

The provenance and palaeobiology of a new multi-vened, chambered frondose organism from the Ediacaran (later Neoproterozoic) of South Australia

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Abstract: The new, large, frondose and stalked, Ediacaran (late Neoproterozoic) ‘petalonamid’ *Pambikalbae hasenohrae* gen. et sp. nov. is preserved in a three-dimensional manner within sandy channel fills occurring directly below the Ediacara Member of the Rawnsley Quartzite on the ‘Nilpena’ pastoral property at a western outlier of the Flinders Ranges, South Australia. *Pambikalbae hasenohrae* was made up of numerous chambered vanes supported by a tapering axial stem and an anchoring stalk. Chambers forming the vanes were commonly infilled with sediment, though variably flattened; groups of vanes representing individual specimens can extend as much as c. 3.7 cm deep through the hosting sandstone matrix. Several series of chambers present in each vane abut at zigzag sutures. *Pambikalbae* is clearly not a cnidarian sea pen, but nevertheless exhibits characteristics suggestive of an evolutionary grade comparable to that of known modern cnidarian divisions. Though the serial geometric configuration of its thin integument seems ideally suited to house symbiotic microbial photoautotrophs, our appraisal of the palaeoecology of *Pambikalbae* is supportive of its being a heterotrophic suspension feeder. *Pambikalbae* may plausibly be a highly derived hydrozoan, part of the ancestral stock of the Siphonophorida, or a sister group to the early Chondrophorina.

The realization that the majority of discoidal remains in Ediacaran biotas are either the basal aspects of anemone-like forms or actually holdfasts of frondose organisms, and not cnidarian medusae (Glaessner 1959; Seilacher 1984, 1989, 1992; Jenkins 1989, 1992, 1996; McMenamin & McMenamin 1990; Narbonne 1998; Preiss 1999; Gehling *et al.* 2000; Steiner & Reitner 2001), necessitates a profound reappraisal of the composition of early metazoan communities. Frondose fossils are the longest studied of any Ediacaran remains, but, despite this, their affinities and biology are amongst the most controversial (Seilacher 1984, 1989, 1992; Fedonkin 1985*a, b*, 1990; Jenkins 1985, 1995; McMenamin & McMenamin 1990; Runnegar 1991, 1995; Fedonkin & Runnegar 1992*a, b*; Conway Morris 1992, 1993*a, b*; Narbonne *et al.* 1997; Narbonne 1998; Dzik 1999, 2002; Narbonne & Gehling 2003; Laflamme *et al.* 2004; Narbonne 2005). This paper describes a new, spectacular, frondose fossil, *Pambikalbae hasenohrae* gen. et sp. nov. preserved in channel sandstones low in the Rawnsley Quartzite in a western outlier of the Flinders Ranges on the ‘Nilpena’ pastoral property (Fig. 1).

An observant amateur, Pamela Hasenhor, drew R.J.F.J.’s attention to fossiliferous exposures in

the area, though Wade (1970) had made an earlier investigation. Lithologies present resemble those at the nearby Ediacara Range, where the fossils have been greatly depleted by long-term collecting.

Geological setting

The late Neoproterozoic soft-bodied Ediacara ‘fauna’ or assemblage has previously been considered as occurring in a mainly recessive stratigraphic interval present in the lower to mid-part of the Rawnsley Quartzite of the Pound Subgroup (Wade 1968, 1970, 1971) described as the Ediacara Member (Jenkins *et al.* 1983; Gehling 1987, 1988, 1999, 2000; Jenkins 1992; 1995, 1996; Preiss 1999). Recent investigations in the western Flinders Ranges indicate that this notion embraces a considerable oversimplification, and three separate faunal levels, sequential in age, are presently identified. Each of these faunal levels holds potential promise for intercontinental biostratigraphic correlation (cf. Jenkins 1995; Nedin & Jenkins 1998) and their individual placement can be established within different sequence stratigraphic cycles or distinct parts of such cycles. A new formal stratigraphic nomenclature for relevant parts of the succession is proposed below.

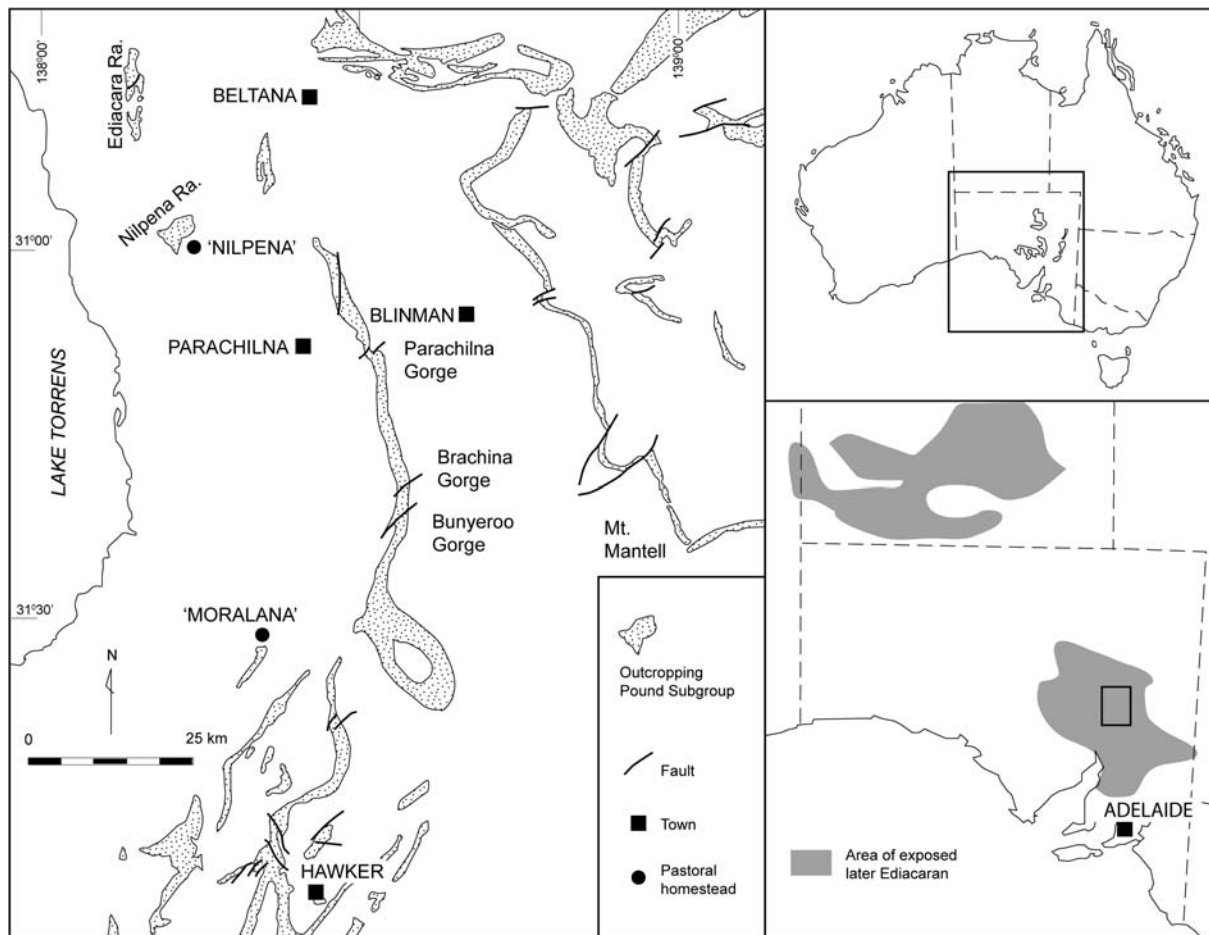


Fig. 1. Locality map for sites of interest in the Flinders Ranges, South Australia. Brachina Gorge is the site of the Global Stratotype Section and Point (GSSP) designated by the International Union of Geological Sciences for the new Ediacaran Period and System.

Transition between Bonney Sandstone and Rawnsley Quartzite

It is recognized that the abrupt change between the maroon-brown Bonney Sandstone and the more boldly outcropping white sandstones or quartzites of the Chase Quartzite Member (Reid & Preiss 1999; Preiss 1999; Gehling 2000) of the Rawnsley Quartzite validly marks a meaningful boundary between these two formations (Fig. 2). The uppermost Bonney Sandstone commonly comprises poorly bedded or wavy-bedded, maroon-brown, sandy siltstones and interbeds of brown sandstone with common polygonal mudcracks on upper surfaces. These lithologies are interpreted as indicating quiet water suspension deposition of silt in a terrigenous, interfluvial, flood plain setting, with episodic sheet flooding and subsequent exposure and desiccation.

Chase Quartzite Member of Rawnsley Quartzite

Within the southern and middle Flinders Ranges the sharp lower boundary of the Chase Quartzite Member (Fig. 2, MEMBER '1') chiefly represents a marine flooding surface with flaggy, granule-

bearing, ripple-bedded, shoreline sandstones above (e.g. Gehling 2000). These grade upwards into thicker bedded, white weathering, feldspathic sandstones with abundant 'dish' structures and sub-polygonal ridges resembling the 'gamma-petee' structures which Reineck *et al.* (1990) attributed to lateral overthrusting of microbial bound sediment laminae due to interstitial crystal growth in a super-saturated/evaporitic upper tidal setting (Gehling 1999, 2000). We concur with Gehling (2000) that deposition occurred in a tidal setting. Near the pastoral homestead 'Moralana', the Chase Quartzite Member measures some 90 m thick and has a thick upper component of sandstone with dish-structures and petee-ridges below a thin development of the fossiliferous Ediacara Member. Though parts of the Chase Quartzite Member commonly include flaggy sand beds, which mould smooth clay partings, such as those that characterize the higher fossiliferous Ediacara Member, few possible indications of animal fossils have been found. A delicate tracery of the kind referred to as 'old elephant skin' structure (Narbonne 1998), attributed to cyanobacterial films or mats (Gehling 1988, 1999; Hagadorn & Bottjer 1997; Gehling *et al.* 2000), commonly marks surfaces.

Breakfast Time Creek Member of Rawnsley Quartzite, new member

Locally, the Chase Quartzite Member is sharply incised by channels containing thin (0–3 m thick) basal sandstones with mud-clast conglomerates, and maroon-brown laminated siltstones which grade upwards into an interval consisting of flaggy, fossiliferous sandstone beds. Uncommon casts of tool marks at the base of these flags are orientated in a variety of directions. Top surfaces show 'rib and furrow' markings, indicating interfering oscillatory currents. These characteristics conform closely to those, which Grey & Benton (1982) and Seilacher (1982) indicated as diagnostic for storm beds or tempestites. Cleaner sandstones with abundant mudcracks on upper surfaces predominate in the upper parts of the cycle. Impurities in the sandstones cause them to weather to a distinctive, dark red-brown colour with abundant black manganese-stainings. These channel deposits reach a local thickness of about 34 m and are formally nominated here as the Breakfast Time Creek Member of the Rawnsley Quartzite (Fig. 2, '2'). The associated fossil remains comprise the 'Rangeid-*Hiemalora*' assemblage (Zone) of Jenkins (1995). Clustered, bag-shaped structures recently found in the older part of one of these channels resemble the *in situ* 'colonies' of *Ernieta* known from the Kliphoeck Member of the Dabis Formation in the Nama

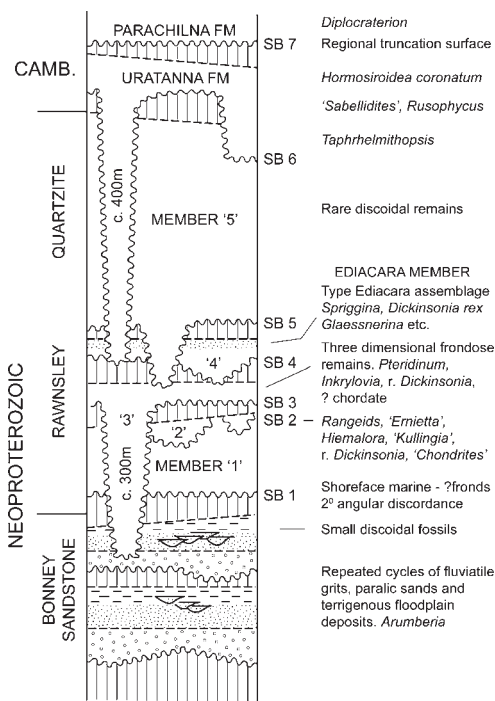


Fig. 2. Stratigraphic diagram of the late-older Ediacaran Cambrian sequence in the Flinders Ranges of South Australia.

Group of Namibia (e.g. Jenkins 1992, fig. 7; Dzik 1999, figs 1d, 3).

The type section of the Breakfast Time Creek Member is located in the east-dipping fill of a large channel, and the section runs NE–SW. This location was sited by satellite coordinates using a new instrument owned by an electronics engineer (WGS 84 standard). The coordinates have been registered with the Australian Stratigraphy Sub-commission for inclusion in the Australian Stratigraphic Units Database with restricted permission for access. The thickness at the type section is measured as close to 34 metres.

