

Review of the Riphean, Vendian and early Cambrian palaeontology of the Otavi and Nama Groups, Namibia

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The Otavi and Nama Groups of Namibia span the late Proterozoic and early Cambrian periods. The fossil record of these two groups documents evolution during a particularly interesting stage of the Earth's history - the period during which the transition from primitive diploblastic organisms to triploblastic, muscle-powered, metazoans with nervous systems, occurred. It was also a period of evolution of an extinct group of organisms, the Vendozoa. Much remains to be learnt about the organisms of this period, this paper being in the nature of a review of work that has already been done on the fossils of the Otavi and Nama Groups.

Introduction

The Otavi and Nama Groups of Namibia are of Riphean and Vendian-Cambrian ages respectively. Fossils from these strata are important for seven main reasons. In particular, organisms of the Proterozoic had major impacts on the superficial parts of the lithosphere, the hydrosphere and the atmosphere.

a) They played an important role in the deposition of immense quantities of carbonates which were later to become the host rocks for massive hypogene sulphide deposits, principally of lead, copper and zinc, and of important supergene ores, especially of vanadium. They also produced vast quantities of organic carbon compounds which were buried in sediments, and they may have played a significant role in the concentration of metallic ions in some situations (e.g. pyrite-fixing bacteria).

b) They played a crucial role during photosynthesis of releasing free oxygen into Earth's atmosphere (and hydrosphere) and in acting as agents for the accumulation of vast quantities of organic carbon in the crust. The latter also led to increases in the partial pressure of oxygen in the atmosphere. Prior to ca. 2 Ga the partial pressure of oxygen in the atmosphere was less than $10^{-3.5}$ bars, whereas after this date oxygen comprised over 20% of the atmosphere (greater than $10^{-2.5}$ bars but less than $10^{-1.5}$ bars). This in turn determined the sorts of metallogenic activity that took place in sedimentary environments.

c) They played an important role in the hydrosphere, principally by removing some ions (Fe, S, Ca, CO₃ etc.) from the water column, and by adding others (O₂) to it. The Vendozoa, in particular, may have played a significant local role in altering water chemistry in shallow marine situations, if indeed they were chemosynthetic organisms.

d) They provide information useful for reconstructing depositional environments. The Otavi stromatolites, for example, accumulated in shallow marine conditions, with reefs, back-reef lagoons, fore-reef debris aprons and so on.

e) They provide important information concerning

the ages of the Otavi (Riphean) and Nama (Vendian-Cambrian) Groups. At present biostratigraphic age estimates for the Otavi and Nama Groups are rather broad and imprecise, but future research on acritarchs and other micro-organisms may well lead to greater precision in biostratigraphy than is now possible.

f) They are potentially of use for reconstructing palaeogeography, including for example, palaeolatitude, on the basis of organismal diversity gradients, which today are generally high near the equator and low in high latitudes.

g) They are of immense palaeontological interest, occurring in strata that pre-date the Cambrian organismic explosion. As such they provide data concerning life forms that are leading towards the evolution of Metazoa and Vascular Plants of the Palaeozoic, Mesozoic and later eras (see Table 1).

This paper is organised into two parts, the first dealing with the Otavi Group, the second with the Nama Group. It is aimed at reviewing previous palaeontological work done in Namibia, which is scattered in the literature and which has not hitherto been the subject of an overall synthesis. As such it is a situation report of what has been achieved in this country, and will hopefully act as a springboard to stimulate future research programmes.

Unfortunately, many of the specimens described in the literature have been lost, or their whereabouts are unknown. Only a few specimens, including the holotype of *Protechiurus edmondsi*, are in the Geological Survey Museum, Windhoek, while a small sample of Vendozoa, including a fine example of *Rangea schneiderhoehni*, is at the South African Museum, Cape Town. Some material may be in Germany, but details are unavailable to the author.

Part 1

OTAVI GROUP PALAEOLOGY

Introduction

The oldest fossils so far recognised in Namibia are

Ga Fossil sites	Main organic events	Other events
O		Glaciation
Karoo		Glaciation
Nama	Plantae	
Otavi	Vendozoa, Metazoa	Glaciation
1 Bittersprings	Stromatolite diversity peak	Glaciation
Belt	Megascopic algae	Glaciation
Amelia	Eukaryotes	
		Oxygen-rich atmosphere
2 Gunflint		
Transvaal	Blue-green algae	Glaciation
	Monera	
Bulawayo	Bacteria	
3		?Glaciation
Fig Tree		
Onverwacht	Osmo-heterotrophs	
	Proteinoid microspheres	
Isua		
4	Proteinoids	
5		

Table 1: Stratigraphic position of the Otavi and Nama Groups relative to the Darwinian Time Scale and to major atmospheric and superficial geological events.

preserved in the middle Proterozoic (Riphean) Otavi Facies of the Damara Sequence (ca. 830-760 Ma) (Pirajno *et al.*, 1993; Table 1). Earlier sediments of the Haib Group (2000-1800 Ma), the Sinclair Sequence (1800-1000 Ma), and the Nosib Group (1000-840 Ma) are potential palaeontological targets, but thus far no fossils have been reported from them.

The Otavi Dolomite Series, over 5300 metres thick, is rich in stromatolites and oncolites of various sorts (Table 2) (Krüger, 1969) yet there has been remarkably little written about them (Kräusel, 1965; Schneiderhöhn, 1921; Schweltnus and Le Roex, 1944; Söhnge, 1954 unpubl., 1957 unpubl.; Van Zijl, 1964, unpubl.; Martin, 1965; Veldsman, 1977; Porada, 1983), and their biogenic origin has been assumed rather than demonstrated.

Definitions

There is some uncertainty and debate about the meaning of the words 'stromatolite' (Kalkowsky, 1908) and 'oncolite' (Pia, 1927; Buick, *et al.*, 1981). For some authors, these terms are purely morphological and the structures so named do not have to have a biogenic origin, whilst for others biogenicity is the *sine qua non* for using the terms. Buick, *et al.* (1981) suggest that 'stromatolite' should be restricted to 'organosedimen-

tary structures predominantly accreted by sediment trapping, binding and/or *in situ* precipitation as a result of the growth and metabolic activity of benthic, principally prokaryotic micro-organisms'. For these authors, similar structures of non-biological or of unproven biological origins, should be called 'stromatoloids'. The term 'oncolite' was coined for mobile, laminated microbial accretions (Pia, 1927) and is thus a sub-category of stromatolites, which are usually sedentary, in the sense that they accrete while their base is fixed relative to the substrate.

When he described the Otavi stromatolites, Krüger (1969) utilised a classification and structural formula of stromatolites published by Logan, *et al.* (1964). This classification was criticised by Buick, *et al.* (1981) on the grounds that the authors allowed inorganic structures that resembled microbially accreted forms to be called stromatolites. In its original definition by Kalkowsky (1908) the term 'stromatolite' was based mainly on the internal and external morphology of the structures, but the role of micro-organisms in their production was clearly intended by Kalkowsky, because he added that "lower vegetal organisms ... initiated the precipitation of the calcium carbonate".

Even though the classification of Logan, *et al.* (1964) has been criticised for its inclusion of abiogenic struc-

Tsumeb Subgroup 3650m	Huttenberg Formation 900m	Dolomite with chert Shale, Limestone Stromatolites, Oölites
	Elandshoek Formation 1100m	Dolomite with chert Stromatolites
	Maiberg Formation 950m	Dolomite, Limestone Slump Breccia
	Chuoss Formation 700m	Mixtite, Dolomite Limestone, Sandstone Itabirite, Oölit, Chert
Abenab Subgroup 1725m	Auros Formation 450m	Dolomite, Limestone, Marl, Shale Stromatolites
	Gauss Formation 750m	Dolomite, Limestone Oölitic chert, Sandstone
	Berg Aukas Formation 525m	Dolomite, Limestone Stromatolites, Arkose Greywacke

Table 2: Stratigraphy and lithology of the Otavi Group, total thickness 5375 metres.

tures within the term stromatolite, it retains some use in palaeo-ecological reconstructions. The morphology of stromatolites yields information concerning depositional environments, including water depth, temperature range, wave action and so on.

Otavi stromatolites

Strictly speaking, the Otavi stromatolites should be called stromatoloids, since their biogenicity has not been demonstrated by appropriate microscopic studies. However, the bulk of the structures described by Schweltnus and Le Roex (1944) and by Krüger (1969) (Figs. 1-12) fulfil most of the macroscopic criteria for recognising stromatolites in the field (Buick *et al.*, 1981) and it would be surprising if most of them were not of biogenic origin. These criteria are as follows :-

- 1.- The structures are in undoubted sedimentary rocks
- 2.- The structures are syndimentary
- 3.- Most of the structures are convex upwards, al-

though many *Conophyton* stromatolites are concave upwards

4.- Laminae thicken over the crests of flexures

5.- Laminations in the structures are wavy, wrinkled and have several orders of curvature.

Ideally, microscopic research should be done to demonstrate the biogenic origin of the Otavi stromatoloids, using the following criteria listed in Buick, *et al.* (1981):-

1.- Microfossils or trace fossils should be present within the structures

2.- Changes in the composition of microfossil assemblages should be accompanied by morphological changes of the stromatoloid

3.- The fossils or trace fossils must be organised in a manner indicating trapping, binding or precipitation of sediment by the living micro-organism.

The Otavi stromatolites and oncolites have been given descriptive names, including 'tütenmergelartige Horn-steineinlagerungen' (Schneiderhöhn, 1921, shortened to 'Tüten' stromatolites by Krüger, 1969), 'Ringel

