

https://dspace.org/

The importance of Nama Group sediments and fossils to the debate about animal origins

Brain, C. K.

1997
Bernard Price Institute for Palaeontological Research
http://hdl.handle.net/10539/16418
None

Downloaded from a DSpace repository. https://dspace.org/

Palaeont. afr., **34**, 1-13 (1997)

THE IMPORTANCE OF NAMA GROUP SEDIMENTS AND FOSSILS TO THE DEBATE ABOUT ANIMAL ORIGINS

by

C. K. Brain

Transvaal Museum, P. O. Box 413, Pretoria 0001, South Africa

ABSTRACT

The purpose of this review is to draw attention to the contribution that Nama sediments and fossils have made, and potentially can make, to the ongoing debate about metazoan origins. Two important features of this debate concern the nature and systematic position of the late Proterozoic "Ediacaran" fauna as well as the reasons for the sudden appearance in the fossil record of representatives of almost all known animal phyla, during the Early-Middle Cambrian radiation. An additional vexing question is the reason for the apparent absence of preserved representatives of ancestral metazoan lineages in Proterozoic sediments, despite the fact that molecular evidence shows that such lineages had a long history, prior to Cambrian times. Nama fossils and their enclosing sediments have made crucial contributions to this debate and will surely continue to do so in the future.

KEYWORDS: Proterozoic, Metazoan origins, Nama Group, Ediacaran fauna.

INTRODUCTION

Between 1908 and 1914, in the early days of German South West Africa as it was then called, the geologists, P. Range, H. Schneiderhöhn and H. Von Staff found impressions of soft-bodied organisms in Nama quartzites on the farms Plateau, Aar and Kuibis, east of Aus, in southern Namibia. These came to the attention of the German palaeontologist G. Gürich, who discussed them at the 15th International Geological Congress, held in Pretoria in 1929 (Gürich 1930). Subsequently he published descriptions of the following five fossil organisms new to science at that time (Gürich 1933): *Rangea schneiderhöhni, Rangea* (?) *brevior, Pteridinium simplex, Orthogonium parallelum* and a medusoid-like impression, *Paramedusium africanum.* The last specimen came from a locality much further to the east, near Ariamsvlei, where S.H. Haughton had found, during geological mapping of the area in 1927, tubular impressions in quartzite that he interpreted as being archaeocyathids (Haughton 1962). Apart from an extensive review of South West African fossils by Richter (1955), little further attention was given to Nama palaeontology until Hans Pflug (1966, 1970a, b, 1972a, b) collected and described large numbers of soft-bodied fossil impressions from the original localities of Plateau and Aar. Gerard J. B. Germs also undertook a major stratigraphic and palaeontological investigation of the Lower Nama Group in southern Namibia, with fieldwork being done between 1967 and 1970, as a doctoral project at the University of Capetown (Germs 1972c). Results of this investigation, which will be discussed shortly, did a great deal to re-kindle interest in the Nama basin as a source of information central to the interpretation of animal origins.

In the interim, during 1946, an Australian geologist, R. C. Sprigg, was examining an old lead mine in the Ediacara Hills north of Adelaide, South Australia, when he came upon impressions of soft-bodied organisms in the Late Proterozoic Pound Quartzite there. The following year he described some of these impressions (Sprigg 1947) as "among the oldest direct records of animal life in the world", observing that "they all appear to lack hard parts and to represent animals of very varied affinities". Since then, a wide variety of taxa based on body-fossil impressions, has been described from the Flinders Ranges of the Adelaide geosyncline (eg. Gehling 1991, Runnegar & Fedonkin 1992) and the term "Ediacaran" was proposed by Jenkins (1981) as the terminal Precambrian subdivision. Subsequently, Cloud and Glaessner (1982) introduced an enlarged concept of "Ediacarian", to embrace the time period from the end of the Upper Proterozoic glacials till the end of the time period of the soft-bodied fossil assemblages. The Ediacaran stratotype occurs in the South Australian Flinders Ranges and the Ediacaran time period corresponds to the proposed Vendian Period (Sokolov & Fedonkin 1984) based on sequences on the Russian Platform.

Assemblages of impressions of soft-bodied organisms, similar to those from Namibia and South Australia have since been found in various parts of the world, though it seems somewhat ironic that these should be referred to as the *Ediacaran* fauna in view of the fact that the first examples were discovered in Namibia, rather than South Australia. But as my Australian friend and colleague,

Malcolm Walter, remarked to me "What matters is not who finds something for the first time, but rather who *does* something with it!". It is true that the Australians have made more of their Proterozoic fossils than have the southern Africans, though this situation is now being corrected.

FEATURES OF THE CURRENT DEBATE ON METAZOAN ORIGINS

The abrupt appearance of fossilised representatives of virtually all extant animal phyla in sediments of early Mid-Cambrian times has commonly been called the Cambrian radiation of animal life. But this event was preceeded by an earlier radiation (Conway Morris 1993), in Late Proterozoic times, of soft-bodied organisms comprising the Ediacaran fauna. As mentioned earlier, the first examples of this fauna came from Namibia, followed by specimens from South Australia. Since then, Ediacaran fossils have come to light in various parts of the world: Morocco in the Adoudou Series in Antiatlas (Houzay 1979); Charnwood Forest, near Leister, England (eg. Ford 1958); South Wales (Cope 1977); County Wexford, Ireland (eg. Palmer 1996); Norway (Kulling 1972); Sardinia (Debrenne & Naud 1981); Finnmark (Farmer *et al* 1991); the White Sea region of Russia (Keller & Fedonkin 1977, Fedonkin 1992); Siberia (eg. Sokolov 1975, Fedonkin 1990); China (eg Xing & Liu 1979); Northwestern Canada (Hofmann, *et al.* 1990); Newfoundland (Anderson & Misra 1968; Anderson & Conway Morris 1982) and Sonora, Mexico (McMenamin 1996).

Ideas as to the affiliation of Ediacaran organisms

There is probably no other group of fossil organisms that has generated such a diversity of opinion, concerning their affinities, as has the Ediacaran fauna. There has been reasonable agreement as to the coelenterate affinities of the medusoid organisms that left impressions in the late Proterozoic sediments, although Seilacher (1992) expressed the opinion that these organisms were very different from the contemporary jellyfish that they superficially resemble. He coined the term Psammocarallia, or sand-corals and wrote (p.611): "In the new interpretation, these fossils are regarded as internal sand skeletons of coelenterates comparable to actinians. They were built of sand grains that entered the gastric cavity and then became phagocytized and deposited in place of a mesogloea between ecto and endoderm".

In an earlier paper (Seilacher 1989) proposed the informal taxon Vendozoa to accommodate remaining elements of the Ediacaran fauna. He believed that all these showed "a unique, quilted type of biological construction that had no counterpart in the modern, or even the Phanerozoic biosphere". In 1992 he went one step further, and reassigned the Vendozoa to a new Kingdom, the Vendobionta, which he defined as follows (p. 607):

"Immobile foliate organisms of diverse geometries that were only a few millimetres thick, but reached several decimetres in size. A shared characteristic is the serial or fractal quilting of the flexible body wall, which stabilized shape, maximized external surface and compartmentalized the living content. Since no organs can be recognised, this content is thought to have been a plasmodial fluid rather than multicellular tissue. Included are the Petalonamae (Pflug 1972b) and a variety of forms previously interpreted as soft-bodied ancestors of metazoan phyla. *Range*: Vendian. Claimed Cambrian survivors seem to show different preservational properties."

In a later development of this concept, Buss and Seilacher (1994) put up the hypothesis that the Vendobionta should be regarded as a phylum, constituting a monophyletic sister group of the Eumetazoa. They speculate that the Vendobionta are cnidarian-like organisms that lacked stinging cells or cnidae and that cnidarians arose later through acquistion of cnidae by symbiosis with microsporidians. In this view, Ediacaran fossils are not thought to have been ancestors of living cnidarians.

The resistant quilted construction of many Ediacaran organisms has also recently impressed Retallack (1994). He suggests that the resistance to compaction shown by these quilted organisms is similar to that of woody fossils preserved in sandstones and has made a case that the Ediacaran organisms were, in fact, lichens. He concludes that "the diversity of Ediacaran body plans can be compared with the variety of form in fungi, algae and lichens". As might have been suspected, the proposal has elicited a good deal of critical comment (eg. Waggoner 1995).

In the course of his studies of quilted organisms from the Nama sandstones in Southern Namibia, Pflug (1972a) concluded that most Ediacaran fossils should be accommodated in a new phylum, the Petalonamae, "distinguished by a characteristic feathered surface structure" (p. 134).