Winnowie Member of Rawnsley Quartzite, new member

Both the older fossiliferous channels and the Chase Quartzite Member may be truncated or deeply incised by thick bedded to massive white quartzites and mud-clast conglomerates comprising ‘nested’ channel deposits. R. Fargher of Parachilna has located distinctive associated faunal remains preserved in a three-dimensional manner in a lensoid transgressive phase towards the top of one of these nested channel fills. These channel deposits often form prominent, blocky outcrops with grey-weathering quartzites demonstrating curved fractures and common moulds of twisted or torn scraps of organic tissues. Other flaggy sandstones can also be present. The equivalent channel deposits present at the southern end of Ediacara Range were described by Wade (1971, p. 183) as occurring 7 m to ‘no more than 18 m below the main fossiliferous unit’ (or Ediacara Member *sensu* Jenkins *et al.* 1983), and known to include *Pteridinium* cf. *simplex* (= *Pteridinium carolinaense*), other frondose remains and *Chondroplon bilobatum*. The erosive base of these channels (e.g. Gehling 1987, 2000), downcutting some 90 m in the southeastern part of Ediacara Range, likely reflects a low-stand of sea level. This 90 m thick suite of channel deposits and its lateral equivalents are recognized formally as the Winnowie Member of the Rawnsley Quartzite (Fig. 2, ‘3’). In the ‘Nilpena’ area, the base of this member may erode down c. 300 m through the Chase Quartzite Member (and the channelized member with *Rangea*) and locally forms deep incisions, well below the top of the Bonney Sandstone.

Faunal elements in these channel sandstones are remarkable for their three-dimensional mode of preservation (‘Nama’ preservation of Narbonne 2005, see also below) and include examples of *Charnia* cf. *masoni*, with the holdfast disc on a bedding sole and the stem and fusiform, chambered frond projecting obliquely upwards into individual event beds (Nedin & Jenkins 1998). Other identified

faunal remains include *Pteridinium carolinaense*, cf. *Inkrylovia*, ‘*Cyclomedusa plana*’, and rare *Dickinsonia costata*. Trace fossils are relatively uncommon, mainly *Planolites*.

The base of the Zimneygory Formation in the White Sea Zimney Gory section, northern Russia, hosts a megascopic biota similar to the classical Ediacara Assemblage of the Flinders Ranges, and is dated utilizing U–Pb zircon concordia intercepts at 555.3 ± 0.3 Ma (Martin *et al.* 2000). Grazhdan-kin (2004, figs 1 and 2) reported a technically unpublished U–Pb zircon age of 558 ± 1 Ma (2σ), for the base of the Verkhovka Formation, which directly underlies the Zimneygory Formation. These ages both reduce to equivalents c. 553 Ma with a change in spike calibration and use of a newly determined ^{235}U decay constant (W. Compston, Australian National University, pers. comm., 2006). On the basis of faunal content, the Winnowie Member correlates approximately with the mid Verkhovka Formation, now indicated at c. 553 Ma.

The type section of the Winnowie Member is located on the SE sector of the large syncline extending through the Ediacara Range, and is placed by the satellite coordinates as 138 08.688 E, 30 49.740 S, (base) and 138 08.564 E, 30 49.733 S (top). The member is 48 m thick at the type section, and is named for the nearby historical dwelling ‘Winnowie Hut’.

Pambikalbae hasenohrae occurs in current-deposited, sheet sands of a channel, and in similar beds towards the top of a thick interval of clean sands filling another large channel scour in the ‘Nilpena’ area.

Ediacara Member of the Rawnsley Quartzite

The base of the Ediacara Member is defined as the erosive, locally downcutting surface between the medium-bedded channel sandstones described above, and the succeeding white-weathering shaley beds (Jenkins *et al.* 1983), which grade upward into flaggy fossiliferous strata (Fig. 2, ‘4’). Evidently, the deeply weathered and leached white shaley beds were formerly a ‘black-shale’ facies, deposited in shallow estuarine embayments under conditions of partial anoxia during an early stage of transgression linked to the deposition of the Ediacara Member. Speckles of red oxide are interpreted as representing weathered pyrite. The member is characterized by its own distinctive faunal association (Jenkins 1992, 1996; Droser *et al.* 2005, 2006). Mid parts of the lower cycle of the Ediacara Member at ‘Nilpena’ include several thin quartzite beds, which preserve numerous remains of *Dickinsonia costata*, probably deposited as a result of local density currents. The abundantly fossiliferous overlying sandstones are ripple-bedded, and it is suggested that near-shore

wave action is responsible for such ripple forms, contrary to previous interpretations. The lower fossiliferous cycle of the member is topped by a narrow interval (several metres) with mud cracks in flaggy sandstones indicative of local emergence. Above this, a second relatively thin flaggy fossiliferous interval is succeeded by medium-bedded fossil-bearing sandstones characterized by large dune forms (Facies 'D' of Jenkins *et al.* 1983; this alphabetical designation does not correspond to that of Gehling 2000). Facies 'D' represents sediments deposited in an upper shoreface setting, and grades up into current-swept, thin-bedded sandstones. Massive bedded channel sandstones characterize the 'upper member' of the Rawnsley Quartzite and become prevalent at about this level.

The presence of three distinctive faunal associations over an apparent vertical stratigraphic interval of as little as *c.* 90 m is an indication that the disjunctive sedimentary cycles represented in this part of the older Rawnsley Quartzite reflect significant condensation, probably manifest principally at the deeply incised surfaces. Gehling (2000) does not recognize separate faunal associations, but it is suggested that taxa unique to each assemblage can be recognized, and sharp changes in the abundance of those species do occur. Each assemblage is considered separated temporally from the next by an erosive surface. Perhaps in the central Flinders Ranges, only the correlative conformities are represented. Alternatively, the earlier fossiliferous cycles may have simply been eroded away completely, or are not locally fossiliferous and have gone unrecognized.

Frondose remains are relatively uncommon in all three assemblages, perhaps because the fossiliferous wave-rippled sandstones were deposited in environments not conducive to their preservation. The fronds likely extended into the water and thus had a different preservational potential to that of their resilient holdfasts, already buried at the time of death (Jenkins 1989, 1992, 1996; Narbonne 2005). Because the integument of the free-living animals, such as the dickinsoniids was 'leather-like' (Seilacher 1989), they were preserved in a manner different from that of the fronds (Wade 1968), and obviously different from trace fossils (see also Fedonkin & Runnegar 1992*b*; Crimes & Fedonkin 1996; Droser *et al.* 2005; Narbonne 2005). Thus it is difficult to assess the original abundance of forms in the communities from counts of the fossil remains present.

Repositories

All studied materials are held in the palaeontology collection of the South Australian Museum and are indicated by register numbers prefixed 'SAM'.

Preservation

Previous studies of the Ediacara assemblage in the Flinders Ranges indicate that the majority of the fossil remains are preserved as low relief markings on the soles of sand beds, which are now resistant sandstone or quartzite. Organisms that had a relatively tough or resilient integument, such as *Dickinsonia*, *Spriggina*, *Parvancorina*, *Tribrachidium*, and *Rugoconites*, tended to support the sand that buried them, so that the interlocking of the sand grains on compaction and subsequent early cementation formed a 'hollow' external mould of the upper surface of their body (Wade 1968; Gehling 1987, 1988, 1991, 1999; Runnegar 1991; Fedonkin & Runnegar 1992*a*; Gehling *et al.* 2000). The primary cementing agent was apparently a fine film of pyrite constituting a 'death-mask' (Gehling 1999).

Other organisms, like *Charniodiscus*, began to decompose soon after burial, and Wade (1968) considered that sand subsiding through their disintegrating tissues settled into an under-mould of the body formed on the thixotropic silts which comprised the substrate at the time the organism came to rest on the bottom (e.g. Gehling 1999, 2000). A taphonomic study of the preservational potential of modern soft-bodied metazoans utilizing freezing of the water-saturated sediment as a means of simulating lithification (Norris 1989) had substantially confirmed Wade's observation.

The flat shapes of most local Ediacaran fossil remains led some workers to conclude that the original organisms were foliate or sheet-like (Raff & Raff 1970; Cloud 1976; Runnegar 1982*a, b*, 1991, 1995; Seilacher 1984, 1989, 1992). While this was probably true for a few forms (e.g. some rare medusiform structures), it seems far from likely for most of the Ediacaran organisms. Where the preserving sands happen to have buried resilient bodies lying on thick, soft clays, deep three-dimensional moulds have resulted, and it is apparent that the more common flat imprints are an artefact of compaction of a 'heavy' sand cover (Gehling 1987, 1988, 1991, 1999; Jenkins 1992, 1995, 1996; Gehling *et al.* 2000). Broad animals, such as the dickinsoniids, were particularly prone to such flattening (e.g. Dzik 2002), and the 5% or so individuals of *Dickinsonia costata* seen compressed into asymmetrical shapes provide an indication that after burial, fluid was squeezed from the organism and the upper and lower tissue layers of the body tended to slide over one another so that the axial line displaced towards one side (Jenkins 1992, 1996).

Retallack (1994) compared the preservation of Ediacaran forms with flattened fossil plant stems and woody logs (mainly Palaeozoic) enveloped by sand and compressed through substantial burial

loading, and also studied Late Carboniferous jellyfish occurring in siderite nodules. Steiner & Reitner (2001) reported Ediacaran fossils from northern Russia to include thin, carbonized layers such as those that commonly accompany plant compressions. In the South Australian material, any such partings have apparently been oxidized, and preservation is apparently due to closely appressed surfaces formed by aligned grains in direct contact, an indication that the tissue layer was thin and membranous, not comprising some substantive cellulose-like substance. This alignment of grains in opposition is not consistent with the idea of Crimes & Fedonkin (1996) that certain forms grew by migration of naked protoplasm through pore spaces. There is abundant evidence of overfolding (Seilacher 1992, fig. 3), creasing and wrinkling (Cloud 1976) or stretching (Runnegar 1982a, fig. 1a) of the integument of some Ediacaran forms (e.g. *Pteridinium*), prior to burial, thus demonstrating that the tissues in these taxa were supple. It appears that the fossil imprints were formed at early stages of burial because they may be cross-cut by fluidized sand injected into fractures as a result of soft-sediment slumping (Wade 1968, fig. 17) or transected by synaeresis cracks (Glaessner 1969, fig. 1e). Gehling (1999; Gehling *et al.* 2000) and others, suggest the possibility that the fixative properties of the sediments in moulding the remains were substantially increased by a high interstitial content of microbial filaments rendering a jelly-like thixotropy. The copious secretion of sticky mucilage by dying or moribund medusoids may similarly act to bind adjacent sediment (L. A. Gerswin, UC Berkeley, pers. comm., 1997).

A chance rock-fall in the high western Flinders Ranges exposed well-preserved counterpart surfaces of large discoidal remains. The several layers of grits and sands incorporated between the enveloping surface moulds of the organism disclose that the preservation is not of a single flattened film (such as a diaphanous 'medusa'), but of a hollow body whose internal spaces were at least partly filled with sediment prior to flattening of the structure during its burial. In the harsh climates which have prevailed in the arid area of Ediacara Range and Nilpena, lower surfaces of the resilient sandstone flags become case-hardened (processes of late Tertiary silicification may be involved), preserving the markings on them, but immediately adjacent tissues were moulded in clay-rich silts and sands that have commonly fretted and crumbled away. Rarely, the actual silt-rich parting 0.1–2.0 mm thick is seen adhering to the fossiliferous undersurface of a sandstone slab. Thus, the simple disc-shaped impressions of one tissue layer usually collected may be an artefact resulting from loss of significant parts of the actual preserved

fossil specimens during the processes of their exhumation and subsequent exposure. The common practice of proposing binomial designations to many of the more 'simple' concentric circular markings commonly observed is not conducive either to a fuller understanding of their biogenic placement or indeed, even justification that some of these forms truly represent organic remains (e.g. Gehling *et al.* 2000; Jensen *et al.* 2002).

The forms *Rangea*, *Pteridinium*, *Ernietta*, *Nasepia* and *Swartpuntia*, occurring in the latest Neoproterozoic Nama System of Namibia, are also preserved in a three-dimensional manner (Richter 1955; Germs 1968, 1973; Pflug 1970a, b, 1972; Jenkins 1985, 1992, 1996; Narbonne *et al.* 1997; Dzik 1999, 2002; Grazhdankin & Seilacher 2002; Narbonne 2005). These forms commonly occur in relatively homogeneous, medium grained, feldspathic sandstones and are seen as leaf- or bag-shaped, film-like partings or compressions, which form curved shapes within the rock matrix. Commonly, several leaf-like forms are conjoined or lie side-by-side so that one foliate element has some random orientation in the rock matrix, and another originating along a suture curves out into the rock in a different direction (Richter 1955; Jenkins 1985, fig. II; Crimes & Fedonkin 1996, pl. 2, fig. c, f). The foliate elements may also overlap, folding over or 'closing' around envelopes of sediment (Jenkins 1985, fig. 1G; Narbonne *et al.* 1997, figs 6, 7, 9; Narbonne 2005). In *Pteridinium*, *Ernietta* and *Swartpuntia* the foliate structures are formed by elongate tubes arranged in a regular array and may be intimately penetrated and moulded by the now lithified sands of the rock matrix (e.g. Narbonne *et al.* 1997, fig. 9.4). Twisted and deformed specimens of *Pteridinium* occur in relatively homogeneous sandstone beds, which probably originated from a process of mass movement, such as a density current, or slumped after deposition (Crimes & Fedonkin 1996, p. 324). On the other hand, Grazhdankin & Seilacher (2002) suggest that some deformed and strangely intertwined examples of *Pteridinium* might have been in life position, where they were buried more or less intact in sand, a view with which we concur, because, in the field, crossbedding can be seen in the fill between individual vanes. Preservation of *Rangea* and *Pteridinium* in sandstones occurring in the Flinders Ranges is analogous to that of the African material.

