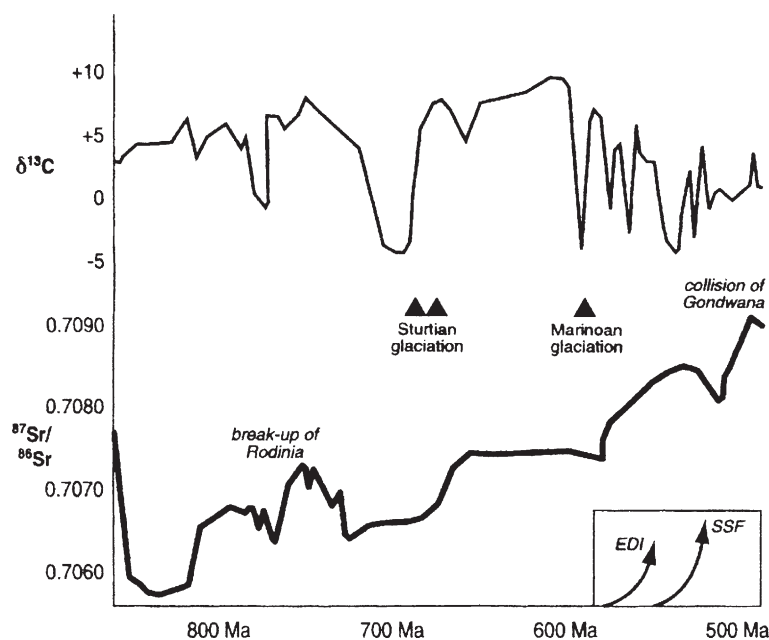


Fig. 165. Summary of Neoproterozoic marine isotope stratigraphy in relation to glaciations (after Shields, 1999). Uncertainties still remain about the correlation of the glacial units. EDI refers to the rise of the Ediacara-type organisms and SSF to the small shelly fossils (from Fairchild, 2001, reprinted with permission of Annual Reviews of Earth and Planetary Science).

Snowball” or “Slush-ball” alternative). The uneven global clustering of the continents at this time would favour such a restricted model. No consensus exists as to the number of Neoproterozoic glacial events, but Kennedy et al. (1998) suggested that it may have been overestimated—a recent synthesis of isotope chemostratigraphy (Shields, 1999) (Fig. 165) assumes that two tillite horizons in Svalbard are both Sturtian and this would appear to be to be a realistic representation. Rising strontium isotope signatures are contrary to the expectation of Hoffman et al. (1998a) that the Sturtian and Marinoan groupings can be taken to represent periods of continental fragmentation with associated carbon dioxide drawdown—tectonic factors alone are inadequate to explain the evidence of extremely rapid climatic fluctuations. There seems to be a lack of evidence of high latitude glaciation, which is a core argument of Williams since 1975 favouring his alternative hypothesis of increased solar obliquity: although the increased obliquity concept (Williams, 1975, 1993; Williams and Schmidt, 2000 really does not account for the detailed sequence of events in the glaciation and its demise. The equatorial configuration of the continents favoured by Hoffman and Schrag (2000) and Kirschvink (1992) is regarded as untenable by Karen Metz and Christopher Scotese (cited by Fairchild), but Hyde et al. (2000) concluded that this configuration was not essential to the “Snowball Earth”

concept. Some critics argue that there is too much evidence for an active hydrological cycle in the extensive erosion and deposition of sediments during the glaciation events, but Fairchild believes that there is a need for much more glaciological modelling of this event, and that most of the evidence for this comes from the waning stage.

The Snowball Earth concept has engendered a vast amount of literature, for, against and neutral. Important recent contributions, generally supportive, are those by Corsetti and Kaufman (1999), Corsetti et al. (2000), Halverson et al. (1998), Hoffman (1999a,b), Hoffman et al. (1998a,b), Hoffman and Schrag (2000), Kaufman et al. (1999), Kirschvink et al. (1999, 2000), Lyons (1999), Schrag and Hoffman (2001), Schrag et al. (1999a,b,c), Tajika (1999), Tojo et al. (1999), and Woods (1999).

Of the neutral publications, those by Evans (1997, 2000) and Evans et al. (1995) are very useful. Evans recognises three models—the Phanerozoic archetype accepting glaciated polar regions and mid-latitudes only (the “Phanerozoic plus” model); the “Snowball Earth” model and the high solar obliquity model. He believes that the first fails to account for several robust determinations of glaciations at low latitudes; also that no single palaeomagnetic determination of glaciation has been recorded poleward of 60°. If such was recognised it would be contrary to the non-uniformitarian high

obliquity model. The “Snowball Earth” model is difficult to disprove or prove based on palaeomagnetism, but more accurate geochronology of the glaciogenic strata may show a degree of diachroneity not compatible with the model. Other important publications of a neutral character are those Gaidos (1999), Runnegar (1998, 1999, 2000), Sohl (1999), Trompette (2000), Yoshioka et al. (1999).

Myrow and Kaufman (1999) described a cap carbonate from Newfoundland with a negative carbon isotope signature, such as has been explained by oceanic turnover and mixing with depleted alkaline water; by the sudden equilibration of a carbon dioxide charged atmosphere after melt-back following a Snowball Earth event; and the near cessation of primary productivity in the oceans. A relatively high palaeolatitude for Avalonia at this time may have resulted here in a shortened or delayed development of the Snowball Earth cap carbonate.

Runnegar (1999), on the sensible premise that there were two major Neoproterozoic glaciations, at c. 750 Ma and c. 600 Ma, stated that the idea that the extraordinary environmental conditions represented by the positive and negative carbon isotope excursions played an important role in the explosive evolution of animal life in the post Cryogenian Proterozoic can be tested by melding biomolecular and geochemical data with the fossil record to examine survivability under “Snowball Earth” conditions (this concept is further considered in the discussions of papers by Erwin and Grey in the succeeding texts).

Some important opposing viewpoints must first be mentioned. Meert and Van der Voo (1994) invoked new palaeomagnetic data indicating that the ice sheets in the Sturtian and Marinoan glaciations may have extended only to just poleward of 25° latitude. Climatic models invoking a juvenile Sun of slightly lower luminosity, lower carbon dioxide levels and coupling of Milankovich cycles suggest that ice sheets could then have extended to about 25° from the Equator. This is consistent with the waxing and waning at intermediate latitudes of ice sheets to form conformable sequences of warm and cold climate strata.

Condon et al. (2002) studied a number glaciogenic successions from both the Sturtian and Marinoan (Vendian) from several cratons and the indications of these studies are that there was a dynamic glacial environment, ‘rain-out’ events being recognised. The evidence is interpreted to show that the seas were not totally frozen over during these glaciations. Studies were carried out of carbon isotope values from in situ peloids, ooids and stromatolitic carbonates from Nami-

bia, North America and Australia. The pattern of the carbon cycle during deglaciation did not support complete coverage of the ocean with sea ice, nor the origin of the cap carbonates with negative excursions in a post-Snowball weathering event.

Another important publication is by Arnaud and Eyles (2001) on the Portaskaig Formation, Islay, Scottish Hebrides. Within the Formation are giant cross-bedded sandstones formed by migration of large sub-aqueous dunes on a marine shelf. Marine ice-free conditions clearly alternated with frozen sea. Large amounts of sand came in intermittently from fluvial/deltaic sources.

A publication by McMechan (2000) on the Vreeland Formation in the Rocky Mountains, British Columbia (Windermere Supergroup), also shows that the hydrological cycle was not eliminated during the glaciation, non glacial sediments being interbedded with non-glacial strata. The deep-water limestone (cap carbonate) also appears to form olistoliths here, rather than a platform overlay.

A study of heat transmissivity by McKay (2000) based on Antarctic dry-valley lakes suggests that the ice cover in tropical regions would be 10 m or less thick and there would be sufficient light transfer for photosynthesis.

Williams and Schmidt (2000) recapitulated the arguments basic to the “Snowball Earth” concept: a global freeze-up extending over the world oceans continuously for 4–30 Myr, caused by the collapse of biological activity, and virtual shut-down of the hydrological cycle, whereas iron formation and carbonates were formed as a result of prolonged volcanic outgassing with nowhere to go (extreme greenhouse). They claim that numerous geological observations in Australia and elsewhere conflict with this scenario and conclude that other explanations must be found for equatorial glaciations.

Other generally questioning publications are those by Crowley et al. (2001), Hyde et al. (2000), Kennedy et al. (1998, 2001a,b), Kerr (2000), Williams et al. (1998), Williams and Schmidt (2000), and Eyles and Januszczak (2004).

The latter authors consider that many long standing assumptions about the character and origin of the Neoproterozoic glacial record are no longer valid. In particular, they question many identifications of tillites. They advance a novel “Zipper-rift” hypothesis for the Neoproterozoic glaciations, emphasizing the strong linkage between the first order reorganization of the Earth’s surface created by diachronous rifting of the supercontinent Rodinia, the climatic effects on uplifted

rift flanks and the resulting sedimentary record in the newly formed rift basins. Many of the tillites recognised are coarse grained syn-rift strata, which initiated sedimentation in the basins—mass-flow diamictites and conglomerates. The diamictites are dominantly the product of subaqueous mass-flow and mixing of coarse and fine sediment (*mixtites*). Olistostromes are also represented. Such facies are not uniquely glacial and are produced independent of climate and latitude. Some sequences include glacial deposits, but many do not. All deposits record a functioning hydrological cycle entirely at odds with a supposed fully permafrozen planet. Many of the deposits with a definite glacial imprint indicate glaciation that was regional or hemispheric, and latitudinally constrained. The regional distribution of glaciation was influenced by tectonic factors, mantle plumes and rift-shoulder uplift. These authors doubt whether the glaciation was any more severe than the Phanerozoic glaciations and they consider the palaeomagnetic evidence for tropical glaciation to be ambiguous. A lower solar luminosity may have contributed to lower snowline elevations and glaciation in lower latitudes. Global tectonic and volcanic activity, and especially rapid burial of organic carbon in new rift basins, may explain the extreme shifts in carbon isotope values.

17.2.4. Doubts about the collapse of biological activity

Grey (2001) published an important extended abstract concerning the ability of organisms to survive the Snowball Earth, based on palynological research in South and Central Australia. This was based on 200 samples and 30 holes. The Ediacarian Leiosphere-dominated Palynoflora (ELP) gave way to the younger Ediacarian Complex Acanthomorph-dominated Palynoflora (Table 19). This biotic change was radical, being accompanied by marked increase in abundance, size and morphological complexity. Nearly 50 species and 20

genera, spiny acritarchs or acanthomorphs, appeared for the first time, a major radiation. The pre-Glacial and post-Marinoan ELP populations are almost identical, with species simple in morphology and of long range. Early Cryogenian populations (c. 850–700 Ma) are taxonomically diverse but dominated by simple leiospheres. The interval between the Sturtian and Marinoan glaciations (c. 700–600 Ma) is poorly documented palynologically. Samples immediately above the Marinoan glaciation are barren, this interval from top of cap dolomite may be 130 m (Amadeus Basin) to 440 m (Adelaide Rift Complex) thick. The first samples above the barren interval resemble Tonian and Cryogenian ones. The ELP may be found through up to 1520 m of section. Although climatic conditions were probably severe in the Marinoan glaciation and resulted in impoverishment in species diversity, there was no major change in the acritarch populations at this time; there is no evidence at all of a new rapidly diversifying taxa from a different type of ecological niche after the glaciation and no taxonomic indications of evolution from extremophiles which could survive in hot spring or ice-dominated refugia. The actual radiation from the ELP to the ECAP occurred not at the end of the glaciation but well after it and, coincidentally or otherwise, synchronously with the giant Acraman impact, which produced a 160 km diameter structure in South Australia. The Marinoan cap dolomite has an estimated age of 595 Ma, the impact 578 Ma, the Ediacaran biota climaxed at 549 Ma and the Proterozoic–Cambrian boundary is now placed at 544 Ma. The conditions predicted by the “Snowball Earth” Hypothesis cannot have precipitated the radiation which was delayed by about 20 Myr after the recovery supposedly marked by the cap carbonates, indeed on the evidence the Acraman event is more likely to have triggered the radiation. This is of course to suppose that animal evolution is likely to have mirrored plant evolution.