As early as 1971, Glaessner argued for the incorporation of the various components of the Ediacaran fauna in existing phyla. This proposal has been accepted by various subsequent workers, with some modifications. For instance, in their review of Proterozoic metazoan body fossils, Runnegar and Fedonkin (1992) assign all known forms to the following phyla: Petalonamae, Trilobozoa (as proposed by Fedonkin, 1985), Cnidaria, "Vermes" (including molluscs and extinct phyla), Arthropoda, Echinodermata and *itncertae sedis*. To this list, a new Phylum, Tribrachidia, has been proposed by Jenkins (1992) to accommodate *Tribrachidium* from the Flinders Ranges.

As an example of the extreme divergence of views as to the affiliations of Ediacaran organisms, the case of *Dickinsonia* can be cited. First described by Sprigg in 1947, *Dickinsonia* was a flat, quilted organism, oval in outline, with prominent ribs radiating from a partial midline. The largest specimens appear to have been about one metre in length (Jenkins 1992). Taxonomic affiliations suggested thus far are as follows:

KINGDOM ANIMALIA	
Phylum **Cnidaria**,	
Class Dipleurozoa	(Harrington & Moore 1955)
Class Actinozoa	(Valentine 1992)
Phylum **Platyhelminthes**	(Termier & Termier 1968, Fedonkin, 1981)
Phylum **Annelida**	(Wade 1972, Runnegar, 1982(c), Glaessner 1984, Jenkins 1992)
Phylum **Petalonomae**	(Pflug 1972(b), Runnegar & Fedonkin 1992)
Phylum **Vendobionta**	(Buss & Seilacher 1994)
KINGDOM VENDOBIONTA	(Seilacher 1992)
KINGDOMS PLANTAE/FUNGI,	Lichens (Retallack 1994)

While most workers on the Ediacaran fauna have considered the organisms involved to have been heterotrophs, McMenamin (1986, 1987), with his concept of "The Garden of Ediacara" visualised them as green photoautotrophs and subsequently as osmotrophs as well (McMenamin 1993).

Questions about the Cambrian radiation

There is no doubt that the early to middle Cambrian Period was a time when a large variety of organisms made their first appearance in the fossil record; there is debate, nevertheless, as to whether their first fossil appearances marked the actual start of their lineages – a discussion that has been underway since the time of Darwin's *Origin of Species*. Following the radiation of Ediacaran organisms during the late Proterozoic, there was a lull in the appearance of new metazoans in the fossil record, followed by a build up of the "small shelly faunas" (eg. Matthews & Missarzhevsky 1975; Bengtson *et al.* 1990), including the very numerous sponge-like archaeocyathids (eg. Debrenne 1992). The fossil residues of early Cambrian limestones are often dominated by calcareous tubes, as well as spicules and sclerites from larger armoured invertebrates, such as the halkeriids, that had relationships to molluscs, brachiopods and annelids (Conway Morris & Peel 1995). Then followed a rapid increase in further appearances, during early Mid-Cambrian times, as manifested in the Cambrian radiation proper. Valentine *et al.* (1990) have documented the first and last appearances of ordinal-level fossil taxa from Vendian and Cambrian sediments as well as ordinal-level standing diversity, which they list as follows (p. 289):

Lower Vendian I: 0; Vendian II: 15 (the Ediacaran radiation); Vendian III: 6; Vendian IV:14; Tommotian: 36; Atdabanian: 61; Botomian: 68; Early Middle Cambrian: 59; Middle Middle Cambrian: 86; Late Middle Cambrian: 51, and Late Cambrian: 63.

A rather similar increase in the record of trace fossil taxa across the Proterozoic-Cambrian boundary has been shown for a number of assemblages (Crimes 1992), particularly from the White-Inyo Mountains in California, the Cassiar Mountains in British Columbia, the Burin Peninsula, Newfoundland and Tanafjord in Norway.

Some of the best-known fossil evidence for the Cambrian radiation comes from the Burgess Shale as it is exposed on Fossil Ridge, close to Mount Field in the Canadian Rockies. Charles D. Walcott, who was Secretary of the Smithsonian Institution (Yochelson 1967), was spending the summer of 1909 exploring Proterozoic and Cambrian rocks in the Canadian Rockies, when he came upon superbly preserved animal fossils. He returned for intermittent excavations at the site between 1910 and 1924, taking back 65000 specimens to the Smithsonian Institution in Washington. In his foreword to a recent book on *The Fossils of the Burgess Shale* (Briggs *et al.*1994), Whittington wrote: "It is to Charles D. Walcott's lasting credit that he found the Burgess Shale, amassed a huge collection of these remarkable fossils, and made the outlines of his find known to paleontologists the world over. How significant his discovery was is only now beginning to be recognised, as not a local aberration to be noted in passing, but as a unique revelation of the extraordinary wealth of Cambrian biota."

Following Walcot's initial work, a resurgence of interest in the fossil assemblage was promoted by the work of Harry Whittington (eg. 1971, 1985) and of his research students at that time, Derek E.G. Briggs and Simon Conway Morris. In the interim, other assemblages of Cambrian soft-bodied fossil organisms have been found in various parts of the world (Conway Morris 1985), in particular the Chengjiang fauna which is somewhat earlier than its Burgess Shale equivalent. It was discovered in 1984 in Yunnan, South China (Zhang & Hou 1985) and has produced a wide variety of fossil organisms, reminiscent of the Burgess Shale fauna, including the recent record of a *Pikaia*-like chordate (Shu *et al.* 1996). A Lower Cambrian fossil lagerstätte in the southern hemisphere has recently been reported (McHenry & Yates 1993), – the Emu Bay Shale on Kangaroo Island, South Australia. From it a new species of *Anomalocaris*, the largest predator in the Burgess Shale assemblage, has been described (Nedin 1995).

As mentioned above, it has long been suspected that the sudden appearance of animals in the fossil record, during the Ediacaran and Cambrian radiations, did not necessarily represent the starting points of the lineages that they represented. Although pre-Ediacaran metazoans have hardly been found as fossils at all, their suspected presence has been linked to the observed decline in the abundance and diversity of stromatolites during the Proterozoic, through grazing and burrowing activities (eg. Awramik 1971). On this topic, Walter and Heys (1985) wrote as follows: "Those stromatolites which formed in quiet subtidal environments began to decline in both abundance and diversity about 1 Ga ago. This was followed by a general decline in all stromatolites beginning 0.7-0.8 Ga ago. Then during the Cambrian there appeared the first thrombolites, stromatolites with a clotted, unlaminated fabric. All three events can be related to the evolutionary history of the Metazoa, and in fact shed new light on that history. We consider that the thrombolites owe their origin to and record the first macroscopic burrowing and possibly boring by animals, an interpretation consistent with the well known first abundant occurrence of vertical burrows in the earliest Cambrian. The 0.7-0.8Ga decline can be attributed to the first widespread grazing by animals (an interpretation made earlier by other authors and supported by our review of new information). The decline of subtidal stromatolites which began about 1Ga ago records the early, subtle effects of grazing, presumably by small acoelomate animals."

Evidence of a different kind for the early existence of animal lineages, prior to the Ediacaran/Cambrian radiations is rapidly coming to light through new research into "molecular clocks" and genetic developmental mechanisms. The concept of a "molecular clock" is based on the assumption that mutational changes, either in the DNA sequences of genes or the amino acids that are assembled on the instructions of such genes, will have arisen at a constant rate over the past history of an organism. In an early application of this technique, Runnegar (1982a&b) made use of the oxygen-carrying proteins, haemoglobins and myoglobins in living vertebrates. For instance, living jawless fish have haemoglobins composed of identical myoglobin-like molecules, but this is not true for sharks and other higher vertebrates. These have tetrameric haemoglobin formed by two pairs of different globins called α and ß chains, presumably because the genes for haemoglobin were duplicated in the ancestors of the jawed fish. Once this happened, the two forms of globin were able to evolve separately, even in the same animal, resulting in a 60% difference in the amino acid sequences of the two globins in living vertebrates, irrespective of their evolutionary grade. Modern sharks and higher vertebrates last shared a common ancestor in late Ordovician or Silurian fish that had inherited the recently acquired duplicate genes. The haemoglobin clock may be calibrated by comparing observed percentage sequence differences with probable times of separation, judged from the isotopically dated fossil record (Runnegar 1982a). Since there is good statistical agreement between these two independent data sets for the last 450 million years, it should be possible to use the same technique to estimate when the invertebrate phyla separated, and hence to date the first major radiation of the animals.

When Runnegar wrote this pioneering paper, few invertebrate globins had been sequenced. Those that had, proved to be about 80% different from each other and from vertebrate globins, leading to the conclusion that the initial radiation of the lower animals probably occurred about 900-1000 Ma ago.