The nature of three-dimensional preservation of all known specimens of *Pambikalbae hasenohrae* closely resembles that of *Rangea*, *Pteridinium* and *Swartpuntia*. The examples of fronds apparently laid over flat during burial and their preservation is similar. The large block including the holotype of *Pambikalbae* (Figs 3a, b, 4a–c, 5a, b) shows

conspicuous hummocky laminations, with several micro-fault displacements. Crossbedding indicates that the flattened, best-preserved frond probably lies on the sole of the flag (Figs 3a, b, 5a). Other frondose elements present show curved, three-dimensional shapes and lie in the general plane of the internal lamination of the matrix (Figs 4b, 6c), except for one ‘vane’ of the paratype SAM P35065, which curves upwards relative to the bedding plane (Fig. 5b) as is commonly seen in many examples of *Pteridinium*. A composite mould (McAlester 1962; Wade 1968; Gehling 1988) has formed between the tapering stem and overlapping frondose elements (Figs 3a, b). The large stalk attributed to *Pambikalbae* (SAM P35067) forms a curved shape extending through

a block of weathered sandstone (Fig. 6e). It appears to comprise a counterpart cast and mould (Wade 1968; Gehling 1988) formed by the sand that filled spaces in the basal parts of overlapping fronds with the internal hollow of the stalk appressing closely against the sand mould of its external surface. Part of another comparable stem extends from the base of the paratype frond SAM P35065 (Fig. 5a).

One or two frondose structures, occurring higher in the rock than the holotype specimen composite mould (SAM P35063) and almost precisely overlapping it, reflect curved longitudinal shapes or possible sand-infillings in line with the stem of the flattened frond (Figs 3a, 4a, b). It was not immediately obvious if these additional frondose

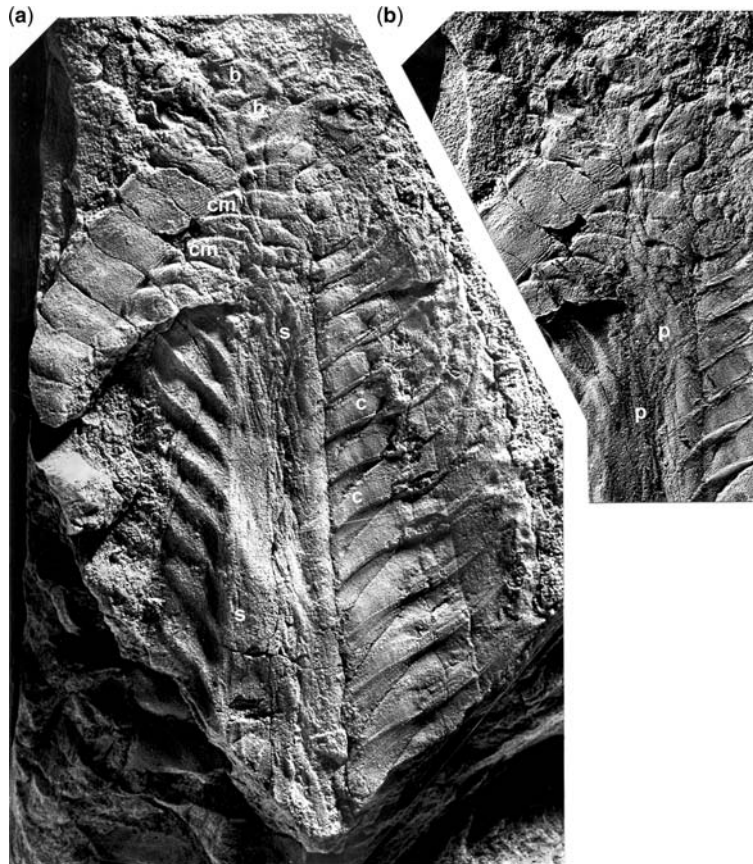


Fig. 3. *Pambikalbae hasenohrae* gen. et sp. nov., SAM P35063, holotype, distal part of frond; Late Neoproterozoic, Winnowie Member, Rawnsley Quartzite; ‘Nilpena’, Flinders Ranges, South Australia. (a) overall aspect with compression of stem (s), indication of faint secondary cross-structure (c) on inner ‘chambers’ of right vane, area of sharp composite moulding of chambers on superimposed vanes (cm) and inflated or bulbous distal ‘chambers’ (b) visible; part of frond illustrated c. 15.5 cm long. (b) distal part of same in different lighting with fine wrinkles or creases marking apparently membranous integument of ‘chambers’ of vane on left side, note criss-cross pattern (p) formed by several vanes collapsed on to and composite moulded against stem compression; scale as for Figure 3a.

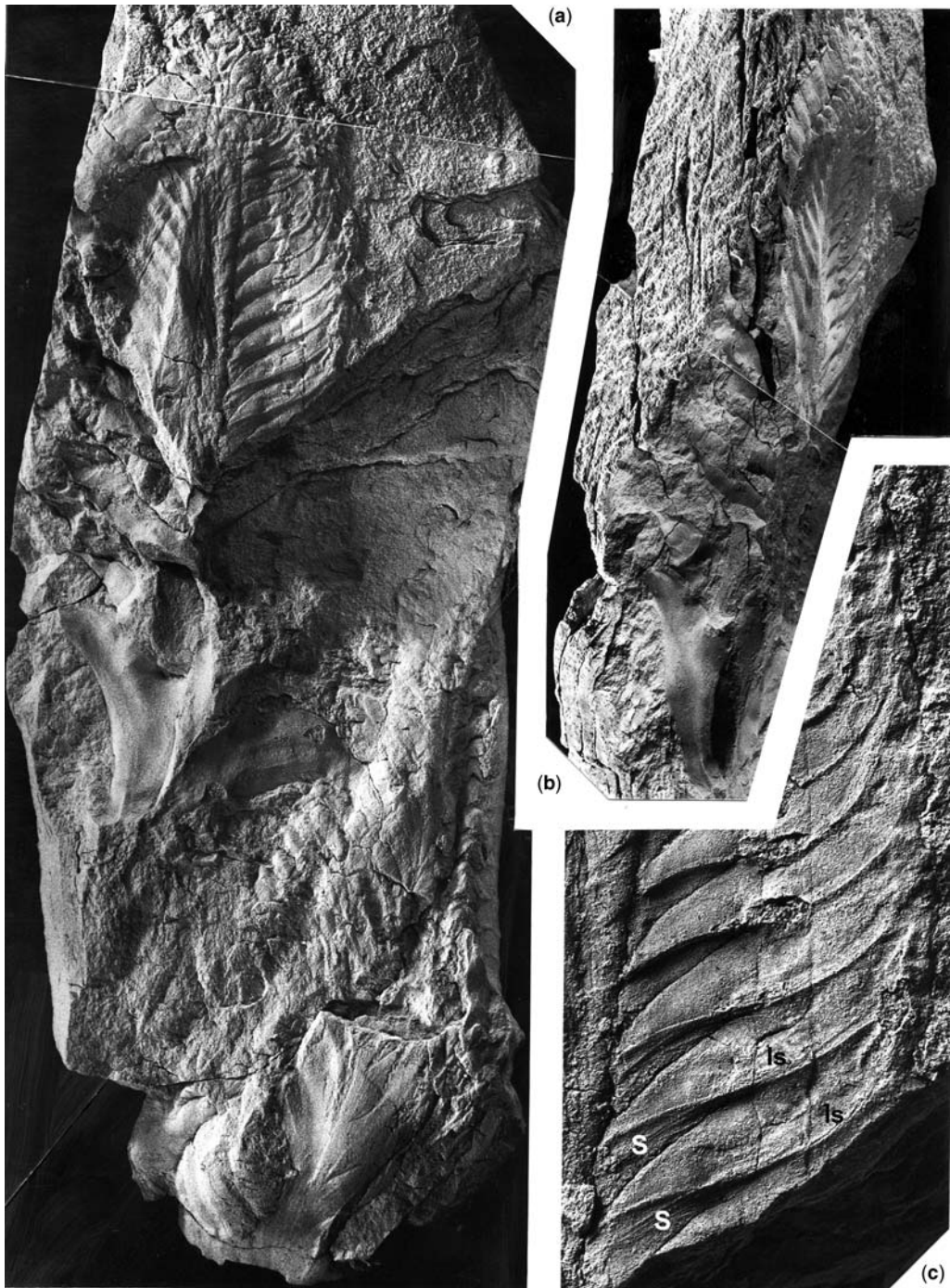


Fig. 4. *Pambikalbae hasenohrae* gen. et sp. nov. (a) SAM P35063, holotype upper left, and SAM P35064, paratype, lower left, on lower aspect of same block of sandstone; visible parts of hosting flag 45 cm long. (b–c) SAM P35063; (b) view of upper left side of hosting sandstone block illustrating parts of holotype interlayered and/or interpenetrating the matrix, the bedding of which is indicated by shadowed vertical cracks mainly on left side of photograph; scale similar to Figure 5a. (c) part of right vane, mid area of frond of holotype, with compressions of possible stolons (s) and slightly zigzag longitudinal sutural traces (ls); illustrated part 12 cm long.

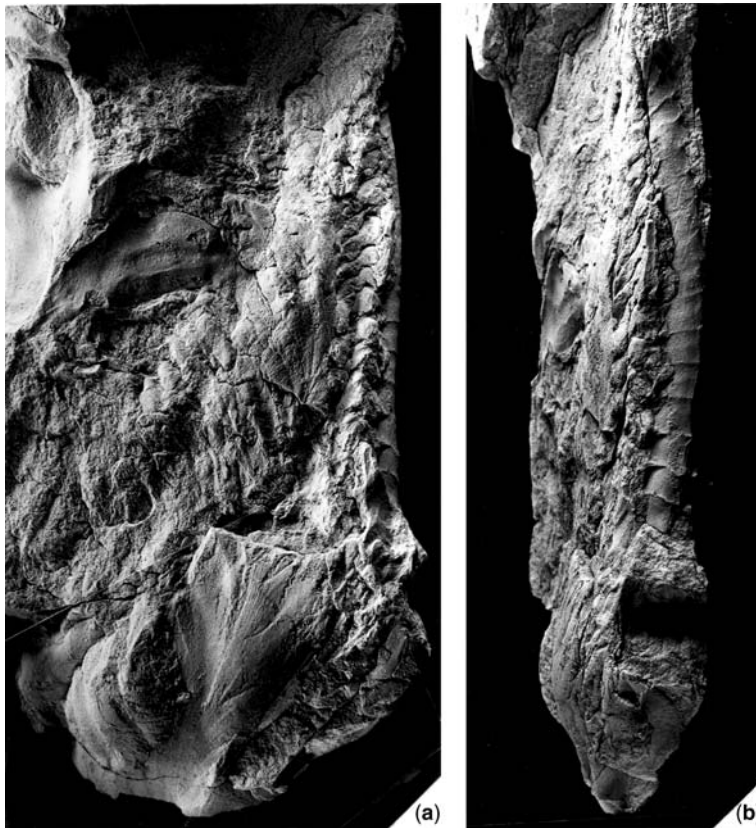


Fig. 5. *Pambikalbae hasenohrae* gen. et sp. nov., SAM P35064, paratype, base and mid parts of frond. (a) overall aspect viewing lower side of compression representing internal mould and composite moulds with suggestion of alternate or sympodial arrangement of 'chambers' near or at mid-line, and some evident secondary cross-structure on 'chambers' at left of base and at right-centre of image; preserved parts of specimen 28 cm long. (b) view of same from right side of hosting sandstone slab showing one vane with strongly developed interchamberal sutures projecting more or less vertically (to right) up through the matrix in the manner commonly evident in specimens of *Pteridinium*; scale similar to Figure 5a.

structures belonged to the holotype or had been juxtaposed accidentally above it. Despite the possibility of some damage to the specimen, a split was made along part of the bedding of the rock in order to resolve this question. This showed that towards the midline of the form, inner chambers of a vane positioned *c.* 1.4 cm higher in the rock curve sharply downwards to meet the stem of the flattened (holotype) frond. Hence, all the structures in proximity to the holotype almost certainly belong to a single individual, which displays a three-dimensional stacked structure or array of parts extending as much as *c.* 3.7 cm deep through the matrix. Some of the fronds or vanes represented have hollow internal spaces packed with sand or are separated by centimetric thicknesses of sand (now lithified), which show both fine, internal lamination and small scale crossbedding. Thus, the

burial of the specimen could not have been instantaneous, but took place progressively as each lamina of sand was deposited, and perhaps represents a time interval spanning some minutes, hours or possibly longer. The hydrodynamic energy associated with the current was sufficient to pack sand into the many hollow spaces.

The paratype SAM P35064 demonstrates complex overlapping of frondose elements partly separated by envelopes of sand (Fig. 5a, b), but the close juxtaposition of the several foliate structures and near register of their base and terminations lends weight to the consideration that they may all be parts of one individual.

