

A re-examination of the Nama-type Vendian organism *Rangea schneiderhoehni*

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Abstract – The need to re-examine *Rangea* has been motivated by two factors: first, by the recent progress in the understanding of three-dimensional mouldic preservation of Vendian fossils, and second, by discoveries of this taxon outside Gondwana albeit in the same sedimentary environment as seen in Namibia. Several important features are revealed, including the *in situ* posture in the sediment, the double-layered quilted structure, the tripartite stemless body and the mucous-supported sheath in the sediment. It is suggested that *Rangea* represents an infaunal organism, and that the similarity with other members of the Nama-type biota reflects convergence in functional and fabricational constraints in relation to infaunal life habit.

Keywords: Neoproterozoic, Vendian, Nama Group, taphonomy, taxonomy.

1. Introduction

The Vendian biota of Namibia comprises an assemblage of forms, exotic to mainstream biology, dominated by serially quilted body plans. Their mouldic preservation within sandstone is intriguing in that the specimens appear in variously curved and oriented shapes, approximately resembling internal moulds of pots and troughs. Among the creatures with a quilted anatomy there is a peculiar frondescent organism *Rangea schneiderhoehni* Gürich, 1929 with a unique dendritic pattern of quilting. Previous studies have dwelt on the importance of the branching pattern of the quilting in determining biological relationships of *Rangea*. The most generally employed interpretation of the dendritic quilting has been to compare it to the branching of an internal gastrovascular organ (Pflug, 1970; Jenkins, 1985; Dzik, 2002a). The gross morphology of *Rangea* convincingly conforms to the body plan of an epibenthic pinnate organism, although even here this apparently straightforward interpretation can be problematic. For example, it has been recognized that although *Rangea* consists of several fronds, the number of fronds varies between four (Dzik, 2002a), five (Pflug, 1970), and possibly more (Jenkins, 1985), according to the interpretations offered. In addition, there is no consensus concerning the reconstruction of the frond arrangement.

In the course of a study of *Pteridinium* Gürich, 1933, we have tested an infaunal model with three-dimensional preservation (see Grazhdankin & Seilacher,

2002) by comparing other fossils occurring in the same taphonomic mode. On the basis of our examination of *Rangea*, we have noticed several otherwise overlooked features suggesting (a) a much higher complexity in the pattern of quilting and (b) a different arrangement and number of the fronds. An important advance was made during the first *in situ* field excavations of *Rangea* in the southeastern White Sea area, northwestern Russia. There we not only extended its stratigraphic and geographic range, but also demonstrated the restriction of this taxon to a specific lithofacies (Grazhdankin, 2004). In this paper we present new data on the biostratigraphy and morphology of *Rangea*, an organism whose biological affinities have yet to be resolved.

2. Material

The holotype and paratype of *Rangea schneiderhoehni* were found in November 1914 by H. Schneiderhöhn (1920, p. 267), who worked as a field assistant of H. von Staff. The specimens were collected in float near trigonometrical point 1438 m, southeast of Kuibis Station (Namibia), in what is currently referred to as the Kliphoek Member of the Dabis Formation, Kuibis Subgroup (Neoproterozoic–Cambrian Nama Group; Saylor, Grotzinger & Germs, 1995). The genus was named after the geologist in the German colonial administration, Dr Paul Range, who earlier in 1908 had collected the holotype of *Rangea brevior* Gürich, 1933. In a letter, written from a prisoner of war camp, H. Schneiderhöhn brought these fossils to the attention of G. Gürich, who at that time was confined in another

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prison camp. The whereabouts of these specimens did not emerge until 1928, when the widow of H. von Staff discovered them in the collection of her husband. The specimens were subsequently described by G. Gürich (1929, 1930a, 1933), and deposited in the Geologisch-Paläontologisches Institut und Museum (GPMH) in Hamburg, where the type material of *Rangaea schneiderhoehni* miraculously escaped destruction in World War II.

In 1968, G. Germs (1973a) found two additional specimens of *R. schneiderhoehni*, one in the Kliphhoek Member (near Vrede) and another in the stratigraphically younger Niederhagen Member (near Chamis) of the Nudaus Formation, Schwarzrand Subgroup (Nama Group). This material is now housed in the South African Museum (SAM) in Cape Town.

The bulk of the material of *R. schneiderhoehni* was collected by the farmer H. Erni from the Kliphhoek Member near Aus. At least ten specimens from this collection were described and figured by H. D. Pflug (1970), R. J. F. Jenkins (1985), and J. Dzik (2002a), and eventually were deposited in the National Earth Science Museum (NESM) in Windhoek. The NESM collection also houses numerous, previously unpublished, albeit mostly poorly preserved material, some of which can be assigned to *Rangaea*.

Beyond Namibia, poorly preserved frondose specimens were reported by M. F. Glaessner (1969) from the Arumbera Formation of Central Australia, and by J. G. Gehling (1991) and R. J. F. Jenkins (1995) from the Ediacara Member of South Australia. These were identified as *Rangaea* sp., but given the uncertainties with identification, these specimens are omitted from our discussion. Outside Gondwana, two specimens of *R. schneiderhoehni* were recently (2002–2003) found by the senior author in the late Neoproterozoic Vendian succession of northwestern Russia. Here, *Rangaea* occurs in the middle reaches of Onega River near the Plesetsk Cosmodrome (see Ivantsov & Grazhdankin, 1997; Ivantsov & Fedonkin, 2002), and in the coastal cliffs of Winter Mountains in the southeastern White Sea area (Grazhdankin, 2004). Stratigraphically these outcrops are correlated with the Verkhovka and Yorga formations, respectively (Grazhdankin, 2003). The specimens are housed in the Paleontological Institute (PIN) in Moscow.

3. Palaeoecological context

The *Rangaea*-bearing Kliphhoek and Niederhagen members consist of medium-grained, thick-bedded and cross-bedded sandstones that are interpreted as upper shoreface, fluvio-marine deposits (Saylor, Grotzinger & Germs, 1995). Specific evidence for a fluvial origin is in the form of unidirectional multistoried cross-bedding (0.1–3.0 m set thickness), abundant channelized and scoured surfaces with flute and groove casts, parting lineations and abundant shale clasts (Germs, 1972,

1983). The precise palaeoecological context of *Rangaea* in Namibia remains obscure on account of the float origin of available specimens.

Rangaea occurs at two horizons in the Vendian succession of Russia (Grazhdankin, 2004). In each case *Rangaea* is confined to medium- to fine-grained, tabular-bedded sandstones that occur in channel casts (0.1–0.5 m thick and several metres wide), with convex-downward erosional bases and nearly flat upper surfaces. The channel casts are uniformly aligned (SW–NE), although locally their traces are sinuous and branching in plan view. They extend beyond the limit of the outcrop and occur within intervals of interbedded wave-rippled sandstone, siltstone and shale. The channel casts are confined to intervals that are characterized by smaller-scale sand-filled gutter casts. The facies also host thicker (up to 1.8 m) sandstone channel casts that tend to have multistoried trough-cross-laminations (SW), where beds or lenses of maroon shale clasts commonly separate the cross-bedded sets. Several centimetres of wave-rippled sandstone with shale clasts cap most channelized sandstones. This facies association records strong current and wave influence and is interpreted as a fluvio-marine overflow gutter and channel setting within a distributary-mouth bar depositional system (Grazhdankin, 2003).