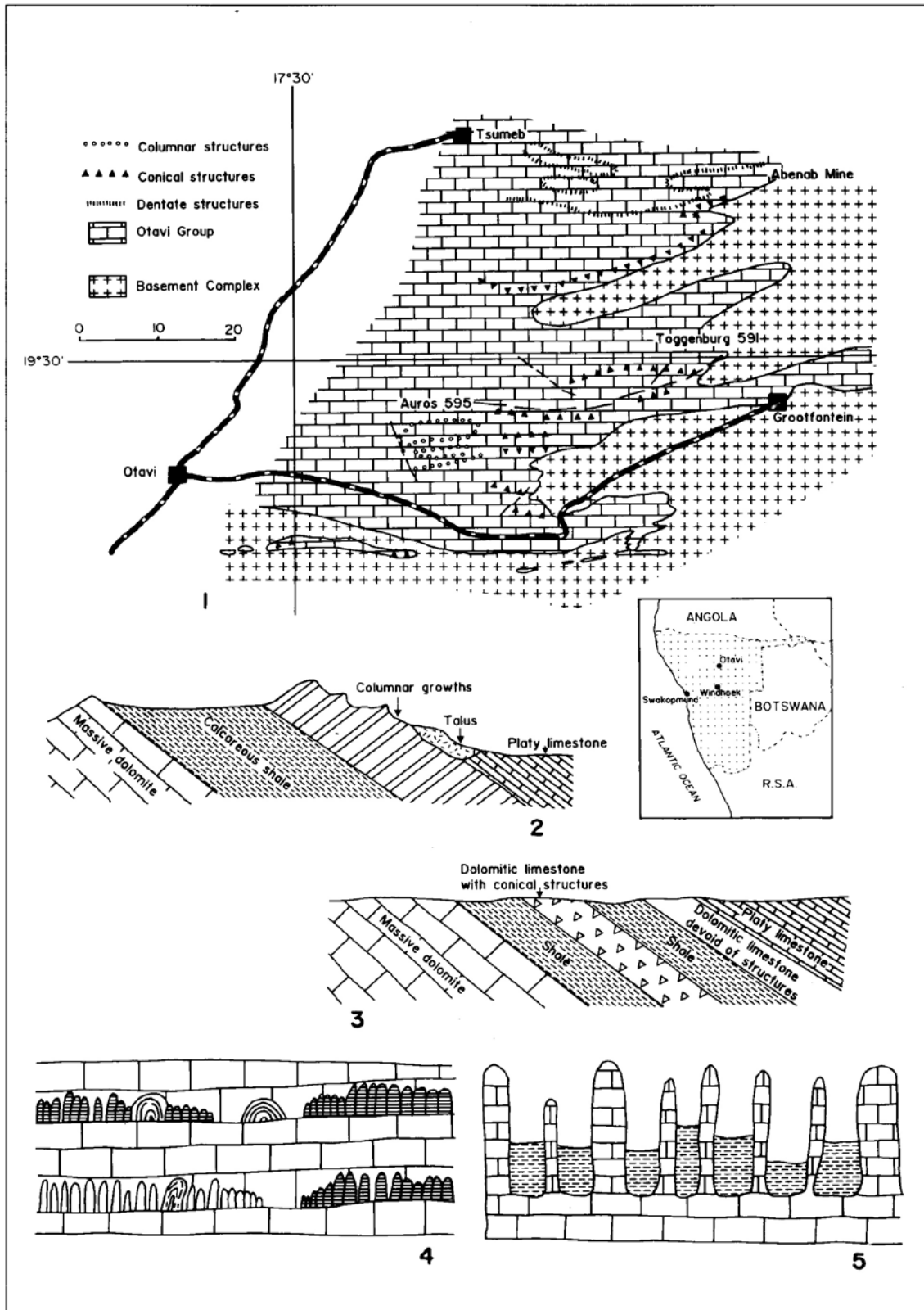


Figure 1: Geological sketch map of the Otavi-Tsumeb-Grootfontein region showing distribution of stromatolitic structures (from Krüger, 1969). **Figure 2:** Section across Shale Band Stage on Auros 595 (from Krüger, 1969). **Figure 3:** Section across Shale Band Stage on Toggenburg 591 (from Krüger, 1969). **Figure 4:** Diagrammatic section through massively bedded dolomite carrying dentate and bun-shaped structures on Abenab 707 (from Krüger, 1969). **Figure 5:** Section illustrating weathering characteristics of dentate structures on Abenab 707 (from Krüger, 1969).

dolomite' (comprised of *Crypiozoon*- and *Collenia*-type stromatolites) (Fig. 7), columnar structures (*Collenia frequens*?-type structure), cylindroids, lateral linked hemispheroids, and *Conophyton* or 'stacked cone' stromatolites. Others include oölites, 'algal buns' (Figs 10-11), algal mats, and spheroidal structures. Some of these, especially the oölites (Fig. 9), may not be biogenic in origin, but the bulk of them probably are.

The high diversity of Otavi stromatolites is suggestive of a relatively low latitude for Namibia at the time of deposition, but further work on a continental basis is required to substantiate this possibility. If low latitude is supported, then it would speak in favour of low latitude glaciation during Chuos times.

Krüger (1969) described the morphology and context of the Otavi stromatolites (Fig. 1) recording specimens from the lower, middle and upper Abenab Stages (or sub-stages) and from the middle and upper Tsumeb Stages (or substages). He reported that the Abenab Stage ended after a change in climate led to the deposition of tillite in the Otavi basin: the lower Tsumeb Stage (Chuos Formation mixtite). The Chuos mixtite (or tillite) may represent the late Proterozoic Glaciation of Sturtian age (800-700 Ma) (Eyles, 1993). It is less likely to have been due to a poorly known glaciation of middle Riphean age (1000 Ma) or the Huronian Glaciation (2200-2100 Ma) (Byles, 1993), since the Nosib Group, which underlies the Otavi Group is estimated to range in age from 1000-840 Ma (Pirajno, *et al.*, 1993).

Stromatolite activity recommenced in the Middle Tsumeb Stage with oölitic beds and wrinkled algal mats, suggesting deposition in deep water with low photic energy levels. The upper Tsumeb Stage is rich in 'Tüten' stromatolites, 'stacked cones' and algal buns indicative of more shallow water conditions. Along the northern rim of the Otavi Basin, reef-type stromatolites formed an incomplete barrier between the open sea and quieter water lagoons on the landward side.

Depositional environments

Krüger discussed the palaeoenvironmental implications of the various types of stromatolites and oncolites based on the scheme of Logan, *et al.* (1964), and reconstructed the depositional environments in which they formed (Fig. 13). He concluded that most of the stromatolites grew in relatively shallow seawaters, those in the Abenab stages in particular, indicating warm water conditions. In the upper Tsumeb Stage, stromatolites and oncolites occur in several depositional facies ranging from shallow water to deeper water as follows :-

1. - Bedded dolomite with silicified algal mats and erratic oncolite layers
 - 2.- Reef-type stromatolites - elongated domes roughly normal to the wave line
 - 3.- Reef detritus
 - 4.- Bedded oölites
- Seawards of the bedded oölites dark grey bedded

shale (now phyllite) with disseminated pyrite was deposited.

Individual reefs contain varied composite stromatolite forms dictated by local palaeoenvironmental conditions. Among the facies considered to be present in the Otavi Sequence, there are wide intertidal flats, shallow lagoons, and gently undulating continental shelf areas which favoured extensive horizontal development of stromatolite-bearing strata. The famous 'tüten' beds, for example, can be mapped for more than 160 km along strike and 10 km along dip.

The algal growths from different stratigraphic units indicated to Krüger (1969) that Stable, and relatively quiet environmental conditions prevailed for long periods, the only exception being on the north side of the Otavi basin where typical reef environments developed, in which more energetic conditions occurred. The latter led to the development of cut and fill structures in the oölitic facies and to the development of talus fans.

Biostratigraphy

Cloud and Semikhatov (1969) discussed the age of the Otavi sequence on the basis of stromatolites. Although stromatolite types have very long ranges, there are several taxa which are confined to the Proterozoic. From the lower Abenab Formation, Cloud and Semikhatov (1969) recorded the species *Baicalia* aff *B. rara* Semikhatov, which suggested to these authors an age less than 1.2 Ga. In the upper Abenab Formation they recorded the species *Conophyton resotii* Menchikoff, which indicated an age of greater than 0.6 Ga.

Discussion

Algae were the dominant life forms for most of the Proterozoic, and were largely responsible for the production and maintenance of the earth's oxygen-rich atmosphere ca. 2 Ga. The Otavi stromatolites lived at a time before the evolution of the Vendozoa in the late Proterozoic, and they played a role in setting up the atmospheric conditions which would eventually enable the Metazoa to evolve at the end of the Proterozoic.

Furthermore, the accumulation of the Otavi Dolomites was to have an important influence on mineralisation and fossil preservation at much later dates than that of their deposition (Pirajno and Joubert, 1993; Pickford, 1993). The dolomites were subjected to karst processes during the Damaran orogeny, the resulting hollows frequently filling with heavy metal sulphides such as galena, chalcopyrite and sphalerite which today form the basis of the Otavi Mountainland economy.

During the Tertiary, these dolomites were exposed to subaerial conditions, with the result that a second cycle of karstification set in, often in the same areas as the previous cycle. This was partly, because certain dolomite beds are more soluble than others, but also because the exposure of sulphide minerals to the atmosphere or

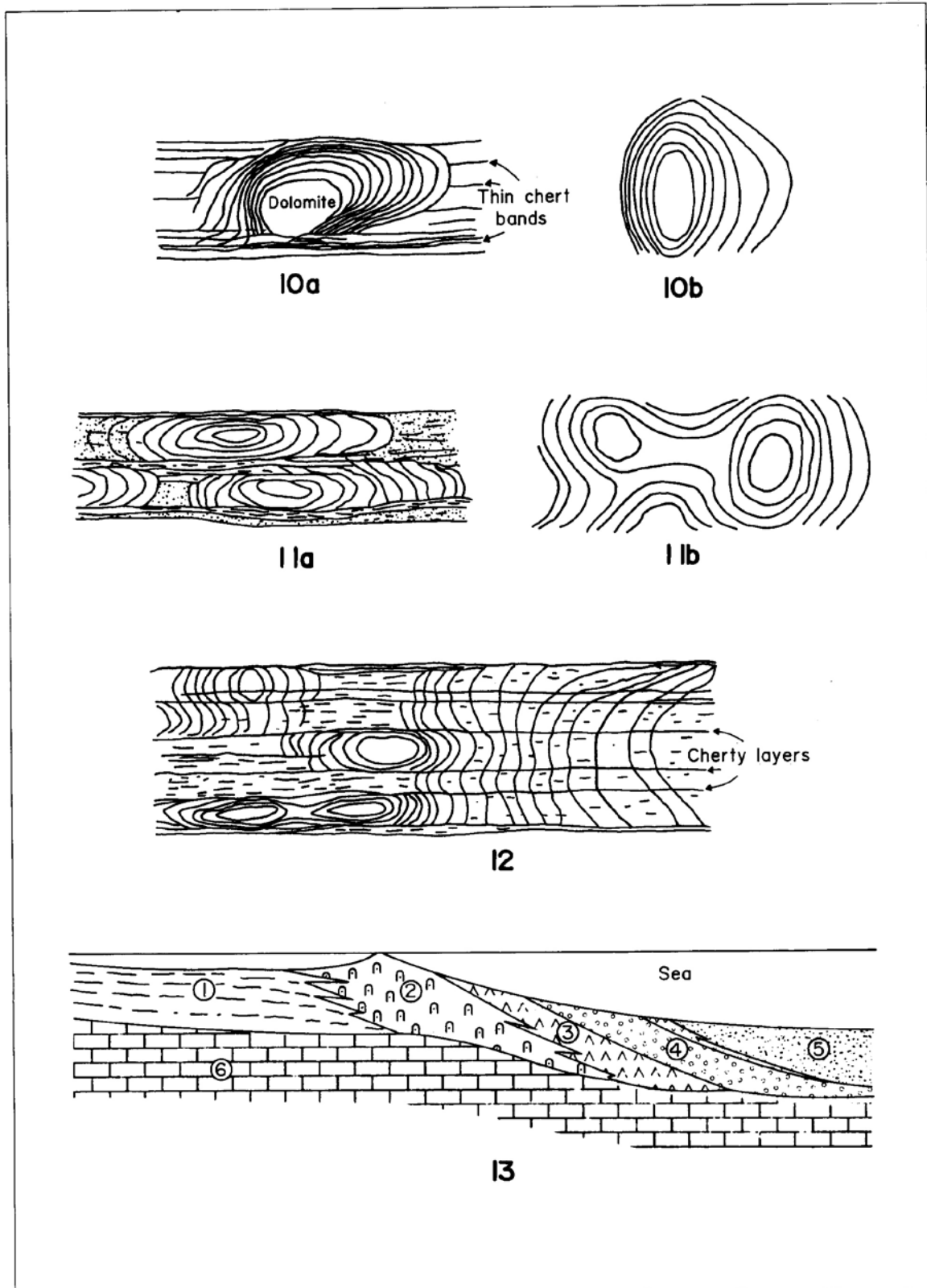


Figure 10: 'Algal buns' (from Krüger, 1969), a. vertical section, b. plan. **Figure 11:** 'Algal buns' (from Krüger, 1969), a. vertical section, b. plan view of structures. **Figure 12:** 'Algal buns' developing into composite structures (from Krüger, 1969). **Figure 13:** Reconstructed local profile through the north flank of the Otavi Basin before tectonic deformation (from Krüger, 1969). 1. bedded dolomite with silicified algal mats and erratic oncolite layers, 2. reef-type stromatolites - elongated domes roughly normal to the shore-line, 3. reef detritus, 4. bedded oolites, 5. dark grey bedded shale (now phyllite), with disseminated pyrite, 6. bedded dolomite of the Upper Tsumeb sub-stage - zone 6.

to oxygen-rich ground waters often results in their oxidation, a by-product of which is sulphuric acid, which promotes the dissolution of dolomite. The caves and fissures thus tended to form near sulphide masses. In proximity to massive sulphide bodies, vanadium in solution in circulating ground waters would precipitate in lead-rich or copper-rich environments as the relatively insoluble minerals descloisite, mottramite and vanadinite, thereby forming the economic vanadium deposits of the Otavi Mountainland, most, if not all, of which are late Tertiary (middle Miocene to Plio-Pleistocene) in age (Pickford, 1993).