The frondose structures of *Pambikalbae* each comprise a series of large tubular elements or chambers that may complexly overlap, forming composite moulds (Figs 3a, b, 4c). The tubular structures are

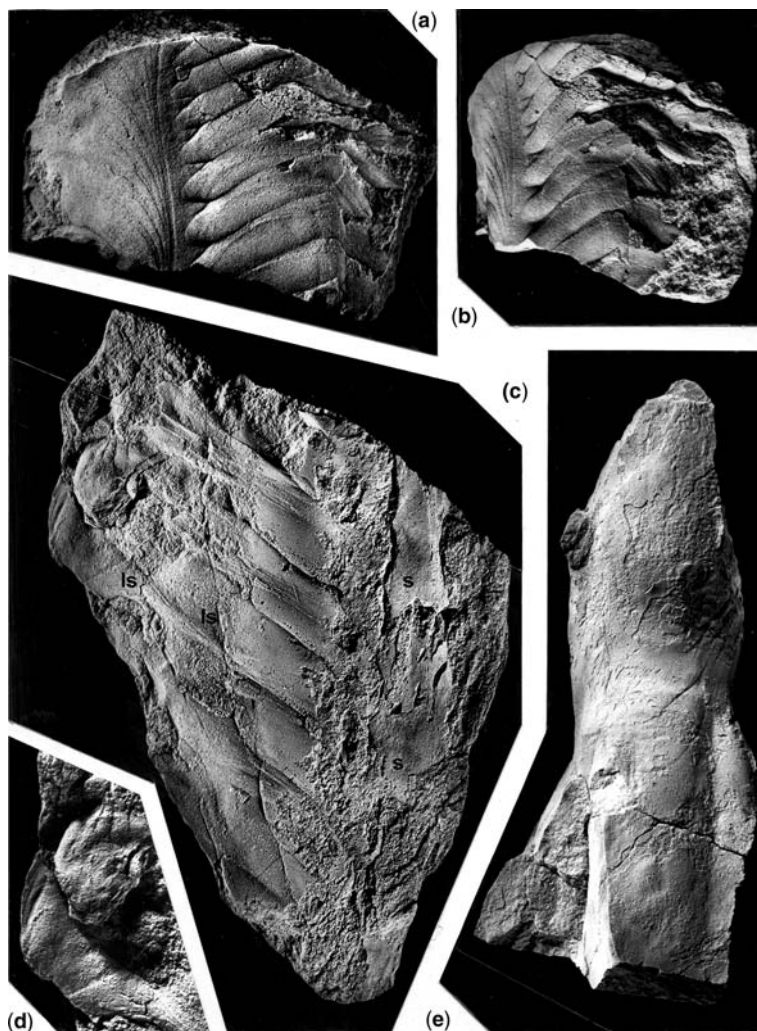


Fig. 6. *Pambikalbae hasenohrae* gen. et sp. nov. (a–b), SAM P35066. (a) internal mould showing axial part of the mid-frond; vertical line of axis 7 cm. (b) same rotated, showing complexity of ‘side’ region in which partings representing an apparently membranous integument forming the ‘floor’ of individual ‘chambers’ extend about 3 cm through the hosting sandstone matrix; vertical line of axis (left of image) 7 cm. (c–d) SAM P35065; (c) internal mould of basal part of frond lying in plane of (wavy) bedding, stem (s), longitudinally sutures (ls) extend approximately through mid-vane; maximum length of rock specimen 25.5 cm. (d) lateral ‘terminations’ of ‘chambers’ of vane with various evident cross grooves or wrinkles; visible part 5.5 cm vertically (in plane of page). (e) SAM P35067, stem preserved as an internal mould ‘in the round’ with oblique grooves evidently representing composite moulds of septal tissues demarking poorly preserved overlapping ‘chambers’; hosting rock 24 cm vertically.

commonly infilled with sand resembling closely appressed butchers’ sausages squeezed against flat surfaces.

The sediments including the holotype likely reflect deposition by a storm-generated waning density current, but the included fossil remains were very likely rooted at their place of life and were simply bent over and aligned with the current.

The matrix of the block including the holotype is a relatively well sorted, but slightly impure, fine-grained sandstone with numerous clay-rich partings including some fine mica. Paratype SAM P35065 is presented within a comparable, but fractionally coarser grained sandstone, and paratypes SAM P35066 and P35067 are both preserved in medium-grained arkosic sandstones.

Systematic palaeontology

Phylum ?CNIDARIA Hatschek, 1888

Class ?HYDROZOA Owen, 1843

Genus *PAMBIKALBAE* nov.

Etymology. Named for *pambi*, a small bag or purse (in reference to the chambers), and *kalbi*, leaf, in the Parnkalla language of the Kujani aboriginal tribe who inhabited the area of the fossil find.

Diagnosis. As for type species.

Pambikalbae hasenohrae sp. nov.

Figures 3–7

Etymology. For Mrs. Pamela Hasenohr who discovered the fossil site.

Diagnosis. Broad, fusiform body comprising multiple vanes conjoined to a tapering axial stem, but sometimes overlapping stem and seemingly meeting at a sinusoidal median groove; stem passing into a broad attachment stalk; vanes showing strong sinusoidal primary furrows reflecting an architecture of three evident serial series of chambers which commonly contain a sediment infill, chambers offset at zigzag sutures, inner series comparatively wide, mid series forming a narrow band, outer series approach breadth of inner set; transverse, more or less faint, serial secondary structure resembling that in *Charnia*.

Dimensions. Body of holotype, SAM P 35063 in excess of 29 cm long and estimated as at least 13 cm wide, stem 2.6 cm wide at about middle of length; paratype SAM P35065 estimated as at least 20 cm wide; paratype SAM P35067 showing stem 6.6 cm wide.

Remarks. Full specific characteristics are outlined in the main text of this study. In general, *P. hasenohrae* is broader than described species of *Charnia* and differs in tending to show only a faint hint of secondary structure transverse to the primary 'branches'; it further differs from *Charnia masoni* in its more tapered overall shape, in the maintenance of relatively wide primary elements towards the distal tips of the vanes or in not showing tertiary grooves. The zigzag sutures evident in the vanes of *Pambikalbae* are unknown in *Charnia*.

Description and interpretation

The morphology of this organism can be divided into two major parts: (1) a broad, tapering axial stem, which extends into a relatively wide basal stalk, and (2) the overlapping, rather broad, foliate, frondose elements. Although there is evidence of at least one of the single 'fronds' being approximately bisymmetrical, it is useful to

describe one 'half' frond extending either side from its join with the stem or the median line as a 'vane'. The composite outline of the overlapping, compressed vanes forms a subovate, fusiform shape tapering somewhat towards free end, which is moderately acute to broadly obtuse and nearly rounded, depending on the degree of distortion (Fig. 3a, b). The number of vanes present in the complete frondose structure is unclear, but the holotype shows evidence of as many as nine vanes, and up to six are recognizable in paratype SAM P35064.

The vanes of *Pambikalbae* have a relatively complex, metameric structure comprising regularly arranged 'tubes' or sub-rectilinear, hollow, elongate box-shaped structures or 'chambers' arranged serially (side by side). The imprints of the membranes, which formed the 'tubes', show fine striations or creases. The frequent distortion, stretching or collapse evident in respect of all the tissues indicates that they were entirely soft, flexible and elastic, and the very faint and delicate imprints of structures on some specimens (Figs 3b, 5a) further suggest that the integument could have been more or less diaphanous.

In the holotype, the tapering axis is outlined partly by the moulding of its infilling sand against the sand fill of the chambers of one vane (right side of Fig. 3a, b), and partly by composite moulding against the termination of wedge-shaped plugs of sand filling chambers of the vane lying on the opposite side. The stem is compressed to a 2.5 cm width near the 'middle' of the preserved frondose structure, and a c. 1.1 cm width near its distal termination. Close examination of the surface of the stem compression indicates that not only is it significantly overlapped by the internal parts of the vanes that lie flat on either side of it, but an eccentrically-positioned zone of thin ridges of sand and patches of criss-crossing furrows suggest that several other vanes collapsed and were compressed into an elongate bundle against the axial element. These vanes either did not include sediment infills or contained only narrow trails of sand. Towards the distal tip of the frondose structure, a substantial portion of a partly collapsed vane has folded flat to overlap the more extended vane on the left side of the axis; the two have become composite moulded so that the collapsed vane has left a serial series of strongly curved imprints which impress the overlapped vane and parts of the mould of the stem.

The structure of the frondose elements is probably made to seem more complex than it really is by the complex counterpart moulding of the sand infillings against adjacent vanes. This makes the presumption that only one layer of chambers or 'tubes' is directly involved with the construction of each vane. The two structures which are at first obvious on one of these counterpart impressions

(e.g. the right side of the holotype frond) are the serial 'wall' sutures between the chambers (Fig. 3a, b), and ridges representing composite moulds of the series of wall sutures of the chambers of the presumably oppressed adjacent vane, where the sand infill of the 'tubes' of this vane have broken away. The wall sutures and the counterpart moulds of the sutures of the adjacent vane form reflexed or sigmoidal curves extending away from the stem towards the free margin of the vane, with the straighter parts of these curves inclined at commonly 45° to 80° relative to the axis of the complete frondose structure. The chambers appear to be blind-ended where they attach to the stem, which they seem simply to abut (SAM P35063) or somewhat overlap, forming scalloped shapes (SAM P35065, P35066; Fig. 6a, c). The tubes of one vane are set along the stem at half an intercept difference from those of the next adjacent vane. Walls of the chambers tend to be rather regularly marked by narrow bands of striations or narrow bands of fibre-like markings made by stringers of very fine sand (Fig. 4c). These striations may represent the collapsed or compressed walls of the chambers of an adjacent vane or, alternatively, collapsed stolon-like tubes with a resistive, fibrous integument, perhaps the most likely notion with respect to the holotype. The chambers vary from about 0.4 cm to 2.2 cm in width (measured approximately parallel to the long axis of the frondose structure), and vary serially in width along the vanes, narrowing towards the distal extremity of the organism.

At about half the breadth of individual vanes, two faint longitudinal grooves are present (Figs 4c & 6c). On close examination of especially well preserved areas, it is evident that these lines mark membranes which divide an inner series of chambers from a narrow medial series of box-shaped structures and thence an external series of longer chambers that form the free edge of the vane. The medial chambers are spaced half an intercept from the inner series, and the outer series are again offset by the same amount. The paratype specimens SAM P35064, P35065 and P35066 all show evidence of these longitudinal structures and pieces of the infilling of adjacent chambers broken away from them; it is apparent that while small parts of these chamber-terminating membranes may lie nearly vertical relative to the surfaces of vanes, in other instances they form oblique configurations, perhaps as a result of distortion. Paratype SAM P35066 is broken in such a way as to show a cross-section of the inner chambers of a vane, and this indicates that the vanes were not at all leaf-like in life, but that their true 'thickness' could have been up to four times the intercept distance between the chambers. Thus, rather than

being tube-like or subquadrate in section during life, the chambers formed a 'stack' of wide, subhorizontal spaces, rather like the juxtaposed, open-plan floors of a high-rise building (presuming that in the live animal the whole frondose structure projected upwards).

The lateral terminations of the outer series of the chambers of the vanes appear poorly preserved. In the holotype, a small curved ridge (or dilation) is associated with the ends of the chambers on the left side, and where one of the overfolded vanes forms a composite mould, narrow subtriangular pits mark the ends of its chambers. Overall, the ends of the chambers seem to have been less resilient than the tissues of the remainder of the vane. Since sand readily entered the chambers during burial of the organism, it seems likely they had a terminal opening. The thickening of the sand infillings near the termination may indicate a rather fragile hood around the aperture. Chambers at the distal tip of the vanes seem to widen and dilate distally, in one instance forming an expanded round shape.

A small, preserved part of SAM P35064 shows two vanes joined medially to form one entire frond, with a sympodial arrangement or alternate positioning of the inner chambers of the vanes at the midline (Fig. 5a). At least one other vane seems to have overlapped the 'frontal' side of the two contiguous vanes, also joining to the midline. Where part of this possibly overlapping vane joins the stem region, several of its chambers show conspicuous transverse ribbing, resembling the transverse markings on the 'branches' of *Charnia* Ford 1958. Low angled lighting reveals that the chambers of other parts of the vanes of this paratype, and lateral parts of the vanes of the holotype and paratype SAM P35065, show indications of metameric transverse markings spaced at intervals of 3–6 mm (Fig. 6d).

The overall disposition of the vanes around the axial stem is not completely clear. On one side of the stem (what we term the 'frontal' side), the vanes seem to have formed entire sheets or 'fronds' with chambers in sympodial arrangements along the midline. At least in the more 'internally' sited 'fronds', the inner series of chambers forming them extended or curved still deeper into the whole frondose structure to join the stem. However, in paratype SAM P35064 the infilling of the chambers of one 'externally' situated vane seems to abut or overlap the surface of an entire frond. In the holotype, vanes seem to both join the sides of and complexly overlap the 'reverse' side of the stem; several may have joined one rather narrow strip of the stem. Paratypes SAM P35065 and P35066 seem to show vanes joining or overlapping relatively wide strips of the stem. It is more or

less clear that in life the stem was largely hidden by its conjoining vanes.

The attachment stalk of *Pambikalbae* was apparently hollow and evidently quite broad (Fig. 6e). Adjacent to the stalk of paratype SAM P35064 are several foliaceous structures separated by or including envelopes of sand, and giving evidence of the chambered construction that characterizes vanes. The curving shapes of these structures seem to indicate their origin from or near the stalk, but it cannot be determined if they actually were parts of the more complete individuals, or were a separate frondose structure with other tissues 'accidentally' appressed against them. The structural similarities of these juxtaposed elements suggest that they all joined, or at least that individuals lived in a tight cluster.

Reconstruction

Since vanes or fronds more or less completely enclosed the axial stem, there can be little doubt

that the whole frondose structure projected into the water column from its presumed anchorage and this is the attitude shown in the reconstructions presented in Figure 7. There is considerable uncertainty as to how auxiliary fronds and extraneous tissues may have related as a whole structure. None of the specimens collected seems to show evidence of any long-distance transport, and there is no evidence that the organism was contractile.