Since 1985, a good deal of work has been done (eg. Raff *et al.* 1996) on the use of DNA sequences in unravelling the Cambrian radiation of animal phyla. A study by Wray *et al.* (1996) made use of sequences from seven genes from a large sample of species in several phyla and concluded that the lines leading to the chordates and the major protostome phyla diverged about 1,2 Ga ago, or a little earlier than Runnegar had surmised. Such a view appears to be gaining considerable support (Bell 1997). Yet it should be mentioned that not all molecular clocks appear to keep the same time. Doolittle *et al.* (1996) made use of amino acid sequence data from 57 different enzymes to determine the divergence times of the major biological groupings. They estimate that deuterostomes and protostomes split about 670 Ma ago, while plants, animals and fungi last shared a common ancestor about 1 Ga ago – considerably less than other estimates. Despite such major discrepancies, all molecular estimates agree that animal lineages originated long before their first appearances in the fossil record. New evidence, now coming to light on the antiquity of developmental control, or hox, genes is sure to further elucidate this question (Erwin *et al.* 1997). Thus it is clear that molecular techniques can provide an enormous amount of information about the branching pattern of animal lineages, and the timing of such branching. But as Conway Morris (1994) has pointed out, palaeontology still remains an indispensable source of information on the nature and structure of the ancient animals themselves.

But if ancestral invertebrate lineages had been in existence for so long before they appeared as fossils, why did they not fossilize? A novel explanation has recently been proposed by Davidson *et al.* (1995), in which they postulate that representatives of the various invertebrate lineages existed prior to the Cambrian radiation in the form of microscopic larvae, constituting "a cryptic, pre-Ediacaran

evolutionary phase that left no fossil record (or at least none so far recovered)". Then, in early Cambrian times, the genetic programmes were evolved that allowed progression form such minute larvae to adult invertebrates, as are known today, showing large size and resistant elements favourable for survival as fossils. This theory, as have many before it, presupposes some striking environmental factor making its sudden appearance in early Cambrian times. Most commonly cited was the oxygen concentration in the late Proterozoic atmosphere that crossed some critical threshold (eg. Nursall 1959; Berkner & Marshall 1965). Runnegar (1982c) for instance estimated that the Ediacaran organism, *Dickinsonia*, would have required 6-10% of the present atmospheric level to have survived. There is a good deal of current research on the topic of oxygenation of the earth's atmosphere (eg. Des Marais et al 1992; Canfield & Teske 1996; Thomas 1997), postulating a rise in atmospheric oxygen concentrations to at least 5-18% of present levels, between 0,6 and 1,0 Ga ago, a change that may have triggered the evolution of animals. Numerous other suggestions have been made as to influences that mediated the metazoan radiations. These include changes in ocean chemistry that promoted the development of skeletons (eg. Daly 1907, Kempe & Degens 1985); the termination of the particularly intense and worldwide late Proterozoic glaciation (eg. Hambrey & Harland 1985); the advent of predation (Stanley 1973) and the premium it placed on the rapid evolution of protective skeletons (eg. Vermeij 1989) and the evolution of sexual reproduction which served to accelerate the tempo of evolution (Stanley 1976).

SOME RECENT DEVELOPMENTS CONCERNING NAMA SEDIMENTS

The Nama basin covers a very large area in southern Namibia, extending from 100kms south of Windhoek in the north to the Orange River in the south and from the western escarpment to beyond the South African border in the east. The basin extends from the Orange River to the vicinity of Springbok and then into the Vanrhynsdorp area. Geological investigations of the Nama basin sediments commenced in early German colonial days when Schenk (1910) correlated the Nama with the Otavi System on the basis of the unmetamorphosed limestones and dolomites found in both successions. Soon afterwards Range (1912) provided the first detailed description of the Nama sequence and proposed the following subdivisions based on exposures in the Bethanie district:

Fish River Series
Schwarzrand Series
Schwarzkalk Series
Kuibis Series and Basal Beds

Martin (1950) concluded that the Nama sequence was younger than the Otavi counterpart and, in 1965 included the Huns limestones in the Schwarzrand Series. The South African Committee for Stratigraphy (1980) set up the Nama Group with three subdivisions: The lowermost Kuibis Subgroup, the Schwarzrand Subgroup and the uppermost Fish River Subgroup, a nomenclature currently in use. Several other related groups, together with the Nama, were regarded as comprising the Damara Supergroup; these are, among others, the Gariep and Witvlei Groups in the southern half of Namibia and the Nosib, Otavi and Mulden Groups further north. The history of the various components of the Damara Supergroup is closely related to that of the cratons on which they rest: the Gariep, Witvlei and Nama Groups lie on the Kalahari Craton, while the Nosib, Otavi and Mulden Group sediments were deposited on the Congo Craton to the north. An understanding of the relative movements of these cratons, together with that of a South American plate, then situated immediately to the west, is crucial to the understanding of the development of the Nama basin.

According to Hoffmann (1992), rifting occurred between the Kalahari and Congo cratons at about 820 Ma ago, into which depression sediments of the Nosib Group were deposited. Marine transgression followed from the ancient Proto-Atlantic, or Adamastor Ocean, with the deposition of the lower carbonates of the Otavi Group. This deposition was interrupted by a glacial episode, represented by the Chuos and Blaubeker Formations (Otavi and Witvlei Groups respectively) at about 720-710 Ma ago. Continental breakup followed with the deposition of further dolomites of the Otavi and Witvlei Groups in the space between the cratons. Northward subduction followed at about 660 million years, followed by a reversal in the relative movements of the Congo and Kalahari cratons, such that they once again approached each other at the time of renewed glaciation, recorded in the Numees tillite, which pre-dates the onset of Nama and Mulden Group sedimentation. In response to mountain-building in the northwest, a foreland basin developed in which the sediments of the Nama group were deposited. Actual continental collision occured during Schwarzrand depositional times, with further mountain building leading to the deposition of the uppermost Fish River Subgroup sediments as a molasse.

Two doctoral projects have provided detailed information about the lower Nama Group in Namibia (Germs 1972c) and the more southerly Vanrhynsdorp Group, as it has become known (Gresse 1986), and stratigraphic correlations between the two groups were then undertaken (Germs & Gresse 1991). Germs and Gresse (1993) have also provided detailed information about the evolution of the Nama foreland basin, bounded to

the northwest by the Damara orogen and to the west by the Gariep orogen and which was divided into the Zaris and Witputs basins in Namibia (separated by the Osis ridge) and the Vanrhynsdorp basin, separated from the first two by the Kamieskroon ridge. Only during the deposition of the upper Fish River beds were the basins continuous. Originally, the lower Nama sediments were derived from the Kalahari craton to the east, while later in the sequence the source was the newly elevated mountains to the north and west.

In 1992, a detailed stratigraphic study of the stratigraphy of the Kuibis and Schwarzrand Subgroups in the Witputs area was started by Beverly Saylor of the Massachusetts Institute of Technology (Saylor 1992/93). This study was designed to apply the concepts of sequence stratigraphy to identify unconformity-bounded depositional sequences which can be used as time lines for interbasinal correlation. The study confirmed the presence of two sequence boundaries in the Kuibis Subgroup sediments, and five in the Schwarzrand Subgroup. In addition, the presence of 11 volcanic ashbeds in the sequence was reported, which have the potential for radiometric dating. This study has been developed considerably (Saylor *et al.* 1995; Grotzinger *et al.* 1995) and, together with earlier investigations, has ensured that the Nama basin sequence is among the best documented terminal Proterozoic successions in the world. Two issues deserve special mention: the use of isotope studies for late Proterozoic correlation and the implications of radiometric dating of the Ediacaran radiation.

Isotope studies and Late Proterozoic glacial episodes

A good deal of attention has been given recently to the secular variation in stable carbon isotope ratios in late Proterozoic successions from various parts of the world (eg. Knoll et al 1986; Kaufman et al 1991; Knoll 1991; Knoll & Walter, 1992; Kaufman *et al.* 1993; Kaufman & Knoll, 1995) and these variations have been shown to be very useful in correlating widely separated stratigraphic sequences. (The numeric value of carbon isotope ratios is conveniently reported as ^{13}C. The number represents the difference between the ratio of ^{13}C to ^{12}C found in a particular sample and the ratio that exists in a universal standard, expressed as a per mill (‰) deviation from the standard).