In the channel casts, the sandstone packages are separated by oscillation wave ripples and microbial structures. Wave ripples tend to have aprons on both sides of their linear crests, spilled over shale drapes in the troughs, indicating alternation of wavy and quiet-water conditions. Evidence for microbial stabilization of the sediment in the channel casts is represented by wrinkle structures, spiral and sinuous shrinkage cracks in the ripple troughs, and sandstone domal and columnar stromatolites. All these features suggest that filling of the channels was interrupted by intervals of cessation in sediment supply and fluvial activity. To summarize, distribution of *Rangaea* in Namibia and the southeastern White Sea area appears to be restricted to the same fluvio-marine distributary-mouth bar lithofacies.

Taphonomical data resulting from studies of oryctocoenoses can be used to resolve the palaeoecology of extinct organisms (e.g. Grazhdankin & Seilacher, 2002). Application of such an approach to the study of *Rangaea* is limited because of insufficient knowledge concerning the occurrence of this taxon in the context of associated fossil assemblages. What we do know is that *Rangaea* co-occurs with *Pteridinium* in at least one specimen (NESM F541) collected in float from the Kliphhoek Member in Namibia (Fig. 1). The larger slab NESM F338 demonstrates an association of several specimens of *Rangaea* (Jenkins, 1985, fig. 7A). H. Pflug (1970) analysed this assemblage, and interpreted the *Rangaea* organisms as living in structured colonies. This may, however, be misleading, given the lack of information about the overall sedimentological context of

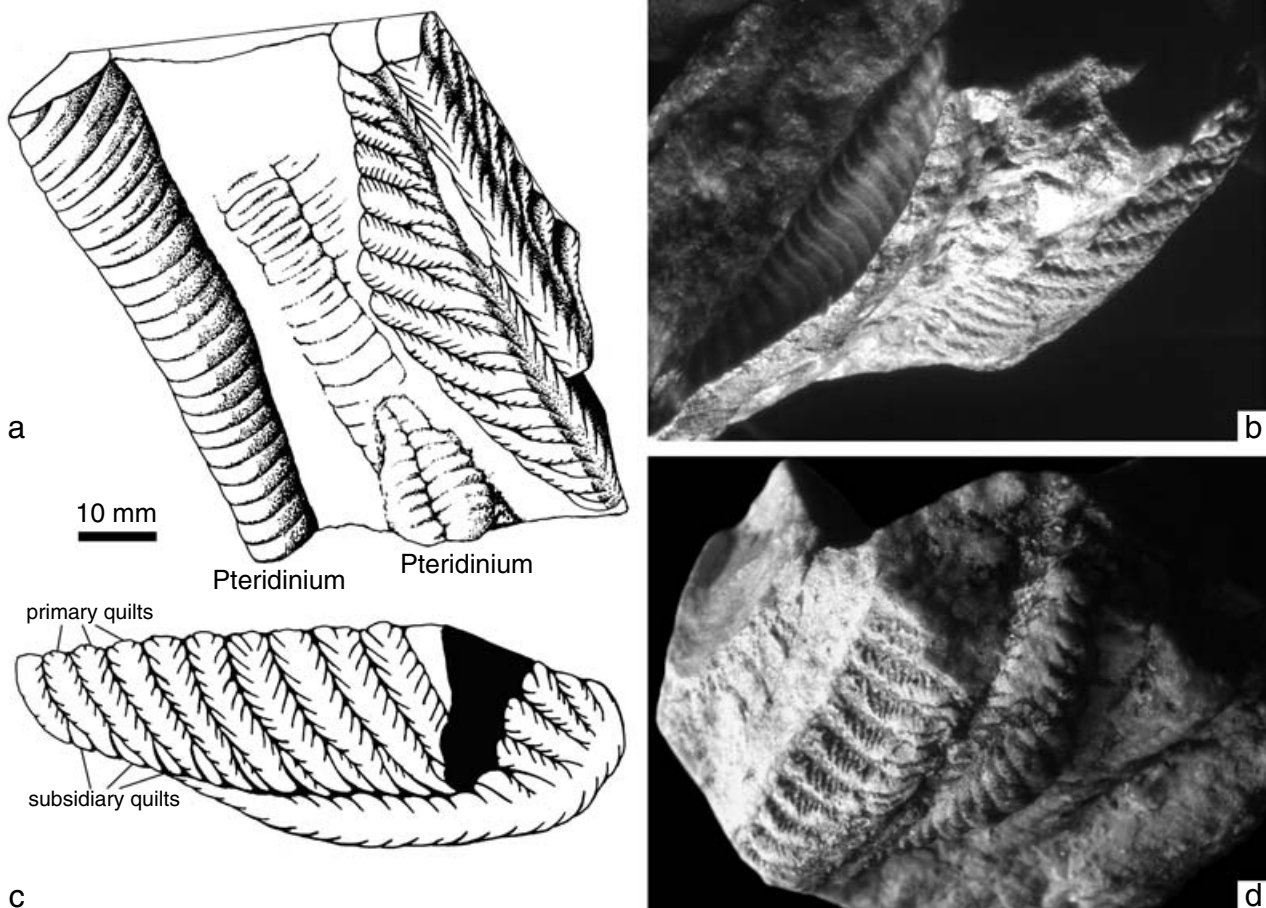


Figure 1. *In situ* biostratinomy of *Rangea* and co-occurrence with *Pteridinium*. Kliphoek Member of the Dabis Formation, Namibia. NESM F541. (a) Bottom view of the assemblage with two casts of *Pteridinium* and a cast of *Rangea* prepared off the sandstone matrix, all confined to the same upper bedding plane. A faint impression of another *Pteridinium* specimen in the central area represents a cast protruding from the overlying assemblage. *Camera lucida* drawing. (b) Vertically extended median vane in the *Pteridinium* cast suggests undisturbed fossilization of the assemblage. (c) Lateral view of the three-dimensionally preserved cast of *Rangea*. *Camera lucida* drawing. (d) View of the *Rangea* cast from the steeper end.

the slab (NESM F338). Preliminary data from field excavations of *Rangea* in the southeastern White Sea area seem to demonstrate the solitary occurrence of this taxon.