Considerations on biological relationships and function

In its disposition of frondose elements or vanes about a stem, *Pambikalbae* shows an organizational grade close to cnidarians and perhaps pennatulaceans. However, there is no evidence of polyp-like elements in the fossil material. Could it be a plant? The apparent flexibility of all the tissues and the manner in which some vanes seem to have collapsed away to almost nothing is more reminiscent of an animal with a collagen-based integument

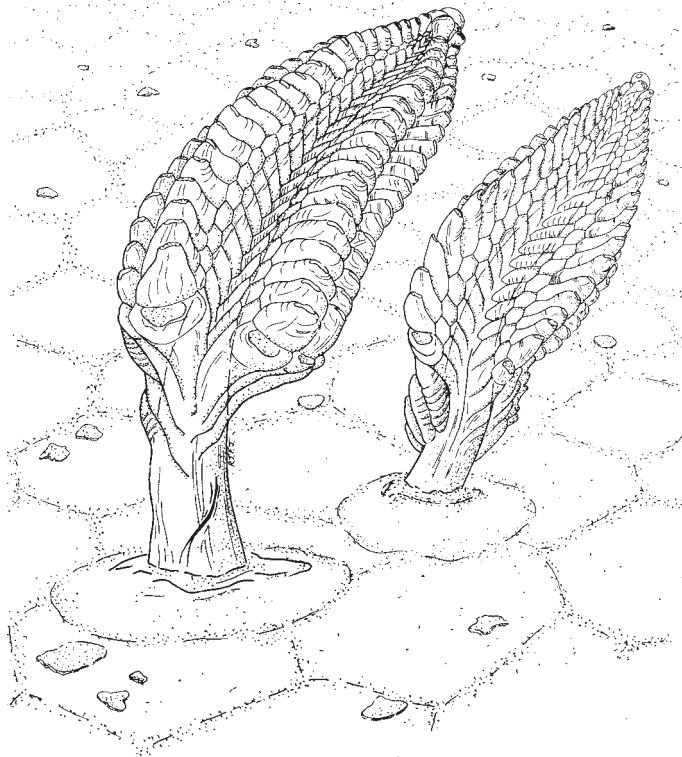


Fig. 7. Reconstructions of *Pambikalbae hasenohrae* anchored in a field of interference ripples, with stray mud flakes. The two interpretations reflect slightly different concepts, that on the left indicating the axial stem enveloped by serial 'chambers' comprising the 'vanes' and that on the right with a 'track' along the stem exposed. Specimens indicate either possibility. The live organism stood about 30–40 cm tall.

rather than a cellulose-based one, but indeed some metazoans, such as tunicates, possess flexible cellulose-based construction.

The regular chambered construction of *Pambikalbae* supports its placement with members of the Ediacaran biota, and is particularly suggestive of an affinity with such forms as *Ernietta*, *Pteridinium*, *Phyllozoon*, *Inkrylovia*, *Ventogyrus*, *Swartpuntia* and possibly *Valdainia*. *Pambikalbae* is also broadly similar in form to the small, frondose structures reported by Jensen *et al.* (1998) in the Early Cambrian of the Uratanna Formation, in the Flinders Ranges. *Ernietta* and *Swartpuntia* occur in Namibia and in the terminal Proterozoic of Nevada (Runnegar *et al.* 1995; Waggoner & Hagadorn 1997; Hagadorn & Waggoner 2000). The time range of *Swartpuntia* extends up into the Early Cambrian in neighbouring southeastern California (Hagadorn *et al.* 2000). The comparable taxon *Pteridinium* is also found in Namibia, on the far north of the Russian platform and in the Ukraine, southern Australia, northwestern Canada and in North Carolina, USA (e.g. Narbonne *et al.* 1997; Weaver *et al.* 2006). *Phyllozoon* occurs in the Neoproterozoic of the Flinders Ranges. *Inkrylovia*, *Ventogyrus* and *Valdainia* are all reported from the northern Russian Platform, but the first is also known from northwest Canada (Hofmann 1981). Pflug (1970a) linked his new phylum 'Petalonamae' to specimens, which Jenkins (1985, p. 351) refers to *Ernietta*.

Ernietta was bag-shaped and composed of several rings of 'tubes' (Jenkins *et al.* 1981, figs 5, 6; Dzik 1999). On the lower aspect of the 'bag', which was likely attached to or partly buried in the substrate, rows of 'tubes' met at a basal zigzag suture; one row of tubules was offset half an intercept relative to the other (e.g. Dzik 1999, fig. 3; Grazhdankin & Seilacher 2002, fig. 9c, e). Approximately half-way up the sides of the 'bag', another suture terminated the lower rings of tubes, and other rings of tubes completed what appears to be the upper part of the structure. These tubes terminated in tapered conical projections in the Nevada material according to B. Runnegar (pers. comm., 1997), but an alternative possibility is that V-shaped portions of sediment project in-between tubes bending into the matrix. Such projections have not been observed in Namibian material, in which, admittedly, the upper tissues uncommonly present seem to be contorted and crumpled. The intercept width between the tubes tends to remain regular, but the cross partitions between the 'walls' of the bag appear as though they were capable of considerable distension. *Ernietta* is commonly preserved in life position with its interior cavity and the 'tubes' packed with sediment (Jenkins *et al.* 1981; Jenkins

1985, fig. 1; 1992, fig. 7; Dzik 1999, fig. 1d). The sac-shaped forms reported herein from the Breakfast Time Greek Member at Nilpena seem to show faint indications of the parallel sutures between the presumed tubes, but no indication of a basal zigzag suture or 'line of budding'.

The several known species of *Pteridinium* comprised three elongate vanes, which joined at a common axis (Fig. 8a). There is limited evidence for each vane consisting of two rows of 'tubes' joined 'back-to-back' but with one row offset half an intercept relative to the other. Where the vanes joined, their tubes were similarly offset, thus forming a zigzag suture (Fig. 8b). The whole fusiform frond was quite flexible, being completely overfolded in slumped beds (the 'winnowed' specimens of Grazhdankin & Seilacher 2002), but the inner parts of the tubes were relatively stiff or resilient and their outer-parts much more membranous and subject to creasing. Fedonkin (1985a) has observed a specimen extending upright through a bed in northern Russia. This orientation may perhaps have come about accidentally due to thixotropic movement of the sediment. No stalk or stem of *Pteridinium* has been observed.

Swartpuntia, first described comprehensively by Narbonne *et al.* (1997; see also Narbonne 1998) from the uppermost Neoproterozoic section of the Nama Group, was constructed of multiple vanes joining a central stem extending from a stalk. From the published illustrations (Narbonne *et al.* 1997), it is possible to infer that as many as five separate vanes were disposed about the stem. Similar to *Pambikalbae*, an inner series of 'lobate projections' lying close to or overlapping the stem and perhaps representing deflated or collapsed chambers, pass into the narrow, 'imbricate', parallel tubes that formed the wider part of the vanes. These tubes are gently recurved or form weakly sigmoidal lines. Such a level of similarity between *Pambikalbae* and *Swartpuntia* and the likelihood of their near concordance in age, surely supports the possibility that they may be closely related, or had a similar lifestyle.

Ventogyrus chistyakovi is described as having the shape of a small boat with a zigzag axis corresponding to the keel-line and sand-infilled 'elements' (chambers) extending away from it at a high angle. Other, shorter second, third, fourth and sometimes fifth order furrows extend away from the central zigzag suture (Ivantsov & Grazhdankin 1997). Of considerable interest, fine parallel striae mark parts of the moulds of the tissues of the chambers and casts of a fan-like array of branching ducts form an 'internal structure' extending lengthwise through the lateral 'elements'. Later study has shown that examples of *Ventogyrus* occurring in a cluster of three nodules were

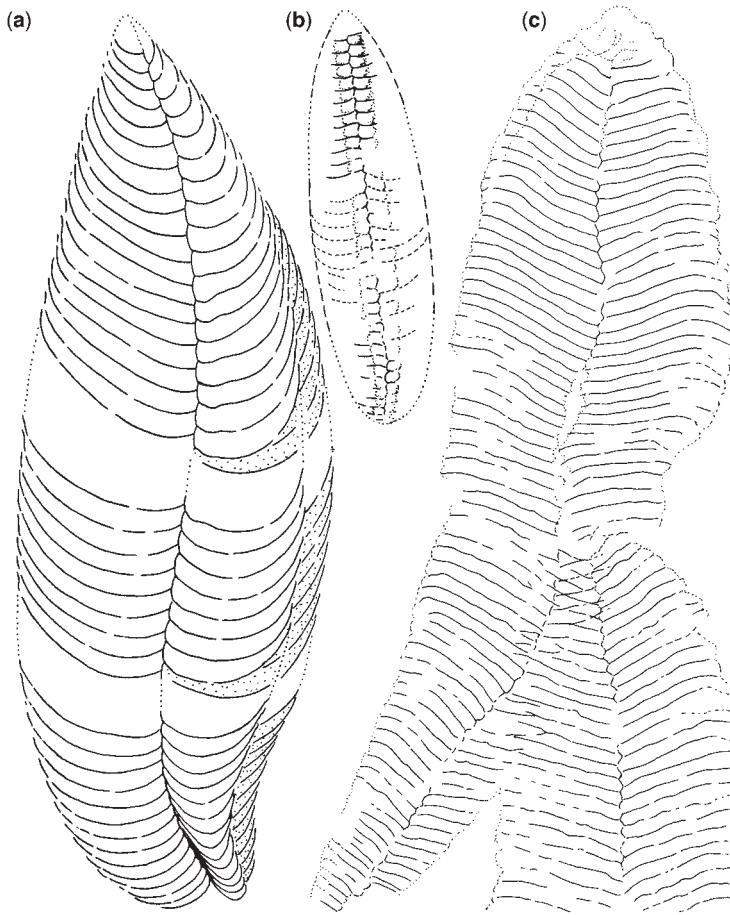


Fig. 8. (a) Reconstruction of *Pteridinium carolinaense* based on material collected from the Winnowie Member, and showing three 'vanes' joined at a median axis. Exposed part of third 'vane' stippled. (b) Compressed 'immature' of presumably the same taxon seen as a very rare element in the Ediacara Member. (c) Type specimens of *Phyllozoon hanseni*, one of the reasonably common elements in the Ediacara Member, with interference pattern formed by composite moulding of resistive walls between the tubules comprising the fronds. Longest frond SAM P19508 (holotype) 18 cm long, Fig. 8a same scale.

originally described as a single organism (Fedonkin & Ivantsov 2007 and references therein).

Other forms which need further comparison with *Pambikalbae* include *Phyllozoon*, a more or less bisymmetrical leaf-shaped structure also composed of serial 'tubes' which met at a zigzag central suture (Fig. 8c). There seems to have been only one layer of tubes forming the 'vanes' of the frond and the integument was relatively 'stiff' or resilient. Numerous individuals are commonly scattered over bedding planes, sometimes overlapping. Such an accidental overlap is incorrectly sketched by Seilacher (1989, fig. 2) and interpreted by him as a join between the fronds. Close inspection reveals the composite moulding of the resilient

'ribs' of the two juxtaposed fronds. The fronds exhibit obvious polarity and their common association with the wide, flattened, tube-like structure which Glaessner (1969) described as a trace fossil designated 'Form D' (e.g. Runnegar 1994, fig. 3) seems too frequent to be due to chance alone. It is possible that this 'tube' constituted a stolon to which the fronds were joined at the narrowly subdivided end (Jenkins 1992). *Valdainia* is a compressed frond with a zigzag suture; the divisions of the vanes show the serial regularity of other members of the 'Petalonamae'.

The foliaceous or frondose taxa, which might have been included in the 'Petalonamae', share the following characteristics: the construction of

the 'body', fronds or vanes consisted of serial rows of 'tubes' or elongate chambers present either in a single 'layer' or several conjoined 'layers'; at least one major join between several series of chambers formed a zigzag suture with one array of chambers abutting the other at half an intercept offset; and all or most forms were likely benthonic, favouring marine shelf settings. Three-dimensional preservation occurs most often in massive sandstones and, as the tubular structure is commonly seen packed with sand, tubes may have had openings to the external environment. The expected placement of these openings (such as at the free edges of the fronds or vanes) seems to have been constructed of fragile tissues and the actual openings themselves have not been observed. *Ernietta* and *Pambikalbae* apparently had membranes which 'blocked' or constricted rows of tubes or chambers that abutted longitudinally; the tubes were of millimetric diameter in most taxa, but centimetric in *Pambikalbae*, which resembles *Swartpuntia* in possessing an axial stem.

Pambikalbae and *Rangea* may have some characteristics in common—multiple foliaceous fronds arranged about an axial stem and anchoring stalk (e.g. Jenkins 1985). The fronds of *Rangea* were also formed by serial elements originating in an alternating manner along the midline, and the edges of the fronds were fragile. *Rangea* is commonly preserved in a three-dimensional manner (Narbonne 2004, 2005), as are the monospecific taxa *Bomakellia* and *Mialsemia*, from northern Russia. Do the similarities between *Rangea* and *Pambikalbae* also reflect close affinity or are they a product of convergence? Of 15 specimens of *Rangea* showing a three-dimensional preservation (Jenkins 1985, p. 342), none seem to show fronds with elongate, hollow tubes packed with sediment. Rather, the fronds seem to include 'branch'-like elements, which further subdivide in an intricate alternating manner. The branches apparently had the capacity to rotate or fold; in compression they are intimately appressed against the interbranch sutures of the neighbouring frond. Thus, close comparison does not presently suggest a near relationship between *Rangea* and *Pambikalbae*, but their similar gross organization does indicate a comparable evolutionary grade ultimately derived from an earlier ancestor.