Relevant to the above is a publication by Erwin (1999) in which he noted that some fossil lineages persisted through the late Proterozoic glaciation—archaeal, eubacterial, simple eukaryote lineages, green and red algae, dinoflagellates. Molecular analysis suggests that these fossils and fungi and the lineage that produced the Metazoa diverged during a pre-Neoproterozoic radiation. This puts constraints on the Snowball Earth concept. He lists three “environmental insults” in the Snowball Earth model, which will have imposed selection regimes on biota and drops in biodiversity:

- (1) gradual decline in atmospheric carbon dioxide and biotic productivity on the onset of glaciation

Table 19
Proposed acritarch zones for the Centralian Superbasin and Adelaide Rift Complex (after Grey, 1998)

Palynoflora	Proposed assemblage zone
Ediacarian Complex	New genus A sp. A/ <i>Ericiasphaera</i>
Acanthomorph	sp. A/ <i>Baltisphaeridium?</i> sp. A
Palynoflora (ECAP)	<i>Tanarium irregulare</i> / New genus A sp. B/ <i>Mutifronsphaeridium pelorium</i> <i>Tanarium conoideum</i> / <i>Schizofusa</i> sp. A/ <i>Variomargosphaeridium litoschum</i> <i>Appendisphaera</i> sp. A/ <i>Alicesphaeridium medusoidum</i> / <i>Cavaspina</i> sp. A
Simple Leiosphere	<i>Leiosphaeridium jacutica</i> /
Palynoflora (SLP)	<i>Leiosphaeridium crassa</i>

- (2) sharply limited solar illumination of ocean and drop in oceanic pH with the onset of glaciation
- (3) release of volcanic carbon dioxide inducing global warming and rapid collapse of glacial conditions, marine waters changing from acidic to highly alkaline (possible transient fresh water layer), gradual return to normal marine conditions at the end of the glaciation.

With a predicted duration of the Snowball Earth condition of 4–30 Myr, harmful mutations may have made populations extinct. Modelling the minimum effective populations for survival shows that for macroscopic algae and early metazoans the size of residual effective populations would have been a greater constraint on survival than for most unicellular lineages. Environmental filters and random variations in population size may have been more important constraints on survival for these organisms.

Evans (2005) reported on palaeomagnetic studies which confirm the uniform tropical palaeolatitude of the pre-glacial Trezona Formation, Elatina Glacial Formation and Nuccaleena cap carbonate. Sporadic magnetic reversals were also recognised through sections in the Flinders Range, as in the Phanerozoic, and also synchronicity of deglaciation. There is thus support for operation of the same palaeomagnetic regimes as in the Phanerozoic (but with more rapid plate movements) and not for a geomagnetic field grossly different to today. Furthermore, the global pattern of humid/arid zones emerging for that time does not support the increased obliquity hypothesis, the main alternative to the “Snowball Earth.” These results mean that we should take the “Snowball Earth” hypothesis seriously, but they, by no means, validate it.

17.3. Conclusion

The reality of complete or partial global glaciation remains a subject of vigorous controversy. Young (1999) recognised two major glacial epochs in the Proterozoic, one at c. 2.3 Ma and one at the end (approx. 750–575 Ma). Williams (2005) has recognised a further glaciation in the Kimberleys, Western Australia at 1.8 Ma. Combination of the Sturtian and Marinoan would seem to be unrealistic in the extreme, involving as it does a 175 Ma long glaciation (compared with a feeble c. 1.5 Myr or so for the Pleistocene glaciation). Though there is a need for more precise geochronology of the Sturtian and basal-Vendian glaciation, there appears to be enough evidence now to separate the Sturtian and Marinoan (Varangian, Laplandian), although the former

and the intervening period are poorly documented. It seems to be well established that there was a uniquely intense and extensive glaciation at about 600 Ma heralding the Vendian Ediacaran, and this was closely followed by the widespread appearance in fossil form of soft-bodied Metazoa with enigmatic biological affinities. It is difficult to believe that this radiation and the glaciation are unrelated, the glaciation acting both as a filter to evolution and as a stimulant in leaving behind a biotically depopulated benthic world, with vast expanses of shallow littoral seas with empty niches. We are really only concerned with the effect on marine life, for the Vendian early animals (and plants) that we know of were all marine. The immediate post-Vendian soft-bodied animals appear to have been mostly (if not all) benthic: was what was triggered the initial spread of life to the benthos? Alternately, was there a prior development of benthic animals, of which we know little or nothing? This aspect will be further considered in Section 18.

The “Snowball Earth” model is countering very strongly founded objections, although low latitude glaciation would seem to be a real possibility at this time, and possibly with no accompanying high latitude glaciation. Geochronological control remains very weak. One must suspect that the objections to the “Snowball Earth” Model will multiply in the future. Some other explanation for low latitude glaciation may have been found.

This discussion of the Neoproterozoic glaciation is best finished by quoting that eminent Australian explorer and geologist Douglas Mawson (1949):

“It must be conceded, in view of the abundance and wide distribution of Precambrian tillites already located, that glaciations of Precambrian time were probably the most severe in Earth history; in fact the world must have experienced its greatest Ice Age”.

Even this statement concerning the basal Vendian (Ediacaran) Ice Age is not uncontroversial (see Eyles and Januszczak, 2004)!

18. Pre-Vendian life

18.1. Introduction

Hypotheses concerning the appearance of the Metazoa in the story of evolution are of two kinds (Signor and Lipps, 1992):

- (1) A long, hidden history of animals, followed by their sudden appearance in the fossil record.

- (2) The sudden appearance of animals linked to some key biological/geological/climatic/environmental event.

The same authors posed 14 questions, although some of them appear to be repetitions of the same question, stated in another manner. These questions are paraphrased below in a condensed form. Recent research suggests that the appearance of skeletons in the fossil record is a quite separate event to the appearance of the first metazoans, which were soft-bodied.

- (1) When did the Metazoa first evolve and why then (what triggered this diversification and was it an adaptive breakthrough)?
- (2) Why was there such a long delay between the appearance of the Monerans and the appearance of the Metazoa?
- (3) Is this long period illusory, the Metazoa having evolved earlier but their existence being not evident from the fossil record because of environmental factors (sedimentological, palaeoecological) or taphonomic factors (non-preservation)?
- (4) Did physical conditions in the early Earth (e.g. oxygen availability) delay the evolution of the Metazoa, and, if so, was this delay due to extrinsic causes or intrinsic (biological) causes?
- (5) Was there a change in the tempo of evolution concurrent with the evolution of the Metazoa?
- (6) Is evolution a directional or steady-state process?

Signor and Lipps (1992) then tabulated the extrinsic factors, suggested by various authorities:

- (1) Lack of sufficient oxygen to develop large and complex organisms.
- (2) Increased carbonate.
- (3) Change in ocean chemistry.
- (4) Emergence of continents.
- (5) Glaciation either causing palaeogeographic changes or changes in the trophic resource supply.
- (6) Sea level variation.

Of these changes (1) is not favoured by some recent evidence and (2) and (3) mainly relate to the emergence of skeletons, which was apparently a later event than the appearance of the Metazoa (although rare skeletalised animals such as *Cloudina* do occur synchronously with Ediacara-type organisms). Continents (4) emerged long before the Neoproterozoic, probably during the Archaean or earliest Proterozoic. (5) and (6) are both very

possible answers, but if (5) is the answer, why did the Ediacara-type fauna not appear immediately after the Sturtian glaciation in stead of the Varanger/Laplandian/Marinoan glaciation?

Intrinsic factors listed were:

- (1) Acquisition of a sedentary habit with resulting competition
- (2) Sedentary habits permitted development of large and morphologically complex organisms
- (3) Organisms invaded habits where preservation could occur at some time after initial evolutionary development.
- (4) Advent of predators/croppers.
- (5) Genetic causes.

18.2. Hidden evolution

The fossil record suggests that Metazoa appeared suddenly in the late Neoproterozoic as soft-bodied organisms, following an immensely long period of Moneran evolution. However, this picture may simply be an artifact of taphonomy and it remains possible that the Metazoa pre-existed the Vendian, of which existence there is little or no trace in the fossil record. No trace fossil of a type produced by metazoans is known prior to the Vendian (according to Signor and Lipps, 1992) and this would seem to indicate that no metazoans existed prior to the Vendian [but there is now some evidence of such trace fossils, those from the Stirling Range, Western Australia, for example, (Rasmussen et al., 2002a,b; Bengtson et al., 2002) and the Vindhyan of India (Seilacher et al., 1998)]. The precursor metazoans may have been largely planktonic or nektonic in life habit and thus left no trace fossils or they could have been very small, in which case, even if traces were left behind they may have been overlooked. If not extremely small, one would expect them to have left behind some body fossils as a record of their existence, however rarely? The suggestion of a small sized precursor meiofauna is thought to be an unlikely answer, because the Ediacara-type soft-bodied fossils include quite large and complex organisms, although the some of the earliest recorded of these, from the Twitya Formation in Northwest Canada are quite small.

The initial reason for postulating a hidden period of evolution of the Metazoa, before the basal-Vandian glaciation is that given by Fedonkin (in Sokolov and Iwanovski, 1985), that they appear to have evolved a considerable distance in time from their probable (flatworm-like?) ancestor—the ancestral Metazoa must

therefore have evolved over a considerable period. The problem here is that we simply do not know how rapidly a major diversification of this sort, from unknown eukaryotic ancestors, could be completed. It had been suggested that novel faunas of the Cambrian such as those of the Burgess Shale or Chengjiang, China, appeared very suddenly, and may have evolved very rapidly, reflecting very sudden evolutionary explosions. However, equally, these faunas may have had precursors which existed over a long period and left no trace in the fossil record. [Conway Morris \(1998\)](#) even suggests possible precursors for individual Burgess members in the Ediacara-type fauna. [Signor and Lipps \(1992\)](#) concluded that some degree of hidden evolution of Metazoan is widely accepted, but the question remaining is how long?

[Knoll \(1994\)](#) noted that the history of evolution is rooted in ongoing biological and environmental change and the Ediacara fauna did not radiate into an empty or static Earth. He also noted that during the past decade reliable records of unicellular protists and metaphytes (megascopic, morphologically complex algae) have moved backwards in time into ever earlier epochs, and, although there are reliable records of multicellularity in c. 1400 Ma rocks from Gaoyuzhuang in China ([Du et al., 1995](#)) and other records of multicellular eukaryotes about this time, the Ediacara fauna remains a fixed basement to the megascopic animal record.

[Runnegar \(1992\)](#) presented a concise account of the problems faced in unravelling the evolution of the earliest animals. The first questions he asked were: Are metazoans derived from a single kind of unicelled organisms (i.e. monophyletic)? If so was it ciliated or of another type? Or were they derived from multicellular eukaryotes such as fungi or plants? How and when did the major taxa of animals evolve?

A vast amount of historical data is stored in the genomes of different creatures, which is digital in character because proteins and nucleic acid are linear polymers of either 20 kinds of amino acids and 4 kinds of nucleotides. This stored information can be used to estimate degrees of relatedness (the recentness of common ancestry). The product is a dendrogram or tree of genealogical relationships expressed in graphic form. Another important development in molecular biology is the recognition of regulatory genes that control the formation of body segments—serial repetition of body parts is an ancient feature of animal design.

