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Possible Ctenophoran Affinities of the Precambrian "Sea-Pen" *Rangea*

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ABSTRACT The Namibian Kuibis Quartzite fossils of *Rangea* are preserved three-dimensionally owing to incomplete collapse of the soft tissues under the load of instantaneously deposited sand. The process of fossilization did not reproduce the original external morphology of the organism but rather the inner surface of collapsed organs, presumably a system of sacs connected by a medial canal. The body of *Rangea* had tetraradial symmetry, a body plan shared also by the White Sea Russian fossil *Bomakellia* and possibly some other Precambrian frond-like fossils. They all had a complex internal anatomy, smooth surface of the body, and radial membranes, making their alleged colonial nature unlikely. Despite a different style of preservation, the Middle Cambrian Burgess Shale frond-like *Thaumaptilon* shows several anatomical similarities to *Rangea*. The body plan of the Burgess Shale ctenophore *Fasciculus*, with its numerous, pinnately arranged comb organs, is in many respects transitional between *Thaumaptilon* and the Early Cambrian ctenophore *Maotianoascus* from the Chengjiang fauna of South China. It is proposed that the irregularly distributed dark spots on the fusiform units of the petaloid of *Thaumaptilon* represent a kind of macrocilia and that the units are homologous with the ctenophoran comb organs. These superficial structures were underlain by the complex serial organs, well represented in the fossils of *Rangea*. The Precambrian "sea-pens" were thus probably sedentary ancestors of the ctenophores. J. Morphol. 252:315–334, 2002.

KEY WORDS: Ediacaran; Cambrian; Chengjiang; Burgess Shale; Vendobionta; Petalonamae; evolution; origins

Rangea was among the first Ediacaran organisms to be named. In Gürich's (1930, 1933) original description, based on three specimens collected by P. Range and H. Schneiderhöhn from the Kuibis Quartzite of Namibia, a ctenophoran nature of this fossil was suggested. This idea has been abandoned by subsequent students, who offered several very different zoological or nonzoological affiliations for *Rangea* and supposedly related organisms (e.g., Jenkins, 1985, 1992; Seilacher, 1989, 1994; Zhuravlev, 1993; Retallack, 1994; Pflug, 1994; Valentine, 1994; Runnegar, 1995). Ironically, recent discoveries of Cambrian ctenophores (Conway Morris and Collins, 1996; Chen and Zhou, 1998) may make Gürich's guess, apparently based only on his intuition, correct.

The key to understanding affinities of the Ediacaran fossils is their taphonomy. Only after knowing what actually is represented by the fossils may one restore the original anatomy and so find a place for the organism in the phylogenetic tree. It is now rather obvious that the taphonomic processes that resulted in fossilization of the late Precambrian and some Early Cambrian soft-bodied organisms in sandstones were not truly uniformitarianistic, as in present-day marine conditions there is no chance for such soft-bodied organisms to fossilize in sand (Dzik and Krumbiegel, 1989). In some cases (for instance, the Namibian *Ernietta*; Dzik, 1999) the shape of the fossil has actually very little to do with the external form of the organism. In certain other cases significant anatomical information can be inferred from the fossil, which originated as a result of embedding in the sediment, collapse of the soft tissues, and injection of the internal cavities with soft sediment (Dzik and Ivantsov, 1999). The Kuibis Quartzite fossils of *Rangea* represent various styles of preservation. Some are just imprints of flattened bodies on the bedding plane. Others, however, seem to have originated as a result of collapse under a load of effectively instantaneously deposited sand.

The Vendian and Cambrian fossil assemblages are so different from each other largely because of taphonomic differences (Dzik, 1994, 1999; Gehling, 1999). Whereas in Ediacara-style fossilization the extractable information concerns differences in pressure of internal body fluids, rigidity of tissues, and flexibility and elasticity of membranes of the

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fossilized organisms, in the Cambrian Burgess Shale-style preservation information is provided mostly on the content of organic matter in particular parts of the body. In the first case these are mechanically produced impressions on the sediment surface; in the second it is a color stain of a chemical nature added to the carbonized originally organic tissue. The anatomical data inferred from the Namibian material can thus be supplemented by those on *Thaumaptilon*, the frond-like organism of Ediacaran affinities from the Middle Cambrian Burgess Shale (Conway Morris, 1993). The Early Cambrian Chengjiang fauna of South China, preserved in a relatively coarse-grained mudstone, offers a mode of fossilization which is, to some degree, transitional between that of the Ediacaran assemblages and of the fine-grained Burgess Shale. As yet, except for the preliminary report by Zhang and Babcock (1996), no frond-like fossils have been found there, but the ctenophore *Maotianoascus* (Chen and Zhou, 1998) shows some features in common with *Rangea*.