Size is not a question in Dzik's (2002) referral of *Rangea* and other 'petalonamids' to the Ctenophora. There are examples of comb jellies reaching up to 60 cm to 1.5 m in length (Haeflinger 1974). However, pelagic members of this phylum are extremely fragile, which renders them both susceptible to renting by storms or damage during capture. An early form of cell determinism during the first cell divisions of the embryo, or 'germ mosaic',

causes the adult to lack regenerative capacity. Thus, at first glance, this would not seem likely to be part of a stock tending to prosper in a regime of strong currents, and with their thick mesogloea jelly split into symmetrical halves by a slit-like central enteron, it seems unlikely that sand could intimately penetrate the entire structure during processes of fossilization. Dzik (2002) considered early benthonic ctenophores may have had a much more robust construction, a position which we cannot refute. Nonetheless, the supposed homology between the 'polyp leaves' of 'petalonamids' and the comb rows of ctenophores is unlikely, as individual polyp leaves are 10–12 cm long in large specimens of *Charniodiscus*, while the individual combs of comb-jellies are comprised of fused cilia. Moreover, the tubules or chambers of some petalonamids seem to have no evident analogue in the Ctenophora.

What was the possible relationship between *Pambikalbae* and *Charnia*, especially in view of the enigmatic secondary structures, which mark parts of the chambers of the first? Close examination of the holotype of *Pambikalbae* and SAM P35064 in very low angle lighting reveals a variety of 'cross-wrinkles' set at about the angle of the secondary divisions of *Charnia*. These 'cross-wrinkles' vary from striae set at millimetric to sub-millimetric spacings, to the faintest of serial ridges repeated at intervals of about 2–3 mm (Figs 3a, 5a). In oblique lighting, similar faint cross grooves, set at a spacing of 3–6 mm, are seen obliquely positioned over the outer parts of the lateral chambers of paratype SAM P35065 (Fig. 6d). The alternating arrangement of major divisions of *Charnia* fronds and their strangely inflated shape indicated by moulds (e.g. Jenkins 1985, Fig. 7b) are similar to these elements in *Pambikalbae*. Steiner & Reitner (2001) document the same morphology in material from northern Russia, and additionally show that the integument of these Russian organisms is represented by a compressed and carbonized film. Fedonkin (1983, 1985a) has observed specimens of *Charnia* from the Khatyspyt Formation of the Olenek Uplift, preserved in a three-dimensional manner, with imprints of overlapping fronds that can be exposed by peeling away bedding lamellae. In an illustration of one specimen such as this (Fedonkin 1985a, pl. 13, fig. 3), part of a frond seems to be marked by faint oblique ridges that evidently represent a composite mould of the 'branches' of an overlapping frond; this is very like the composite moulding present in the holotype of *Pambikalbae*. However, the Australian material of *Charnia* provides evidence that the serial secondary (crosswise) divisions of the branches were apparently small, hollow chambers, which became infilled with sediment. Thus, while the similarities

between *Pambikalbae* and *Charnia* are suggestive of affinity, their fronds show important constructional differences.

Seilacher's ideas (1984, 1989) that the majority of known Ediacaran body-fossil remains belong in the 'Vendozoa' or the notion (Seilacher 1992; Buss & Seilacher 1994) of their representing two major taxonomic entities, the 'Vendobionta' and the 'Psammocorallia' are well reviewed by Crimes & Fedonkin (1996) and Narbonne *et al.* (1997) (for viewpoints at variance with Seilacher, see Gehling 1991; Runnegar 1991, 1994, 1995; Conway Morris 1992, 1993*a, b*). A restricted interpretation of the 'Vendobionta' might place all late Precambrian frondose remains within this division (e.g. Narbonne *et al.* 1997), a notion lent tangential support by the suggestion of Glaessner (1984, pp. 57, 87) and Runnegar (1991, p. 76) that the supposed sea-pen-like taxa *Glaessnerina* Germs, 1973 and *Charnia* could be synonymous.

Of two specimens of *Glaessnerina grandis* Glaessner & Wade, 1966, known from Ediacara Range, both are positive hyporelief casts exhibiting the 'frontal' side of the 'frond'. One specimen in Bunyeroo Gorge, referable to this taxon, shows a prominent axial stem. Other recently located material includes a large 'frond' in excess of 73 cm long, preserved compressed, yet in a three-dimensional manner, with smaller and larger segments of the counterpart, a second adjacent specimen on the same rock flag and its counterpart, a separate incompletely preserved part of a large frond, and part of yet another large frond, including the mould of a short convex portion of an axial stem. These new specimens indicate that this taxon had a particularly complex construction. The rather broad (?tapering) stem is evident on only one or two specimens. The 'fronds' themselves were not integral structures or single sheet-like layers of tissue, but were formed by separate 'branches' or large leaf-shaped elements arranged in overlapping series and preserved with thin layers or wedges of sand up to a few millimetres thick spacing the moulds of the tissues of each 'leaf' from its neighbour. Evidently, the leaves were broad, perhaps rather more than a third as wide as long. A long, tapering part attached them to one side of the stem at widely-spaced intervals equal to about half the length of each individual leaf in series, and another series of leaves on the opposite side of the mid-line of the stem was attached at the mid-intercept spacing of the first series. The margins of individual leaves are incompletely preserved but seem to have formed strong sigmoidal curves. On one margin of each leaf about one third of the width of the leaf was marked by deep 'grooves' or sutures separating a row of up to 16 or more serial elements, each

perhaps four times longer than wide and commonly showing some curvature. These serial divisions are sometimes preserved by an infilling body of sand forming internal moulds and thus seem to have been hollow originally.

In our view, the marginal divisions of the leaves could have been sites of polyps (e.g. Jenkins 1996, fig. 4.1), and as the individual leaves in series were widely separated, free circulation of water was possible for feeding and respiration. However, no polyp impressions have been found with certainty.

When the whole organism came to rest on the substrate, possibly undergoing contraction immediately prior to its burial, various leaves forming the 'frond' likely were compressed in juxtaposition to form complicated, composite moulds as their more resistive elements pressed together and through different layers of tissue. The resultant conspicuous 'ribbing' related to the compaction of the secondary divisions is typically more or less parallel with, or at a slight angle to the mid-line of the whole 'frond'.

The separation of the individual 'branches' of *Glaessnerina*, their general leaf-like form, and the occurrence of 'hollow' divisions on one margin of each leaf are all characteristics shared with living pennatulaceans. In contradistinction, there seems to be no evidence that the primary divisions of *Charnia* were constructed of a broad, smooth leaf-like part or any indication that they were clearly separate. Moreover, the secondary divisions marking the branches of *Charnia* can decrease in width towards the midline of the frond (Fedonkin 1985*a*, pl. 13, fig. 3), making it unlikely that they represent serially-budded polyps (arising in sequence on the terminal parts of the branches). The sometimes well marked, oblique tertiary structure has been interpreted as indicating the presence of polyps (Glaessner 1984, pp. 57, 87), but this is now not likely because of evident similarities between *Charnia* and *Pambikalbae*. Thus, it is possible to maintain that there is *not* an obvious relationship between *Charnia* and *Glaessnerina* and the gross geometric resemblance between these forms (Glaessner 1984; Runnegar 1991; Laflamme *et al.* 2007) is not compelling evidence of their structural homology.

Overfolded specimens of *Charniodiscus* indicate that each frond was a single, leaf-shaped entity (Jenkins & Gehling 1978; Jenkins 1992). Three-dimensional compressions of the holdfast are discussed above, and the specimen illustrated by Runnegar (1991, fig. 4c) is likely the imprint of the upper surface of such an anchoring device.

The holotype of *Charniodiscus oppositus* Jenkins & Gehling, 1978 is preserved in three-dimensions and shows the linked 'branches' markedly inflated, with grooves between (ridges in the

preserved external mould; Jenkins & Gehling 1978, fig. 6). No fine sutures indicative of subdividing membranes are evident. Rather, each 'branch' supported a foliate, half-leaf-shaped element, which projected out from the frond towards the surrounding water, and on burial was folded back against the frond, either compressed lying towards the distal end of the frond, or rotated 180° and lying towards the proximal direction (e.g. Glaessner & Wade 1966). In a specimen recently recovered from Bunyeroo Gorge in the Flinders Ranges, some of these 'polyp-leaves' are well displayed, either bent back towards the stalk end of the frond, or partly folded on themselves. They show wide, oblique secondary divisions (spaced at *c.* 15–29 mm) marked by transverse structures resembling the polyp anthosteles of some modern sea pens. However, their arrangement is unique because the 'polyp-leaves' evidently formed a kind of hood or cover (wide enough to fold partly back on itself) and the polyps may be reconstructed as standing in numerous diagonal rows on the upper side of each leaf (Jenkins 1996, fig. 3). During feeding, the muscular polyp-leaves may have folded outward and downward so that the many rows of polyps could project into the water to catch micro-organisms with their tentacles. The polyp-leaves of even small individuals of *Charniodiscus* (*c.* 10–12 cm tall) projected 3–4 mm out from the surface of the frond, and in large individuals (*c.* >1 m tall) extended some 2.5–3 cm out from the surface. This separation could clearly have enhanced the circulation of adjacent waters necessary for efficient feeding and respiration. At times of current influence or perhaps emergence, contraction of the polyps was possibly followed by polyp-leaves folding up over to cover them, so that they would have been contained in a closed pocket. The lips of the 'leathery' covers may have tightly appressed against the sides of the frond to keep out sand or prevent dehydration. Specimens of *Charniodiscus* may show wrinkling and folding, perhaps as a result of partial decomposition prior to burial and the fixative processes which resulted in their casting and composite moulding. There is evidence of a ribbon of supportive tissue underling the basal line of each polyp-leaf. The probability that the close-spaced, short imprints commonly marking stems or stalks represent spicules has been investigated to the limits of preservation the material permits (Jenkins & Gehling 1978).

While *Pambikalbae*, *Glaessnerina* and *Charniodiscus* show obvious similarities in their gross morphology, closer study reveals marked differences. *Pambikalbae* does not exhibit the conspicuous structures interpreted as polyp anthosteles in *Glaessnerina*, and the latter does not reveal the

sutural membranes indicative of a chambered construction. Similarly, the single foliate frond of *Charniodiscus* seems to form an integral element with the stem (cf. Laflamme *et al.* 2004) and not consist of chambered vanes abutting sutures. Moreover, its tissues seem to have been fleshy, and while it might well have had a hydrostatic skeleton pressured by water filling pervasive canals (certainly the stalk appears to have been hollow), there is no evidence in the *c.* 100 specimens known that the fronds included tubular or box-shaped spaces which became packed with sand. Furthermore, 'polyp-leaves' are not apparent in *Pambikalbae*, nor are the imprints that might be attributed to spicules.

The possibility of some considerable separation of the branches and the converse compressive overlap of the 'polyp anthosteles' in *Glaessnerina*, and the distinctive 'polyp-leaves' of *Charniodiscus* (e.g. Jenkins 1996) obviate Seilacher's (1989, p. 231) suggestions that these genera were 'leaf-like structures without branch separation which would have been necessary to let the filter currents past the polyps' and that 'it would be difficult to identify the places of the individual polyps'.

The preceding discussion highlights the gross similarities between Ediacaran frondose fossils, but also points out structural differences that may indicate deep separations at high systematic levels (cf. Laflamme *et al.* 2007). At present, the significance of these differences is unclear. There is little doubt that the bizarre, tubular- or box-like construction has major systematic importance, and the designation 'Petalonamae' holds priority and is potentially available (Ivantsov & Grazhdankin 1997; Narbonne 2004, 2005; Narbonne *et al.* 1997). The taxa which might belong to this division are *Ernietta*, *Pteridinium*, *Phyllozoon*, *Inkrylovia*, *Ventogyrus*, *Swartpuntia* and *Pambikalbae*, plus (with less certainty) *Charnia* and possibly *Valdania*. *Rangea* shows an enigmatic similarity to *Pambikalbae*, but there seems to be no convincing indication that it was constructed of tubes or chambers. In this it approaches a second significant division, which includes forms that show possible evidence of polyps, but no suggestion of the tubular construction of the 'Petalonamae'; this section embraces *Glaessnerina* and *Charniodiscus*, and possibly the Russian form *Vaizitsinia*. *Thaumaptilon*, from the Middle Cambrian of British Columbia, also resembles this group; it apparently lacks a membranous edge to the frond and lacks obvious preserved polyp leaves, but possesses a more elongate holdfast. The small, round markings on the surface of the frond and patches of the stem of *Thaumaptilon* are interpreted as probable siphonozooids rather than the autozooids as interpreted by Conway Morris (1993a). The grade of

organization of these forms is consistent with that of the Cnidaria and more particularly pennatulaceans, specifically the probable presence of zooids (e.g. Jenkins 1992, 1995; Conway Morris 1993a), evidence for a system of internal canals (Conway Morris 1993b) and overall shape. While mere resemblance is not proof of affinity, it is a primary yardstick of biological classification. *Thaumaptilon* broadly resembles *Charniodiscus* and the possible indication of zooids in either is consistent with their designation within the cnidarian Anthozoa. Thus, there seems no particular reason to exclude this second major clade from the Cnidaria unless proof of some difference is ultimately unearthed. Deep divergences between major polypoid cnidarian clades suggested by molecular data (Bridge *et al.* 1995) may well portend early morphological diversity such as might be reflected in their older fossil record. The mosaic of similarities and differences members of the 'Petalonamae,' including *Pambikalbae*, show to the more or less coeval sea-pen-like taxa certainly enhance the kind of morphological spectrum expected to accompany a primal cnidarian radiation.