These are the techniques which led [Runnegar \(1982b\)](#) to put forward a quite different, intrinsically based argument. He applied the “molecular clock” method to the sequence of divergence of globin genes

(also collagen genes, cytochrome c and 5S RNA), to estimate the time of divergence for metazoan phyla, and obtained a range of 800–1000 Ma compared with the date of the Ediacaran radiation (at less than 600 Ma). Objections, however, have been raised to this method, in particular that the mutations involved are chronologically very irregular, and the latitude of error is very wide. [Knoll \(1994\)](#) concluded that this estimate could be reconciled with the lack of evidence of pre-Vendian fossils if the precursors were small and effectively unfossilisable. (e.g. tiny architecturally simple animals such as meiofaunal nematodes). He proposed that the physiology of megascopic animals could only be supported towards the end of the Proterozoic Eon, when massive rifting and extensional basin formation occurred of one or more supercontinent (e.g. Rodinia, Pannotia) and high rates of carbon burial associated with this event generated sufficient amounts of oxygen. He also suggested a number of ways this problem can be further researched, including a number of isotope-based methods and comparison of oxygen levels in the Jurassic. Especially important is the suggestion that improved palaeontological data might refine the “present murky picture” of pre-Ediacaran protist and metaphyte radiations, and diversification of algal seaweed. Also he noted our present lack of knowledge about the environmental conditions during the interval preceding the late Proterozoic era.

[Valentine \(2002\)](#) considered that the richness of body design in the relatively narrow slice of geological time immediately after the Cambrian explosion (including the Sirius Passet, Greenland and Chengjiang, China, faunas which, due to unusual preservation revealed details of their soft-bodied anatomy), implies a significant evolutionary prehistory. There must have been an interval between the origin of the Metazoa and Cambrian explosion which witnessed divergence and radiation of numerous lineages in which many unique body plans were assembled. The sequence of fossils that extends back c. 40 Ma before the explosion does not contain fossils that permit tracing the steps in morphological evolution that led along divergent branches to the Cambrian forms.

Valentine included a diagram illustrating the chronology of events through the Vendian and Early Cambrian as now widely accepted ([Fig. 166](#)). He recognised as the earliest metazoan fossils that are well characterised, those of the Doushantou Formation, constrained to 590–550 Ma ([Knoll, 1999](#)). These occur in phosphorites and include eggs and blastula-stage embryos ([Xiao et al., 1998](#)), probable sponge spicules ([Li et al., 1998](#)) and possible cnidarians ([Xiao et al.,](#)

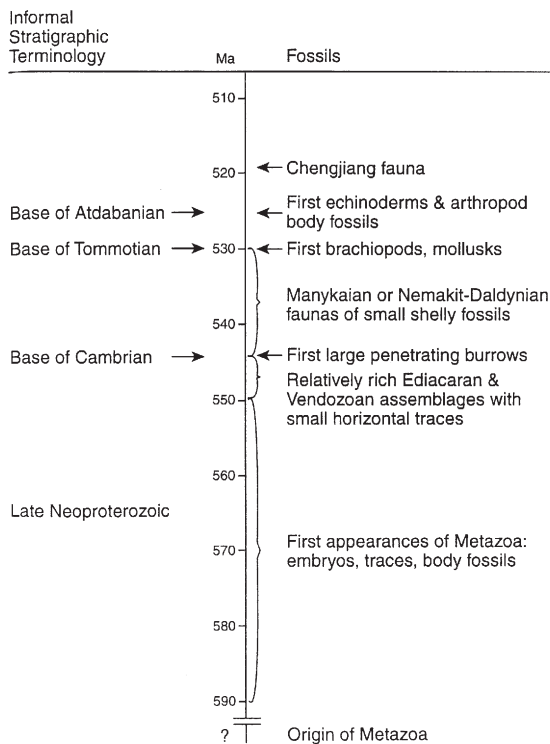


Fig. 166. The sequence of appearance of key fossils during Neoproterozoic and Early Cambrian time (after Valentine, 2002, reprinted with permission of Annual Reviews of Earth and Planetary Science).

2000). These are spectacularly illustrated by Xiao (2005). The embryos are undoubtedly metazoan. Valentine considered the Ediacara-type fossils, known from all continents but Antarctica, to be putative metazoans—only the sponges can be assigned to crown groups of phyla. Brasier et al. (1997) reported extremely convincing sponge spicules from very late Neoproterozoic rocks in Mongolia.

Valentine considered that the most likely group to have living descendants of the Ediacara-type fossils in Neoproterozoic assemblages are the shallow cone-shaped forms (“medusoids”) which may have tentacles and ?oral disks, and were most likely benthic in life habit; and may be the stem of cnidarians, possibly sea-anemone-like anthozoans. There are also possible pelagic forms. The frond-like forms and bag-shaped forms have not been shown to share features with any derived phyla. Minute mineralised skeletons (e.g. *Cloudina*) appeared towards the close of Neoproterozoic time. He published a diagram showing the earliest appearance of crown-phylum level groups (Fig. 167). He discussed the ‘molecular clock’ evidence and concluded that it has a bias towards exaggerating the

age of diversification of the Metazoa. The results obtained can range from c. 1500 Ma to 600–700 Ma. Non-clock methods are emerging but applying them to the very ancient nodes will be challenging.

Valentine (2002) noted that the ambulatory benthic animals of the Neoproterozoic were small-bodied. The fossil evidence suggests this, but larger-bodied ambulatory organisms may have escaped fossilisation or their evolution occurred in the deep sea (though these exceptions were considered to be unlikely). Metazoan evolution of the platform fauna during the ‘Prelude to the Cambrian Explosion’ was thought to be characterised by radiations and significant linear divergence of a small-bodied benthic fauna. There were no mineralised skeletons and cuticles were lacking or thin. Such organisms would only fossilise under exceptional conditions and it is not surprising there is no record of such a minute bilateria fauna. This concept appears to be well supported by the evidence, but it is difficult to use studies of later small-bodied organisms to research meiofaunal body plans, because most of these are later modifications of larger animals. It was, however, inferred that the prelude fauna was bilaterian, of small-bodied worms, some creepers and some shallowly burrowing horizontally. There may also have been some larger-bodied bilaterians? It was noted that all living Metazoa have a sponge in their ancestry (Fig. 167).

It was concluded that there was a lengthy pre-explosion history of Metazoa, but only sponges, radiates and non coelomate bilaterian grades were present during the Neoproterozoic segment. A period only of up to 47 Ma is actually recorded of this prelude by actual Metazoan fossils. The Cambrian explosion represents the culmination of an evolutionary ramp, which produced the body plan of the complex animals. The Metazoa originated from choanflagellates or their relatives at some unknown time likely to have been before 600 Ma and their appearance marked the evolution of a genome capable of production and organisation of differentiated cell types. By about 570 Ma, trace fossils appeared which suggest the presence of creeping bilaterians. Valentine (2002) believed that as many lineages of prokaryotes and protists, and presumably fungi and metazoans weathered the severity of the Neoproterozoic glaciations, in which, in his opinion, it is unlikely that the Earth was completely frozen over. Just how far metazoans reached along the trajectory of increasing complexity that culminated in the body plans of the explosion fauna and how diverse the faunas were remains uncertain. Future studies that combine geological and palaeontological

identification, but they could be egg cases or algal cysts. The phosphatic rocks included cellular tissues of possible sponges, small tubes that might be cnidarians and varied algal remains.

Xiao (2005) reported that the Doushantuo and Dengying Formations of China provide several taphonomic windows into the late Neoproterozoic biosphere. The taxa of macroscopic carbonaceous compressions can be unambiguously interpreted as multicellular algae. A few have been interpreted as sponges or cnidarians, but these are not unique interpretations and algal interpretations can neither be completely falsified. None can be interpreted as macroscopic bilaterians (bilaterally symmetrical animals). There was a diversification at this time of large acanthomorphic acritarchs, found in chert and phosphorite, but this was ephemeral, these disappearing with the appearance of the Ediacara animals at c. 575 Ma (a real event, not a preservational artifact). The phosphatic globular microfossils at Weng'an in Guizhou Province (embryos or egg cases) had geometry consistent with them being blastula, but they displayed a mixture of individual features of sponges, cnidarians and bilaterians—they may belong to stem groups at animal, eumetazoan or bilaterian levels. Other Weng'an. Microfossils had been interpreted as sponges, adult cnidarians or bilaterian gastrula.

18.5. 'Molecular clocks' and the fossil record

Seilacher et al. (1998) wrote:

“There are two seemingly contradictory views amongst zoologists and palaeontologists about the early history of the metazoans. The Cambrian Explosion scenario is based on Cambrian shelly fossils and Burgess type lagerstätten. This scenario suggests that animal phyla originated rather suddenly ~540 Myr ago (Ma) during the Proterozoic–Phanerozoic transition. This view was first modified by the discovery of Ediacaran fossils of late Proterozoic (Vendian) age in many parts of the world. Although most of these fossils are not metazoan (according to the Vendobionta hypothesis), the presence of true, but soft-bodied, triploblasts in Ediacaran biota is now documented by worm burrows, radular markings and body impressions of early mollusks, and by phosphatised embryos. These discoveries lengthened the palaeontological record of animals to ~580 Ma. The alternative “slow burn” scenario suggests that animals developed more slowly—according to some molecular analysis beginning more than 1 Byr ago.”

This was written in a paper which described more than 1 Byr old traces of a worm-like triploblastic animal.

This is not the place to argue the merits or demerits of the two alternative scenarios. Suffice it to say that the molecular clock method is well covered by Donoghue and Smith (2004). These authors state that the *raison d'être* of the molecular clock method is “the unlikelihood of fossilization of the earliest representative taxa, for which the record is perhaps unreliable...”

These authors accept that there are real problems with the molecular clock method based on genetic molecular chemistry. Graur and Martin (2004) go further, presenting a demolition job.

The evidence from the present study of the Vendian (Ediacaran) and the rather meager evidence from the earlier part of the Neoproterozoic and Mesoproterozoic suggests a longer run-in history for the soft-bodied animals extending from the Mesoproterozoic to the Cambrian boundary and there is even slender (but convincing) evidence that the Ediacara medusoid organisms (whatever their taxonomic affinities) may have had a pre-Vendian (Ediacaran) history. The “phylogenetic fuse” concept of Fortey et al. (2004)—the idea of a prolonged period of cryptic animal evolution, poorly represented by soft-bodied fossils, prior to the Cambrian explosion—seems to be equally compatible with the actual factual record.

In saying this, although the molecular clock method gives more or less the correct chronological scale for the early development of metazoans, this by no means endorses the accuracy of the method—the coincidence may be pure chance.

18.6. Conclusion

The fossil record of the pre-Vendian (pre-Ediacaran) Neoproterozoic, Mesoproterozoic and Palaeoproterozoic has been well covered by Xiao (2005). Whereas the record of pre-Vendian fossils of the characteristic Ediacaran soft-bodied assemblage is restricted to isolated minimal occurrences (e.g. Stirling Range, Kimberleys), there is a diverse record of eukaryotes way back through the Mesoproterozoic, sponges and cnidarians have been tentatively identified and algae show evidence of diversification. The evidence of trace fossils is of critical importance in this respect. Biogeochemical markers suggest that eukaryotes may range back to the earliest Proterozoic.