Late Proterozoic sedimentary sequences have shown ^{13}C values to be generally positive, indicating generally high rates of organic carbon burial during their deposition. However there have been episodes in the record when the enrichment in ^{13}C declined rapidly and the ^{13}C values became strikingly negative. Such deviations were found to coincide with glacial episodes, such as the 600Ma Varanger glaciation, evidence for which has been found to underlie strata containing Ediacaran fossils in various parts of the world including the Nama basin. Immediately beneath the Nama sequence lies the Numees tillite of the Gariep group, apparently with an unconformable contact (Kröner & Germs 1971), though Martin (1965, p. 105) found the contact to be conformable in the area west of Witputs.

In the course of a detailed study of carbon isotope ratios of Damara Supergroup carbonates, Kaufman *et al.* (1991) have shown that at the base of the Nama group, ^{13}C values rise dramatically from -4 to +5 ‰, within a short stratigraphic interval. A similar trend was observed in dolomites of the Otavi Group immediately above the Chuos tillite, which was correlated in this study with the Kaigas tillite of the Gariep Group and the Blaubeker tillite of the Witvlei Group. Thus, one of the particularly significant conclusions of the carbon isotope study on Namibian Proterozoic carbonates is that the trends in isotope concentrations allow for correlations with equivalent sediments in other basins of the world, as well as between carbonates on the adjacent Congo and Kalahari cratons. It has been observed (eg. Hambrey & Harland 1985; Hambrey 1992) that the Varanger glaciation, to which the pre-Nama Numees tillite bears witness, was not only the most intense in the the history of the earth, but also spread throughout low equatorial latitudes. It is a vexing question as to what circumstances would have been required to allow for such low latitute glaciation, but new evidence suggests that this may have been a feature of other Proterozoic glaciations as well. For instance, a new study on glaciogenic deposits of the much older (2,2 Ga) Transvaal Supergroup on the Kaapvaal Craton in South Africa (Evans et al 1997), show that these were deposited well within the tropics.

Evidence for two other glacial episodes within the Nama Group sediments has been reported. Over 50 years ago, Schwellnus (1941) found glacial pavements, tillite and other features of glacial activity in the Klein Karas mountains. With some reservations, this evidence was accepted by Martin (1965) who re-examined the exposure and concluded that floating and grounded ice-flows, rather than true glaciers, had been responsible for the observed effects. Germs (1972c) also reassessed the field evidence and found that the glacial indications, which he did not question, occured close to the base of the Schwarzrand Subgroup, between the Nudaus and Urusis Formations. He also found further evidence for glacial activity close to the top of the Schwarzrand Subgroup. This took the form of steep-sided channels, partially filled with conglomeritic debris, which had been cut after the deposition of the Spitskopf limestone. More recently Saylor (1992/3) questioned the glacial interpretation of these features, though she did not rule it out. Support for

a glacial episode at, or close to, the Proterozoic-Cambrian boundary, comes from a marked negative Carbon isotope excursion at this time, reported from elsewhere in the world (Knoll & Walter 1992), though not shown in the Namibian curve, probably as a result of the time-hiatus represented by the Spitskopf-Nomtsas unconformity (Grotzinger *et al.* 1995).

The various lines of evidence discussed above combine to show that the terminal Proterozoic time period was an environmentally turbulent one. There is worldwide evidence of tectonic activity and mountain-building; of increased hydrothermal activity (Knoll 1991); of high rates of organic carbon burial that would have increased the oxygen concentration of the atmosphere, and there are indications of extremely severe glacial episodes, extending into tropical latitudes. It was in such circumstances that the first radiation of metazoans appears to have occurred in the Nama basin and elsewhere.

Precise dating of the Ediacaran radiation

Until recently, the dating of Nama Group sediments has been somewhat imprecise. For instance, measurements on detrital white micas in upper Schwarzrand sediments gave an age of about 630Ma, while micas in younger Fish River sediments suggested approximately 530Ma (Ahrendt *et al.* 1978). The post-tectonic Kuboos and Bremen igneous suites, which are intrusive into the Kuibis and Schwarzrand Subgroups yielded ages of between 500 and 550 Ma (Allsopp *et al.* 1979), suggesting a minimum age of 500Ma for the uppermost Schwarzrand Subgroup. Further determinations by Horstmann et al. (1990) of detrital white mica, narrowed the sedimentation time of upper Schwarzrand and Fish River Subgroups to between 570 and 500Ma.

As mentioned above, the fieldwork undertaken by Saylor (1992/3) in the Nama basin confirmed the presence of a number of volcanic ashbeds in the sequence. Four of these were selected for dating by Bowring at the Massachusetts Institute of Technology, using the uranium-lead method applied to single zircon crystals (Grotzinger *et al.* 1995). The samples were positioned in the Nama stratigraphic column as follows: 1. From the northern subbasin, a 30 cm-thick ashbed that lies in the Hoogland carbonate member, 270 m above the base of the Kuibis Subgroup; 2. In the southern subbasin, a 50 cm-thick ashbed in the lower part of the Spitskopf carbonate member at Witputs; 3. a 20 cm-thick ash in the uppermost Spitskopf limestone at Swartpunt, 135 m above sample 2; 4. The stratigraphically highest ash, in the lowermost Nomtsas Formation at Swartkloofberg.

The best age estimates for these samples are as follows:

Basal Nomtsas Formation (sample 4): 539.4 ±1 Ma
Upper Spitskopf Member (sample 3): 543.3 ±1 Ma
Lower Spitskopf Member (sample 2): 545.1 ±1 Ma
Lower Hoogland Member (sample 1): 548.8 ±1 Ma

These results constrain the Precambrain-Cambrian boundary in Namibia to be younger than 543.3 ±1 Ma and older than 539.4 ±1 Ma, in good agreement with a date from the lowermost Cambrian strata in Siberia.

Grotzinger *et al.* (1995) report the finding of body fossils of *Pteridinium* and "a Dickinsonid-like fossil that may be *Nasepia* or possibly a new taxon" near the top of the Spitskopf Member, 90-100 m above the upper Spitskopf ash. This extends the stratigraphic range of such fossils in the Nama Group upwards considerably and shows they existed until virtually the Cambrian boundary. The fact that the Nama dates can be tied to the carbon isotope curve, which has world-wide application, means that the time span of other Ediacaran assemblages, such as that in the Flinders Ranges of Australia, can be estimated with greater assurance than in the past. The general conclusion is thus reached that the most diverse Ediacaran fossil assemblages are no more than about 6 million years older than the Precambrian-Cambrian boundary. However, the minimum lower limit for the age range of the Ediacaran fauna is 565 Ma, as has been measured at Mistaken Point, Newfoundland. Generally, Ediacaran fossils have not been thought to occur below the Varanger glacial beds, although simple disk and ring-shaped impressions from the Twitya Formation of northwestern Canada (Hofmann et al. 1990) suggest that macroscopic metazoans may predate the glaciation. If this is so, the Ediacaran radiation has a time range of at least 55 million years, though the span of the lower Nama sediments is considerably shorter than had been estimated previously. An important implication of the new Nama dates is that the upper limit of the Ediacaran radiation is brought to the Cambrian boundary. This, taken with the fact that new dates for early Cambrian strata in Siberia (Bowring *et al.* 1993) show that that the initial phases of the Cambrian Period were much briefer than previously thought, accentuates the rapidity of faunal diversification leading to the main Cambrian radiation itself.

SOME COMMENTS ON THE NAMAN FOSSIL ASSEMBLAGES

Martin Pickford (1995) has recently provided a comprehensive overview of the fossil fauna from Nama Group sediments. The majority of taxa, being members of the soft-bodied Ediacaran fauna, are listed by him under "Vendozoa", as follows:

Pteridinium simplex Gürich 1930, originally spelt *Pteridium*
Rangea schneiderhöhni Gürich 1929
Orthogonium parallelum Gürich 1930
Ernietta plateauensis Pflug 1966
Ausia fenestra Hahn & Pflug 1985
Paramedusium africanum Gürich 1933
Nasepia altae Germs 1973
Cyclomedusa davidi Sprigg 1947
Velancorina martina Pflug 1966
Petalastroma kuibis Pflug 1973

In addition to these Vendozoan texa, Pflug (1972a) described the following taxa from the farms Plateau and Aar, which are regarded by Runnegar & Fedonkin (1992) as synonyms of *Ernietta plateauensis*:

Ernietta aarensis, Ernietta tschanabis, Erniobaris baroides, Erniobaris epistula, Erniobaris gula, Erniobaris parietalis, Erniaster apertus, Erniaster patellus, Erniobeta forensis, Erniocarpus carpoides, Erniocarpus sermo, Erniocentris centriformis, Erniocoris orbiformis, Erniodiscus clipeus, Erniodiscus rutilus, Erniofossa prognatha, Erniograndis paraglossa, Erniograndis sandalix, Ernionorma abyssoides, Ernionorma clausula, Ernionorma corrector, Ernionorma peltis, Ernionorma rector, Ernionorma tribunalis, Erniopelta scrupula and *Erniotaxis segmentrix*. Other possible synonyms of *Ernietta plateauensis* are *Namalia villiersiensis* Germs 1968, and *Kuibisia glabra* Hahn & Pflug 1985.