Like caves and fissures all over the world, the Otavi cavities tended to act as traps for sediments and for fossils if they were open to the surface. In the Otavi dolomite facies all over northern Namibia, cave fills of diverse ages ranging from middle Miocene to Holocene are preserved. Many of these are fossiliferous, and have yielded a fine succession of vertebrate faunas (Senut *et al.*, 1992; Pickford, 1993).

Part 2

NAMA GROUP PALAEOLOGY

Introduction

The Nama Group, of late Proterozoic and early Phanerozoic age (567 -537 Ma according to Runnegar and Fedonkin, 1992), which crops out extensively in the south central region of Namibia, with important extensions in South Africa, is of immense palaeontological interest for three main reasons.

1.- At its base it contains abundant evidence of Vendozoa, sometimes considered to be a sort of half-way stage between single celled organisms (Monera and Protoctista) of the early and middle Proterozoic and multicellular organisms (Metazoa) which evolved towards the end of the Proterozoic. Vendozoa appear to have been sedentary organisms that were not subjected to serious predation pressures until the end of the Proterozoic, principally because the diversity of independently locomoting organisms (capable of predation) was restricted. Once such metazoan predators evolved, the sessile soft-bodied Vendozoa proved 'easy fare' and it has been postulated that they may have been eaten to extinction by the time of the Cambrian organismic explosion.

2.- The Nama Group documents the evolution of Metazoa, principally as traces of their activity which are preserved in fine-grained sedimentary facies. In effect, the Nama Group is one of the few rock units known which spans the record of the onset of voluntary muscle-driven locomotion and of predation by multi-cellular organisms. Brain (1994) has discovered microscopic metazoan body fossils preserved in glassy cherts of the Mooifontein Formation. These are among the earliest known body fossils of this group.

3.- Surely not coincidental with 2 above, is that the Nama Group contains the earliest known evidence of the development of hard skeletal parts in organisms - in *Cloudina* - probably as a defence mechanism against predation by freely moving metazoans. Other organisms with external body 'armour' may include *Archaeichnium haughtoni* in which a body coating of sand grains may have covered and 'protected' the soft-bodied organism inside it, and *Hagenetta aarensis* which is reported to have had two non-calcareous, but nevertheless durable, presumably resistant, valves.

Thus, the Nama Group is of the greatest scientific interest, documenting as it does, three of the early evolutionary stages which led towards the biological 'arms race', the earliest and most dramatic expression of which was the Cambrian Biological Explosion. Because it existed prior to the days of predation, the Vendian bionta is sometimes said to have lived in the 'Garden of Ediacara'.

Stratigraphy and age

The Nama Group has been subdivided into three major units: from below upwards they are the Kuibis, Schwarzrand and Fish River Subgroups (Martin, 1965; Germs, 1972, 1974; Saylor, 1993) (Table 3). The basal Kuibis Subgroup accumulated in two basins separated by the Osis Ridge, which became progressively buried so that by Schwarzrand time the ridge no longer divided the basin into two, allowing the overlying Schwarzrand and Fish River Subgroups to accumulate in continuous beds from north to south. Each of the Nama subgroups is comprised of several formations and members (Table 3) many of which are fossiliferous (Tables 4 and 5).

The Vendozoa or Vendobionta

Because the Vendozoa have no hard parts, fossil occurrences tend to be rare - there are only a score of sites known in the world (Morris, 1990; Runnegar and Fedonkin, 1992). Where they do occur they are usually localised and are comprised of impressions in various sedimentary rocks, often indurated sands of various sorts. In the Nama Group, the principal fossiliferous facies for finding Vendozoa are quartzites (the Kuibis Quartzites, Gürich, 1933; the Niederhagen and Nasep Members, Germs, 1983). The Nama vendozoan fossil preservation thus resembles that of the world famous Ediacara bionta of the Pound Quartzite, Australia, while other occurrences such as Mistaken Point, Newfoundland, consist of impressions of soft-bodied organisms in pelagic sediments that were covered by volcanic ash.

Ediacara-like fossils were first reported from Namibia in 1929 (Gürich, 1929, 1930a, b, 1933; Haughton, 1929), long before they were found in Australia (Runnegar and Fedonkin, 1992). They had been found as early as 1908 by Range and 1914 by Schneiderhöhn in the debris of small shelters built of quartzitic rock

P e r i o d	Subgroup	FORMATION Member	Body fossils	Trace Fossils
C a m b r i a n	Uppermost Schwartzrand	NOMTSAS		<i>Diplichnites</i> <i>Neonereites</i> <i>Phycodes pedum</i>
v e n d i a n	Schwartzrand	URUSIS Spitskop Member ----- Huns Member ----- Nasep Member ----- NUDAUS	<i>Cloudina</i> <i>Stromatolites</i> <i>Cloudina</i> <i>Cyclomedusa</i> <i>Stromatolites</i> <i>Nasepia</i> <i>Paramedusium</i> <i>Pteridinium</i> <i>Pteridinium</i> <i>Rangea</i>	<i>Brooksella</i> <i>Curvolithus</i> <i>?Didymaulichnus</i>
v e n d i a n	Kuibus Upper	ZARIS Mooi- fontein	<i>Cloudina</i>	
v e n d i a n	Kuibus Lower	DABIS ----- Kliphock Member ----- Mara Member ----- Kanies Member	<i>Ernietta</i> <i>Namalia</i> <i>Orthogonium</i> <i>Pteridinium</i> <i>Rangea</i> <i>Ausia</i> <i>Kuibisia</i> <i>Hagenetta</i> <i>Erniobaris</i> <i>Cloudina</i>	<i>Bergaueria</i> <i>Buchholzbrunn- ichnus</i> <i>kroneri</i> <i>Skolithos</i>

Table 3: Summary of Nama Group stratigraphy and fossil content.

slabs by the German Schutztruppe on the farms Plateau and Aar. They have excited interested commentary and controversy ever since. In general, the Nama Vendozoa are well preserved, abundant and relatively widely distributed within the Kuibis Quartzite and other formations, several famous localities having been discovered along the western scarp of the Nama Group in Lüderitz and Bethanien Districts.

Because vendozoan fossils are generally preserved as impressions, there has been a great deal of debate as to the interpretation and reconstruction of the various organisms comprising the bionta. Even today there is no consensus of opinion among Ediacaran palaeontologists as to their place in nature. Some researchers try to 'shoe-horn' them into one of the five extant kingdoms (Monera, Protoctista, Animalia, Fungi, Plantae) or into some subcategory of these kingdoms (Glaessner, 1959, 1976, 1979; Germs, 1973b; Hahn and Pflug, 1985b; Haughton, 1959), while others prefer to locate them in a phylum of their own, the Vendozoa (Seilacher, 1989) or even a kingdom of their own, the Vendobionta (Seilacher, 1992).

Some palaeontologists consider Vendozoa to be multicellular heterotrophs (that is metazoans), while others consider them to be immense single-celled autotrophs with the ability to absorb nutrients through the body wall. A third suggestion has been that they possessed photosynthetic endosymbionts. Various theses are to be found in the literature, summarised by Runnegar and Fedonkin (1992). For example, some of the Nama biotic forms have been considered to be primitive precursors of brachiopods, molluscs or crustaceans.

The important question is whether the Nama fossils should form the basis for the erection of a sixth kingdom, thereby radically altering current notions of past organismal diversity at the highest taxonomic level, or whether they can be accommodated in one of the five presently accepted kingdoms.

The concept of Vendozoa (Seilacher, 1989) (or Vendobionta Seilacher, 1992) has been useful in that it has obviated the tendency to 'shoe-horn' the organisms into extant phyla, with the concomitant tendency to 'impose' interpretations on them, as for example was done by Pflug (1966, 1970a, b, 1971, 1972a, b, 1974; Hahn and Pflug, 1985, 1988) Glaessner (1963, 1971) and others, under the perhaps mistaken impression that they were dealing with early forms of corals, worms and other Phanerozoic organisms.

It has become evident during the past decade that the study of *in situ* occurrences of these fossils is of the greatest importance, many of the older studies being rendered obsolete or of doubtful value because no record was made of the field orientation, especially of the way-up, of the fossils, or of the spatial relationship between individuals within fossil populations. Until 1992, for example, the leaf-like Germs *Pteridinium* was habitually figured upside down, and its life position reconstructed in such a position. Examination of *in situ*

material showed the error and has profoundly altered our perception of its life position, life style, growth and reproductive pathways. Furthermore, museum collections tended to be of fragments of organisms, so that parts of single organisms could and did end up being described as different species or even genera.

Body Fossils

Body fossils in the Nama Group fall into two main categories - those composed only of soft parts and those with shells or other durable body coverings. Among the former group, growth is both fractal and serial, the basic structure of the body being quilted, which imparts a ribbed appearance to the fossils. Quilting is a particular strategy for maintaining rigidity (or semi rigid bodies) in soft tissues, much as an inflatable mattress is given rigidity by the simple tactic of making it in compartments. Seilacher (1989, 1992) has called this morphology the 'pneu structure' (Fig. 15), from the French word for tyre. It implies that the hollow pneus were filled with liquid or jelly-like substances. When the organism is compressed after death, the roof and floor of the pneus tend to collapse, while the side walls retain their form, thus giving rise to the ribbed appearance of many of the Vendobionta. Gürich (1933) described *Orthogonium parallellum* as a fossil in which box-shaped sections were separated by gaps. The specimen on which this Germs is based could conceivably represent a specimen in which the pneu structure was infilled with sediment prior to fossilisation, thus preserving in three dimensions the positive structure of the organisms, rather than the compressed structures that usually are bequeathed to us. If this should be the case, then Seilacher's interpretation of the ridges in fossils of Vendozoa would appear to be seductive.

Soft bodied sessile Vendian organisms of Namibia: Vendobionta Seilacher, 1992 (or Vendozoa Seilacher, 1989)

More than a dozen species of Vendobionta are known from the Nama Group, and there are undoubtedly several others awaiting description and naming.