19. Metazoa or Vendobionta

19.1. Vendobionta

Seilacher (1984, 1985, 1989) suggested that the Ediacara fossils are fundamentally different from Palaeozoic and younger metazoans, and few, if any, can be referred to living phyla or even the animal kingdom. We were dealing with a time signature that had no counterparts in the Phanerozoic record. It was difficult to draw a boundary between body fossils and trace fossils, both in many cases being mere impressions on sandstone surfaces. Any investigator would be influenced strongly by previous experience and preconceptions. He believed that it was no longer possible to rely on homologues with living animals when attempting to interpret these enigmatic fossils. Seilacher (1985) did however accept that traces were made at this time by worm-like coelomates with a peristaltic mode of locomotion. The Vendian medusoids were, he believed, probably a mixed group, some being radial feeding burrows, some radial or concentric versions of his “Vendozoa”. If symmetry classes are disregarded, apparently very different forms can be classed together as variants of a single constructional principle: that of foliate pneu-structures whose shapes are held constant by internal quilting. These forms, which include *Dickinsonia*, have been interpreted otherwise as members of modern phyla—sea-pens, annelids, arthropods, echinoderms or as extinct phyla (Petalonamae of Pflug, 1972).

He interpreted them as extrovert benthic organisms of which the external surface was maximised for the uptake of food and possibly also light. Rather than being ancestral to modern Metazoa, the group was taken to represent an independent evolution of large organisms, which, despite low oxygen pressures, were only possible in a world that was ‘paradise’, because of the lack of predators and ubiquity of bacterial food.

19.2. Traditional interpretations

The Vendian fossils are of lower quality and quantity than those of the Cambrian and no-one can argue that they are not odd. Logical and experimental approaches are therefore necessary. The task becomes even more difficult when interpreting the spaghetti-like fossil, *Grypania spiralis* found in c. 1300 Ma rocks in Montana, China and India (Sun Weiguo, 1994) (Fig. 168). We simply do not know what sort of organism it was, nor its mode of life. Seilacher’s views are, however, contrary to the majority of workers on the Ediacara fauna, who have treated the fossils as being of precursor metazoans and

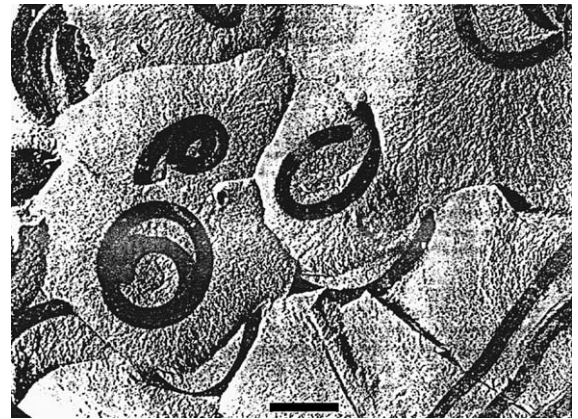


Fig. 168. The enigmatic fossil *Grypania spiralis* from the 1.4 Ga old Gaoyuzhuang Formation, upper Changcheng Group, Jixian Section, N. China. This form has been reported from 2.1 Ga old rocks in Michigan, and suggests that the history of multicellularity in life dates to very far back in geological time (scale bar=3 mm) (from Sun Weiguo, 1994).

attempted to find analogies with known later taxa. Glaessner referred most of them to modern animal groups, Pflug interpreted some as being of extinct phyla, whereas Fedonkin regarded them as descendant of older Precambrian metazoans, still unknown to us; and erected a model for the early history of the Metazoa based on symmetry-related changes in gross body form.

19.3. Approaches to the problem

Runnegar (1992) illustrated the degree of disparity in interpretation between Seilacher and the traditional interpreters by noting that *Mawsonites*, the very large ‘medusoid’ that figures in many museum collections throughout the world as a body-fossil, was interpreted by Seilacher as a trace fossil, the complex burrow of a bilateral metazoan (this idea was later abandoned according to Runnegar, 1995, but Seilacher et al., 2003 restated the possibility, suggesting a burrow of a worm-like organism with a systematic search pattern). Runnegar then attempted to eliminate this divide. Turning to trace fossils, he argued that the presence of bilaterally symmetrical animals is demonstrated by looping or spiralling surface trails up to several millimetres in width, and strings of faecal pellets, accompanying Ediacaran fauna, for example in the White Sea Region. These traces point to the existence of soft-bodied bilateria with a well-developed nervous system. There are also grazing trails, formed by animals foraging over microbial mats? Seilacher (1985) appeared to accept the

existence of coelomate Metazoa at this time (see above), but believed that the Ediacaran fossils are something different.

Runnegar observed that the core members of the Ediacara fauna are those that appear to have a quilted or mattress construction: these include *Charnia*, *Pteridinium*, *Dickinsonia* and *Phyllozoon*. These were referred by Seilacher (1989) to the ‘Vendozoa’, but it is possible that they are not animals (Bergstrom, 1989, 1990), hence the later term ‘Vendobionta’, applied by Seilacher to a new kingdom. Seilacher interpreted these as members of an extinct monophyletic clade, into which he ‘shoehorned nearly all other Ediacaran body fossils’ (Runnegar, 1992), taking all linear structures to be compartment boundaries in the quilted structure, the sites of flexible walls. Runnegar (1992) described the differences between the five genera above in some detail, and also noted the fact that Seilacher had reversed the interpretation of *Spriggina floundersi* (the most complicated Ediacaran species), turning it on its tail and planting it in the substrate-like *Charniodiscus*.

McMenamin (1986) proposed that the Ediacara-fauna may have housed unicellular photosynthetic algae, like some corals, obtaining their energy in this way. The fact that Ediacara-type fossils, including *Pteridinium* (a quilted form), have been found in deep-water settings in Newfoundland and Northwest Canada makes this unlikely. Seilacher (1989) suggested that they obtained their food by chemosymbiosis (the process utilised by the gutless tube worms of the deep-sea ‘black-smokers’). Runnegar (1992) considered this to be a possibility.

McMenamin has published a number of times on the Ediacaran occurrences (McMenamin, 1981, 1986, 1992, 1993, 1998, 2003, 2005; McMenamin and McMenamin, 1990), and coined the term “Garden of Ediacara”, which has, however been severely criticised (Lipps et al., 2000; Lipps and Fedonkin, 2002). His views, which tend to favour the Vendobiont concept, were incorporated in a book (McMenamin, 1998). His essential theme was that the Ediacara fossils represent sessile organisms which were photoautotrophic, extracting their energy directly from sunlight. He adopted Fischer’s idea of inverted medusoids acting as a receptor dish, doubted whether they were animals at all and would appear to prefer the word ‘biota’ to ‘fauna’. Photoautotrophism, has however been questioned by Crimes (1999) on the grounds that some of the biota were living either buried away from light or in water deeper than the limits of the photic zone. McMenamin questioned the evidence for some of the Ediacara organisms living in deep water, especially

the evidence of occurrence in slope turbidite deposits suggested by Narbonne and Aitken (1990) in the case of Sekwi Brook, NW Canada, occurrences, but this seems to be well-established there and in Newfoundland (Narbonne, 2004).

Very interesting, in McMenamin (1998), is the explanation of *Vermiforma* (Cloud et al., 1976) as the track of a discoid holdfast-based normally sessile organism, gliding forward, while filter feeding, and the corollary that the ovoid *Aspidella* (Gehling et al., 2000) was a “non-gliding” analogous trace. His treatment of the “frond fossils” is non-committal. He simply asks the question whether Conway Morris (1998), in suggesting a biological relationship between his reconstruction of the Burgess Shale (Cambrian) *Thaumaptilon* and *Charniodiscus*, was too much influenced by conventional Australian reconstructions of the latter. The leaf-shaped *Rangaea*, is thought to be mainly preserved in storm-deposited sandstones (Jenkins, 1985), but McMenamin noted that Seilacher believed that it lived in the sediment, and considered its fronds to be well suited to absorb sunlight. Regarding the extraordinary bag-shaped *Ernietta*, he noted that it was gregarious, and believed that it had sand infillings during life. *Dickinsonia* had been described as “a jellyfish, coral, annelid or polychaete worm, an arthropod, a bacterium, a protozoan, a member of a new phylum, and even an alien creature from outer space!”. There were difficulties in determining which end is which and whether this flexible organism exchanged gas and absorbed nutrients from the sea water through its cuticle or in another way, and there were also problems in its preservation under the crushing pressures of rock lithification. *Spriggina* and an unnamed form called a “soft-bodied trilobite” were discussed; the former previously referred to annelids and arthropods, and also considered to be an autotrophic Vendobiont frond fossil with unipolar growth by Seilacher. The supposed cephalon is possibly its rear end. The “soft trilobite” of Jenkins (1992) was considered to have unlikely structural features in a trilobite, but McMenamin admitted that *Parvancorina* from South Australia does resemble a trilobite and concluded that it and the “soft-trilobite” provide a “fascinating puzzle” He added the intriguing suggestion that the Vendobionts may have been evolving heads and brains independently of animals. He noted the ‘fragile evidence of Ediacaran sponges’ (surely not so fragile?) and mentioned the unusual forms *Corumbella*, *Inaria*, and *Akarua*, the latter said to resemble Echinoderms; however, in his view, the similarities may prove to be superficial.

McMenamin provided an entire chapter on *Clou-dina*, listing three genera. Glaessner saw them as tube-dwelling annelid worms. They are, McMenamin believed, without question the first animal-style shelly organisms to occur in the fossil record. He was doubtful about borings in Cloudinids identified by Bengtson and Yue (1992) and in any case suggested that such small borers would not have posed a threat to them. This argument with Bengtson relates to the “Garden of Ediacara” concept, one of its tenets being that large predators were rare or absent in the Precambrian.

Summarising the objections to the Vendozoa interpretation, and the erection of a new kingdom of ‘Vendobionta’ (Seilacher, 1992), Runnegar (1995) noted that the Vendobionts were considered to be “immobile, megascopic, compartmentalised, acellular creatures filled with a mass of naked protoplasm formed by fusion of amoeboid bodies without fusion of their nuclei (‘plasmodial fluid’). How they obtained their energy was the subject of a number of suggestions. It was not stated where they fitted into the tree of life. He concluded that the morphological similarities of *Char-niodiscus*, *Charnia* and *Thaumaptilon* (a Middle Cambrian Burgess Shale fossil) (Conway Morris, 1998) to the living pennatulacean *Virgularia presbytes* were sufficient to challenge the Vendobiont scenario, but not to falsify it. However, his arguments based on cellularity, symmetry, growth and complexity of Ediacaran organisms, make the Vendobionta scenario more difficult to accept. The more realistic alternative is that Ediacaran “fauna” is a sample of the Neoproterozoic biosphere: which contained sponges, cnidarians, bilaterians, a possible echinoderm and various problematical metaphytes (?*Phyllozoon*, ?*Ernietta*, ?*Pteridinium*), as well as trace fossils and worm tubes. The “fauna” is merely a sample of Neoproterozoic diversity. It may be added that it is a sample which can be considered in no way necessarily representative because of filtering by preservational constraints.

Conway Morris (1998) put forward arguments against the ‘Vendobionta’ as an independent kingdom. In citing the similarity between *Thaumaptilon* and the frond-like Ediacaran fossils, he maintained that the latter were Cnidarians, as probably were many other Ediacara-type organisms. Sponges were more primitive than the Cnidarians and they had now been recognised (Gehling and Rigby, 1986) (unequivocal sponge spicules had also been described by Brasier et al., 1997). Chemical biomarkers diagnostic of this phylum had also been recognised (McCaffery et al., 1994). The more advanced forms with well-developed anterior ends (cephalisa-

tion), bilateral symmetry and in some genera transverse segmentation, were likely to have given rise to the bulk of the Cambrian forms. Although their exact taxonomic position remains questionable, these forms were clearly on the route leading to arthropods and annelids.