Other faunal taxa listed by Pickford (1995) are these:

Hagenetta aarensis Hahn & Pflug 1988.

This was a small almost circular fossil, about 5mm in diameter, with an upper valve of roughly triangular outline. Runnegar & Fedonkin (1992) consider *H. aarensis* to be a synonym of *Beltanelliformis brunsae*, from Vendian sediments of the Russian platform. It was possibly a sessile organism that lived on sandy substrates and fed on phytoplankton.

Protoechiurus edmondsi Glaessner 1979.

This was a cigar-shaped organism, about 7 cm long from the Kuibis quartzite on Plateau farm. Glaessner reconstructed as an echiurid worm with a spatulate proboscis and eight longitudinal muscle bands. Runnegar & Fedonkin (1992) regards it to be a dubiofossil.

Spriginnidae ?

Germs (1973b) described the imprint of a flat, elongate fossil about 10 cm long and 1 cm wide from shale underlying the Mooifontein limestone Member on the farm Buchholzbrunn 99. The organism appeared to have had at least 34 segments, with lateral ribs and possible intestinal tract and protostomium. Unfortunately the specimen, that had been lodged in the State Museum, Windhoek, has since been lost. Germs compared this specimen to *Spriggina ovata* from Ediacara in south Australia.

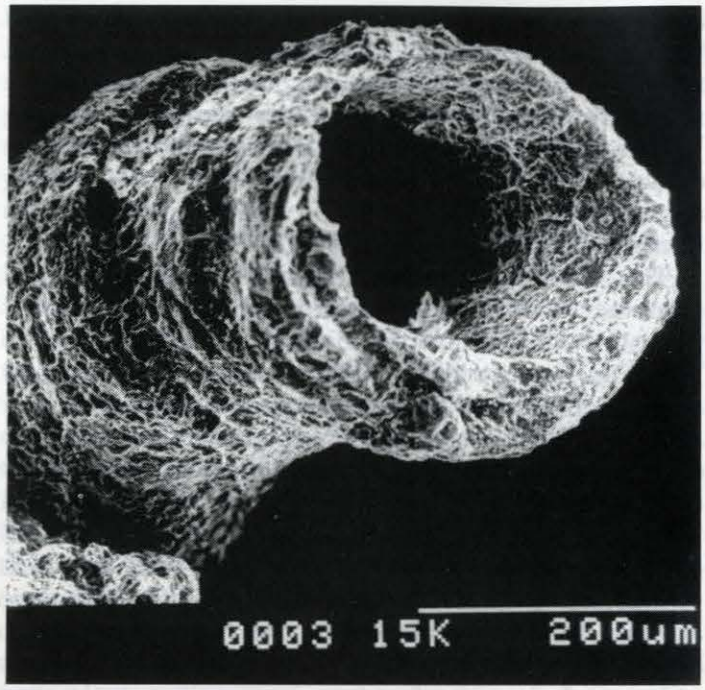


Figure 1. The calcareous tube of *Cloudina* sp. from the Mooifontein limestone of the Nama Group, seen as a SEM image. *Cloudina* is the earliest known organism to have made use of biomineralisation, a process crucial to the later development of skeletonised animals. First described from the Nama Group by G. J. B. Germs, *Cloudina* has since been found in many parts of the world and is regarded as a terminal Proterozoic index fossil.
Photo: C. K. Brain.

Archaeichnium haughtoni Glaessner 1963.

Haughton (1962) described tubular structures on two slabs of Kuibis Subgroup quartzite from Gründoorn, in SE Namibia and regarded these as archaeocyathids. He noted that they consisted of long tubes, conical at one end and open at the other, showing "a number of elongate pustulate ridges". On the basis of plaster casts of these slabs, Glaessner (1963) named these fossils *Archaeichnium haughtoni*, which he considered as worm tubes or worm burrows. Glaessner (1977) later made a close examination of the original specimens in the South African Museum, and concluded that the impressions consist of "agglutinated sand grains and are similar to tubes made actively by living polychate worms ..... In the absence of any taxonomically significant characters of tube construction the systematic position of the originator of these fossils remains uncertain".

Cloudina hartmannae and *C. riemkeae* Germs 1972

Germs (1972a) described these two species of calcareous tube-building organisms, that occur in limestones throughout the Kuibis and Schwarzrand

subgroups, but are particularly numerous in the "bioherm" that Germs described from Driedoring-vlakte, near Schlip on the northern margin of the Nama basin. The two species were designated on the basis of tube-size, with the larger species, *C.harmannae*, 2,5-6,5 mm wide as opposed to 0,3-1,3mm for *C.riemkeae* (Figure 1). The tubes were found to consist of a cone-in-cone structure, closed at one end, but flared at the open ends, where space existed between each of the eccentric layers. Germs considered that *Cloudina* should possibly be placed in the Class Cribricyathea, of the Phylum Archaeocyatha. Subsequently Hahn and Pflug (1985) described *Cloudina* from Brasil and set up the Family Cloudinidae.

Grant (1990) undertook a detailed study of the shell structure and distribution of *Cloudina*, after which he maintained the two species described by Germs and showed that representatives of the genus have now been found in many parts of the world, including Antarctica. He concluded that *Cloudina* can be regarded as an index fossil for the terminal Proterozoic. He considered that *Sinotubulites* from China, *Nevadatubulus* and *Wyattia* from North America are "either closely related to or congeneric with *Cloudina*." Grant regarded the phylum, class, order and family as uncertain and concluded that "the organism that secreted these shells appears to have had to move up the tube between the deposition of successive shell layers implying a musculature and internal complexity consistent with a diploblastic or even triploblastic animal. Thus the *Cloudina* organism was probably a metazoan of at least a cnidarian grade of organisation."

The particular significance of *Cloudina* is that it represents the earliest known metazoan to have made use of biomineralisation, a process crucial to the later evolution of skeletonised animals. As was the case with Ediacaran body fossils, it was the Nama sediments that first yielded evidence of this animal, later found to occur in many other countries.

In addition to the actual fossil taxa listed above, at least 18 taxa of trace- or ichnofossils are known from the Nama sediments as reported by Germs (1972b) and Crimes and Germs (1982). These include the trace fossil *Phycodes pedum*, which is considered to be an important Cambrian indicator and has been found to occur in the Nomtsas Formation and the overlying Fish River Subgroup beds (Saylor et al 1995).

Apart from fossils of animals discussed above, the Nama sediments have produced remains of organic-walled microfossils (Germs *et al.* 1986) and probable calcified metaphytes (Grant *et al.* 1991).

For the last three years the present writer has been investigating Nama limestones, particularly at ashbed-chert/limestone interfaces for the presence of preserved micro-organisms. The aim is to reconstruct the community of which *Cloudina* formed a part. This community must have included representatives of the invertebrate lineages whose later members made their fossil appearance during the Cambrian radiation. The micro-organisms are being investigated in thin-sections and by way of SEM images of silicified remains that are picked from acetic acid residues. One such image is that of a *Cloudina* from the Mooifontein limestone shown in Figure 1. The results of this investigation will be published separately.

CONCLUSIONS

As will have become apparent from the overview presented above, the Nama basin contains a remarkable sequence of sediments, approximately 3000m thick, which cover a critical period of the Ediacaran and early Cambrian radiations. These sediments are largely unaltered and unafffected by tectonism, except along the western margin of the basin. The sequence has been studied in considerable detail and the volcanic ashbeds which occur at intervals throughout its depth have provided precise dates. These can be correlated with the curve for carbon isotope values that have been determined and which can be used for inter-basinal correlations on other continents.

The palaeontological significance of the Nama basin is very considerable and the potential for further discoveries is great. In fact, the unique combination of Naman fossil, sedimentological and chronological information can be used to address almost every facet of the current debate on animal origins.

ACKNOWLEDGEMENTS

In particular, I would like to thank Gerard Germs for introducing me to the pleasures, excitements and frustations of the Nama basin and its fossils. Throughout this recent project, Laura Brain has given me invaluable support. I am also very grateful to the following people for help and advice both in the field and laboratory: J. E. Almond, S. Conway Morris, J. G. Gehling, P. G. Gresse, M. A. Fedonkin, W. Hegenberger, K. H. Hoffmann, A. H. Knoll, M.-A. S. McMenamin, M. H. L. Pickford, B. Runnegar, W. J. Schopf, A. Seilacher and M.R. Walter. Bruce Runnegar and John Almond kindly provided useful comments on the manuscript and I am grateful to Bruce Rubidge for editorial help. The research was supported by a grant from the Foundation for Research Development in Pretoria.