These have been classified in many different ways. Some authors including Glaessner (1971) have endeavoured to fit them into groups known from the Phanerozoic, such as Coelenterata, Hydrozoa, Conulata, Scyphozoa, Anthozoa, Annelida, Polychaeta, Trilobitomorpha and Crustacea, while others have created new families, orders, sub-orders, phyla and even a kingdom for them. One of the early names created for a subgroup of Vendobionta was Petalonamae Pflug, 1970 - the Nama petals - for the large sessile, colonial and gregarious soft-bodied organisms. Other suprafamilial names proposed for these organisms include Rangeomorpha Pflug, 1972, and Psammocorallia Seilacher, 1992.

In this report, I do not use supra-generic names, on

Behoboth District	
Dreidoornvlakte 490	<i>Cloudina</i>
Berghoek 506	<i>Diplocraterion, Nereites</i>
Maltahöhe District	
Grootplaats	<i>Skolithos</i>
Harughas	<i>Diplocraterion</i>
Hauchabfontein	<i>Cloudina</i>
Kuderup	? <i>Chondrites, Diplocraterion</i>
Osis	<i>Skolithos, Diplocraterion, ?Chondrites</i>
Zaris Pass	<i>Cloudina</i>
Lüderitz District	
Aar 16	Vendobionta
Hoogland	<i>Cloudina</i>
Kolke	Phylloid alga
Plateau 38	Vendobionta
Schakalskuppe	<i>Velancorina martina</i>
Swartkloofberg	<i>Cloudina</i>
Bethanien District	
Arimas	<i>Nasepia altae</i> , Phylloid alga
Buchholzbrunn	<i>Buchholzbrunnichnus</i>
Chamis	<i>Rangea</i>
Helmeringhausen	<i>Cloudina</i>
Huns 106	<i>Brooksella</i>
Kalkfontein	<i>Rangea</i>
Kuibis Nord	Vendobionta
Mooifontein	<i>Cloudina</i>
Quaggaspoort	<i>Cloudina</i>
Uitsig	<i>Cloudina</i>
Vergelee	<i>Diplichnites, Neonereites</i>
Vrede	<i>Rangea, Namalia</i>
Keetmanshoop District	
Gainachas	<i>Enigmatichnus africanus</i>
Gavaams	<i>Phycodes pedum</i>
Gründoorn	<i>Archaeichnium haughtoni, Orthogonium</i>
Hooolog	<i>Cloudina</i>
Naute	Trace fossils
Karasburg District	
Ai-Ais	?Radiolaria

Table 4: Fossiliferous localities in the Nama Group

account of the fact that no two authors appear to agree on supra-generic placement of any of the Nama Group fossils, a fact that not only highlights the complexities of interpreting such fossils, but also indicates how ignorant we are of the life forms that inhabited Earth in the late Proterozoic period. In question are the origins of at least two kingdoms, Plantae and Animalia. One cannot overemphasize the scientific value of the Nama fossils for settling, or more correctly, for stimulating the debates that revolve around the origins of organisms that dominate the Earth today.

Pteridinium simplex (Gürich) 1930, (originally listed as *Pteridium simplex*).

Pteridinium (Fig. 14c, d) is a bath-tub shaped organism with a median ridge running down the length of the tub. Specimens occur in 'colonies' and can be over 30 cm long. Initially, the organism was thought to be horse-shoe shaped in section, with the convex side upwards (Pflug, 1972), but study of *in situ* specimens reveals that without exception, the specimens had the convex side oriented downwards during life (Seilacher, 1992). *Pteridinium* had unipolar growth and was quilted serially. It appears that budding of new individuals took place along the central ridge in the 'bath tub' or along the tops of the 'bath tub walls'. The geometry of the organism indicates that it probably lived just below the surface of the sand, which in turn indicates that it was very probably a chemosynthesiser, and not a photosynthesiser: it may have been a sort of living battery, getting its energy from the bath of chemically charged interstitial waters that characterises marine sands.

The sedimentary environment appears to have been shallow marine, with enough background sedimentation that the walls of the organisms had to grow upwards as sedimentation tended to bury them, and thereby produced 'sediment stickers'. In contrast to sediment stickers, in areas of low sedimentation there lived flat reclining organisms, in which a mat-like body profile occurred.

Pteridinium was first collected in the Kuibis Quartzite on Farm Kuibis, but it has since been found in various places, especially on Farms Plateau, Kalkfontein, Aar, Schakalskuppe, and Kolke (Germs, 1972a).

Rangea schneiderhoehni Gürich, 1929 (1930)

The Germs *Rangea* (Fig. 16) is common in Namibia, where minor variations of form have led to taxonomic splitting. Gürich himself named two 'forms' of *Rangea schneiderhoehni*, forma *plana* and forma *turgida*. He also erected a separate species *Rangea ? brevior*, which appears to belong to the species *R. schneiderhoehni*.

Rangea has unipolar growth, and exhibits fractal quilting (Seilacher, 1989) and, like *Pteridinium*, it appears to have been a sediment sticker. The holotype was found on Farm Kuibis, and other samples have been reported from Farms Chamis and Vrede.

Germs (1973) described this Germs in detail. The

known specimens have leaf-like bodies with primary and secondary branches, or vein-like structures. These are now interpreted as being part of a network of pneu morphology. One of the specimens is 6.5 cm wide and 7.5 cm long. The primary branches form an angle of 40-60° with the somewhat obscure median line. The secondary branches are bilateral and form angles of 45-55° with the primary branches in the plane of the 'leaf'. The spacing between the primary furrows is 4-5 mm, and that between the secondary furrows is 0.9-1.1 mm. Near the axis there are commisure ribs between the prominent primary ones. The inner extremities of the primary branches slope and taper towards the median line and then show secondary branches in one direction.

A second specimen is 9 cm long and 4.7 cm wide, of which the outer flange is 4 mm wide. Germs (1973) considered that the specimens originally had an epidermis, which is preserved in patches near the base of the 'leaf'.

Orthogonium parallelum Gürich, 1930

According to the original description by Gürich (1933), *Orthogonium parallelum* consists of 8 parallel rows of elongated tubes which are square in section lying on a bedding plane of sediment. These tubes are divided into sections, the longest preserved tube being 58 mm long and having 28 mesh-like sections, each of which is 2 mm high and 3 mm wide, each section being separated from its neighbour by a more or less sharply defined groove. Rows 5+6 and 7+8 of the holotype are closer to each other than they are to their neighbours, thus forming pairs of tubes which are further apart from each other than are the rows in each pair. These square-section tubes could represent original pneu structures that did not collapse during fossilisation, but were filled with sediment, thereby preserving the three dimensional form of the pneu. At the base of the fossil, the organism bends down into the sediment layer, thereby forming a bulge. This suggests perhaps that during life, part of the organism was embedded in the sediment, and part of it extended upwards into the overlying water. When it was buried, the free part was bent downwards onto the bedding plane.

Gürich compared the structure with that of crinoids, but its precise relationships, like those of many of the other Vendozoa, remains enigmatic. Judging from the photographs published by Gürich (1933) *Orthogonium parallelum* was probably a serially quilted organism with unipolar growth, but this needs to be verified by examination of the original specimen (which may be lost (Runnegar and Fedonkin, 1992))

Orthogonium parallelum was found on Farm Kuibis along with *Pteridinium simplex* and *Rangea schneiderhoehni*.

Namalia villiersiensis Germs, 1968

This Germs and species was erected by Germs (1968) for a conical fossil, oval to round in section, with sever-

Table 5

Algae	
<i>Vendotaenia</i> sp.	
<i>Conophyton</i> (?)	
<i>Boxonia</i> (?), <i>Katavia</i> (?), <i>Gymnosolen</i> (?)	
<i>Acaciella</i> (?), <i>Kulparia</i> (?)	
Phytoplankton	
<i>Favosphaeridium</i>	
<i>Protosphaeridium</i>	
cf <i>Leiosphaeridia aurata</i>	
<i>Rifenita ovalis</i> (?)	
<i>Chuarina</i> sp.	
Leiosphaeridacean acritarchs	
Vendozoa	
<i>Pteridinium</i> * <i>simplex</i> *	(originally <i>Pteridium simplex</i>)
<i>Rangea</i> * <i>schneiderhoehni</i> *	(includes <i>Rangea brevior</i> *)
<i>Orthogonium</i> * <i>parallelum</i> *	
<i>Namalia</i> * <i>villiersiensis</i> *	(?= <i>Ernietta plateauensis</i>)
<i>Ernietta</i> * <i>plateauensis</i> *	
<i>Ernietta aarensis</i> *	(= <i>Ernietta plateauensis</i>)
<i>Ernietta tschanabis</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniobaris</i> * <i>baroides</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniobaris epistula</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniobaris gula</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniobaris parietalis</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniaster</i> * <i>apertus</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniaster patellus</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniobeta</i> * <i>forensis</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniocarpus</i> * <i>carpoides</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniocarpus sermo</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniocentris</i> * <i>centriformis</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniocoris</i> * <i>orbiformis</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniodiscus</i> * <i>clipeus</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniodiscus rutilus</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniofossa</i> * <i>prognatha</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniograndis</i> * <i>paraglossa</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniograndis sandalix</i> *	(= <i>Ernietta plateauensis</i>)
<i>Ernionorma</i> * <i>abyssoides</i> *	(= <i>Ernietta plateauensis</i>)
<i>Ernionorma clausula</i> *	(= <i>Ernietta plateauensis</i>)
<i>Ernionorma corrector</i> *	(= <i>Ernietta plateauensis</i>)
<i>Ernionorma peltis</i> *	(= <i>Ernietta plateauensis</i>)
<i>Ernionorma rector</i> *	(= <i>Ernietta plateauensis</i>)
<i>Ernionorma tribunalis</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniopelta</i> * <i>scrupula</i> *	(= <i>Ernietta plateauensis</i>)
<i>Erniotaxis</i> * <i>segmentrix</i> *	(= <i>Ernietta plateauensis</i>)
<i>Ausia</i> * <i>fenestrata</i> *	
<i>Paramedusium</i> * <i>africanum</i> *	
<i>Nasepia</i> * <i>altae</i> *	
<i>Cyclomedusa</i>	
<i>Velancorina</i> * <i>martina</i> *	
<i>Kuibisia</i> * <i>glabra</i> *	(?= <i>Ernietta plateauensis</i>)
<i>Petalostroma</i> * <i>kuibis</i> *	

Table 5: List of organisms and trace fossils from the Nama Group, Namibia (* - Holotype from Namibia)

Metazoa or Animalia?	
<i>Hagenetta* aarensis*</i>	(?= <i>Beltanelliformis brunsa</i>)
<i>Protechiurus* edmondsi*</i>	
Body coating fossils (?Metazoa)	
<i>Archaeichnium* haughtoni*</i>	
Cloudinidae (? Metazoa)	
<i>Cloudina* hartmannae*</i>	(includes <i>Cloudina hartmannae</i>)
<i>Cloudina* riemkeae*</i>	(?= <i>Cloudina hartmannae</i>)
Ichnofossils (?Metazoa)	
<i>Skolithos</i>	
<i>Buchholzbrunnichnus* kroeneri*</i>	
<i>Bergaueria</i> (or <i>Intrites</i>)	
? <i>Didymaulichnus</i>	
<i>Planolites</i>	
<i>Helminthoidichnus?</i> (or <i>Taphrhelminthopsis circularis</i>)	
<i>Curvolithos</i>	
<i>Brooksella</i>	
<i>Scolicia?</i>	
<i>Taenidium, Muensteria, Scolepecopus</i>	
? <i>Chondrites</i>	
<i>Diplocraterion</i>	
<i>Enigmatichnus* africana*</i>	
<i>Phycodes cf pedum</i>	
<i>Neonereites biserialis</i>	
<i>Neonereites uniserialis</i>	
<i>Nereites</i>	
? <i>Diplichnites</i>	

Table 5: (continuation).

al longitudinal ridges, that he collected from the Kuibis Formation on Farm Buchholzbrunn (Germs, 1972a). A second locality with this species occurs on Vrede (Germs, 1972a). The fossils occur in groups of up to 30 individuals which range in length from 5.2 to 9 cm and in diameter from 1.5 to 7 cm and there are 27-40 ridges. Many of the fossils occur as upright cones in the sediment, with the narrow end down, suggesting that they lived in the sediment in such an orientation. Others were found lying in the bedding plane, indicating that some reworking may have occurred.