19.4. The case for Ediacaran fossil roots to the Metazoan Tree

Gehling (1991) suggested that attempts by Seilacher (1984, 1985, 1989) and Fedonkin (1985a) to invent structural bases for unifying all Ediacaran taxa represent general emotional embarrassment because these organisms do not appear to conform to the notional ancestors of prominent Cambrian taxa (small slug-like ancestors predicted by Bergstrom, 1989, 1990). He suggested that the actual Precambrian organisms (multicellular with large, specialised body forms) require as much onus to be placed on revising these phylogenetic models as revising the phylogenetic assignment of the earlier organisms known from fossils.

Gehling published a table listing the generalisations concerning the Ediacara fauna (Table 20) and a list of popular misconceptions (Table 21): a critical review reveals a heterogeneous array of organisms in size and shape and there has been too much description of them without reference to taphonomic processes. Different preservational aspects of the same taxon can be recognised, enabling three-dimensional restoration (Narbonne and Hofmann, 1987; Gehling, 1988). The flattened form, taken by Seilacher (1984, 1989) to be diagnostic, is in many cases secondary; the original shape being conical or hemispherical. The flattened form of *Dickinsonia* is illusory; some small forms are hemispherical, whereas larger forms are flattened. The two ends are differentiated in many specimens. Gigantism is confined to three groups: some discoids, Dickinsonids and frondose forms, rare forms being up to a metre scale, but the greatest number of Ediacara organisms are much smaller. Transportation before burial, favoured by Jenkins (1989a,b), is not borne out by recent sedimentological studies. Many of the imputed medusoids are more likely to have been benthic polyps, where one side is always preserved as a convex cast of the pedal surface (Fedonkin, 1985b; Jenkins, 1989a,b). It is difficult to consider annulate forms (*Ovatoscutum*, *Chondroplon*) as anything but chambered, float-bearing organisms. True pelagic organisms should be randomly oriented on the substrate, but, except for *Dickinsonia costata*, no free-living Ediacara taxa have been shown, convincingly, to have both dorsal and ventral surfaces exposed.

Table 20

Alternative classifications for some of the core members of the Ediacara fauna (crosses in brackets indicate extinct higher taxa) (after Gehling, 1991)

Australians	M. A. Fedonkin	A. Seilacher
Coelenterata	Coelenterata	Coelenterata
Hydrozoa	Cyclozoa(†)	Psammocorallia(†)
<i>Ovatoscutum</i>	<i>Ovatoscutum</i>	<i>Beltanelliformis</i>
Scyphozoa	<i>Beltanelliformis</i>	
<i>Ediacaria</i>	<i>Ediacaria</i>	Trace Fossil
<i>Mawsonites</i>	<i>Mawsonites</i>	<i>Mawsonites</i>
Anthozoa	Trilobozoa(†)	
<i>Charnia</i>	<i>Albumares</i>	
<i>Charniodiscus</i>	<i>Tribrachidium</i>	
<i>Rangea</i>		
Petalonamae(†)	Petalonamae(†)	Vendozoa(†)
	<i>Charnia</i>	<i>Charnia</i>
	<i>Charniodiscus</i>	<i>Charniodiscus</i>
<i>Pteridinium</i>	<i>Pteridinium</i>	<i>Pteridinium</i>
<i>Phyllozoon</i>	<i>Phyllozoon</i>	<i>Phyllozoon</i>
	<i>Rangea</i>	<i>Rangea</i>
Annelida	Proarticulata(†)	<i>Ovatoscutum</i>
<i>Dickinsonia</i>	<i>Dickinsonia</i>	<i>Dickinsonia</i>
<i>Spriggina</i>	<i>Praecambridium</i>	<i>Spriggina</i>
Arthropoda	Arthropoda	<i>Albumares</i>
<i>Praecambridium</i>	<i>Spriggina</i>	<i>Tribrachidium</i>
Incertae Sedis		
<i>Albumares</i>		
<i>Tribrachidium</i>		

Gehling believed that Seilacher (1984, 1989) had chosen the simpler approach by considering these organisms as an evolutionary dead-end, a failed experiment, avoiding the need for phylogenetic comparison and sidestepping the real issues that arise in taxonomy and taphonomy. Gehling tabulated the elements of Seilacher's new "Vendozoa" paradigm

Table 21

Misleading preconceptions about the structure and ecology evident in recent questioning of the phyletic affinities of the Ediacaran taxa: set alongside new interpretations suggested on the basis of new collections and re-examination of depositional setting of organisms (from Gehling, 1991)

Existing preconceptions	Interpretations in this ^a paper
Gigantic compared with Cambrian faunas	Small taxa make up a large part of the assemblage
Two-dimensional disc, foliate or ribbon forms	Restored form most often conical, hemispherical or tabular
Dominated by medusoids pelagic cnidarians	Most organisms benthic-sessile and vagile forms
Transported assemblage	Life assemblage with few pelagic taxa
Trace fossils unrelated to body fossils	Small bilateral organisms as potential trace makers
Only macroscopic animals	Simple frond-like forms may be macrophytes

^a Gehling's.

Table 22

Elements of Seilacher's Vendozoa paradigm (from Gehling, 1991)

1. Development based on a number of fractal growth patterns.
2. Achieving structural rigidity by use of tubular elements.
3. Being devoid of functional locomotional appendages, internal digestive organs and concentrated sensory organs (thus not functional animals).
4. Having no clear evidence of musculature.
5. Being pseudo-segmented bilateral organisms (with asymmetrical halves).
6. Encasement in a tough but flexible cuticle.

(Table 22). Seilacher interpreted many of the organisms with radial and concentric patterns as trace fossils of a cryptic, soft-bodied metazoan fauna.

The Vendozoan paradigm, Gehling believed, provides no clear answer to the biological problems that all palaeontologists must address. If Vendozoan organisms possessed no musculature or digestive system, then the following functions remain problematic:

Nutrition: if there was no mouth or digestive system, photoautotrophism or some chemical system would be necessary. A large surface area to volume ratio would also be required.

Mobility: vulnerability to some form of blanketing by silt would be a problem for immobile forms with no attachment. *Dickinsonia* reached such a size that a habit of life supine on the soft substrate appears unlikely.

Epidermis: a cuticular integument would limit permeability required for metabolic activity.

Gehling found *Dickinsonia* not to be so simply constructed as Seilacher supposed, the dorsal and ventral surfaces being different. The segments on the supposed ventral surface extend across the body with no interruption by a midline and the ends are differentiated, the segments decreasing in size towards one end, where segments are added (Wade, 1972b). The anterior segments are fused at the proximal ends of the mid-line. There is evidence of musculature contraction of some segments at the time of burial, quite distinct from post-burial shrinkage. The evidence that it possessed muscles strongly indicates a metazoan grade organism, and there is evidence in some specimens of a worm-like creeping habit. There is evidence that the mid-line is a narrow gut and that *Dickinsonia* was a coelomate grade organism, and able to react to sensory input. Seilacher suggested autotrophic feeding, but this is not adopted by modern organisms which augment their feeding with the aid of microbial symbionts.

Referring to the ‘pseudosegmentation’; of some Ediacaran organisms, favoured by Fedonkin (1985a)—alternation of segments on either side of the median line—the ventral side of *Dickinsonia* does not show this, so it is deduced that, where it is seen on the dorsal side, it is a product of flattening. In rare sections of *Dickinsonia elongata*, the displacement is admittedly difficult to explain.

Gehling considered that *Ovatoscutum*, *Chondroplon*, *Phyllozoon* and *Pteridinium* are more likely

candidates for the Vendozoa. It appears to be unlikely that the last two genera represent organisms with the same degree of organisation as the other frond-like forms, and a possible relationship to the metaphytic algae should be considered. There was no relationship between size of segments, annuli and branches to overall body size of a given taxon, contrary to Seilacher’s requirement that the tabular compartments should be of the same order of cross-sectional size.

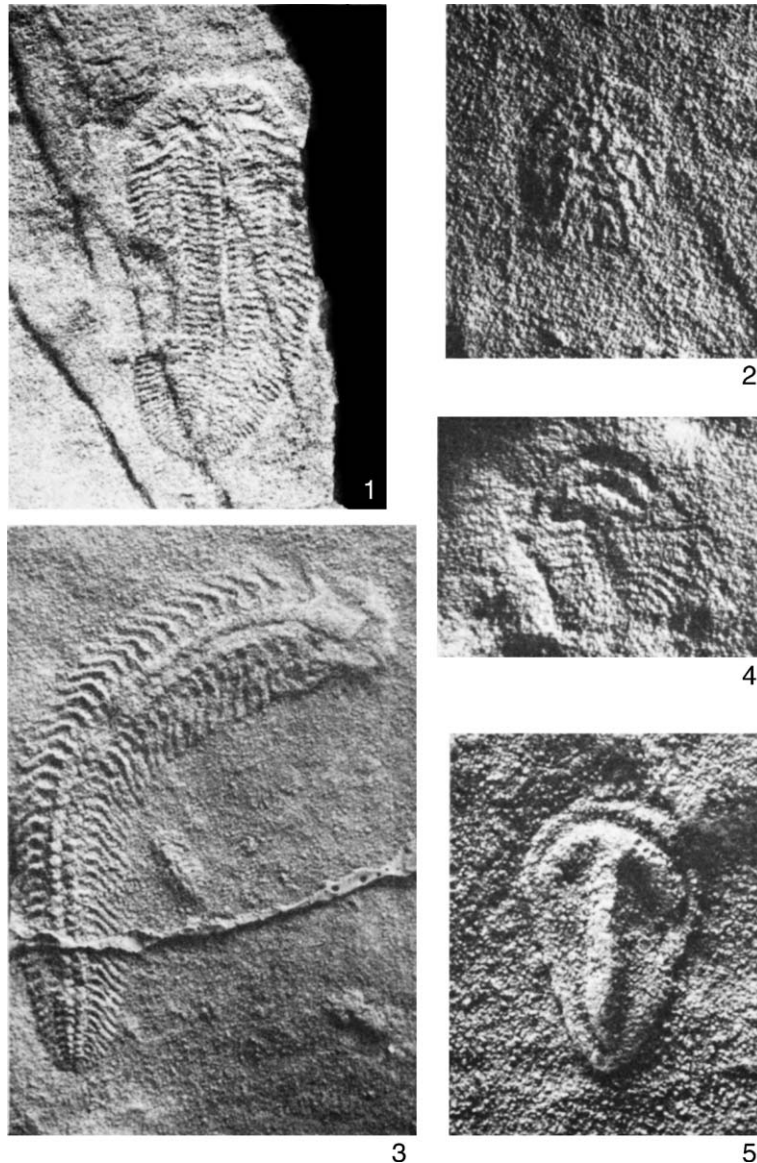


Fig. 169. Five examples of fossil organisms that do not fit into the Vendozoa paradigm and are considered to be vagile metazoa (from Gehling, 1991). (1) *Marywadea*, natural external mould ($\times 1.6$). (2) *Praecambrium sigillum*, rubber cast of natural external mould ($\times 4.5$). (3) *Spriggina flouderesi*, rubber cast of natural external mould ($\times 2$). (4) Metameric organism, rubber cast of natural external mould ($\times 3$). (5) *Parvancorina minchami*, rubber cast of natural external mould ($\times 4.5$).

In many Ediacaran organisms, the structures recorded cannot be reconstructed as ‘quilted’—*Cyclomedusa*, *Parvancorina* and *Spriggina* have external morphologies that can in no way be related to the structural elements of *Charnia*, *Phyllozoon*, and *Ovatoscutum*. Only with a very broad brush could all Ediacaran organisms be represented as fractal growth variations based on the same units of construction.