In this article, the way in which the original body shape of *Rangea* and *Maotianoascus* can be restored will be presented. This can be done by a kind of retrodiction, from the present form of the fossil to the original three-dimensional arrangement of the soft tissues. The results will be used to infer their anatomy and then identify the probable position of the Precambrian "sea-pens" in the phylogenetic tree. This is of special importance as the allegedly pennatulacean affinities of the Ediacaran "sea-pens" play a crucial role in the scenario of a colonial origin of some Metazoa (Dewel, 2000).

MATERIAL AND TAPHONOMY OF *RANGEA*

The classic fossiliferous horizons of the Precambrian in Namibia are within the Kliphoek Member of the Dabis Formation, Nama Group. Radiometric evidence indicates that they are just older than the base of the Cambrian (Bowring et al., 1993; Grotzinger et al., 1995), that is, about 545 Ma. All the specimens from Namibia referred to in this article are now under the care of Hans Pflug in Lich near Giessen, where most of my study was done. The Georg Gürich originals borrowed by him from Hamburg University are prefixed here with the acronym HU. Specimens prefixed with GU Pf are temporarily at the University of Giessen, but their final placement is unknown (see Jenkins et al., 1981, p. 68). The specimens have been collected from loose weathered material and only a few larger blocks show the original position of the fossils in the rock.

The specimens from the Kuibis Quartzite show a variety of preservation modes but, with a few exceptions, are preserved within unstratified sandstone or mudstone beds that apparently were deposited very rapidly as a result of a mass flow or storm event. The best *Rangea* specimens were found close to the station Kuibis (Richter, 1955; Punkte A and B of Pflug, 1966). They are preserved either at the bedding plane surface (those of Gürich, 1933), in which case they are flattened (Fig. 1), or within mass-flow sandstone beds. The most informative sandstone block with several *Rangea* in situ, GU Pf 247 (Fig. 2; Pflug, 1970b, pl. 34:5, 35:1–2), was thoroughly redescribed by Jenkins (1985), who has convincingly demonstrated that it shows effects of sediment transport resulting in a directional arrangement of enclosed fossil fronds. Sediments of the Kliphoek Member originated in shallow-marine to even fluviatile environments with offshore facies represented only occasionally (Grant et al., 1991). An extensive mass flow of the sediment is thus unlikely. However, some local events of limited extent seem to have been sufficient to produce the *Rangea*-yielding bed.

In the Namibian material, the *Rangea* petaloids show unusually prominent relief. Its preservation was explained by Jenkins (1985, p. 338) as being a result of limited compaction of the sandstone. Pflug (1970a) proposed, and Jenkins (1992) followed, a similar way of reasoning, that the Namibian specimens were subject to early diagenetic silicification and it was this that enabled their three-dimensional preservation. Potentially this is possible, but in any event other interpretations are more likely in this particular case. It is proposed here that the present morphology of the specimens of *Rangea* in the Namibian material is rather an effect of a collapse of the soft tissue under a heavy sand load. This means that the elevations and depressions on the frond surface do not necessarily need to correspond strictly to similar surface structures in the soft body. Rather, they reflect differences in mechanical resistance of internal organs.

The Kuibis Quartzite fossils thus offer only limited evidence on the original soft-tissue morphology. Certainly in the case of *Ernietta* and *Pteridinium*, and possibly in some *Rangea* specimens, soft organs were not present in the specimens even at the stage of filling with sand and prior to being transported (Dzik, 1999). The important point is that the observed morphologic features of the fossils should not be taken as literally representing the soft anatomy of the original organisms.

The leaf-shaped units of the *Rangea* body, of a fractal organization (Seilacher, 1995), were named "petaloids" by Pflug (1970b), but the term "fronds" has been applied by Jenkins (1985). While Pflug was apparently impressed by a similarity of these structures to the blastoid hydrocoel, Jenkins' nomenclature has been influenced by his contention that this fossil organism belongs to an extinct group of the octocorals. I prefer Pflug's term, which is more neutral, even if it is also used as referring to leaf-shaped segments of ambulacra in some echinoderms. Particular units of the petaloid are here referred to as "petals." It seems more reasonable to use the term "frond" for the whole petaloid-bearing part of the rangeid body, with the "rachis" in its center. Halves