The complex chambering of the 'Petalonamae' poses a question as to their functioning and mode of life in respect of this adaptation. Their common manner of three-dimensional preservation may be an indication that their tissues were in some way especially resilient, perhaps toughened by an abundant connective compound, or perhaps more likely, chitinous material. This is lent support by the occurrence of little deformed specimens of *Swartpuntia* in association with mud-flake conglomerates that presumably reflect energetic transport (Narbonne *et al.* 1997). Hence, the chambered construction of the 'Petalonamae' could have functioned principally in the role of mechanical support rather than more dynamic processes related to feeding or ingestion of nutrients.

If the 'Petalonamae' harboured photosynthetic symbionts, then it might be expected that their preferred life habit was one of shallow, clean, clear waters. However, lithologies preserving the organisms suggest that they tended to live offshore or in channels, where there may have been some attenuation of light levels. The matrix of many of the remains includes an admixture of clay or silt that helped form the 'moulding sand' (Milner *et al.* 1962, pp. 576–577; Jenkins 1985) that was probably important in their preservation. The silt suggests turbid water, not a favoured characteristic in the environment of organisms dependent on photosymbionts. The propensity of some 'Petalonamae' to be preserved in channel deposits or even to have colonised current-scoured pot holes (*Ventogyrus*, see Ivantsov & Grazhdankin 1997) further explains their requirement for a tough integument

as a necessity to withstand buffeting by sediment-charged, storm currents (see Fedonkin & Ivantsov 2007).

Gentle movement of currents along such surge channels during fair conditions likely carried a rain of fine detrital food particles released by inshore wave-winnowing of sandy sediments known to have included abundant decaying remains (those that formed the characteristic, abundant shallow-water fossil assemblages). Perhaps the chambers of *Pambikalbae* were carpeted with flagellate cells similar to the choanocytes of sponges, or otherwise bore bands of cilia that helped waft in suspended food particles. One appraisal is that the 'Petalonamae' may have had an oxidative metabolism with their tubes/chambers connected to the surrounding waters, and they were possibly heterotrophic suspension feeders. The possibility that the tubes or chambers actually housed polypoid zooids interconnected by thin stolons can not be ruled out, though the mathematical regularity of *Ernietta* which seems to have some 64 tubes in each cirlet comprising the body irrespective of the size of the individuals, poses major questions as to how the zooids could have reproduced with such precision, and the manner in which the complete structure increased in size. Moreover, if the interpretation of Runnegar (pers. comm., 1997) that the tubules of *Ernietta* terminate in conical projections is correct, no obvious peripheral apertures are apparent for the extension of the polypoid feeding device. Narbonne *et al.* (1997) suggested that the open ends of the tubes of a sand infilled specimen of *Swartpuntia* were either original or due to damage by storm action, and described the serrated segment terminations of other specimens as surrounded by a smooth groove along the entire margin of the petaloid, implying that the tubes were closed at their ends.

Even more bizarre is the possibility that members of the 'Petalonamae' either tended to 'ingest' sediment while still alive, or were packed with sand so near to death that their tissues did not lose any of their vital resilience (e.g. Jenkins *et al.* 1981, p. 75; Seilacher 1992; Buss & Seilacher 1994; Crimes & Fedonkin 1996; Narbonne *et al.* 1997; Grazhdankin & Seilacher 2002). Thus, colonies of complete individuals of *Ernietta* evidently preserved in life position have the body spaces packed with fine sand and even show discontinuities in the sediments forming the clastic infill of the central space (Jenkins *et al.* 1981, figs 5b, c). If the organisms died during their infilling or had a large amount of sediment suddenly dumped upon them, then surely their tissues would have collapsed flat; the inference is that the organism's structure was sufficiently robust to maintain its gross shape even as the creature was intimately permeated

with sand over some finite interval of time (minutes? days?). This trait seemingly militates against the presence of corporal zooids within the tubes. The idea of growth of protoplasm through interstices between sediment grains (Crimes & Fedonkin 1996) is not supported to the extent that *Ernietta* is preserved by direct contact moulding of grains, and its internal fill shows miniature erosive unconformities indicating its interior space was truly a confined hollow, and filled subsequently by the entry of current-transported sediment.

The likelihood that *Pteridinium simplex* lived partially buried in the substrate (Grazhdankin & Seilacher 2002) is lent support by study of the site Seilacher (1992) investigated on Farm Aar (the Aarhausier site) in Namibia. The numerous associated individuals present at one level in medium bedded sandstone (Saylor *et al.* 1995) are mostly aligned as though orientated by the current (e.g. Jenkins 1985, fig. 1e), but almost all are positioned with the convex aspect of the joined vanes downward in the 'virgin' association of Grazhdankin & Seilacher 2002. Moreover, some long examples show curious snake-like bends or kinks, which would surely have resulted in juxtaposition of specimens if their placement were simply due to chance. Instead, they evidently represent a life assemblage, the two lower vanes of each formed into a shape like a canoe (Grazhdankin & Seilacher 2002), which was partly filled with sand, but still with the encircling free margins projecting above the substrate. Thus, the projecting margins were probably subject to abrasion and imperfectly preserved, or not evident at all. The level filling of the enveloping sand (Crimes & Fedonkin 1996) can be attributed to the equal upward accumulation of sediment settling from currents varying in strength and direction (as tidal sands are sometimes seen to bury moribund anemones); this fill rarely shows small-scale cross-bedding. For the most part, the ends of the fronds also curved upwards above the substrate and are rarely observed. Broken beds reveal that the central medial ('third') vane also projected upwards and probably through the substrate almost like a longitudinal sail. The alignment of the fronds then becomes a necessity for growth as the ends of the creatures prolonged between their neighbouring fellows Fedonkin (2000) has reconstructed *Pteridinium* as an elongated tubular organism that had three longitudinal 'septa', very similar to the body plan of *Ventogyrus*. The evidence of interpenetration of specimens considered by Grazhdankin & Seilacher (2002) to indicate growth of individuals through sediment is open to interpretation. One of us (R.J.F.J.) has observed two individual (calcareous) bivalve shells at right angles in an event bed with a thick valve cleanly cutting a lighter one, clearly an example of post

mortem impact, suggestive of the old hack of using a gun to fire a straw through a barn door. Whether or not *Pteridinium* had to be buried before a growing one worked its way through the dead and decaying integument of another is a further issue. Ivantsov & Grazhdankin (1997) present analogous information for the life orientation of *Ventogyrus*, with its remarkable colonisation of the successive sediment levels filling potholes.

The robust or leather-like (Seilacher 1992) consistency of some members of the 'Petalonamae' mitigates against their being of syncytial grade (tissue comprising multinucleate protoplasm) as posed by Runnegar (1995), and if, as he considers, they were of 'algal' rather than animal affinities, how could their habits of living partly buried or colonisation of channels and/or pot holes favour photosynthesis?

Vanes of some members of the 'Petalonamae' incorporated resistive but flexible material; the 'stiff' septa forming the walls of the tubes in *Phyllozoon* are one example (Jenkins 1992; Runnegar 1995). The characteristics of this material on preservation simulate the same geometry as the chambered structures which represent the identified chondrophores *Ovatoscutum*, and *Chondroplon*. Hofmann's (1981) interpretation of the latter as a deformed *Dickinsonia* completely failed to appreciate the resilience of *Chondroplon* implied by the broad, radiating folds, which deform its centre (Wade 1971) or its unique marginal lappets. For comparable reasons it is probable that a 'chitinoid' stiffening was present in some of the 'Petalonamae'.

Living relatives?

Possible tunicate affinities have been suggested for several Neoproterozoic forms, with the sac-shaped *Yarnemia* (in Chistyakov *et al.* 1984) from the middle Onega River, and also *Inkrylovia*, interpreted to form a broadly hollow bag (Chistyakov *et al.* 1984; Fedonkin 1990). The characteristics of colonial tunicates, including a tough but flexible integument composed of tunicin, the metamerism associated with replication of the body parts, the occurrence of stolons and the overall size of the colonies, provide a possible basis for comparison with the 'Petalonamae'. The large chambers forming the 'vanes' of *Pambikalbae* are wide enough to have housed the barrel-shaped, ciliated branchial chamber that is diagnostic of the tunicates, but while fine mouldings reflect their membranous construction, no indication of any branchial apparatus is evident. It is perhaps noteworthy that in the pelagic salps, the gill apparatus

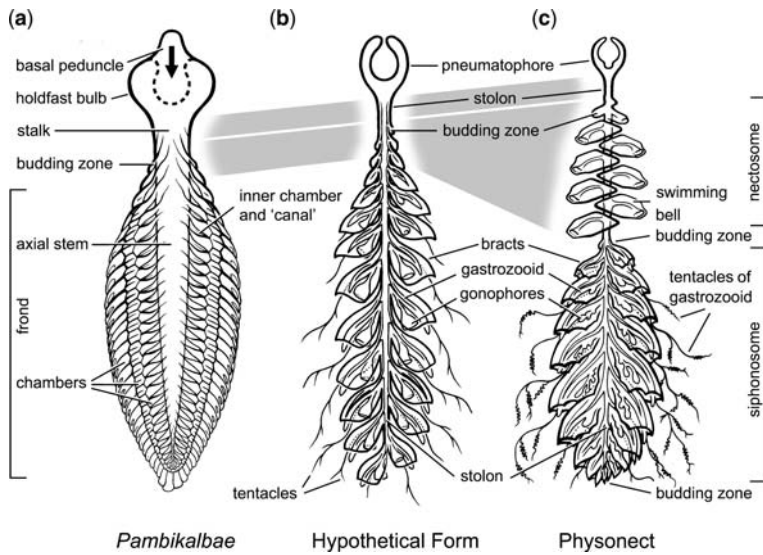


Fig. 9. Comparison between an 'inverted' *Pambikalbae*. (a), a hypothetical ancestral 'calycophore' siphonophore in which the swimming bell (nectophore) has yet to evolve (b), and a generalized modern physonect (c). The frondose fossil animal represented might well have adapted the holdfast to a pneumatophore by simple invagination of the basal peduncle and development of gas secreting cells. The gross homology of the 'colony' is indicated. Modern calycophores have a swimming bell, but have apparently 'lost' the pneumatophore. The further point of comparison is that in *Pambikalbae*, the 'vanes' are comprised of three serial rows of chambers, and in calycophore and physonect siphonophores, the serial 'persons' arrayed along the stem are tripartite, consisting of a more or less enveloping passive bract, a feeding gastrozoid, and the reproductive gonophore which doubles as a swimming bell.

is reduced to a pair of slits on either side of a sloping bar and the potential for this device to be preserved is minimal.

There are at least superficial similarities between the strangely flattened 'horizontal' chambers of *Pambikalbae* and the compressed swimming-bells and cormidia variously crowding the trailing stolon-like coenosarc of the pelagic cnidarian calycophore and physophorid Siphonophorida (Fig. 9). These fragile nectonic creatures comprise either an upper swimming-bell or compound swimming-bells, or a gas-filled primary float or pneumatophore, and a succeeding coenosarc or extensile hollow stem of varying length from which numerous medusa-buds or cormidia ('persons' in earlier works) arise asexually (Fig. 9b, c). The cormidia develop at one or several growth loci (Hyman 1940; Totton 1954; 1965).

The widened chambers of *Pambikalbae* show enigmatic structural parallelisms with the extraordinary compound cormidia and eudoxids (separate free living cormidia) of some calycophores. In these compound elements, several medusa-buds or individuals may insert one within the other to become inextricably interlocking, a circumstance at least reminiscent of the distinctive longitudinal suturing of the 'vanes' of *Pambikalbae* and its

internal transverse partitioning of the chambers. Walls in the calycophores and physophorids tend to be muscular and, unlike other hydrozoans, have thick developments of mesogloea, which makes the elements relatively resistive, in contrast with their fragile, stolon-like or membranous connections to the coenosarc. The narrow ribbon-like line extending through the 'horizontal' walls of the chambers of *Pambikalbae* is similar to the 'principle radial canal' which links all of the cormidia of a compound medusa-bud back to its attachment stolon. The branched, stolon-like tubules in *Ventogyrus* might be considered as having functioned in a comparative role. Both single swimming-bells and compound elements in the living animals may show unusual ribs, grooves and sutures; for example the nectophores of *Halistemma striata* show serial side ribs.

Totton (1954, 1965) considered the pneumatophore, stem (coenosarc) and distal gastrozoid of the physonects as representing the primary oozoid. The stem of *Pambikalbae* might also be considered as representing a primary oozoid (as it is in pennatulaceans) and its 'vanes' to be formed of compound 'cormidia' at least analogous to those in siphonophorids (9a–c). Presuming that *Pambikalbae* had a discoidal holdfast as occurs in

its assumed fossil allies, perhaps such a structure became secondarily modified as the physophorid pneumatophore by simple invagination of its base, evolution of a gas gland and some chitinous stiffening of the inner gas vesicle (Figs 9a, b, 10a, b). It is noteworthy that the pneumatophore has no mesogloea, but possesses simple two-layered walls which are highly muscular (Hyman 1940, p. 469) as also might be expected for a holdfast. The gastrovascular cavity of the pneumatophore passes directly into the central hollow of the stem, and the sand infilling comprising internal moulds of Ediacaran discoidal holdfasts and stems of frondose remains indicates both that the holdfasts were hollow and that this cavity was in open connection with a wide hollow extending through the stalk and stem.