Gehling concluded that the ‘promorphological’ method of Fedonkin (1983a,b, 1984, 1985a, 1986) is too dependent on 2-D body plan analysis and largely disregards the 3-D architecture, palaeontology and ontogeny. Characteristics like ‘irregular segmentation’ recognised by Fedonkin (1985a) have been assumed to be real, but may be due to secondary deformation. Gehling quotes Clark (1979):

“hypothetical animals must have been real animals in a real world”.

He also noted that Glaessner (1984) warned of the danger of constructing hypothetical animals without explaining their functional anatomy, and interpreted the taxonomic diversification of the cnidarians as the product of a long, cryptic history of evolution, whereas Fedonkin regarded the various forms of radial symmetry as indicative of rapid experimentation that culminated in forms with 3- and 4-fold symmetry.

Gehling then mentioned three groups of Ediacara-type organisms:

Attached and benthic organisms: the similarity of the frond-like organisms such as *Charniodictis* to pennatulids may be due to true evolutionary conservation or convergence, but comparison with this group is preferable to comparison with marine macrophytes.

Metameric organisms: in this group are included *Spriggina*, *Marywadea*, *Praecambridium* and *Parvancorina* (Gehling might also have mentioned the White Sea forms such as *Vendia*, *Vendomia* and *Onega*). Seilacher (1989) turned these on their heads, and viewed them as small fronds with holdfasts. Gehling considers that to reconstruct small segmented Ediacaran taxa as other than vagile metazoans requires an appeal to the absurd. Though some descriptions of orifices and internal organs on these fossils may be treated with skepticism, some impressions do provide unequivocal evidence of internal organs. *Spriggina* has been found associated with minute versions, identical with the adults except in number of segments, so *Praecambridium*

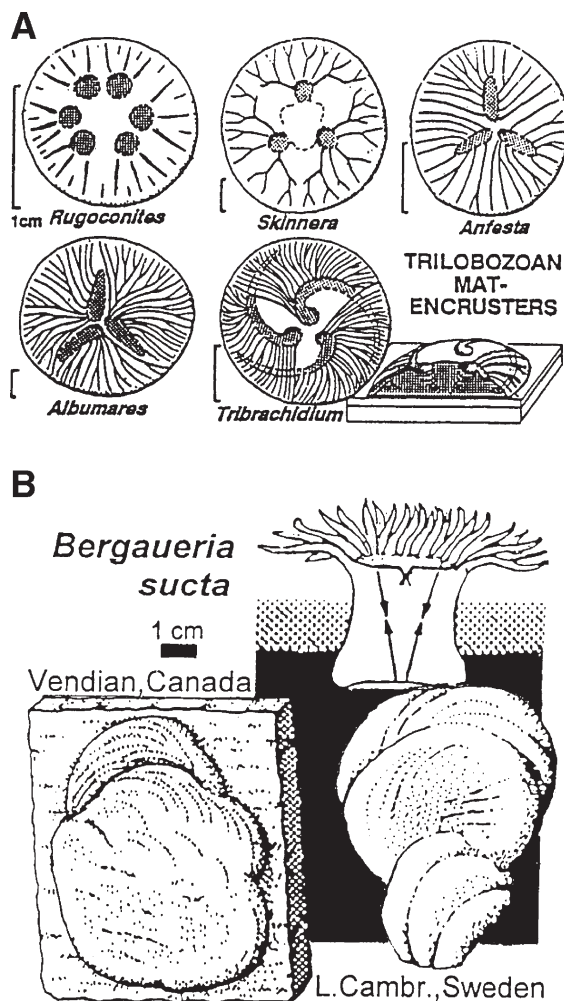


Fig. 170. (A) The shield shape of Trilobozoa reflects the mat-encrusting life style, the finer canals being for inhalation and the wider ones for exhalation, as in sponges (after Seilacher et al., 2003). (B) Assumed resting traces of *Bergaueria* show the round body outline and its active lateral displacement (after Seilacher et al., 2003).

cannot be its larval stage (as suggested by Birket-Smith, 1981b); likewise small juvenile (?) specimens have been found associated with *Dickinsonia*. *Spriggina* was interpreted as an arthropod by Birket-Smith, but as a polychaete worm by Glaessner (1984). A new metameric form with greater external resemblance to a trilobite than any other Ediacaran soft-bodied fossil was under investigation at the time Gehling was writing (Fig. 169). This is, presumably, the ‘soft-bodied trilobite’ mentioned by Jenkins (1992) and which impressed McMenemy (1998). *Parvancorina*, which Glaessner (1979a) interpreted as an arthropod, is now known to have had a convex profile, not flat shield-shape. Gehling concluded that animals with heads

and that are segmented are almost certainly annelids or arthropods.

Radial and concentric forms: Gehling found no evidence to support the interpretation of some of these as trace fossils, pedal disc impressions or radial burrows (Seilacher, 1990). It was difficult to interpret the tentacle-bearing forms as anything but sedentary, bottom-dwelling polyps of cnidarian grade. A number of the forms with this geometry may have affinities with sponges.

Contrary to many expressed views, Gehling considered that the scale of many feeding traces of Vendian age is consistent with the size of a number of Ediacaran animal taxa and that the patterns are consistent with the evidence of sensory organs in the metameric forms: thus they might be the actual traces of metameric forms found as fossils. Paired hypichnial ridges are consistent with an origin as arthropod feeding scratches.

Regarding the unusual preservation of fossils in sandstones, Gehling attributed to the effect of microbial mats, which allow preservation of ‘death masks’.

He concluded that *Parvancorina* and *Arkarua* are closely related to arthropods and echinoderms respectively. Other small Ediacaran organisms must be considered as members of shell-less lineages which survived into the Phanerozoic. Molluscs should not be overlooked in making comparisons with Ediacaran organisms: *Conomedusites* appears to have direct Palaeozoic descendants in the Conulata. Recognition of ancestral groups among the Ediacaran fauna must be disproved before the mass extinction proposed by Seilacher (1984) is accepted. Autotrophism, as proposed by McMenamin and McMenamin (1990) should not, in itself, be an argument against relationships with existing phyla. The symbiotic method of obtaining food is quite common among deep-sea worms and bivalves, corals, sedentary jellyfish, anemones, flatworms and nudibranchs. The Vendozoan paradigm is not, in his view, appropriate for the majority of Ediacaran organisms. Using the “widely branching tree” metaphor for metazoan evolution, the Ediacaran fauna provides our only glimpse below the Precambrian–Cambrian boundary, of the roots of the metazoan tree.

19.5. The latest words on the Vendobionta

Seilacher et al. (2003) presented a restatement of the Vendobionta paradigm. The reinterpretation of the seemingly complex trace fossils and assumed metazoan body fossils from Vendian lagerstätten was led by functional, constructional and preservational crite-

ria. In the new scenario, the Ediacaran biota were dominated by prokaryote biomats and giant Protozoa (Xenophyophoria and Vendobionta), which developed a variety of shapes and lifestyles in the “golden age” that followed the ‘Snowball Earth’. It was now accepted that contemporary metazoans (sponges, polyps, soft-bodied mollusks, possible echinoderms, and worm-like burrowers) were adapted to this non-uniformitarian environment, although scarce and relatively small. Some phyla (arthropods, brachiopods) appear to have been absent). This peaceful “Garden of Ediacara” was terminated by the Cambrian explosion, the formerly dominant taxa becoming extinct or restricted to less favourable environments. A new and more dangerous world for animals was then initiated, and it persists to the present day.

These authors illustrated the morphology of the Trilobozoa forms which they believed were adapted to the life style of mat encrusters, their canal pattern for inhalation and exhalation resembling the irrigation system of sponges. They also illustrated the active lateral displacement of *Bergaueria* (Fig. 170). They believed that there was evidence from the White Sea region that *Kimberella* was a mollusk (a “soft limpet”). They interpreted *Spriggina*, *Parvancorina*, *Mialsema*, *Vendomia* and *Vendia* as bilateral Vendobionts that grew by the serial addition of new quilts, citing the lack of appendages and absence of arthropod trackways from the Vendian (such trackways they say do not require a hard skeleton and would be easy to recognise). They are doubtful about *Arkarua*, the only echinoderm tentatively recognised among the Ediacaran fauna. They illustrated *Aulozoon* traversing *Dickinsonia* and *Phyllozoon* on a slab from South Australia; and considered *Cloudina* and *Namacalathus* probably to be Protozoa. The last part of their statement covered the requirements for unicellular giantism, a description of Xenophyophoria (obscure abyssal marine rhizopodian protists) and Vendobionta.

Wagoner (2003) presented the opposing viewpoint. The Ediacaran organisms, which preceded and overlapped the Cambrian radiation of metazoans, include many fossils which, despite 50 yrs of study, are obscure as to their systematic positions. Despite this, analysis of their distribution in time and space is useful. Study of palaeoecology, palaeoenvironments and age relations reveal three major clusters, the Avalon (Newfoundland) being the oldest, the Russian White Sea the next, and the Nama extending into the base of the Cambrian. The frond-like taxa, and the medusoids to a lesser extent, show longer stratigraphic ranges, broader geographical and palaeoenvironmental ranges, and less provinciality

than the bilaterians and tubular taxa, which tend to be combined to areas that were equatorial—the other taxa show weak or no latitudinal diversity gradients. Waggoner concluded that the Ediacara organisms reveal a diverse range of responses to environmental parameters. He finds no basis for classifying them as having a single body plan or mode of life, as has been done in the past.

Valentine (2004) took a similar viewpoint. He believed that a few of the Ediacara taxa may be bilaterians. *Spriggina* has a jointed construction and cephalic shield. *Parvancorina* resembles the probable stem arthropod fossil for the Early Cambrian arthropods. The slug-like *Kimberella* may well be a mollusk (Fedonkin and Waggoner, 1997) and the borings in *Cloudina* have been attributed to a mollusk (Hua Hong et al., 2003). Valentine also considered the trace fossil evidence. The latest Neoproterozoic shows little evidence of bioturbation, a lack of mixing by animal activity—this gives a greater chance of trace and body fossil preservation. Some traces do penetrate the sediment but penetration burrows are short, small and rare. In the Manakayan, there is an increase in diversity, mixing and penetration, body size and biological activity. The latest Neoproterozoic traces are generally conceded to represent the activity of bilaterians, chiefly worms. Diploblastic animals likely contributed, also.

Parker (2003) accepted the ‘soft trilobite’ as a ‘proto-trilobite’, a grazer which fed on algal mats and probably dead animal matter on the seafloor. He envisaged these organisms as peaceful grazers (though they may have preyed on each other), yet were the forerunners of the voracious predators of the Cambrian. However, the anonymous reviewer of this present work noted:

“if there is a Vendian soft trilobite, then phylogenetic analysis shows where the trilobites appear in the arthropod phylogeny and there *has* to be an earlier history of the group to account for branching patterns. In turn there has to be an earlier history to account for the common ancestry of the proto-stome phyla. This means that the argument is not completely rehearsed.”

Lipps and Fedonkin (2002) argued against the two suggested trophic processes for the Ediacara-type organisms—uptake of dissolved organic material or algal symbiosis. They considered that there was no evidence to support photoendosymbiosis or utilisation of dissolved organic materials. In their opinion, these organisms

included herbivores, detritivores and suspension feeders. The ‘peaceful garden’ metaphor was incorrect—the environment was neither peaceful nor a garden—and predation was widespread.