REFERENCES

AHRENDT, H., HUNZIKER, J. C. & WEBER, K. 1978. Age and degree of metamorphism and time of nappe emplacement along the southern margin of the Damara Orogen, Namibia. *Geol. Rundsch.* **67,** 719-742.

ALLSOP, H. L., KOSTLIN, E. O., WELKE, H. H., BURGER, A. J., KRÖNER, A. & BLIGNAUT, H. J. 1979. Rb-Sr and U-Pb geochronology of the late Precambrian- Early Palaeozoic igneous activity in the Richtersveld and southern South West Africa. *Trans. Geol. Soc. S. Afr.* **82,** 185-204.

ANDERSON, M. M. & CONWAY MORRIS, S. 1982. A review, with description of four unusual forms of soft-bodied fauna of the Conception and St. John's Groups (Late Precambrian), Avalon Peninsula, Newfoundland. **In:** Mamet, B. & Copeland, M. J., Eds, *Proceedings of the North American Palaeontological Convention*, **1,** 1-8.

-------- & MISRA, S. B. 1968. Fossils found in the Precambrian Conception Group in southeastern Newfoundland. *Nature*, **220,** 680-681.

AWRAMIK, S. M. 1971. Precambrian columnar stromatolite diversity: reflection of metazoan appearance. *Science* **174,** 825-827.

BELL, M A. 1997. Origin of metazoan phyla: Cambrian explosion or Proterozoic slow burn?. *TREE* **12**(1), 1-2.

BENGTSON, S., CONWAY MORRIS, S., COOPER, B. J., JELL, P. A. & RUNNEGAR, B. N. 1990. Early Cambrian fossils from South Australia. *Association of Australasian Palaeontologists,* Memoir **9,** 1-364. Brisbane.

BERKNER, L. V. & MARSHALL, L. C. 1965. History of major atmospheric components. *Proc. Natl. Acad. Sci. USA* **53,** 1215-1225.

BOWRING, S. A., GROTZINGER, J. P., ISACHSEN, C. E., KNOLL, A. H., PELECHATY, S. M. & KOLOSOV, P. 1993. Calibrating rates of early Cambrian evolution. *Science* **61,**1293-1298.

BRIGGS, D. E. G., ERWIN, D. H. & COLLIER, F. J. 1994. *The fossils of the Burgess Shale.* Washington, Smithsonian Institution Press.

BRINK, W. C. 1950. The geology, structure and petrology of the Nuwerus area, Cape Province. *Ann. Univ. Stellenbosch* **26**(3-11),97-221.

BUSS, L. W. & SEILACHER, A. 1994. The Phylum Vendobionta: a sister group of the Eumetazoa. *Paleobiology* **20**(1), 1-4.

CANFIELD, D. E. & TESKE, A. 1996. Late Proterozoic rise in atmospheric oxygen concentration inferred from phylogenetic and sulphur-isotope studies. *Nature* **382**:127- 132.

CLOUD, P. & GLAESSNER, M. F. 1982. The Ediacaran Period and System: metazoa inherit the earth. *Science* **217,** 783-792.

CONWAY MORRIS, S. 1985. Cambrian Lagerstätten: their distribution and significance. *Phil. Trans. Roy. Soc.* London B**311,** 49-65.

-------- 1993. The fossil record and the early evolution of the metazoa. *Nature* **361,** 219-225.

-------- 1994. Why molecular biology needs palaeontology. *Development*, 1994 Supplement, 1-13.

-------- & PEEL, J. S. 1995. Articulated halkariids from the Lower Cambrian of North Greenland and their role in early Protostome evolution. *Phil. Trans. Roy. Soc.* London B **347**:305-358.

COPE, J. C. W., 1977. An Ediacaran fauna from South Wales. *Nature* **268,** 624.

CRIMES, T. P. 1992. The record of trace fossils across the Proterozoic-Cambrian boundary. **In:** Lipps, J. H. & Signor, P. W. Eds., *Origin and Early Evolution of the Metazoa*, pp. 117-202. New York, Plenum.

-------- & GERMS, G. J. B. 1982. Trace fossils from the Nama Group (Precambrian-Cambrian) of South West Africa \Namibia. *J. Palaeontology* **65,** 890- 907.

DALY, R. A. 1907. The limeless oceans of Precambrian time. *Am. J. Sci.* **23,** 93-115.

DAVIDSON, E. H., PETERSON, K. H. & CAMERON, R. H., 1995. Origin of bilaterian body plans: evolution of developmental regulatory mechanisms. *Science* **270,** 1319- 1325.

DEBRENNE, F. 1992. Diversification of Archaeocyatha. **In:** Lipps, J. H. & Signor, P. W., Eds., *Origin and Early Evolution of the Metazoa*, pp. 425-439. New York, Plenum.

-------- & NAUD, G. 1981. Méduses et traces fossiles supposées précambriennes dans la formation de San Vito, Sarrabus, Sud-Est de la Sardaigne. *Bull. Geol. Soc. France* **23,** 23-31.

DES MARAIS, D. J., STRAUSS, H., SUMMONS, R. E. & HAYES, J. M., 1992. Carbon isotope evidence for the stepwise oxidation of the Proterozoic environment. *Nature* **359,** 605-609.

DOOLITTLE, R. F., FENG, D. F., TSANG, S., CHO, G. & LITTLE, E. 1996. Determining divergence times of the major kingdoms of living organisms with a protein clock. *Science* **271,** 470-477.

ERWIN, D., VALENTINE, J & JABLONSKI, D. 1997. The origin of animal body plans. *American Scientist* **85**, 126-137.

EVANS, D. A., BEUKES, N. J. & KIRSCHVINK, J. L. 1997. Low-latitude glaciation in the Palaeoproterozoic era. *Nature* **386,** 262-266.

FARMER, J. D., VIDAL, G., STRAUSS, H. MOSZYDLOWSKA, M., AHLBERG, P. & SIEDLECKA, A. 1991. Ediacaran medusoids from the Innerelv Member (late Proterozoic) Tanafjorden area of N. E. Finnmark. *Geol. Soc. Am. Abstracts* **23**(5), 97.

FEDONKIN, M. A. 1981. White Sea biota of the Vendian. Precambrian non-skeletal fauna of the Russian Platform. Moscow, Nauka. (In Russian).

-------- 1985. Precambrian metazoans: the problems of preservation, systematics and evolution. *Phil. Trans. Zool. Soc.* London B**311,** 27-45.

-------- 1990. Systematic description of the Vendian metazoa. **In:** Sokolov, B. S. & Iwanowski, A. B. Eds., *The Vendian System*, Vol. 1 (Palaeontology) pp. 77- 120. New York, Springer Verlag.

-------- 1992. Vendian faunas and the early evolution of metazoa. **In:** Lipps, J. H. & Signor, P. W., Eds., *Origin and Early Evolution of the Metazoa*, pp. 87-129. New York, Plenum.

FORD, T. D. 1958. Pre-Cambrian fossils from Charnwood Forest. *Proc. Yorkshire Geol. Soc.* **31,** 211-217.

GERMS, G. J. B. 1968. Discovery of a new fossil in the Nama System, South West Africa. *Nature* **219,** 53-54.

-------- 1972a New shelly fossils from the Nama Group, South West Africa. *Amer. J. Sci.* **272,** 752-761.

-------- 1972b. Trace fossils from the Nama Group, South West Africa. *J. Palaeont.* **46,** 864-870.

-------- 1972c. The stratigraphy and palaeontology of the lower Nama Group, South West Africa. *Bull. Pre-Cambrian Research Unit*, Univ. of Cape Town **12,** 1-250.

-------- 1973a. A reinterpretation of *Rangea schneiderhöhni* and the discovery of a related new fossil from the Nama Group, South West Africa *Lethaia* **6,** 1-10.

-------- 1973b. Possible sprigginid worm and a new trace fossil from the Nama Group, South West Africa. *Geology* **1**(2), 69-70.

-------- 1974. The Nama Group in South West Africa and its relation to the Pan-African Geosyncline. *J. Geol.* **82,** 301-317.

-------- 1983. Implications of a sedimentary facies and depositional analysis of the Nama Group in South West Africa \Namibia. **In:** Miller, R. Mc. Ed., *The Damara Orogen.* Special Publication of the Geol. Soc. S. Afr. **11,** 89-114.

-------- 1995. The Neoproterozoic of South West Africa, with emphasis on platform stratigraphy and palaeontology. *Precambrian Research* **73,** 137-151.