Runnegar (1995) cautioned that there is a danger of overlooking true fossil representatives of the primary stock of major clades because the expected character states of crown-group members may not be present. Thus, the probably benthonic *Pambikalbae* is certainly distant from the living Siphonophorida, but shows several analogous characteristics and a general organizational grade consistent with it potentially representing a highly derived member of the cnidarian class Hydrozoa. Perhaps *Pambikalbae* and some of its near allies are an evolutionary plesion broadly related to the stem stock of the siphonophorids, which may have had a benthonic origin in the Neoproterozoic and secondarily evolved a float, a more fragile colony

and specialized adaptations related to their becoming pelagic (Fig. 9).

The question as to whether any of the other known Ediacaran frondose remains may represent hydrozoans (Glaessner 1979, 1984; Boynton & Ford 1995) and indeed the reality of any zoological affinities between suggested members of the 'Petalonamae' remains opaque in-so-far as the state of knowledge of most is relatively incomplete. The sympodial growth of the 'branches' in *Rangea*, *Bradgatia* Boynton & Ford 1995, and the spindle-shaped fossils in southeastern Newfoundland may be compared with modern hydroid colonies such as *Halecium*, but by no means compel a hydrozoan placement. *Rangea* certainly had a central oozoidal stem or polypoid-like *Pambikalbae* and multiple foliate fronds. An alternative possible interpretation of the branching elements in *Rangea* is as relatively elaborate gonodendra, with the major and subsidiary series of branches signalling different developmental maturity, or somewhat less likely, physically separate male and female gonodendra. The fine third order structure of the branches (Jenkins 1985, figs 4a, 5) could just possibly be an actual indication of the gonophores. In some siphonophorids the tentacles bear the nematocysts on small serial tentilla and when these are strongly withdrawn the coils form little, serial, knob-like projections at the sides of the clumped structure, a configuration somewhat resembling the third order structure on the branches of *Rangea*.

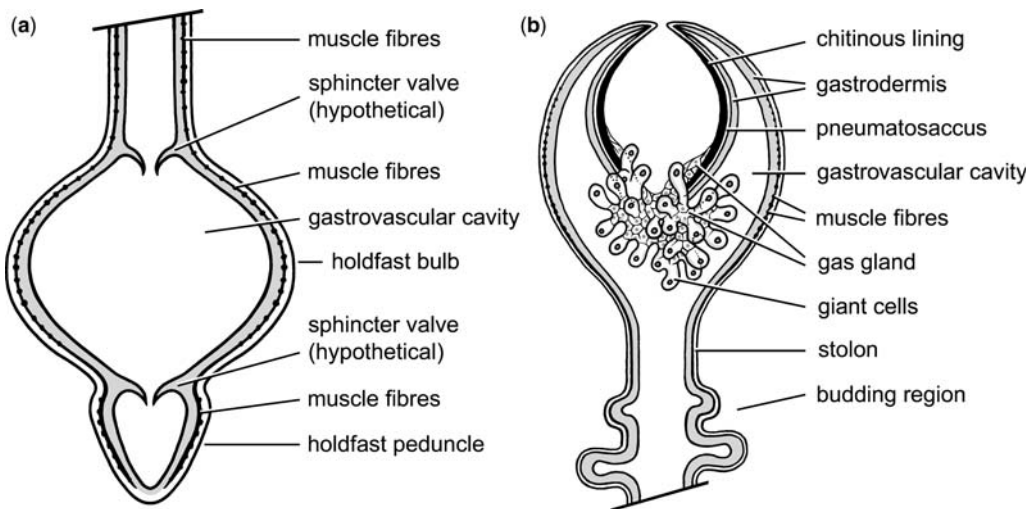


Fig. 10. Comparison between the holdfast of an Ediacaran frondose fossil as hypothesized from characteristics of preserved material (a), and the 'float' or pneumatophore of a physonect siphonophore (b) (adapted after Hyman 1940, p. 472), exploring the possibility of their homologous construction. Of particular note, both have muscle fibres in the wall of the bulb, a necessary adaptive characteristic for a holdfast, and the pneumatophore may have a chitinous lining, a possible synapomorphy in relation to the stiff material making some frondose fossil remains (e.g. *Phyllozoon*).

On the other hand, considering that *Pambikalbae* shows striking similarities to several other coeval fossil forms, its possible placement relative to any modern division can hardly be argued in isolation. What, then, of its evident alliance with *Swartpuntia*, which in turn is apparently a near relative of *Pteridinium*? It is noteworthy that an aspect of the geometric construction of *Swartpuntia*, the way in which the tubes forming the vanes parallel the inferred proximal margin of the later (Narbonne *et al.* 1997, figs 6, 7, 9.1) and directly intersect the remaining margins, sometimes widening slightly and curving inwards near the distal (medial) tip of the frond, resembles the disposition of the comparable elements in the unique South Australian specimen of *Chondroplon*, which is preserved in an identical manner. Both occur in near association with *Pteridinium carolinaense* and in broad terms, must be of similar age. *Chondroplon* apparently lacks the elaboration of the medial axis evident in *Swartpuntia* and the end with the widened chambers shows a deep inflection. *Swartpuntia* and *Chondroplon* were evidently similar in their stiff or resilient integument.

If *Chondroplon* is truly a chondrophore as posed by Wade (1971), then by comparison with the ontogeny of living examples, the central chamber of the 'float' formed first and the subsequent (narrowing chambers) progressively added in a concentric manner towards the free margin, and indeed decrease to only fractions of a millimetre in width at the youngest formed pole. It needs to be clearly stated that unlike '*Kullingia*', which Jensen *et al.* (2002) consider as a marks made by a tethered and ribbed strand twisting about in currents, *Chondroplon* is not a scratch circle and shows both complicated moulding of the ends of chambers and radial flexure attributed to a stiff integument (Wade 1971). Intuitively it might be expected that the manner of increase in the tubes in the vanes of *Swartpuntia* was exactly the reverse, that is, the new elements grew sequentially at the 'distal' tip of the frond. But what if this was not true and the apparently membranous fragile tissues at the 'proximal' end of the frond (Narbonne *et al.* 1997, figs 6, 7, 9.1) formed the actual site of increase?

Exactly the same question may be posed for *Pteridinium carolinaense* where specimens from Ediacara indicate that the tubes were shorter and narrower at the blunt or rounded end of the frond and comparatively wide at the more pointed (? 'distal') tip. Likewise, in *Phyllozoon* the part of the frond that might be interpreted as 'basal' or proximal has the narrowest and shortest tubes consistent with their being relatively immature. In *Pambikalbae* it is again the 'distal' end of the frond which shows the most highly ordered metamerism, while on the stalk and basal or proximal

part of the stem incompletely defined 'chambers' are marked by grooves with an irregular geometry, bulges or 'branches' with poorly defined cross structure and virtually shapeless or irregular foliaceous outgrowths. Are these evidence of growing tissues incompletely organized into the rhythmical metameric format of the more mature distal frond? A valid question is whether any living Cnidaria show such a retrograde pattern of growth, and immediate examples occur within the Siphonophorids where new nectophores bud off the proximal end of the coenosarc in the physophorids and a budding zone at the join of the siphosome (trailing coenosarc with secondary cormidia) with the nectosome or first definitive nectophores gives rise to the cormidia in both the physophorids and calycophores (e.g. Totton 1965). Additional budding zones may also be present.

Chondroplon provides a bridging morphotype between the characteristic fusiform bipolar organization evident in various genera of the 'Petalonanae' or 'Vendobionta' and the concentric, but still approximately bisymmetrical geometry of both the presumed Ediacaran chondrophore *Ovatoscutum*, and the living *Verella*, in which the vertically orientated, chitin-supported sail (see Kaestner 1967, fig. 4.42) is at least the analogue of one of multiple vanes of the frond or the 'third' vane of *Pteridinium*.

These observations pose a basis for a new morphostructural interpretation of the 'Petalonanae', not as a hollow translucent device to house symbiotic photoautotrophs, and not forming tubes or chambers to house enigmatic zooids, but as a resistive and likely chitinous tubular or chambered endoskeleton made by communal hydrozoans phylogenetically near the ancestors of the Chondrophorina. As in the living animals, the endoskeleton could have been secreted by an aboral ectodermal invagination of the communal coenosarc.

As primarily simple diploblasts without the supportive advantage of the 'stiff' mesoglea present in the Anthozoa, the constructional fragility of poly-poid hydrozoans greatly limits their potential for size increase in energetic environments. This is overcome to an extent by their tendency to secrete a chitinous periderm, which forms a tubular support enclosing the stolons and cups or bells housing the polyps or hydranths, as in the extant *Gymnblastina*. The Hydroactinidae make a chitinous or calcareous mat from a periderm of tangled hydrorhizae. By the process of invaginating the secretory membrane of their basal coenosarc the Chondrophorina are able to completely envelope their hollow, chambered chitinous skeleton or 'support', which constitutes the gas-filled float. However, there is no *a priori* reason why the forms that first evolved the capacity to secrete an internal chambered device should have been

pelagic, and its potential benefit in enabling early hydrozoans to reach large colony-size and exploit the inner neritic realm of the terminal Proterozoic is readily apparent. The imbricate series of tubes forming individual vanes of the supportive endoskeleton would have similar stiffening properties to flat cardboard sandwiching a plicate medial sheet, and the occurrence of multiple vanes extending from a common axis evidently served to increase the surface area of the whole colony. Presumably the stalk and stem in essence comprised a single 'giant' polyp.

This model is useful in explaining the peculiar modes of life of some 'Petalonamae' as the living coenosarc and myriad supported polyps enveloped a 'dead' chitinous frame, which could become progressively buried in the substrate. The coenosarc would presumably die on the buried parts, but free margins of vanes extending above into the water may have been maintained in growth as they supported live tissue and hydranths. A difficulty with this hypothesis lies in the extraordinary near-mathematical constancy of the number of tubules in each sheath of *Ernietta*; because the construction is in essence bisymmetrical, it follows the tubules must form an even number to generate a closed circuit, but what characteristic in a 'primitive' invertebrate could control their fixed number?

Without more definitive evidence of the problematic placement of the frondose Neoproterozoic forms relative to the Hydrozoa or Anthozoa, Glaessner (1979) chose to maintain his several newly-erected family divisions within the informal section 'Petalonamae'. Noting that the division of the 'Petalonamae' was first used by Pflug (1970a, p. 228) with reference to synonyms of *Ernietta*, which is surely among the most aberrant of all Neoproterozoic foliate remains, Jenkins (1985) promoted the 'order' Rangeomorpha Pflug, 1972, as a section of the subclass Octocorallia. The striking and (in the sense of fossil remains) singular characteristics of *Pambikalbae* and its potential identification as a hydrozoan lead us to nominate it to a separate section, *Pambikalbiidae* fam. nov., assigned to the new order Palaeophorina, which may possibly be considered as part of an early hydrozoan radiation that evolved structural traits showing some analogies with, or broadly foreshadowing either the Siphonophorida or Chondrophorina.

The extraordinary diversity present among modern cnidarians and likelihood that numerous past clades within this phylum have become extinct over the geological ages, as is true for most kinds of multicellular life, hardly makes the exercise of suggesting a possible classification for *Pambikalbae* one of artificial 'shoehorning' into the Hydrozoa. This classification is not 'proved', but appeals to the time honoured approach of comparative

morphology as providing a philosophical basis for arguing the ancestry or subsequent diversification of taxa. In respect of this, morphological traits are unable to be detected in *Pambikalbae* that place it outside the known variability of the Cnidaria, notwithstanding that other problematic fossil remains of similar age, to which it may or may not be directly related, can not presently be confined to any modern phylum with a level of certainty. Thus, we do not view *Pambikalbae* as lending support to Seilacher's (1992) Kingdom 'Vendozoa', which is defined to include the characteristics of the present form, nor particular merit in the notion that organisms of essentially cnidarian grade should have evolved twice over (e.g. Gould 1998; McMenamin 1998), separated by the arbitrary historical dichotomy of the Neoproterozoic/Phanerozoic transition. The Cambrian similarly contains highly derived cnidarians (Conway Morris 1993b) as well as representatives of the sister phylum Ctenophora showing considerable evolutionary divergence (Conway Morris & Collins 1996; Dzik 2002). The possibility that several of the earliest phyla had overlapping characteristics or generated highly convergent morphologies, is in essence an expected consequence near the rootstock of major radiations. In soft-bodied remains these subtleties of overlap and convergence will be further mantled by the vagaries of preservation, including accidental retention of particular body parts, and the bias of the observer.

Molecular sequence data for ribosomal RNA provides indications that the Cnidaria are among the most primitive of the metazoans and that their ancestry is appreciably deeper in time than the diversification of the 'deuterostome' and 'protostome' phyla whose early history is shown directly by body fossil remains or inferred from trace fossils to be embodied in the terminal Proterozoic/older Cambrian evolutionary 'explosion' (Lake 1990; Adoutte & Philippe 1993; Conway Morris 1993a, b; Halanych *et al.* 1995). Studies of the homology of the relatively diverse homeobox genes now known in hydrozoans and anthozoans also supports the archaic evolutionary placement of the Cnidaria, either as the rootstock of higher animals (Finnerty & Martindale 1997; Valentine 2001), or as a sister clade to the form which provided the monophyletic origins of the articulates and vertebrates (Carroll *et al.* 2001, Peterson *et al.* 2005; Sempere *et al.* 2006).

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