Runnegar (1992) considered that *Namalia* is based on a fossil of *Ernietta plateauensis*.

Ernietta plateauensis Pflug, 1966

According to Pflug (1966) the body of *Ernietta plateauensis* (Fig. 21) is bilaterally symmetric and segmented. The body axis is bent into the form of a U and is covered, in this position, by a test which consists of parts of segments of the back and sides. There is a zig-zag median dorsal suture line, at which the segments of sides meet alternatively. Jenkins (1985) described *Ernietta* as sack-shaped with striations.

Pflug (1972) described several genera from either the farms Aar or Plateau which are considered by Runnegar (1992) to be synonyms of *Ernietta plateauensis*. These include *Erniaster* (species *E. apertus* and *E. patellus*), *Erniobaris*, *Erniobeta*, *Erniocarpus*, *Erniocentris*, *Erniocoris*, *Erniodiscus*, *Erniofossa*, *Erniograndis*,

Ernionorma, *Erniopelta* and *Erniotaxis* all erected by Pflug in 1972.

Seilacher (1992) considered that *Ernietta* was a sediment stalker, in which the sides of the organisms grew upwards as sediment accumulated round and inside it. The body was thus convex downwards, with the open top uppermost.

Ernietta plateauensis has been collected from the Kuibis Quartzite on Farm Aar 16, at Radfortputs, Kokkerboomkloof, Twyfel and Helmeringhausen (Germs, 1972a).

Paramedusium africanum Gürich, 1933

Gürich (1933) provided a detailed description of this species, which was found in micaceous sandstone at Groendorn, 3 km northwest of the railway station at Ham Rivier. The fossil is broken, with large parts missing, but the surviving portion is approximately semi-circular and is flat, with a diameter of about 170 mm. It has three concentric furrows and ridges (or bulges) along its margin which differ in width, the outermost ridge being the weakest, the innermost one being the widest and lowest. The outermost groove is the sharpest. The middle and innermost grooves are shallower, and fade out towards the 'top' of the specimen.

The innermost ridge (or bulge) is covered by radiating ribs 2 to 3 mm from each other which occasionally show net-like connections to each other. These ridges cross the middle furrow and pass onto the middle ridge.

Locally, the radiating ribs in the middle furrow swell to form knots or they include rounded hollows.

In the better preserved 'left' quadrant of the specimen, the surface is depressed slightly to form a rounded trough. In the 'right' quadrant there appears to be a similar trough, but it is filled with sediment. The two troughs are separated from each other by a flat ridge which extends from the periphery towards the centre.

Judging from the description and figures, *Paramedusium africanum* was probably a flat recliner - a mat-like organism that lay sessile on the sea bed. It appears to have had radial growth and serial quilting, although this needs confirmation by examination of the original specimen.

Nasepia altae Germs, 1973

Germs (1973) described this Germs and species as having leaf-like bodies with thin ribs, mostly in one direction and then usually subparallel to the long axis. In some places he noted the presence of transverse ribs. These leaf-like structures, or petaloids (Pflug, 1970a, 1970b) bundled together in *Nasepia* to form a petalodium (Fig. 19). There is a feather structure on the margin of a petaloid, which Germs considered might represent commissures where each body is perforated by an axial channel which would have served for water circulation through the body of the organism.

The petaloid is 10.5 cm across, and the width of the ribs ranges between 0.1-1.0 mm.

Seilacher (1989) indicated that *Nasepia* had bipolar growth and had serially arranged pneus. It may well have been a flat recliner, lying on the sands of the sea bed like a mat.

Nasepia is known from the Nasep Member on Farm Arimas.

Cyclomedusa davidi Sprigg, 1947.

Cyclomedusa davidi is a roughly circular organism with radial growth (Germs, 1972a; Seilacher, 1989). The centre of the body is comprised of circular traces, while the outer parts are comprised of radially arranged ribs of serial type (Fig. 20).

In Namibia it has been found in the Huns Limestone Member on Farm Simplon (Germs, 1972a), although there is some discussion whether the Australian and Namibian specimens represent the same species of organisms, or whether the resemblances are fortuitous.

Velancorina martina Pflug, 1966

The body of *Velancorina* is roughly oval or elliptical and is bipolar, there being a distinct furrow down the long axis of the oval. There are furrows leading sideways from the central groove, suggesting the presence of a serial pneu structure, but the fossils are not well enough preserved for certainty in this matter. The fossil described by Pflug (1966) is about 24 mm long and appears to have different structures at its two extremities.

It resembles other Vendozoa which were flat reclin-

ing forms, and may have lain on the sandy sea bed like a mat.

The holotype of *Velancorina martina* was collected on Farm Aar 16 and other material from Schakalskuppe 18.

Erniobaris baroides Pflug, 1972

Pflug and Meinel (1974) illustrate this bipolar species of soft-bodied organism, which was found on Plateau Farm east of Aus. It is roughly oval in outline and approximately 30 mm wide and 44 mm long. It has a fore and aft furrow from which ribs spread laterally on both sides, those near the end being distinctly curved, while those near the middle of the body are straight becoming slightly curved towards the margin of the body (Fig. 18). It appears that quilting was of the serial kind.

Runnegar (1992) considered *Erniobaris* to be a synonym of *Ernietta plateauensis*.

Ausia fenestrata Hahn and Pflug, 1985

Hahn and Pflug (1985) reported that *Ausia* has the shape of a large, tube-shaped central polyp occupied entirely by small secondary polyps. The latter are arranged in a regular pattern consisting of whorls and co-axial lines. The holotype specimen from Plateau Farm, is 7.5 cm long and its width increases from 1.5 cm near the base to 3 cm near the middle.

Kuibisia glabra Hahn and Pflug, 1985

Kuibisia is a solitary 'polyp' with approximately conical shape about 10 cm long and 3.5 cm broad at its widest. As reconstructed by Hahn and Pflug (1985), the margin of its apically located 'mouth' was densely covered by tentacles which are connected at their base. They develop from co-axial ribs that cover the surface of the polyp. These ribs are all approximately the same shape and size.

The holotype specimen came from Plateau Farm.

Runnegar (1992) considers *Kuibisia glabra* to be based on a specimen of *Ernietta plateauensis*.

Petalostroma kuibis Pflug, 1973

In 1973 Pflug erected the new Germs and species *Petalostroma kuibis* on the basis of a fossil from the Dabis Formation on Aar, but Runnegar (1992) considers it to be *incertae sedis*.

Soft bodied mobile Vendian organisms of Namibia: Metazoa, Echiura and Sprigginiidae

Protechiurus edmondsi Glaessner, 1979

According to Glaessner (1979) *Protechiurus edmondsi* was a cigar shaped echiurid with a broad based, spatulate proboscis and eight more or less prominent longitudinal muscle bands (Fig. 22). The holotype which came from Plateau Farm east of Aus, is 74 mm long and its maximum width is 19 mm while its 'height' measured at right angles to the maximum width is 11

mm. If this interpretation of the fossil is correct, then this Germs would indicate the presence of an independently mobile organism in the Kuibis Quartzite.

Runnegar (1992) considered this Germs to be a du-biofossil.

Spriginnidae?

Germs (1973) described the imprint of a flat, elongated oval fossil about 10 mm wide, that he found on Fanu Buchholzbrunn 99. He observed three different units in it. One of these was endowed with fine ribs which were curved in places and 0.1 to 0.2 mm wide, which faded out sideways. A second unit was coarse and segmented, and showed longitudinal and transverse subdivisions. There were at least 34 segments in this unit, the lengths of which ranged between 0.6 and 0.7 mm. The third unit showed ribs which were 0.1 to 0.2 mm wide, subparallel to the long axis of the body. Germs also thought that he could make out parts of an intestinal tract and a protostomium. He compared the fossil with *Spriginnia ovata* from Ediacara in Australia (Fig. 17). If Germs is correct about this specimen, then it provides evidence of the existence of locomoting organisms (and macro-predation) in the Vendian of Namibia.

Shell-bearing Vendian organisms of Namibia: Cloudinidae Hahn and Pflug, 1985

Claudina hartmannae Germs, 1972

According to Hahn and Pflug, 1985, *Claudina* were apparently worm-like animals which secreted calcareous tubes. The tube as a whole was composed of several smaller single tubes which were set one into the other as in a telescope, being open distally and proximally. Only the first of the tubes is closed at the bottom (Fig. 35). The tubes are of organic material, but with cones of calcium carbonate inserted. Unlike *Serpulidae* which secrete calcareous rings, *Claudina* was unable to do so, but could only produce calcareous cones which were limited to one side of each single tube. In cross-section, therefore, the tube as a whole is composed of many calcareous cones, which were secreted one after the other by different single tubes, each one offset against the other.

Claudina possessed tubes which ranged in size from 1.5 mm to 150 mm. These were straight or only slightly curved and there is little change in diameter along the tube as a whole. Different species of *Claudina* are recognised on the basis of overall tube length, single tube length, breadth of the tube as a whole, and the diameter of their walls. *Claudina hartmannae* is appreciably larger than *C. riemkeae*.

Because the method of construction of the tubes as a whole and of the arrangement of the calcareous cones appear to be unique in the biosphere, the systematic position of the Cloudinidae remains unsolved.

Claudina is widespread in limestones of the Nama Series. The holotypes of *C. hartmannae* and *C. riemkeae*

were collected on Fanu Driedoornvlakte, not far from Schlip, where *Claudina* forms reefs. In other occurrences such as Quaggaspoort Fanu, Hauchabfontein, Zaris Pass, Hoogland, Swartklootberg, Helmeringhausen, Mooifontein, Holoog and Uitsig, it occurs as scattered and isolated shells which 'float' in limestone like plums in a pudding.

Claudina riemkeae Germs, 1972

C. riemkeae is a smaller version of the type species *C. hartmannae*. Both species occur together in the fossil record of Namibia, especially at Driedoornvlakte.

Runnegar (1992) considered that there is only one species of *Claudina* in Namibia, the two size groups being parts of a single species.

Microscopic organisms preserved in chert

Brain (1994) has discovered a diversity of microscopic metazoan-like organisms in cherts of the Mooifontein carbonates. The material is still under study, but promises to yield evidence of major interest to furthering our understanding of the origins of macroscopic metazoans at the onset of the Cambrian, by providing information about their possible precursors of Vendian age.