-------- & GRESSE, P. G. 1991. The foreland basin of the Damara and Gariep orogens in Namaqualand and southern Namibia: stratigraphic correlations and basin dynamics. *S. Afr. J. Geol.* **4,** 159-169.

-------- , KNOLL, A. H. & VIDAL, G. 1986. Latest Proterozoic microfossils from the Nama Group, Namibia (South West Africa). *Precambrian Research* **32,** 45-62.
GEHLING, J. G. 1991. The case for Ediacaran fossil roots to the metazoan tree. **In:** Radhakrishna, B. P., ed., *The World of Martin Glaessner*. Geol. Soc. India Memoir **20,** 181-224.
GLAESSNER, M. F. 1963. Zur Kenntnis der Nama-Fossilien Südwest-Afrikas. *Ann. Naturhistor. Mus. Wien.* **66,** 113-120.
-------- 1971. Geographic distribution and time range of the Ediacaran Precambrian fauna. *Geol. Soc. Amer. Bull.* **82,** 509-514.
-------- 1977. Re-examination of *Archaeichnium*, a fossil from the Nama Group. *Ann. S. Afr. Mus.* **74**(13), 335-342.
-------- 1979. An echiurid worm from the late Precambrian. *Lethaia* **12,** 121-124.
-------- 1984. *The Dawn of Animal Life: a Biohistorical Study*. Cambridge, Cambridge University Press.
GRESSE, P. G. 1986. The tectono-sedimentary history of the Vanrhynsdorp Group. Unpublished PhD thesis, Univ. Stellenbosch, 155pp.
-------- & GERMS, G. J. B. 1993. The Nama foreland basin: sedimentation, major unconformity-bounded sequences and multisided active margin advance. *Precambrian Res.* **63,** 247-272.
GRANT, S. W. F. 1990. Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic. *Amer. J. Sci.* **290,** 261-294.
-------- , KNOLL, A. H. & GERMS, G. J. B. 1991. Possible calcified metaphytes in the latest Proterozoic Nama Group, Namibia; origin, diagenesis and implications. *J. Palaeont.* **65,** 1-18.
GROTZINGER, J. P., BOWRING, S. A., SAYLOR, B. Z. & KAUFMAN, A. J. 1995. Biostratigraphic and geochronologic constraints on early animal evolution. Science **270**, 598-604.
GÜRICH, G. 1929. Die ältesten Fossilien Südafrikas. *Z. Prakt Geol.* **37,** 85.
-------- 1930. Die bislang ältesten Spuren von Organismen in Südafrika. *C. R. 2, 15th Int. Geol. Cong. S. Afr.* 1929, 670-680.
-------- 1933. Die Kuibis-Fossilien der Nama-Formation von Südwestafrika. *Palaont.Z.* **15,** 137-154.
HAHN, G. & PFLUG, H. D. 1985. Polypenartige Organismen aus dem Jung- Präkambrium (Nama-Gruppe) von Namibia. *Geologica Palaeontologica* **19,** 1-13.
-------- 1988. Zweischalige organismen aus dem Jung- Präkrambrium (Vendium) von Namibia (S. W. Afrika). *Geologica Palaeontologica* **22,** 1-19.
HAMBREY, M. 1992. Secrets of a tropical ice age. *New Scientist* Feb. 1992, 42-49
-------- & HARLAND, W. B. 1985. The Late Proterozoic glacial era. *Palaeogeogr., Palaeoclimatol, Palaeoecol.* **51,** 255-272.
HARLAND, W. B. 1989. Palaeoclimatology. **In:** Cowie, J. W. & Brasier, M. D. Eds., The Precambrian-Cambrian Boundary. *Oxford Monographs on Geology and Geophysics*, **12,** 199-204.
HARRINGTON, H. J. & MOORE, R. C. 1955. Fossil jellyfish from Pennsylvanian rocks and elsewhere. *State Geol. Surv. of Kansas Bull.* **114,** 153-164.
HAUGHTON, S. H. 1962. A archaeocyathid from the Nama System. *Trans. Roy.* Soc. *S. Afr.* **36,** 57-60.
-------- & MARTIN, H. 1956. The Nama System in South and South West Africa. *Congresso Internat. Mexico El Sistema Cambrico* **1,** 323-329.
HOFFMANN, K. H. 1992. Depositional history of the Damara Belt in Namibia: evidence for major ocean closure and continental collision in the late Proterozoic. *Unpublished ms.*
HOFMANN, H. J., NARBONNE, G. M. & AITKEN, J. D. 1990. Ediacaran fossils from intertillite beds in northwestern Canada. *Geology* **18,** 1199-1202.
HORSTMANN, U. E., AHRENDT, H. CLAUER, N. & PORADA, H. 1990. The metamorphic history of the Damara Orogen based on K/Ar data of detrital white micas from the Nama Group, Namibia. *Precambrian Res.* **48,** 41-61.
HOUZAY, J. P. 1979. Empreintes attribuables à des mèduses dans la sèrie de base de l'Adoudounien (Precambrian termaina de l'Anti-Atlas, Maroc). *Gèol. Med.* **6,** 379- 384.
JENKINS, R. F. J. 1981. The concept of an "Ediacaran Period" and its stratigraphic significance in Australia. *Trans. Roy. Soc. S. Aust.* **105**(4), 179-194.
-------- 1992. Functional and ecological aspects of Ediacaran assemblages. **In:** Lipps, J. H. & Signor, P. W., Eds. *Origin and Evolution of the Metazoa,* pp. 131-176. New York, Plenum.
KAUFMAN, A, J. & KNOLL, A. H. 1995. Neoproterozoic variations in the C-isotopic composition of seawater: stratigraphic and biogeochemical implications. *Precambrian Res.* **73,** 27-49.
-------- , HAYES, J. M., KNOLL, A. H. & GERMS, G. J. B. 1991. Isotopic compositions of carbonates and organic carbon from upper Proterozoic successions in Namibia: stratigraphic variation and the effects of diagenesis and metamorphism. *Precambrian Res.* **49,** 301-327.
-------- , JACOBSEN, S. B. & KNOLL, A. H. 1993. The Vendian record of Sr and C isotopic variations in seawater: implications for tectonics and paleoclimate. *Earth & Planetary Science Letters* **120,** 409-430.
KELLER, B. M. & FEDONKIN, M. A. 1977. New organic fossil finds in the Precambrian Valdai Series on the Syuzma River. *Izv. Akad. Nauk SSSR* Ser. Geol. **3**, 38-44.
KEMPE, S. & DEGENS, E. T. 1985. An early soda ocean? *Chem. Geol.* **53,** 95-108.
KNOLL, A. H. & WALTER, M. R. 1992. Latest Proterozoic stratigraphy and earth history. *Nature* **356,** 673-678.
-------- , HAYES, J. M., KAUFMAN, A. J., SWETT, K. & LAMBERT, I. B. 1986. Secular variation in carbon isotope ratios from upper Proterozoic successions of Svalbard and East Greenland. *Nature* **321,** 832-838.
KRÖNER, A. & GERMS, G. J. B. 1971. A re-interpretation of the Numees-Nama contact at Aussenkjer, South West Africa. *Trans. Geol. Soc. S. Afr.*. 74, 69-74.
-------- McWILLIAMS, M. O., GERMS, G. J. B., REID, A. B. & SCHALK, K. E. 1980. Paleomagnetism of Late Precambrian to Early Paleozoic mixtite-bearing formations in southern Namibia (S.W. Africa); the Nama Group and Blaubeker Formation. *Am. J. Sci.* **280,** 942-968.
KULLING, O. 1972. The Swedish Caledonides. **In:** Strand, T. & Kulling, O. Eds., *Scandinavian Caledonides*, pp. 147-302. London, Wiley.
MARTIN, H. 1950. Südwestafrika. *Geol. Rundsch.* **38,** 6-14.
-------- 1965. *The Precambrian Geology of South West Africa and Namaqualand*. The Precambrian Res. Unit, Univ. of Capetown.
MATTHEWS, S. C. & MISSARZHEVSKY, V. V. 1975. Small shelly fossils of Late Precambrian and early Cambrian age: a review of recent work. *J. Geol. Soc. London* **131,** 289-304.
McHENRY, B. & YATES, A. 1993. First report of the enigmatic metazoan *Anomalocaris* from the southern hemisphere and a trilobite with preserved appendages from the Early Cambrian of Kangaroo Island, South Australia. *Rec. S. Aust. Mus.* **26**(2), 77- 86.
McMENAMIN, M. A. S., 1986. The garden of Ediacara. *Palaios* **1,** 178-182.