Apart from *Rangea schneiderhoehni*, species diversity in the Kliphoek Member encompasses *Pteridinium simplex* Gürich, 1933; *Ernietta plateauensis* Pflug, 1966; and *Namalia villiersiensis* Germs, 1968. More problematic taxa include *Orthogonium parallelum* Gürich, 1930b; *Petalostroma kuibis* Pflug, 1973; *Protechiurus edmondsi* Glaessner, 1979b; *Ausia fenestrata* Hahn & Pflug, 1985; and *Nemiana simplex* Palij, 1976 (= *Hagenetta aarensis* Hahn & Pflug, 1988), nor need this be a complete list, because not all of the taxa described by Pflug (1972) can be readily re-interpreted as preservational modes of *Ernietta*. In the authors' view, the specimens described from the Kliphoek Member as a putative sprigginiid (Germs, 1973b) and *Kuibisia glabra* Hahn & Pflug, 1985 actually represent wave-winnowed preservation of *Pteridinium* and

Namalia respectively (see Grazhdankin & Seilacher, 2002).

Found in close association with *Rangea* in the outcrop of the Verkhovka Formation on the Onega River is a fossil assemblage that includes *Yarnemia ascidiformis* Nesson in Chistyakov *et al.* 1984, *Ventogyrus chistyakovi* Ivantsov & Grazhdankin, 1997, *Vendoconularia triradiata* Ivantsov & Fedonkin, 2002, as well as several problematic fossils. The *Rangea*-bearing interval in the Yorga Formation in the Winter Mountains has yielded *Petalostroma kuibis*, *Nemiana simplex* and *Bomakellia kelleri* Fedonkin, 1985 (= *Mialsemia semichatovi* Fedonkin, 1985).

4. Biostratinomy

Rangea is preserved as three-dimensional sandstone casts, either swollen or flattened (*forma turgida* and *forma plana* in Gürich, 1933). To date, in Namibia *Rangea* is known only from float specimens.

Nevertheless, in the slab NESM F541 (Fig. 1), the convex-down position of a three-dimensional cast of *Rangea* is in association with an *in situ* three-dimensional cast of *Pteridinium* with a specific relation to the top bedding plane. In addition, in the slab NESM F338 several three-dimensionally preserved specimens of *Rangea* demonstrate uniform convex-down fossilization with respect to the top bedding plane (Jenkins, 1985). Finally, similar convex-down occurrences of *Rangea* have been observed during *in situ* excavation in northwestern Russia.

The swollen, three-dimensional casts of *Rangea* 'float' in a convex-downward position in the upper part of sandstone event beds, with their edges reaching the top bedding plane. As such they resemble casts of a narrow boat with arching sides (Fig. 1c). In plan view the casts are ovoidal, with one end more pointed than the other. The maximum thickness of the casts is in their widest part (Fig. 1a, c). The casts demonstrate a gently rising angle towards the tapering end (Fig. 1c), whereas the opposite end is steeper (Fig. 1d). There is self-evident similarity to the mode of preservation of *Pteridinium* and *Onegia*, and the three-dimensional appearance of *Rangea* can therefore be reasonably interpreted as a result of *in situ* fossilization of infaunal organisms (Crimes & Fedonkin, 1996; Grazhdankin & Seilacher, 2002; Grazhdankin, 2004). The specimens of *Rangea* found on internal parting surfaces within tabular-bedded sandstones, which are spread out and flattened, are interpreted as resulting from the preservation of winnowed individuals in reworked sediment (Fig. 2). This winnowing does not imply, however, protracted transport, because the flattened casts are never crumpled, folded over, pursed or stacked. In addition, the three-dimensional and flattened casts are confined to the same facies, albeit having different biostratigraphic contexts.

The common reconstruction of *Rangea* (Jenkins, 1985, 1992; Dzik, 2002a) in the form of an epibenthic frondose organism is based on the assumption that corpses were smothered in a sand flow during storm deposition and adapted a three-dimensional, convex-downward shape under the sediment load. The opportunity to test this assumption is presented in the southeastern White Sea area. There, several specimens of *Charniodiscus* Ford, 1958 were found, preserved within the sandstone matrix of a prodelta event bed, in precisely the burial mode proposed by Jenkins (1985). The occurrence of these fronds, however, is either flat or gently convex upward. Likewise, *Dickinsonia* Sprigg, 1947, found in the same bed, does not mould itself into a convex-downward shape, even though it was presumably trapped in density currents (Grazhdankin, 2004; *contra* Dzik, 1999, 2002a). *Rangea* is, therefore, very unlikely to represent an epibenthic frondose (Jenkins, 1985) or ovoid (Dzik, 2002a) organism, deformed into a convex-downward shape during burial.

Rather all the taphonomic features suggest an infaunal habit.

5. Morphology

5.a. Quilting

Fossilized *Rangea* consists of several fronds. Each frond has a foliate shape with a series of recessed furrows that run outwards at varying angles from a prominent smooth median zone to define a series of chevron-like units called quilts (Fig. 1). There is some evidence for a geniculation of the quilts near the median zone, although the strength and persistence of this feature is variable. The frond is bilaterally symmetrical; there is, however, a slight deviation in the disposition of quilts. Thus, quilts on each side of the body are slightly offset by one-half of a quilt along the median zone relative to quilts of the neighbouring side (Fig. 2). Furthermore, along the length of the body the quilts are arranged in two rows, that is, as long petaliform primary quilts and short lanceolate subsidiary quilts (Pflug, 1970; Germs, 1973a). The subsidiary quilts pinch out a short distance from the median zone as the primary quilts expand (Figs 1c, 2), whereas the primary quilts extend to the edge of the frond where they taper bluntly.

In no specimen can an exact total of primary quilts be counted, on account of either missing areas or incomplete preservation. In SAM 4368 (Germs, 1973a, fig. 1F, G) it is estimated that on each side there were at least 20 primary quilts. Other relatively complete specimens have fewer quilts. The primary quilts also vary in size. The largest quilts are observed in PIN 3993-7021, the respective length and maximum width being 34 and 9 mm (Fig. 2). The quilts become progressively narrower and shorter towards the tapering ends of the frond.

Each primary and subsidiary quilt is further patterned by less prominent and evenly spaced second-order furrows (Fig. 2). They define a series of second-order chevron-like quilts that, in turn, appear to be subdivided by third-order furrows. The character of the secondary subdivision is similar to the primary quilting of the frond, and this is repeated in the third-order quilting. There is a positive correlation between the length of the first-order quilts and the number of second-order quilts within the same specimen (Fig. 2). It may be significant, however, that the maximum number of second-order quilts is generally similar among different specimens and is in the range of 14 to 16, regardless of the maximum quilt length. Accordingly, width of the second-order quilts varies between different specimens.