Valve-bearing organisms of the Nama Group

Hagenetta aarensis Hahn and Pflug, 1988

According to Hahn and Pflug (1988) *Hagenetta* is almost circular, about 5 mm in diameter (Fig. 23) with an upper valve of roughly triangular outline. It appears to have been a bilateral shell-bearing animal, the shell being predominantly organic, only a small proportion of it being mineralised. The shell consists of two valves located on the animal's dorsal and ventral sides, as in brachiopods. The dorsal valve is smaller than the ventral one, and fits exactly into the opening of the ventral valve, like the lid of a cooking pot, and is not attached to it by a hinge. There is no opening for a stalk in the ventral shell and the dorsal valve is like a pot lid rather than a door, meaning that *Hagenetta* was not related to brachiopods or to any other molluscs.

Runnegar (1992) considers that *Hagenetta aarensis* is a synonym of *Beltanelliformis brunsaе*.

Hagenetta was possibly a sessile epibenthont that inhabited sandy substrates in shallow marine conditions, and it probably fed on phytoplankton, some of which have been found associated with it. It is quite common on Fanus Aar and Plateau.

Soft-bodied Nama organisms with coatings of agglutinated sand grains

The Nama Group has yielded a further category of fossils which are neither body fossils, such as Vendozoa, nor trace fossils in the strict sense. It appears that by Vendian times, some organisms were 'protecting'

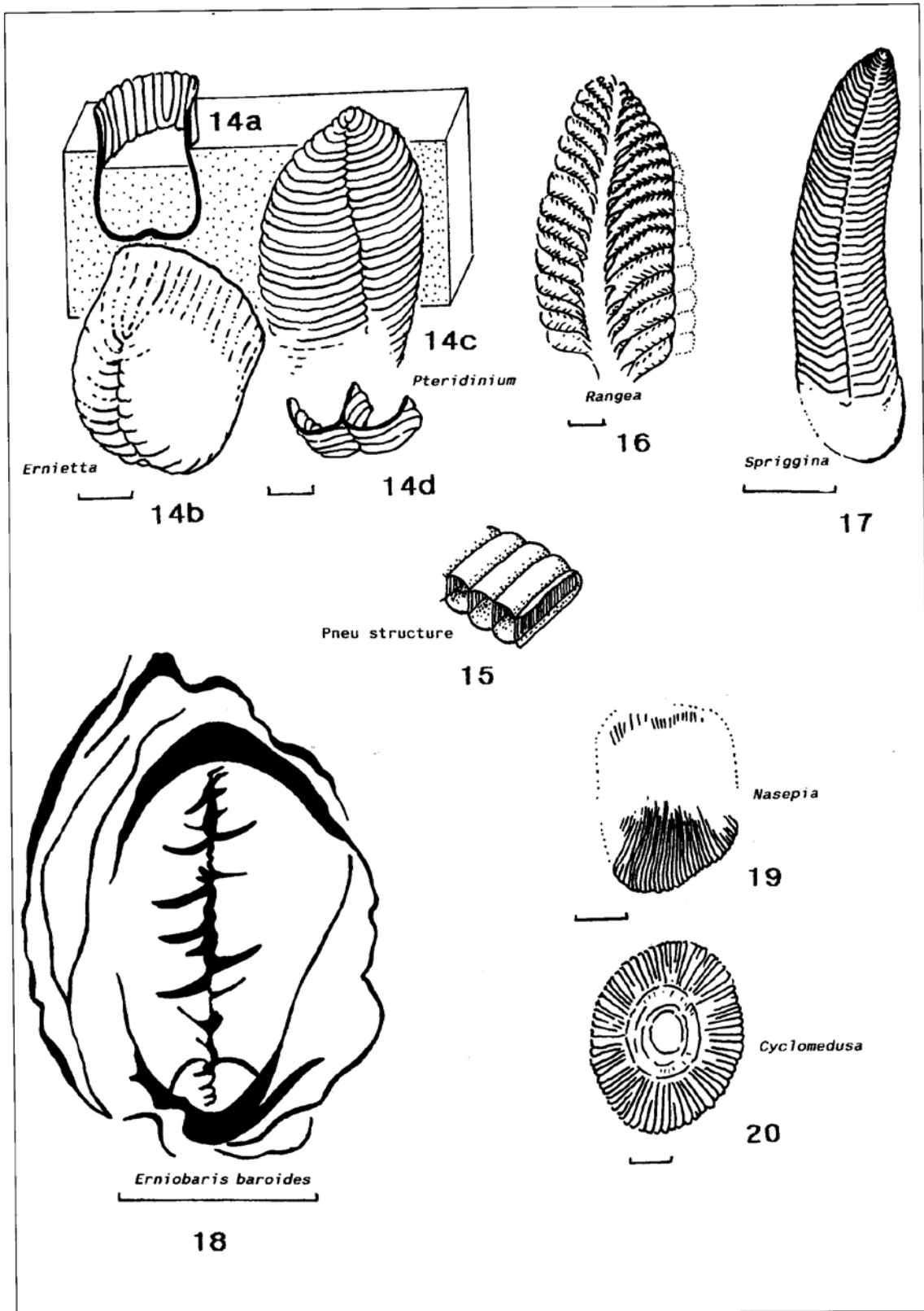


Figure 14: a, b, *Ernietta* and c, d, *Pteridinium* (from Seilacher, 1992), a. section through individual in growth position, b. oblique view of entire individual c. view of underside of individual, d. section through individual to show median wall (scale bars: 1 cm). **Figure 15:** Pneu structure according to Seilacher (1992). **Figure 16:** *Rangea* (from Seilacher, 1992) (scale bar: 1 cm). **Figure 17:** *Spriggina* (from Seilacher, 1992) (scale bar: 1 cm). **Figure 18:** *Erniobaris baroides* (from Pflug, 1966) (scale bar: 1 cm). **Figure 19:** *Nasepia* (from Seilacher, 1989) (scale bar: 1 cm). **Figure 20:** *Cyclomedusa* (from Seilacher, 1989) (scale bar: 1 cm).

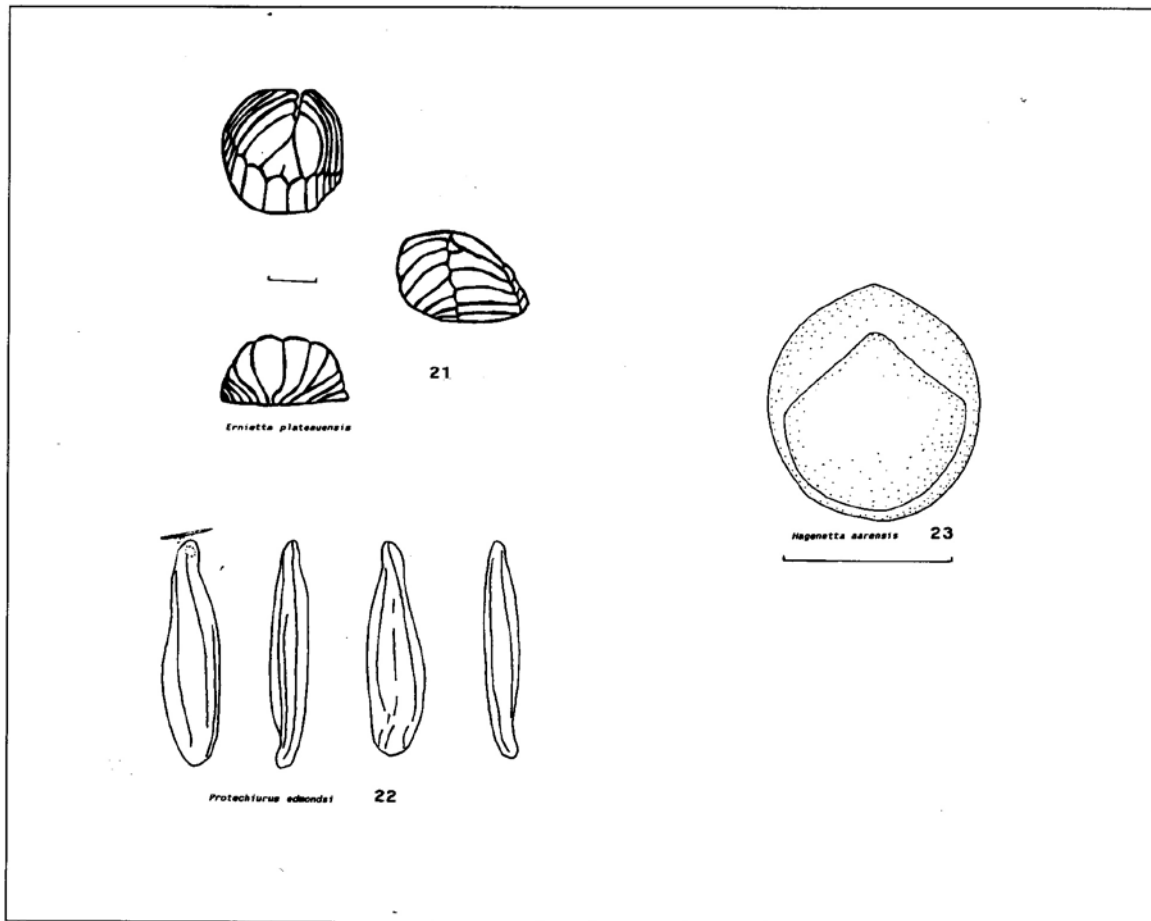


Figure 21: *Ernietta plateauensis* (from Pflug, 1966), three views of an individual (scale bar: 1 cm). **Figure 22:** *Protechiurus edmondsi* (from Glaessner, 1979), four views of the holotype specimen (total length of specimen: 7.4cm). **Figure 23:** *Hagenetta aarenensis* (from Hahn and Pflug, 1988) (scale bar: 5mm).

their soft tissues by sticking sand grains to the outside of their bodies, sometimes in semi-regular to regular patterns. During fossilisation, the bodies of such organisms tended to rot away entirely, while occasionally the 'skin' of sand grains was preserved more or less intact, even if compressed and twisted or torn.

Archaeichnium haughtoni Glaessner, 1963

This fossil consists of agglutinated sand grains and appears to have been similar to tubes made by living polychaete worms. As such the fossil is not a trace fossil - it occurs as a sharp semi-relief on the surface of a block of quartzite, now appearing as flattened and sometimes twisted tubes ranging in diameter from 1 mm to 5 mm.

The style of preservation suggests that the tubes were thin-walled, compressible and flexible, since none of them is broken but several are twisted and flattened. Irregular forms are more common than geometrically regular ones, and several of the specimens narrow abruptly at one end to form a long thin twisted 'tail'. The holotype of *Archaeichnium haughtoni* which was

collected from Gründorn, near the Ham River, is over 70 mm long and has a maximum width of almost 5 mm. The wall is about 1 mm thick and shows pronounced transverse layering of sand grains. The tube is filled with sand grains which show a much fainter and less regular transverse fabric. The outer surface of the tube is marked by fine longitudinal ribs, which are only faintly visible near the ends of the tube. This particular tube is 'split' for most of its length.

Originally interpreted as an archaeocyathid by Haughton (1960), it was reinterpreted by Glaessner (1977) as an agglomeration of sand grains built up by a worm-shaped animal which agglutinated sand grains using an organic cement which allowed the overall structure to remain flexible. For this reason the fossil is neither a body fossil nor a trace fossil in the strict senses of these concepts, but is most conveniently considered to be a body-coating fossil. The implications are that by the time that this organism lived, protection of the body from predators was a necessary strategy for survival of the species, which in turn would indicate that macro-predators were already active on Earth. Another opin-

ion is that the specimens are merely trace fossils, but if this is the case, then it is difficult to explain the twisted and collapsed parts of the trace, and the longitudinal split that occurs on the holotype.