-------- 1987. The emergence of animals. *Scientific American* **256,** 94- 102.
-------- 1993. Osmotrophy in fossil protoctists and early animals. *Invertebrate Reproduction and Development* **23**(2-3), 165-169.
-------- 1996. Ediacaran biota from Sonora, Mexico. *Proc. Natl. Acad. Sci. USA* **93**, 4990-4993.
-------- & McMENAMIN, D. L. S. 1990. *The Emergence of Animals: the Cambrian Breakthrough*. New York, Columbia University Press.
NEDIN, C. 1995. The Emu Bay Shale, a Lower Cambrian Lagerstätten, Kangaroo Island, South Australia. *Mem. Ass. Australas. Palaeontols.* **18,** 31-40.
NURSALL, J. R. 1959. Oxygen as a prerequisite to the origin of Metazoa. *Nature* **183,** 1170-1172.
PALMER, D. 1996. Ediacarans in deep water. *Nature* **379,** 114.
PFLUG, H. D. 1966. Neue Fossilreste aus den Nama-Schichten in Südwest Afrika. *Palaeont. Z.* **40**(1-2), 14-25.
-------- 1970a. Zur fauna der Nama-Schichten in Südwest-Afrika I. Pteridinia, Bau und systematische Zugehörigkeit. *Palaeontographica* A**134,** 226-262.
-------- 1970b. Zur fauna der Nama-Schichten in Südwest-Afrika. II. Rangeidae, Bau und systematische Zugehörigkeit. *Palaeontographica* A**135,** 198-231.
-------- 1972a. Zur fauna der Nama-Schichten in Südwest-Afrika. III. Erniettomorpha, Bau und Systematik. *Palaeontographica* A**139,** 134-170.
-------- 1972b. Systematik der jung-präkambrischen Petalonamae. *Palaeont. Z.* **46,** 56-67.
-------- 1973. Zur fauna der Nama-Schichten in Südwest-Afrika. IV. Mikroskopische Anatomie der Petalo-organismen. *Palaeontographica* A**144,** 166- 202.
PICKFORD, M. H. L. 1995. Review of the Riphean Vendian and early Cambrian palaeontology of the Otavi and Nama Groups, Namibia. *Communs. Geol. Surv. Namibia* **10,** 57-81.
RAFF, R. A., MARSHALL, C. R. & TURBEVILLE, J. M. 1994. Using DNA sequences to unravel the Cambrian radiation of animal phyla. *Ann. Rev. of Ecology and Systematics* **25,** 351-375.
RANGE, P. 1912. Geologie des deutschen Namalandes. *Beitr. Geol. Erforsch dt. Schutzgeb.* **II**.
RETALLACK, G. J. 1994. Were the Ediacaran fossils lichens? *Paleobiology* **20**(4), 523- 544.
RICHTER, R. 1955. Die ältesten Fossilien Südafrikas. *Senckenb. Leth.* **36,** 243-289.
RUNNEGAR, B. 1982a. The Cambrian explosion: animals or fossils. *J. Geol. Soc. Aust.* **29,** 395-411.
-------- 1982b. A molecular clock date for the origin of animal phyla. *Lethaia* **15,** 199-205.
-------- 1982c Oxygen requirements, a biology and phylogenetic significance of the late Precambrian worm, *Dickensonia* and the evolution of the burrowing habit. *Alcheringa* **6,** 223-239.
-------- 1995. Vendobionta or Metazoa? Developments in the understanding of the Ediacara 'fauna'. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **195,** 305-318.
-------- & FEDONKIN, M. A. 1992. Proterozoic metazoan body fossils. **In:** Schopf, J. W. & Klein, C. Eds., *The Proterozoic Biosphere. A Multidisciplinary Study*. pp. 369-388. Cambridge University Press.
SAYLOR, B. Z. 1992/3. Progress report on the sedimentology and stratigraphy of the Kuibis and Schwarzrand Subgroups, Witputs area, southwestern Namibia. *Communs geol. Surv. Namibia* **8,** 127-135.
--------, GROTZINGER, J. P. & GERMS, G. J. B. 1995. Sequence stratigraphy and sedimentology of the Neoproterozoic Kuibis and Schwarzrand Subgroups (Nama Group) southwestern Namibia. *Precambrian Research* **73,** 153-170.
SCHENK, A. 1910. Bemerkungen zur geologischen Karte von Deutsch-Südwestafrika. *Meyer, Kolonialreich* II.
SCHWELLNUS, C. M. 1941. The Nama tillite in the Klein Karas Mountains, South West Africa. *Trans Geol. Soc. S. Afr.* **44,** 19-33.
SEILACHER, A. 1989. Vendozoa: organismic construction in the Proterozoic biosphere. *Lethaia* **22,** 229-239.
-------- 1992. Vendobionta and psammocorallia: lost constructions of Precambrian evolution. *J. Geol. Soc. London* **149,** 607-613.
SHU, D., CONWAY MORRIS, S. & ZHANG, X. -L. 1966. A *Pikaia*-like chordate from the Lower Cambrian of China. *Nature* **384,** 157-158.
SOKOLOV, B. S. 1975. On palaeontological finds in the pre-Usol deposits at Irkutsk Amphitheatre. *Trudy Inst. Geol. Geofiz. Sibirsk. Otd. SSSR Akad. Nauk* **232,** 112-117 (in Russian).
-------- & FEDONKIN, M. A. 1984. The Vendian as the terminal system of the Precambrian. *Episodes* **7**(1), 12-19.
SOUTH AFRICAN COMMITTEE FOR STRATIGRAPHY 1980. Stratigraphy of South Africa, Kent, L. E., compiler. *Handbook Geol. Surv. S. Afr.* **8,** 1-690.
SPRIGG, R. C. 1947. Early Cambrian (?) "Jellyfishes" from the Flinders Ranges, South Australia. *Trans. Roy. Soc. S. Aust.* **71,** 212-224.
STANISTREET, I. G., KUKLA, P. A. & HENRY, G. 1991. Sedimentary basinal responses to a Late Precambrian Wilson Cycle: the Damara Orogen and Nama Foreland, Namibia. *J. Afr. Earth Sci.* **13,** 141-156.
STANLEY, S. M. 1973. An ecological theory for the sudden origin of multicellular life in the Late Precambrian. *Proc. Nat. Acad. Sci. USA* **70**, 1486-1489.
-------- 1976. Ideas on the timing of metazoan diversification. *Paleobiology* **2,** 209-219.
TERMIER, H. & TERMIER, G. 1968. *Évolution et biocinèse. Les invertébrés dans l'histoire du monde vivant*. Paris, Masson.
THOMAS, A. L. R. 1997. The breath of life - did increased oxygen levels trigger the Cambrian explosion? *TREE* 12, 44-45.
VALENTINE, J. W. 1992. *Dickensonia* as a polypoid organism. *Paleobiology* **18,** 378- 382.
--------, AWRAMIK, S. M., SIGNOR, P. W. & SADLER, P. M. 1990. The biological explosion at the Precambrian-Cambrian boundary. *Evolutionary Biology* **25,** 279-356.
VERMEIJ, G. J. 1989. The origin of skeletons. *Palaios* **4,** 579-584.
VON BACKSTRÖM, J. W. 1960. Die geologie van die gebied om Nieuwoudville, Kaapprovinsie. *Geol Surv. Explanation of sheet 241*.
WADE, M. 1972. *Dickensonia*: polychaete worms from the late Precambrian Ediacaran fauna, South Australia. *Mem. Queensland Mus.* **16**(2), 171-190.
WAGGONER, B. M. 1995. Ediacaran lichens: a critique. *Paleobiology* **21**(3), 393-397.
WALTER, M. R. & HEYS, G. R. 1985. Links between the rise of the metazoa and the decline of stromatolites. *Precambrian Research* **29,** 149-174.
WHITTINGTON, H. B. 1971. The Burgess Shale, history of research and preservation of fossils. *Proc. N. Amer. Paleon. Convention* 1969, **1,** 1170-1201.
-------- 1985. *The Burgess Shale*. New Haven, Yale Univ. Press.
WRAY, G. A., LEVINTON, J. S. & SHAPIRO, L. H. 1996. Molecular evidence for deep Precambrian divergences among Metazoan phyla. *Science* **274,** 568-573.

XING, Y., & LIU, G. 1979. Coelenterate fossils from the Sinian System of southern Liaoning and its stratigraphic significance. *Acta. Geol. Sinica* **53,** 167-172.

YOCHELSON, E. L. 1967. Charles Doolittle Walcott, 1850-1927. A biographical memoir. *Biographical Memoirs* **39,** 471-540.

ZHANG, W. -T. & HOU, X. -G. 1985. Preliminary notes on the occurrence of the unusual trilobite *Naraoia* in Asia. *Acta Palaeontologia Sinica* **24**(6), 591-595.