The apices of the quilts are sharply delimited by wedge-shaped fields of either smooth or wrinkled relief that give this part of the body a scalloped appearance

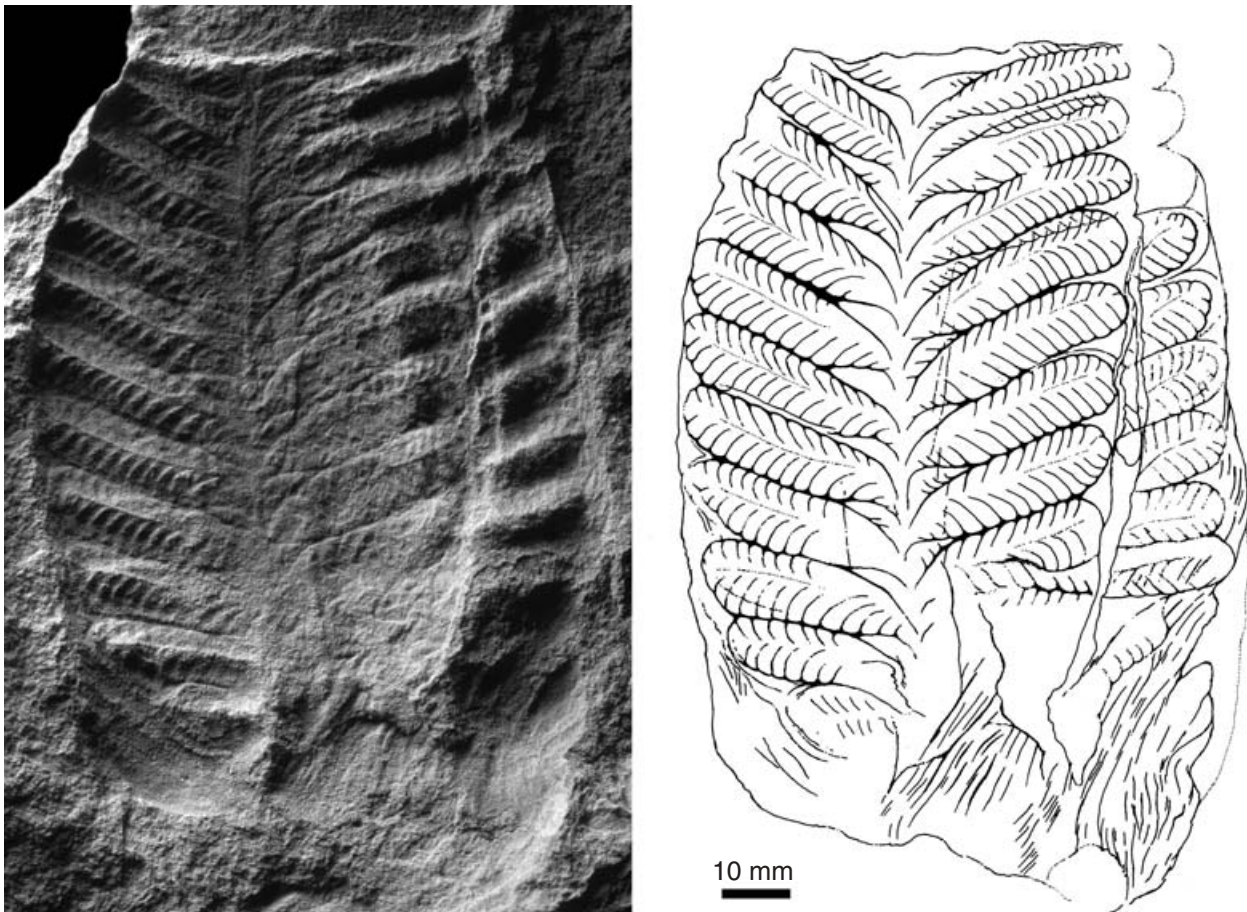


Figure 2. Winnowed preservation of *Rangea* showing the fractal quilting of the frond, the margin of the second frond, and the sheath. Yorga Formation, Russia. PIN 3993-7021.

(Fig. 2). These incised fields represent a part of the body by means of which the quilts were connected.

5.b. Double-layered structure of the frond

In most specimens the quilts are preserved with the chevrons of the second-order furrows flaring towards their apices (Fig. 2). Upon changing light direction, however, the furrow patterns in some specimens switch to an opposite inclination (Fig. 3). This is best explained by an overprinting of second-order furrows by another layer of quilts, the furrows of which must run in opposite directions due to the alternating position of the quilts. We hypothesize, therefore, that the subsidiary quilts extended into another plane to form a closely attached second layer (Fig. 4). The alternative possibility, that the overprint corresponds to an adjacent frond, has been considered and rejected, not least because the superimposed furrows in PIN 3993-7021 (Fig. 2) could be traced and linked to the subsidiary quilts.

Apart from the lateral offset due to the alternating position of the quilts, the overprinted features appear with inverted relief. Thus, the quilts are typically preserved in positive hyporelief separated by recessed furrows,

whereas the superimposed quilts have a shallow negative relief and are separated by sharp-crested ridges. This inversion can be explained as differential collapse of quilts from either side of a double-layered frond.

Composite moulding of the double-layered structure has produced a variety of preservational features that can be easily misinterpreted. For instance, superimposition of quilts from two layers in the poorly preserved holotype (GPMH 179) might have misguided a number of authors (Germis, 1973a; Jenkins, 1985; Dzik, 2002a) when they concluded that the tubular quilts had twisted around their axes (which could only happen if they were free). These effects are best revealed in specimens PIN 3993-7021 and PIN 4564-2000, where overprinting of second-order furrows from the two layers gives the illusion of an oblique secondary quilting (Figs 2, 3). Furthermore, superposition of alternating quilt boundaries from the two layers locally produces sharp-crested ridges running along the median zone of the quilts (Fig. 2). In our opinion this represents a taphonomic feature, but it has been interpreted by Dzik (2002a) as the impressions of medial canals of an otherwise hypothetical gastrovascular system. Under close inspection, however, the ridges appear to be extensions of

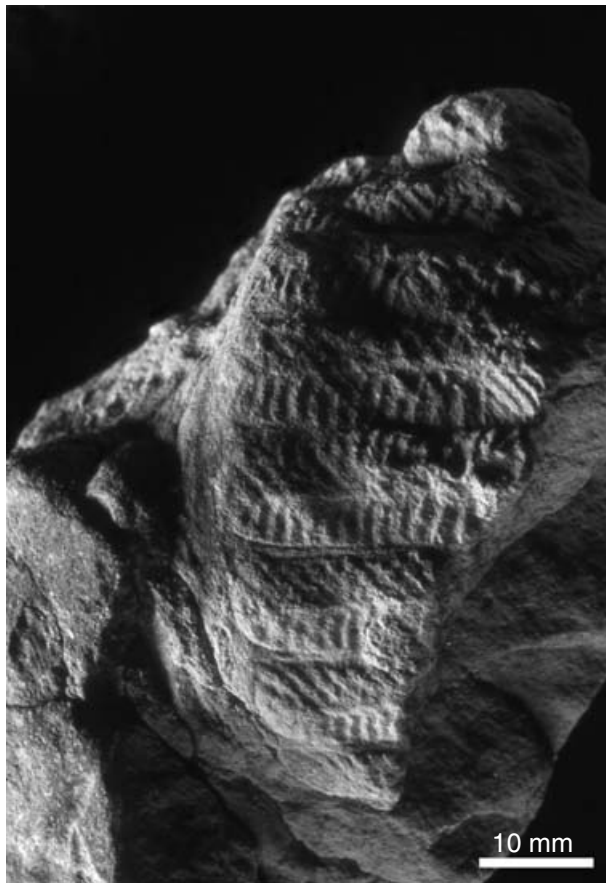


Figure 3. *In situ* preservation of *Rangea* showing the overprinting of quilts from the double-layered structure of the frond. Verkhovka Formation, Russia. PIN 4564-2000.