Nama Group Trace Fossils

The Nama Group is known for the richness and variety of its trace fossils. These have been fairly intensively studied on account of their extreme geological ages, and up to now over a dozen genera of ichnofossils have been described from Namibia.

Skolithos (Fig. 32)

Five blocks of sandstone, containing more than 100 burrows each have been reported from the Nama Group on Geinochas (or Gainachas) and Grootplaats Farms. This Germs has also been found in the Kuibis Quartzite on Churutabis Farm and at Osis Farm. The only parts of the burrows visible are their tops where they emerge from the bedding plane as protuberances mostly 1-2 mm in diameter and about 1 mm high. These protuberances are thought by Crimes and Germs (1972) to be the tops of vertically oriented *Skolithos* tubes originally present in the underlying mud stratum.

Buchholzbrunnichnus kroeneri Germs, 1973

This trace fossil was described and named by Germs (1973) on the basis of material from Farm Buchholzbrunn. The trace has a width of about 4.8 mm and consists of two parts. The first shows three parallel ridges, all of which are built up by slanting planes. On the crest of each ridge a small narrow ridge is present. The second part is about 0.8 mm thick and has three grooves which correspond more or less in position with the ridges of the first part.

Bergaueria (or *Intrites*) (Fig. 31)

Crimes and Germs (1982) were the first to record this Germs from the Nama Group. He found specimens in the Urikos Member of the Zaris Formation, on Kuibis Farm. The trace fossils appear as positive relief on the sole of a grey sandstone bed which has also been affected slightly by scour. They are cylindrical sacs with rounded lower ends and with a shallow, minute, but well defined, circular central depression. The specimens are 1-5 mm in diameter and their height is always less than their width. The central depression is a fraction of a millimeter in diameter and depth, yet is well developed in almost all the specimens. These traces have no ornamentation and occur in profusion on the block of sediment, appearing like a collection of small buns with central dimples, crowded together on the bedding plane.

They are thought to be coelenterate burrows, and have been recorded from many sites around the world, including several in the Cambrian Period. Crimes (1989) considered that the Nama fossils assigned to *Bergau-*

eria belong to the Germs *Intrites* (Fig. 30).

?*Didymaulichnus* (Fig. 24)

This ichnofossil appears as a relatively straight ridge, the centre of which is scored by a shallow depression, thereby forming two parallel ridglets.

Planolites (Fig. 26)

This trace fossil has been reported from the Nama Group by Crimes and Germs (1972). It consists of simple wormlike ridges that wander over the upper surface of sediment blocks, sometimes crossing other traces,

?*Helminthoidichnus* (or *Taphrhelminthopsis circularis*) (Fig. 25)

This worm-like trace fossil was identified by Germs (1972) as a worm trace, but Crimes (1989) considers that it is bilobed and circling, in which case it is more likely to represent the species *Taphrhelminthopsis circularis*. Glaessner (1963) illustrated a specimen which probably belongs to this Germs from Chamaites 13, south of Seeheim, Keetmanshoop District.

Curvolithos

Curvolithos has been listed as occurring in Namibia, but details of its appearance and locality are not available.

Brooksella

The ichnogenus *Brooksella* was also described for the first time from Namibia by Crimes and Germs (1982). The specimen was found on Huns Farm, in the Nasep Member of the Urusis Formation. There are 18 trace fossils on the surface of the block, which are disc-like structures, 2-4 mm deep, 5-12 mm in diameter and showing a radiating structure. Each structure has 3-8 arms which radiate regularly from a centre which may be elevated or distinctly depressed in its innermost part.

Crimes and Germs thought that these traces could have been made either by resting coelenterates or by some small worm-like animal. The variability of fine structure suggests that the latter explanation is more likely.

?*Scolicia*

Germs (1972) described a smooth double-ridged cast from the Nasep Quartzite on Arimas Farm, as ?*Scolicia*. If the identification is correct, then this would be one of the earliest known systematically backfilled burrows. It is of Tommotian age, somewhat younger than the Vendian.

Taenidium, *Muensteria*, *Scolecocopus*

Germs (1972) described and illustrated some trails in sediments of the Schwarzrand Formation on Sonntagsbrunn Farm. They are 3.5 to 4 mm wide with transverse ribs approximately 1.3 mm apart. This trace is a well

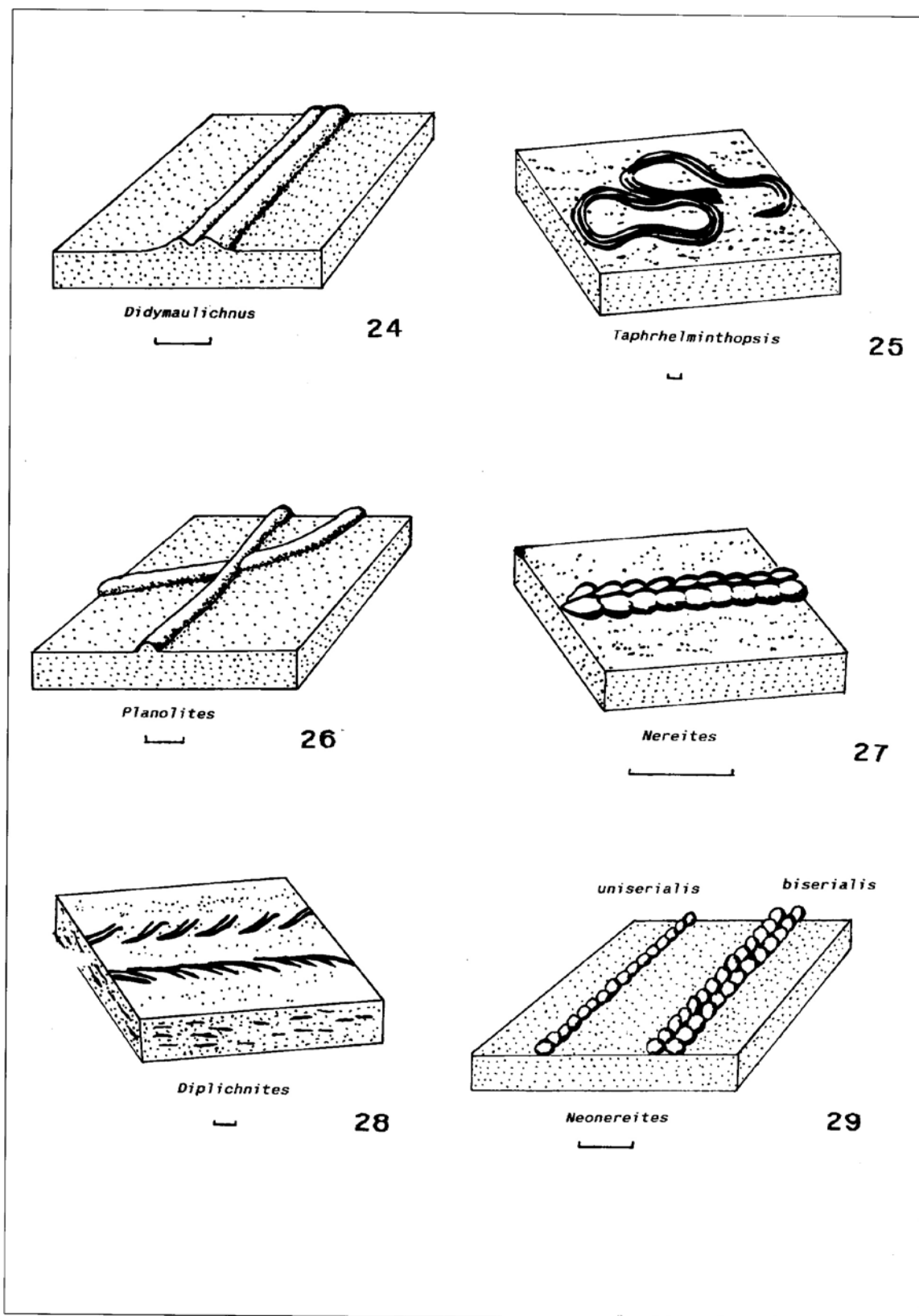


Figure 24: *Didymaulichnus* (from Crimes, 1987) (scale bar: 1cm). **Figure 25:** *Taphrhelminthopsis* (from Crimes, 1989) (scale bar: 1 cm). **Figure 26:** *Planolites* (from Crimes, 1987) (scale bar: 1cm). **Figure 27:** *Nereites* (from Crimes, 1989) (scale bar: 1cm). **Figure 28:** *Diplichnites* (from Crimes, 1989) (scale bar: 1cm). **Figure 29:** *Neonereites* (from Crimes, 1987) (scale bar: 1cm)

known type in other parts of the world, where it is variously known as *Taenidium*, *Muensteria* and *Scolecocoprurus*.

?*Chondrites*

The record of this Gründorn in the Nama Group is not certain - the traces could be of abiogenic origin. However, Crimes and Germs (1982) considered that the furrow structures that they found in the Vingerbreek Member on Kuderup Farm and at Osis Farm, are more organised than abiogenic wrinkle marks usually are. The furrows form a dendritic pattern on the upper surface of a bed, and consist of occasionally branching furrows and associated ridges, which diverge from a restricted zone. In neither of the available specimens is this zone preserved.

Diplocraterion (Fig. 33)

This trace fossil is common in the Vingerbreek Member on Haruchas Farm and it has also been found at Berghoek, Kuderup and Osis Farms. Various sites have yielded many blocks with more than a hundred traces on them. The traces consist of vertically oriented U-shaped burrows infilled with sandstone and mudstone within beds of sandstone, and with spreite between the limbs of the U. The tube diameter ranges from 1 to 3 mm, the distance between the tubes is between 4 and 21 mm, and the width of the spreite is 1 to 3 mm. A few of the vertical limbs have a concentric arrangement of sediment revealed as darker mud laminae. In some examples, the spreite of two *Diplocraterion* cross each other.

Most of the tubes can be traced into the sediment for a few millimetres, but a few pass through as much as 12 mm. The sedimentary structures in the same strata include smallscale cross-bedding, wrinkle marks and mud cracks, suggesting that deposition was in shallow water, fairly energetic conditions, possibly tidal channel sands and associated intertidal sand and mudflats.

Enigmatichnus africanus Crimes and Germs, 1972

Traces called *Enigmatichnus* consist of pairs of steep-sided, more or less parallel slits 3 to 7 mm long and about 1 mm wide, preserved as negative features on the upper surface of sandstone beds. Individual slits of a pair are separated by 1 to 2 mm so that the width of the trace is 3 to 5 mm.

These traces are thought to have been made by some kind of arthropod of unknown affinities. The samples came from the Rosenhof Member on Geinochas Farm.

Phycodes cf pedom (Fig. 34)

Crimes and Germs (1972) described a specimen of this ichnofossil found on Gavaams Farm in the Rosenhof Member of the Fish River Subgroup. It is also known from Autsas Farm. It consists of a sand-filled main burrow about 15 mm long and 2-3 mm in diameter

with four smaller bundled branches on one side.