19.6. Conclusion

Conway Morris (1998) suggested that the emergence of the Vendozoa hypothesis as an alternative to the traditional approaches had reduced research activity on Ediacaran fauna. Fortunately, the present library-based study shows no evidence of this. The lucid account of Gehling (1991) does suggest that the quite different traditional approaches of Glaessner, Jenkins, Gehling and Fedonkin should not be dismissed lightly, in favour of the novel approaches of Seilacher and McMenamin, and both Waggoner and Valentine endorsed this viewpoint. During this study, the author has read the works of Glaessner and Fedonkin, exhaustively, and, although there is a different approach to Glaessner in the emphasis on symmetry by Fedonkin, both would seem to have accepted a prior history of metazoan life (whatever the duration), and both drew comparisons with known later taxa. Whereas, Seilacher’s approach conflicts with these approaches, he does accept, like them, that there was metazoan life in the Vendian. While it appears to be quite possible that Vendobionta may



Fig. 171. Images of *Cyclomedusa davidi* displaying twinning of the polyps, suggested of asexual reproduction by fission ($\times 0.7$) (from Gehling, 1991).

have existed alongside early metazoans, there is appears to be no need for a comprehensive shoe-horning. The reversal of metameric forms to depict attached frond-like forms appears to be questionable. If the similarity of the metameric forms, especially the ‘soft trilobite’ and *Parvancorina* to trilobites in design is coincidental, it is a remarkable example of convergence.

One point omitted by Gehling (1991) and perhaps underscored in the literature, is that there is evidence of apparent asexual multiplication by fission in some specimens of ‘medusoids’ (for example, Fig. 171). This appears to be a highly anomalous feature, if it occurred in early metazoans.

20. Summing up

20.1. Introduction

The term “Vendian” has in 2004 been substituted by the term “Ediacaran”, this being the last *period* of the Proterozoic and extending from ~600 to 543 Ma. This review, which was initiated purely out of interest—the author having been triggered by seeing some excellent specimens of Ediacaran fossils in the Western Australian Museum during a visit in 2001, and having known both Reg Sprigg and Martin Glaessner while at the University of Western Australia from 1960–1970—constitutes a review of

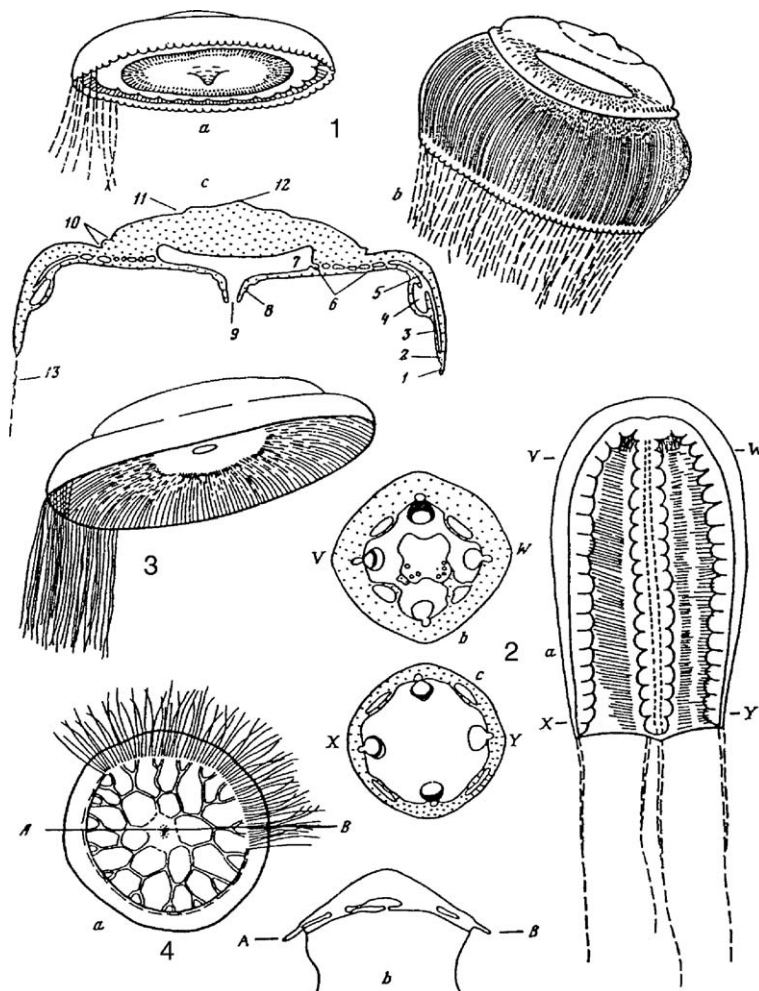


Fig. 172. Some typical medusae of the Ediacaran biota according to Wade's (1972a) interpretation. (1) a, b, c *Brachina delicata* Wade, three views. (2) a, b, c *Kimberella quadrata* Glaessner and Wade, three views. (3) *Ediacara flindersi* Sprigg. (4) a, b *Rugoconites enigmaticus* Glaessner and Wade, two views. Modern interpretations tend to favour sessile polyp modes of life for most of the ‘medusoids’, the jellyfish-like mode of life illustrated here being only favoured for a few forms (after Fedonkin, 1985a).

the literature published in the six decades since Sprigg's discovery.

The record in the rocks from the beginning of the period to the beginning of the Cambrian is truly extraordinary. In no more than a span of ~60 Myr or less, life apparently developed from the initial but global colonisation of the marine benthos by a fauna of megascopic soft-bodied marine creatures (some of them at least primitive Metazoa) to a much more diverse, highly organised and abundant population of skeletalised marine metazoans during the Cambrian. The Ediacaran radiation was quite separate to the Cambrian explosion of skeletalised animals. The fauna, is cosmopolitan, spread over the globe. Suggestions have been made that it represents a taphonomic window and is unrepresentative; certainly, it is the product of remarkable preservation of soft-bodied fossils, not fully explained, and such preservation became almost impossible once burrowing organisms went deep enough to cause wholesale bioturbation of the host sediments—although a few fossils have been found in Cambrian sediments.

This terminal period of the Precambrian, once obscure in its life details, is now becoming quite well delineated, and thus of great interest; both intrinsically and as a platform from which to launch future studies of the record of life both covering the Ediacaran and also in the earlier Proterozoic periods of the Geological record (the Cryogenian and Tonian of the Neoproterozoic and the Mesoproterozoic), at present very sketchily known from algae, acritarchs, obscure worm-like fossils and microorganisms; and also, importantly, reported trace fossils. The Ediacaran Period is of critical importance to Geoscientists at the present time, in trying to obtain more knowledge of the evolutionary gap between the earliest eukaryotes and the highly organised metazoans of the Cambrian radiation, and also their forerunners.

The period reveals a much richer fossil record than our geological predecessors realized—the unusual form of fossilisation in sandstones rather than the usual Phanerozoic fossilized rock types may be the cause of delayed fossil discovery—provides a fertile source of information concerning the early history of development of life forms on the planet during the latest Neoproterozoic. It is now certain that soft-bodied metazoans existed through the Ediacaran and prior to it, although some or even the majority of the taxa may not be metazoans. Besides the soft-bodied fauna, there is also evidence from the Ediacaran in a number of regions of the globe of cloudinids, with incipient mineralised

skeletons, apparently the forerunners of the skeletalised Cambrian organisms. Their taxonomic affiliations also remain obscure, but it is apparent from recent discoveries in Uruguay, Namibia, China and Oman, that the cloudinid fauna was to a degree already diversified by this time and even included an agglutinated form—a (?) forerunner of the agglutinated foraminifera. The recent discovery of *Namapoikia* establishes a pre-Cambrian development of colonial skeletalised forms in reefal assemblages with stromatolites and thrombolites. In Oman, such an assemblage alternates uniquely with evaporitic deposits, due to repeated uplift, and it hosts hydrocarbons. A few small shelly fossils similar to the Meishucunian fauna also appeared in the late Ediacaran, forming a distinctive precursor fauna.

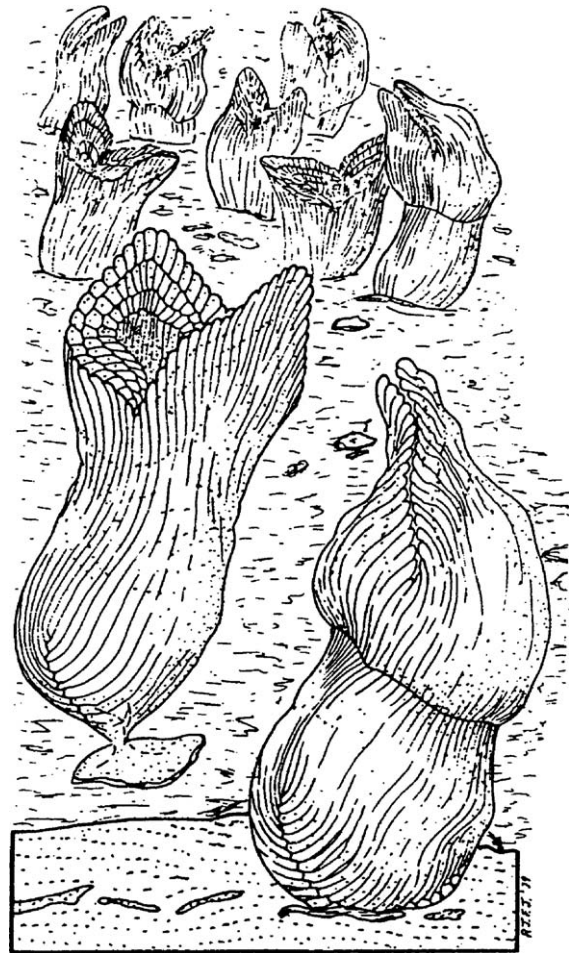


Fig. 173. Reconstruction of *Ernietta* showing the sessile, benthic mode of life now widely favoured for most Ediacara-type medusoids and pennatulids (after Jenkins, 1992).

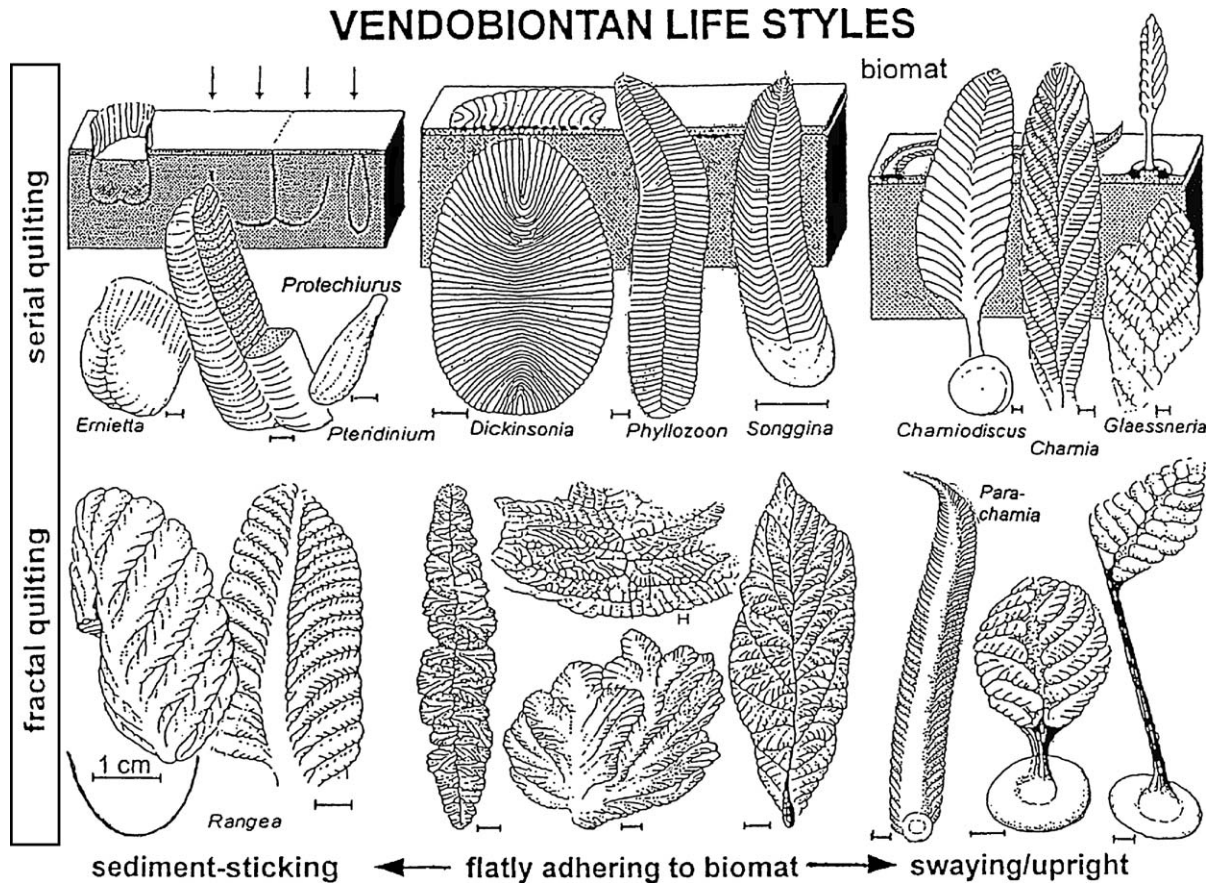


Fig. 174. "Vendobiontan lifestyles" (after Seilacher et al., 2003).