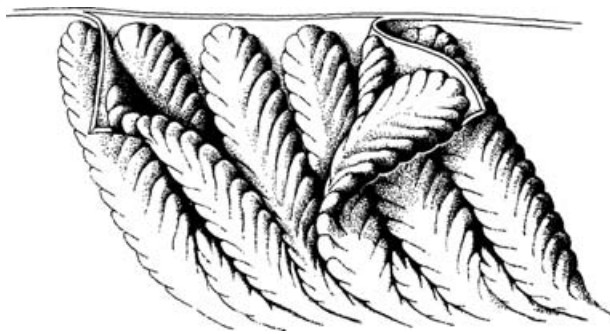


Figure 4. The authors' reconstruction of the double-layered structure of the frond.

the boundaries of subsidiary quilts when they continue into another plane to form a second layer (Fig. 2).

In winnowed specimens the median zone, including the subsidiary quilts, is often delineated on both sides by a sharp flexure in relief ('Seitenkante' in Gürich, 1933) (Fig. 2). The position of this flexure coincides with the curvature of the trough-shaped frond in three-dimensional specimens. We interpret the flexure as a taphonomic feature related to flattening, which arguably is supporting evidence for the frond being trough-shaped in life.

5.c. Compound body

Another peculiarity of *Rangea* is the clustering of several fronds ('petaloids' in Pflug, 1970) into a closely packed compound structure ('petalodium'). This clustering is clearly not accidental, because in each cluster all the constituent fronds demonstrate a similarity in quilt morphology and uniformity of quilt arrangement. Furthermore, these clusters maintain their integrity in winnowed specimens of *Rangea* (Fig. 2). This implies, therefore, certain stability and resistance of the cluster to mechanical stress.

Pflug (1970) argued that a compound body consisted of three fronds (internal, external and frontal 'petaloids'), although some specimens were thought to have additional in- and ex-counter petaloids. These specimens were re-examined in the NESM and the structures noted. The structures interpreted as in- and ex-counter petaloids join along a common seam, are serially quilted, and appear simply to be three-dimensional casts of *Pteridinium* (Fig. 1a). All specimens of *Rangea* are preserved in clusters of two or three fronds, and complete specimens always have three fronds. Jenkins (1985) and Dzik (2002a) identified four fronds in the clusters NESM F338-2 and F338-5. We were able to examine NESM F338-2, and concluded that at least in this specimen, a pair of well-preserved fronds and another deeply weathered frond constitute the tripartite cluster, whereas the evidence for the fourth frond refers to an inorganic feature (Fig. 5a). In the tripartite cluster NESM F338-5 (Fig. 5b), either side of the middle frond was misinterpreted by Jenkins (1985, fig. 2C) and Dzik (2002a) as a separate frond. However, in the same paper Jenkins (1985, fig. 4B) offered an alternative interpretation of the cluster NESM F338-5, suggesting that one of fronds could possibly represent several fronds stacked together and separated by narrow, 1–2 mm thick wedges of sediment. We re-examined this specimen in the NESM and concluded that deformation of the frond 1 (Fig. 5b) resulted in imbrication of the quilts, a common mode of three-dimensional preservation in siliciclastic sediments (Ivantsov & Grazhdankin, 1997; Grazhdankin & Seilacher, 2002). The interior of two of the three-dimensionally preserved quilts was misinterpreted by Jenkins (1985) as sediment in-filling 'obverse cavities' of separate fronds. To summarize, there is no conclusive evidence that the *Rangea* fronds cluster in four. The compound body of *Rangea* consists of no more than three fronds.

Jenkins (1985) and Dzik (2002a) have argued that the clustering occurs around a common axis, although they could identify a stem-like structure in only a single specimen (NESM F338-5) (Fig. 5b). When the specimen was examined in the NESM we came to the conclusion that the 'axial cavity filling' is, in fact, the interior of the three-dimensional cast of a frond in a tripartite cluster (frond 1 in Fig. 5b). Another structure

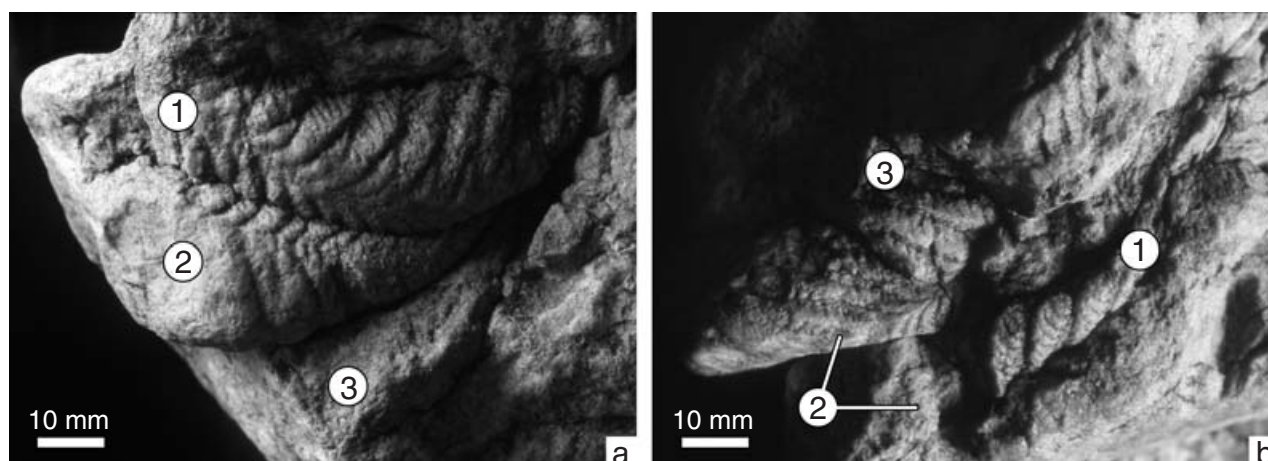


Figure 5. *In situ* preservation of *Rangea* showing the tripartite and stemless structure of the body. Numbers 1 to 3 indicate the three parts of the body. Kliphhoek Member of the Dabis Formation, Namibia. NESM F338-2 (a), F338-5 (b).

in the same specimen, interpreted by Jenkins (1985) and Dzik (2002a) as the ‘basal bulb’ of an inferred peduncle, is not connected with the cluster of three-dimensional casts and could be fortuitous. This structure was also noted by Pflug (1970; the ‘annulus’), but interpreted as an organ by which all petaloids could be connected. Apart from NESM F338-5, the available specimens of *Rangea* are devoid of any indication that would suggest an axial stem-like structure.