Neonereites biserialis (Fig. 29 right)

This trace fossil is preserved in two ways. In some specimens there is a double row of sand-filled spheres or ellipsoids with their longest dimension 3 to 5 mm and forming a gently and irregularly curving string 7-10 mm wide. In the other, there are hollows where the spheres or ellipsoids have fallen out of the burrows. Two of the three known Nama specimens found on Vergelee Farm in the Nomtsas Formation, are 11 cm and 8 cm long. The spheres or ellipsoids of one row are offset with respect to those in the other row. The spacing of spheres or ellipsoids within or between rows is not more than 1 mm, and adjacent pellets are often touching each other. Some of the pellets show indistinct fine striations on their surface.

Neonereites traces are thought to be post-depositional internal burrows, while the spheres or ellipsoids are considered to be faecal pellets back-filling the burrow.

Neonereites uniserialis (Fig. 29 left)

There are three specimens of this species known from Vergelee Farm in the Nomtsas Formation of the Nama Group (Crimes and Germs, 1972). The traces consist of a chain of sand-filled unornamented spheres with no neighbouring structures outside them. The diameter of the spheres ranges between 3 and 8 mm. Some spheres are isolated by gaps of up to 4 mm, but they are commonly juxtaposed or even overlap. The chain of spheres curves slightly in some specimens, while it can be tightly curved in others. The Nama specimens are 5 cm, 12 cm and 20 cm long.

Nereites (Fig. 27)

Five specimens assigned to *Nereites* have been reported from the Nama Group (Crimes and Germs, 1972). They were collected from the Vingerbreek Member on Harughas Farm and on Berghoek 506. They consist of meandering traces on the top surface of beds, comprising a narrow median furrow flanked on both sides by spherical or ovate to pinnate lobes. Where the lobes are closely spaced they usually have a pinnate form, but with greater spacing they are more spherical in shape. In well preserved specimens, the pinnate lobes show faint striations roughly parallel to the outline of the lobe. These trace fossils are 4-6 mm wide with lobes not normally exceeding 2 mm in length.

Nereites is often thought of as being a deep water form, although it has also been recorded in shallow water facies.

?*Diplichnites* (Fig. 28)

The basis for recording ?*Diplichnites* in the Nama Group is a block of finely laminated red Nomtsas sandstone from Vergelee Farm, which is marked by a track which forms a winding row of marks, each consisting of two slightly elongated imprints meeting approxi-

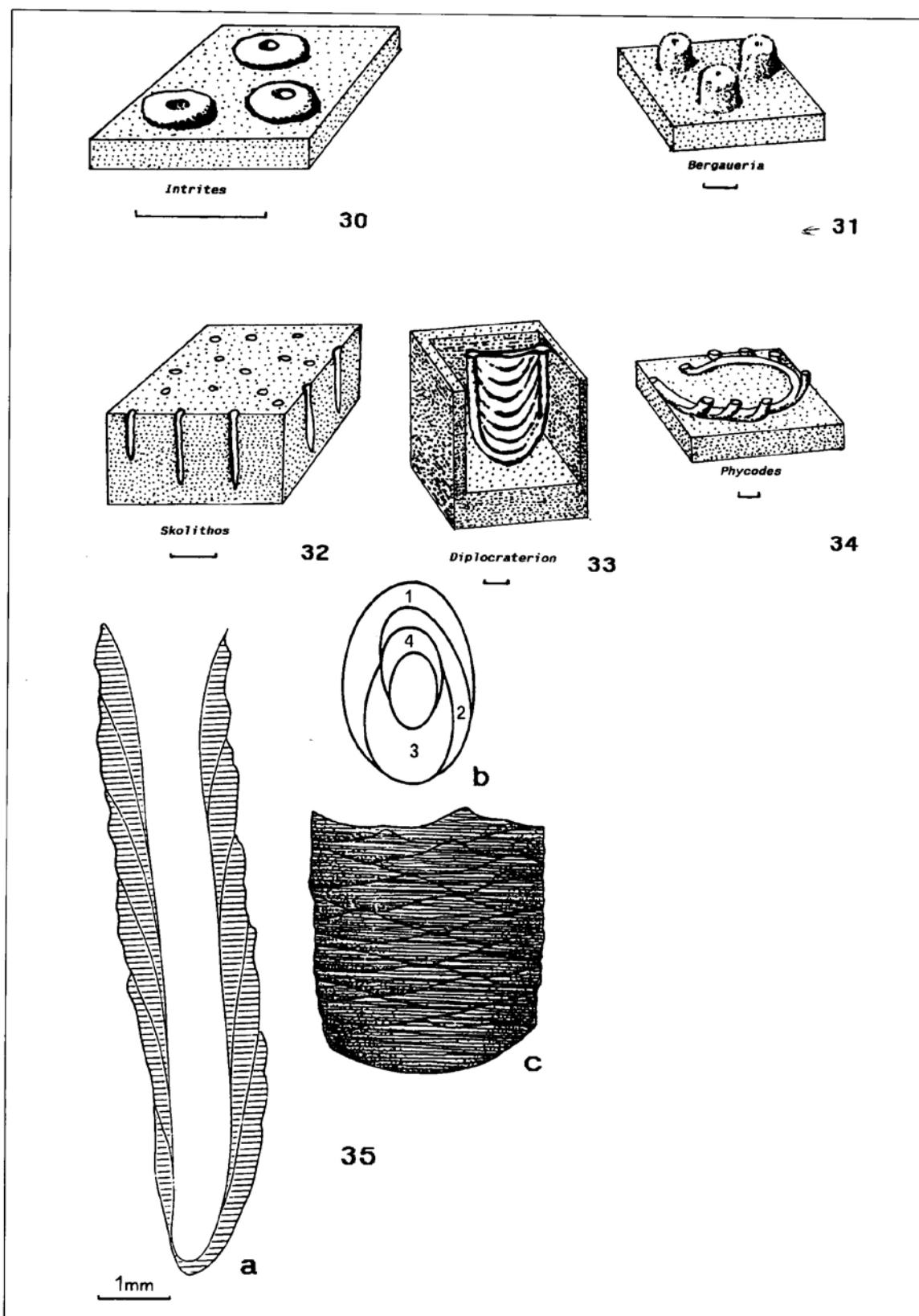


Figure 30: *Intrites* (from Crimes, 1987) (scale bar: 1cm). **Figure 31:** *Bergaueria* (from Crimes, 1987) (scale bar: 1cm). **Figure 32:** *Skolithos* (from Crimes, 1987) (scale bar: 1cm). **Figure 33:** *Diplocraterion* (from Crimes, 1989) (scale bar: 1cm). **Figure 34:** *Phycodes* (from Crimes, 1987) (scale bar: 1cm). **Figure 35:** *Cloudina hartmannae* (from Hahn and Pflug, 1985) a. vertical section through an individual, b. transverse section showing disposition of shell elements (1-4), c. microstructure of outer surface.

mately at right angles. The imprints are about 2 mm long and are spaced at 8 mm intervals. As preserved the track consists of 8 imprints covering a distance of 6 cm. There are also three other imprints on the immediately overlying lamina, which are aligned parallel to the main track but 3 cm away from it, and which may represent parts of the same trace preserved as an undertrack duplicate.

Crimes and Germs (1972) thought that this track could be one side of a double row of imprints. Although the preservation is not very clear, the biological origin of the track is not in doubt, even though its identification as *Diplichnites* remains uncertain.

Stromatolites

Although it has been known for a long time that the Nama Group contains stromatolites, almost no palaeontological research has been done on them. We thus remain in ignorance concerning the organisms responsible for secreting the stromatolites, and even of details of their palaeoecological significance. Nevertheless, stromatolites can be classified on the basis of their overall morphology without having evidence concerning the precise identification of the organism that secreted them. As such the various described 'genera' and 'species' of stromatolites are based on their form rather than on the systematic affinities of the organisms that produced them.

Vidal (in Germs, 1983) mentioned that the alga *Vendotaenia* had been found in the Nama Group and phylloid algae have been reported from the Farm Arimas and at Kolke.

Among the seven types of stromatolites recorded by Germs (1972a) only three were identified with doubt to recognised taxa.

- 1) *Conophyton* (7)
- 2) *Boxonia* (7), *Katavia* (7), *Gymnosolen* (7)
- 3) *Acaciella* (7), *Kulparia* (7)

Germs (1983) reported that the stromatolites in the Kuibis Subgroup and Urusis Formation built huge bioherms, those in the Kuibis Subgroup forming vast barrier reefs north of the Osis Ridge. In shelf lagoon environments there occur patch reefs built by the same kind of organism that was responsible for the huge bioherms. Earlier bioherms in other parts of the world are usually constructed by a wide diversity of organisms, and it has been suggested that there was an important decrease in stromatolite diversity towards the end of the Proterozoic (Awramik, 1971), perhaps following the evolution of macropredatorial grazers of stromatolite secreters. The latter might explain the apparently low diversity of Nama stromatolites reported in the literature, although low diversity could, instead, be due to lack of detailed research.

Phytoplankton

Hahn and Pflug (1988) recorded the presence of phytoplankton in association with *Hagenetta aarensis* in the Kuibis Quartzite. Vidal, in a personal communication to Germs (1983) mentioned that acritarchs (*Chuarina* sp.) had been found in the Nama Group. Germs (1972a) recorded the presence of the following taxa of microfossils from various limestones of the Nama Series;-

- Favosphaeridium* Timofeev, 1959
- Protosphaeridium* Timofeev, 1966
- cf *Leiosphaeridia aurata* Deflandre, 1944
- Rifenita ovalis* (7) Naumova, 1961
- Leiosphaeridacean acritarchs

The research on microscopic organisms of the Nama sediments could profitably be continued, as so little has been done so far, and there is so much to be learnt about the evolution of early photosynthetic and heterotrophic organisms.

Discussion

The Nama Group, which spans the period Vendian to Cambrian, provides important evidence concerning the evolution of various groups of organisms, including stromatolites, phytoplankton and other microscopic single-celled organisms such as acritarchs, the Vendobionta and the earliest known organisms with calcareous shells, *Cloudina*. Its record of trace fossils -presumably made by metazoans - is also impressive.

Study of the diversity of these Proterozoic organisms on a world-wide basis reveals several patterns which are probably inter-related. For example, during much of the Proterozoic, the diversity of stromatolite building organisms increased steadily to a peak during the Upper Riphean, just prior to the Vendian. Thereafter, their diversity decreased dramatically (Awramik, 1971). There may well be a cause for this decline, which was the dramatic increase in diversity of trace fossils during the same period (Crimes, 1987, 1992) which suggest that independently mobile predatory organisms (Animalia or Metazoa) evolved during this period and were putting pressure on soft-bodied autotrophs such as the stromatolites and Vendobionta for the first time in the palaeontological history of the Earth. The Vendobionta which were very diverse during the Vendian, especially in Namibia, had disappeared by the onset of the Cambrian, probably as a direct result of predator pressure.

It is surely no coincidence that during the same period (Vendian to Cambrian) we witness the evolution of the earliest known organisms with calcareous shells (*Cloudina*), and others which were agglutinating sand grains to cover their bodies (*Archaeichnium haughtoni*), or secreting durable 'valves' (*Hagenetta aarensis*) presumably as a defence mechanism against predation.

The Nama Group thus yields evidence of several

major stages in the early evolution of simple and complex life forms prior to and including the metazoan diversity explosion at the onset of the Cambrian. There is no doubt that much, more could be learnt from the extensive Nama Series, regarding the early evolution of the plant and animal kingdoms. The sediments are widespread in southern Namibia - what is required is an appropriate research effort aimed at sampling the palaeontological record in a systematic and scientific way in order to build on the solid foundation laid by previous researchers.

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