20.2. Key questions

Three key questions are:

- (1) What were the Ediacara-type organisms?
- (2) Was there a hidden pre-Ediacaran evolution of the Metazoa?
- (3) Do these organisms tell us anything new about evolution?

20.2.1. What were the Ediacaran organisms?

The fauna seems to be three-fold in character: medusoids, frond-like organisms and metameric organisms. It is now widely accepted that the Ediacara fauna represents a diverse assemblage of megascopic, soft-bodied marine organisms of latest Neoproterozoic age, including impressions of discoidal and pennate organisms, which have been tentatively assigned to the Phyla Arthropoda, Cnidaria, Annelida, Porifera. The image of jellyfish floating, like fairy lamps, with their tentacles suspended, as delightfully portrayed in the illustration due to Mary Wade (Fig. 172), has not been sustained by

the evidence since accruing and the benthic mode of life, well illustrated by Jenkins for *Ernietta* (Fig. 173) and Seilacher et al. (2003) (Fig. 174), is characteristic of these organisms, although there were very likely some planktonic/nektonic forms.

The phyletic affinities of the Ediacaran organism remains controversial despite the now general acceptance that some metazoans are represented, although possibly only as a minority. The alternative to the traditional interpretations of Glaessner and Wade, and later Jenkins and Gehling, is stated by Seilacher et al. (2003); and also by Steiner and Reitner (2001), who reported evidence of organic structures in Ediacara-type fossils and microbial mats; and endorsed the conclusions of Seilacher and Bengtson that some at least of the Ediacara soft-bodied fossils were prokaryotes and that the ancient wrinkled structures were microbial mats. They concluded that, despite some morphological and structural evidences supporting this attribution, the Charniidae were not pennatulaceans (Fig. 175). They considered that part of the Ediacaran colonies were colonial prokaryotes or symbiotic organisms involving



Robert Bolland

Fig. 175. A living sea-pen (pennatulid), a filter feeder which can if attacked by a predator expel water from its body and sink into the sand (reproduced from Gosliner et al., 1996).

prokaryotes, but also considered the possibility that the Charniidae might be a stem group of poriferans.

Waggoner and Collins (2004) noted that there had been many referrals of the Ediacara fossils to Cnidarians. Representatives of living groups had been identified as preserved in a number of Ediacara fossil species, but although some were plausible, others had problems. These authors had tested these identifications by means of extensive molecular phylogeny studies based in extant species, calibrating divergence dates across the cnidaria. This method, assuming the existence of Cnidarians within the Ediacaran biota, produced a value for the root of two of three groups of the Cnidarians, Penatulacea and Scyphozoa, of between 800 and 1000 Ma, figures not out of place with previous molecular clock estimates. For the Chondrophorines, figures between 1500 and 2000 Ma were obtained—considered to be most unlikely. The conclusion reached by these authors was that the Pennatulacea and Scyphozoa were represented amongst the Ediacaran organisms, but that the Chondrophorines had been mis-identified.

Waggoner (2001) had earlier recognised layers in stromatolitic material from the Johnnie Formation, Inyo County, California (not finely dated, but correlated in time with the Doushantuo Formation of China): these included microbial pseudomorphs and acid resistant material provisionally identified, by analogy with certain

trace fossils, as faecal pellets of an unknown micro-metazoan with a complete gut. McMenamin (2003) also strengthened the case for metazoans among the Ediacara body fossils, by recognising homologies between the spines and cephalic region of *Spriggina* (sometime referred to as an annelid, as an arthropod and as a frondose Vendobiont) and those of fallotaspid and paradoxid trilobites—so endorsing Birket-Smith's previous identification. Yet another support for the existence among the Ediacaran body fossils of metazoans comes from the recognition by Lin-Jih-Pai (2003) of a *Parvancorina*-like arthropod in the middle Cambrian Kaili biota of Guizhou Province, China.

The occurrence of medusae and other types of Ediacaran taxa in deep water environments in Canada has been frequently quoted against the prokaryote assignment (the Vendobionta hypothesis) and the illustration of *Dickinsonia* (a strong candidate for the Vendobionta), accompanied by what is surely its larva (Fig. 50), is possibly another inconsistency. McMenamin (2005) argued against the biomat/deathmask explanation for the preservation of Ediacaran fossils based on a slab showing *Charnia* superimposed on a spindle-shaped fossil, in a specimen from Mistaken Point, Newfoundland.

Although metazoans are thus now widely accepted as living during the Ediacaran period, it is not likely that many of the latest Neoproterozoic trace fossils are due to the Ediacaran biota.

Retallack (1994) suggested that the Ediacara fossils were of lichens, but this appears to be unlikely.

It is surprising that, after almost six decades have passed since the Ediacara discovery, so much uncertainty still exists concerning the phyletic assignments, or even the extreme possibilities, that the majority are giant protozoa or an evolutionary dead end group with no descendents among Phanerozoic organisms. However, the reality would seem to be that we must await better fossil evidence or some new indirect methodology. It is possible that the biogeochemical markers now being exhaustively studied (see Eglinton and Pancost, 2004), although mainly at present applied to microorganisms, might be used to resolve the problem of definite identification of the phyletic relationships of the Ediacaran organisms, now preserved as fossils.

20.2.2. Was there a hidden pre-Ediacaran evolution of Ediacara-type organisms or metazoans?

This has been covered in Section 18. The evidence from trace fossils seems to indicate that metazoans or at least worm-like organisms existed even as far back as the Mesoproterozoic (Seilacher et al., 1998). There is

also evidence, albeit slender, from Western Australia (Stirling Range, Kimberleys), that Ediacara-type medusoids developed prior to the Ediacaran Period.

20.2.3. Do the Ediacara fossils tell us anything new about evolution?

The uncertainty about phyletic affinities does at present limit the value of these organisms in contributing to the ongoing development of evolutionary science, yet the evidence from them does favour a long precursor history of animals prior to the Cambrian explosion (the “Phyletic Fuse” concept: [Fortey et al., 2004](#)) and not a sudden appearance of them at that time. There is also evidence that the stem taxa to skeletalised metazoans may well have been soft-bodied and that the ancestors of skeletalised predators like trilobites may have been soft-bodied, peaceful grazers ([Parker, 2003](#)).

Another contribution is surely what they tell us about likely environmental influences on the tempo of evolution. The global radiation of the Ediacaran organisms occurred just after the break up of Rodinia and the Maranoan/Laplandian/Varanger glaciation, and surely this was not coincidental. These events must have made available copious habitats for these organisms to occupy throughout the globe. The Ediacaran organisms were extremely sensitive to environmental conditions on a local scale as is shown by the recent studies of [Droser et al. \(2003\)](#) and [Grazhdankin \(2004\)](#), and the same is true on the scale of geographical provinces ([Waggoner, 2002](#)). The story of the Ediacaran would seem to endorse the view expressed in the following quotation, which the author found by chance in a book about the mammoth:

“The evolutionary history of organisms cannot be reduced to a study of evolutionary mechanisms at the cellular level. It has its own tempos and modes; and it raises other questions, other parameters and other forms of causality” ([Cohen, 2002](#)).

The Ediacaran world was a simpler world than our present world in terms of life. Besides the facts that plant life was restricted to algae (there were no trees or other plant vegetation as we know it today) and the bare continents, if occupied by life at all, were probably at the most only habitats of algae and microbes; this world experienced the first great radiation, the first invasion by megascopic animals (or proto-animals) of the marine benthos in the extensive littorals made available by the breakup of Rodinia and the glaciation. It seems that in this early, simpler world, evolutionary pressures operated along-

side largely inanimate geological developments of the planet, which imposed environmental constraints on it (albeit there were also constraints imposed by life itself, for example the onset of predation). Evolution was constrained in both its nature and tempo by the limitations of the habitats available for occupation at any one time. It was surely never a smooth tempo process controlled solely by the intrinsic forces of molecular genetics. The picture of Ediacaran life surely favours punctuated evolution. The global radiation of Ediacara fauna occurred because the evolutionary time was ripe and because the geological development of the marine realm was favourable. The subsequent course of evolution was surely to some extent decided by this radiation (although some of the Ediacaran lineages may have been blind alleys).

One can make a similar assumption for the later Cambrian explosion of skeletalised organisms, which had its forerunners in the late Ediacaran, but the exact reason for this second radiation remains conjectural.

Another lesson that we get from the Ediacaran picture is that Nature (=evolution) then, as now, had no favourites. Even at this early date, it evolved new genera and species, but at the same time was already evolving organisms that destroyed them (for example, that ate them and bored into them).

20.3. An Ediacaran GSSP

A Global Stratigraphic Section and Point has been established at the base of the Nuccaleena Formation, above the Elatina Formation, Enorma Creek, Flinders Range National Park ([Gehling and Cooper, 2005](#)).

20.4. The future

A review of this sort is useful on different levels. It is in part a historical document, in part a database. It will be useful in encouraging future research, including research in provinces in which latest Neoproterozoic sequences are developed with body fossils or trace fossils, but which call for more rigorous and detailed research. There are still reports coming in of new finds—for example *Thectardis* by [Clapham et al. \(2004\)](#) in Newfoundland; *Vendoconularia* (a conularid-like fossil) by [Ivantsov and Fedonkin \(2002\)](#) from the Onega River; and *Yorgia*, a new Dickinsonid, by [Ivantsov \(1999\)](#) from the White Sea (Winter Coast). These are from well-trodden provinces, but there is surely much potential in the less well-trodden areas for new and important

finds. China is an obvious example, but other provinces such as the Vindhyan of Central India [where there are thick sections of little metamorphosed Proterozoic rocks and a new discovery has been made by De (2003)]; Uruguay (Gaucher and Sprechmann, 1999), which must surely be the other half of the Namibian developments, separated by Atlantic opening; and the Puncoviscana Province of northwest Argentina [where Buatois and Mangano (2003) have re-evaluated the ichnofauna].

Surely, we are by no means at the end of exciting new finds from the Ediacaran rock sequences so liberally spread out throughout the world.

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