Winnowing of the compound body never resulted in separation of the fronds, nor has it ever involved their sharp deformation (Figs 2, 6). This arguably implies certain resistance of the double-layered fronds against bending and pursing.

5.d. Sheath

In winnowed specimens PIN 3993-7021 and SAM K4367 the cluster of collapsed fronds is underlain by a thin discontinuous wrinkled veneer of sediment (Figs 2, 7). In SAM K4367 this veneer preserves a faint impression of a frond with primary and subsidiary branching (Fig. 7). The branches, however, are not geniculated and connected in the median zone, but rather terminate at a stem-like structure (Fig. 7). Under close inspection the relief of the impression appears to be inverted as compared to three-dimensional casts, whereas the stem-like structure corresponds to the axial trough between the fronds (Fig. 7).

Germis (1973a) noted this structure and interpreted it as the epidermis. Alternatively, the sand veneer could represent sediment that was in contact with the infaunal *Rangea* and became cemented to the organism by a secreted mucous sheath. This interpretation is reasonable assuming that the sheath was thin and enveloped the tripartite cluster of *Rangea*. The structure of the sheath may have been delicate and seldom preserved unless sediment penetrated and moulded the space between the fronds and the sheath. The faint

branch-like structures seen on this mould could be traces of quilts where they contacted the sheath. The connection between the putative sheath and fronds, however, was weak, and the former could exfoliate as a result of deformation, as is evident from a misalignment between the traces of quilts in the sheath and the quilts in the fronds in SAM K4367 (Fig. 7).

6. Discussion

Rangea is reconstructed as an immobile benthic creature, whose body consisted of three closely-packed trough-shaped fronds enveloped by a mucous sheath. Three-dimensional preservation and biostratinomy of the fossils suggest that in life *Rangea* was completely immersed into sand, and that the sand filled the cavities of the trough-shaped fronds. Living *Rangea* had a convex-down posture within the sediment, with the edges of all three fronds rising to the sediment–water interface (Fig. 1). Each frond consisted of two membranes, and the space between these membranes was inflated and fractally quilted (Fig. 4). The quilts were probably hydrostatically supported. Composite moulding of the frond suggests that the quilt boundaries correspond to structures stiff enough to press through the integument.

The infaunal habit poses certain problems, particularly regarding the intrasedimentary growth and morphogenesis. The trough-shaped appearance of the fronds suggests that *Rangea* grew in length by displacing the sediment, whereas the rising angle of their basal area could be a result of the resistance offered by the sand during the growth (Figs 1, 5). There is a variation in the length and proportions of the quilts, implying that they also contributed to growth by lateral expansion. The arrangement of the first-order quilts in two layers presumably solved the space problem arising from quilts expansion away from the median zone (Fig. 4). We hypothesize that early in the ontogeny

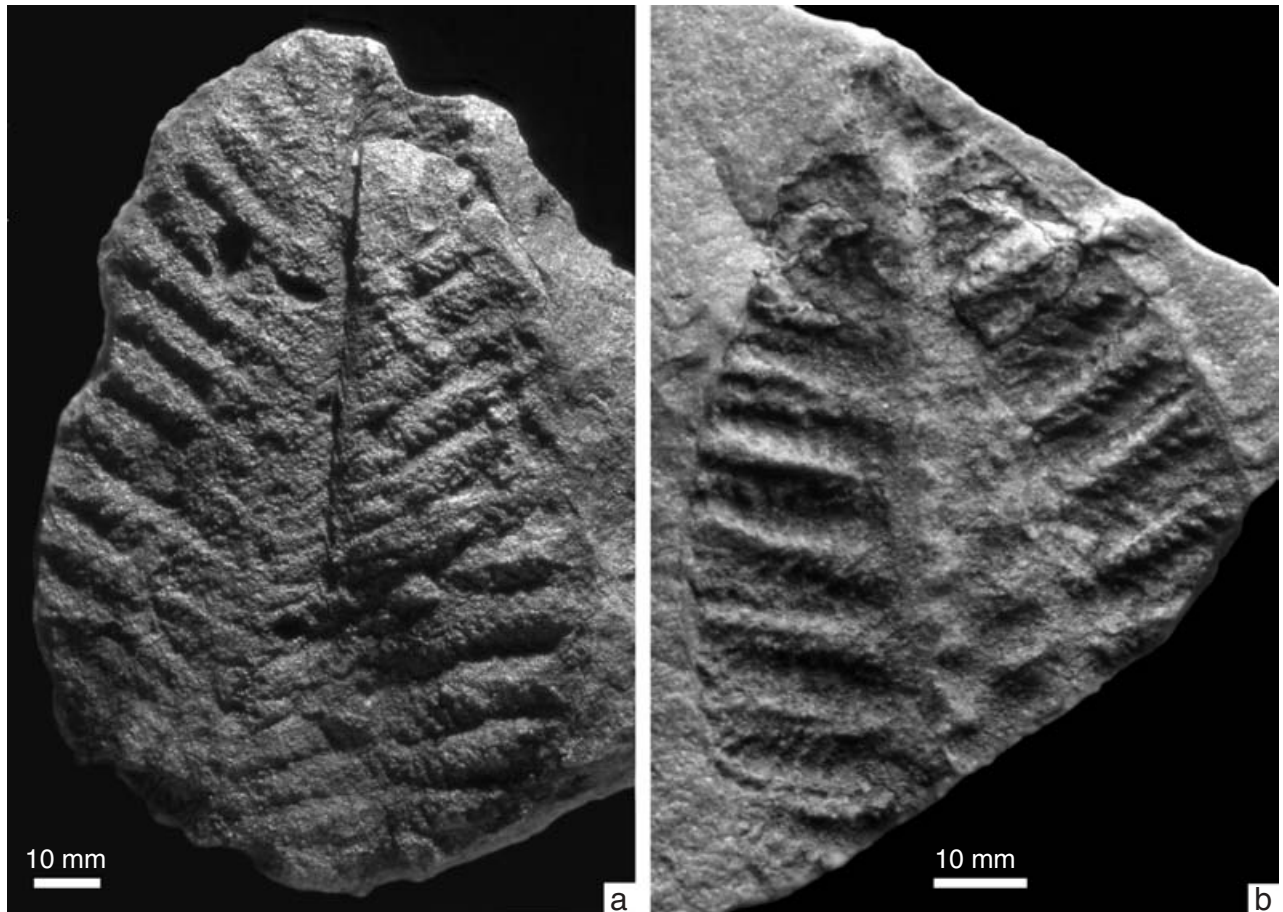


Figure 6. (a) In winnowed *Rangea* specimens, one of the three fronds is commonly preserved spread along the parting surface. Another frond is compressed laterally and preserved as a wedge-shaped three-dimensional cast. The third frond is thought to be lost during weathering. NESM F530. (b) Weathered specimen showing a poorly preserved frond. A fragment of the three-dimensional cast of another frond is seen adhered to the right-hand side of the mould. NESM F379. These specimens have never been previously figured. Kliphoek Member of the Dabis Formation, Namibia.

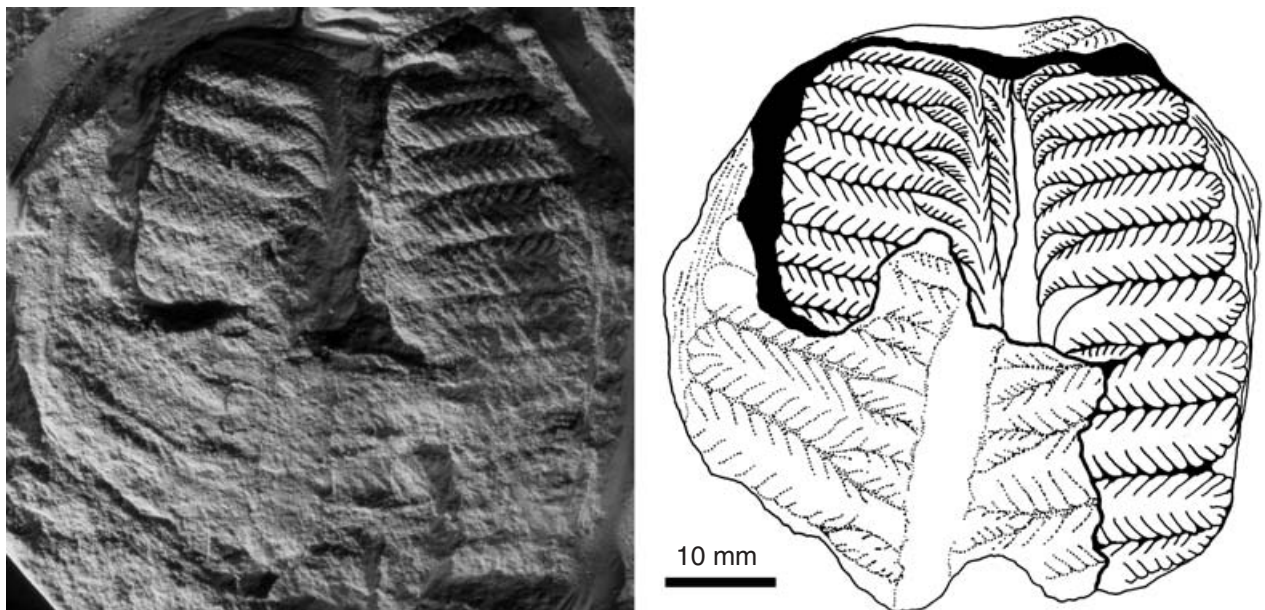


Figure 7. Winnowed preservation of *Rangea* showing the three collapsed fronds and the sheath. Niederhagen Member of the Nudaus Formation, Namibia. SAM K4367.

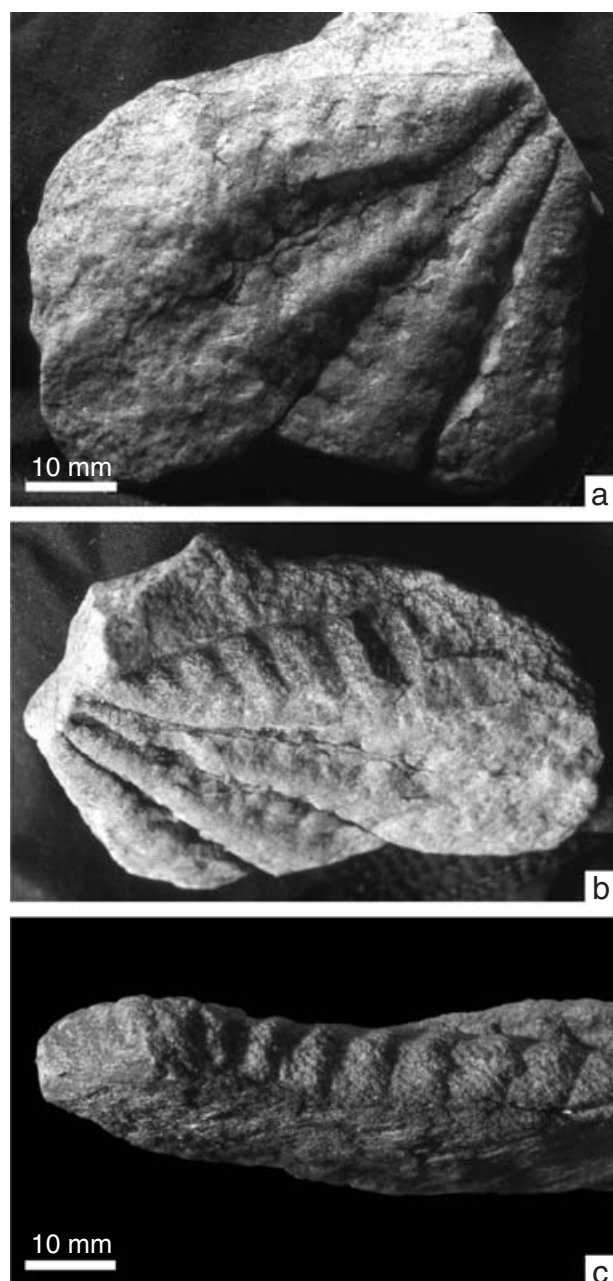


Figure 8. Problematic fossils showing some similarity to *Rangea*. Kliphoek Member of the Dabis Formation, Namibia. (a, b) NESM F540; (c) F566.

Rangea inhabited shallower depths in the sediment, and that the edges of trough-shaped fronds grew upward in response to continued sedimentation.

That the *Rangea* fronds are arranged around a common stem-like structure is impossible to demonstrate unambiguously. Previous account of there being four fronds also cannot be confirmed. These conclusions, by Jenkins (1985, 1992) and Dzik (2002a), were inspired by two peculiar specimens, which were also examined albeit never discussed by Pflug (1970). One of these specimens (NESM F566; Fig. 8c) is a low-sided three-dimensional cast of a solitary frond, while the other

(NESM F540; Fig. 8a, b) consists of four such casts; both are reminiscent of *Rangea*. The casts have a pronounced sagittate shape when viewed from the underside, with a tapering and a blunter end. Their sides are quilted; however, the quilts appear not to be differentiated into primary and subsidiary series (Fig. 8). The low-sided appearance of the specimens is unlikely to be a result of vertical compression. NESM F540 (Fig. 8a, b) is interpreted by Dzik (2002a) as a cast of an exfoliated tetramerous organic skeleton unrolled into one plane. However, Jenkins (1985, p. 343) expressed doubts upon the completeness of its preservation. Considering the distinct quilting and the low-sided sagittate appearance of individual fronds, these specimens are better kept as a separate species of *Rangea*.

Rangea has been enthusiastically thrown into several schemes of metazoan phylogeny, including stem-group hemichordates (Pflug, 1970), anthozoans (Richter, 1955; Jenkins, 1985, 1992; Dewel, Dewel & McKinney, 2001), and ctenophores (Gürich, 1930a, 1933; Dzik, 2002a,b, 2003). The stemless reconstruction of *Rangea*, the double-layered arrangement of the quilts, and the close-packing of the fronds in a cluster enveloped by a common sheath make all of these interpretations difficult to accept. Furthermore, we argue that the infaunal life habit better explains the taphonomic and morphological features of *Rangea*, but we also admit that it renders the biological affinities more enigmatic. Nevertheless, *Rangea* shares an infaunal habit with other members of the Nama-type biota, representing a distinctive assemblage of ecologically specialized late Neoproterozoic organisms that inhabited fluviomarine settings (Grazhdankin, 2004). Any similarity in body plan with *Pteridinium*, as proposed by Gürich (1933), Richter (1955), and notably by Pflug (1970), is interpreted here as a convergence related to adaptation and specialization to infaunal life habit.

The relationships of *Rangea* are very uncertain. The diagnostic fractal quilting of *Rangea* is seen in the similarly problematic and morphologically disparate *Charnia* Ford, 1958, *Bradgatia* Boynton & Ford, 1995, and several imperfectly described fusiform, frondose and plumose fossils from Newfoundland that together are referred to as Rangeomorpha (Anderson & Conway Morris, 1982; Jenkins, 1985; Narbonne & Gehling, 2003; Narbonne, 2004; Brasier & Antcliffe, 2004; O'Brien & King, 2004). It is interesting to note in this connection that biostratigraphic evidence also suggests an infaunal *in situ* preservation of *Charnia*, indicating that the fractally quilted frondose base gradually immersed itself into the sediment with only the clusters of miniature 'frondlets' continuing to protrude above the sediment surface, keeping pace with the sedimentation (Grazhdankin, 2004). Thus when smothered by sand, the upper side of *Charnia* is preserved as wedge-shaped sandstone infillings that cast the boundaries between the protruding frondlets (Grazhdankin, 2004,

fig. 2A). That *Charnia* was likely to be an infaunal organism is also evident in a recently discovered specimen from the Trepassey Formation at Spaniard's Bay, Avalon Peninsula. Preservation of this specimen (Narbonne, 2004, fig. 3D) is very peculiar, because it exhibits a mouldic impression of the upper side and fragments of the weathered-out three-dimensional cast bearing impressions of the frondlets. Narbonne (2004) misinterpreted the impression of the upper side as a hypothetical 'internal organic skeleton' of rangeomorphs. This, of course, echoes the reconstruction of *Rangea* by Dzik (2002a), also featuring an imaginary 'internal organic skeleton'. Neither of these hypotheses is complete, because each fails to take taphonomy into full account.

Overall, Rangeomorpha seems best compared with the Vendobionta on account of the quilted morphology, although this need not necessarily be strictly homologous. More precise comparisons with known groups are elusive. Ninety years since its discovery, *Rangea* remains a fossil oddity challenging palaeontologists' minds to the limit of imagination and common sense.

7. Systematic palaeontology

Subgroup RANGEOMORPHA Pflug, 1972

Rangea Gürich, 1929

Emended diagnosis. Compound body consisting of three closely-packed almost identical trough-shaped fronds. Fronds fractally subdivided by equidistant furrows into chevrons of quilts of at least three orders. Median zone well defined. First-order quilts have open connections in median zone along the bottom of trough-shaped fronds, and are arranged in two layers along their sides. Quilts of each side are slightly offset by one-half of a quilt along the median zone relative to quilts of the opposite side.

Rangea schneiderhoehni Gürich, 1929

- 1929 *Rangea Schneiderhöhni* [sic]; Gürich, p. 85.
 1930a *Rangea Schneiderhöhni* [sic]; Gürich, p. 673, figs 2–4.
 1933 *Rangea schneiderhöhni* [sic]; Gürich, p. 139, text-figs 1, 2 [cop. Gürich, 1930a, figs 3, 4].
 1933 *Rangea* (?) *brevior* [sic]; Gürich, p. 142, text-fig. 3 [cop. Gürich, 1930a, fig. 2].
 1955 *Rangea schneiderhöhni* [sic]; Richter, p. 264, pl. 7, figs 12, 13 [cop. Gürich, 1930a, figs 3, 4].
 1970 *Rangea schneiderhöhni* [sic]; Pflug, pls 33–35.
 1972 *Rangea schneiderhoehni*; Germs, pp. 169–73, pl. 20, figs 1–3 [cop. Gürich, 1930a, figs 3, 4], 5–7.
 1973a *Rangea schneiderhoehni*; Germs, text-fig. 1 [cop. Gürich, 1930a, figs 3, 4; Germs, 1972, pl. 20, figs 5–7].

- 1979a *Rangea schneiderhoehni*; Glaessner, p. A99, text-fig. 11.2 [cop. Pflug, 1970, pl. 33, fig. 2].
 1985 *Rangea schneiderhoehni*; Jenkins, p. 355, text-figs 1, 7A [cop. Gürich, 1930a, figs 3, 4; Pflug, 1970, pl. 33, fig. 2, pl. 34, figs 4–6, pl. 35, figs 1, 2].
 2002a *Rangea schneiderhoehni*; Dzik, text-figs 1A, 1C [cop. Gürich, 1930a, fig. 3], 2 [cop. Pflug, 1970, pl. 34, fig. 5, pl. 35, figs 1, 2] [non fig. 1B = n.sp.].

Remarks. G. Gürich (1933) described *Rangea brevior* based on a single poorly preserved specimen that has been lost since World War II. The specimen was a flattened ovoidal mould that consisted of two crescentic structures, with transverse quilting, surrounding a relatively inflated mid-area. Faint markings on some of the quilts suggested second-order subdivisions. *R. brevior* was distinguished from *R. schneiderhoehni* by its different proportions and by variation in quilt arrangement (Gürich, 1933). The holotype of *R. brevior* appears to be very similar to NESM F379, which is interpreted as a winnowed specimen of *R. schneiderhoehni* (Fig. 6b). The crescentic appearance of the fronds and the featureless median zone in the holotype have resulted from deep weathering of the specimen. *R. brevior* must therefore be taken as a junior synonym of *R. schneiderhoehni*.

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