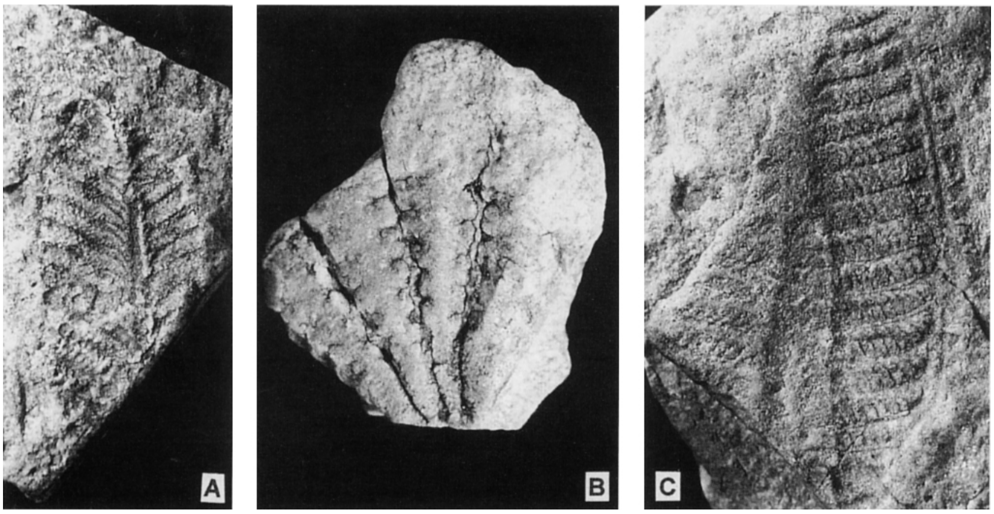

Fig. 1. Specimens of *Rangea schneiderhoehni* Gürich, 1930, from the Kliphoek Member of the Dabis Formation, Nama Group of Namibia, preserved on the sandstone bedding plane; all ×1. **A**: Specimen GU Pf 534 with compressed petaloids, imprints of which form a multilayered structure; pinnate organization of the units (petals) well preserved. This is a preservation style somewhat similar to that of *Maotianoascus* from the Early Cambrian of Chengjiang, with sandstone wedges reaching the axial canal. **B**: Specimen GU Pf 523 probably representing completely exfoliated and flattened basal lining of petaloids; details of morphology not preserved in effect of compression, probably the basal surface of a sandstone bed. **C**: Holotype HU 179 (illustrated also in Jenkins, 1985, fig. 2A) with perpendicular arrangement of the petals in oblique compression and imprints of petals outside the margin of the frond, suggestive of partial exfoliation of the membrane.

of each of the neighboring petaloids in *Rangea* protruded together, forming relatively flat units, longitudinally extended and radiating from the axis, here referred to as vanes. The free end of the rachis of *Rangea* is expanded into a bulb. Both the rachis and the bulb are completely filled with sand, at least in some specimens.

Axial Cavity Filling

In block GU Pf 247 (Fig. 2; Jenkins, 1985) the current-oriented *Rangea* specimens are arranged in such a way as if they were pulled during the sediment flow, their sand-filled basal disc being anchored to the bottom. This indicates that both the basal disc and the axial cavity in the *Rangea* shaft (rachis) were already full of sand during transport. The fleshy petaloid remained partially erect despite strong deformation. This opens the possibility for at least two opposing lines of inference: either the axial cavity was sand-filled during the life of the organism, or the sand penetrated it during postmortem processes.

The first interpretation may be supported by some similarity between the mode of preservation of *Rangea* and related organisms on a sandstone bedding plane from the Mistaken Point Formation of Newfoundland. In the Newfoundland assemblage numerous specimens with fronds are preserved as impressions on the sediment surface, and the rachises with their bulbs behaved as being either filled with sediment or being originally composed of firm skeletal tissue (Seilacher, 1992). The overlying volcanic ash layer shows that the community was catastrophically buried. If they were free-floating organisms they would not have been the first to sink to the sea bottom. This means that they were originally anchored in the sediment (Jenkins, 1992, p. 137). The Namibian community of *Rangea* animals may have also been originally anchored in the sediment and were subsequently killed by a mass flow of sediment. Fronds would then have been deformed by the moving sand. Subsequently, the soft tissue collapsed, with the originally sand-filled basal bulbs being preserved in situ.

The alternative, that sediment penetrated the axial cavity in the *Rangea* shaft after its death, does not seem much less likely. In the most complete specimen in the block some darker mudstone pebbles cross the axial cavity boundary, showing that the rachis was partially split before the sediment flow ended (Fig. 2B). If the transport lasted long enough, the cavity could have been easily filled with sand. Certainly, the narrow appendages of *Xenusion*

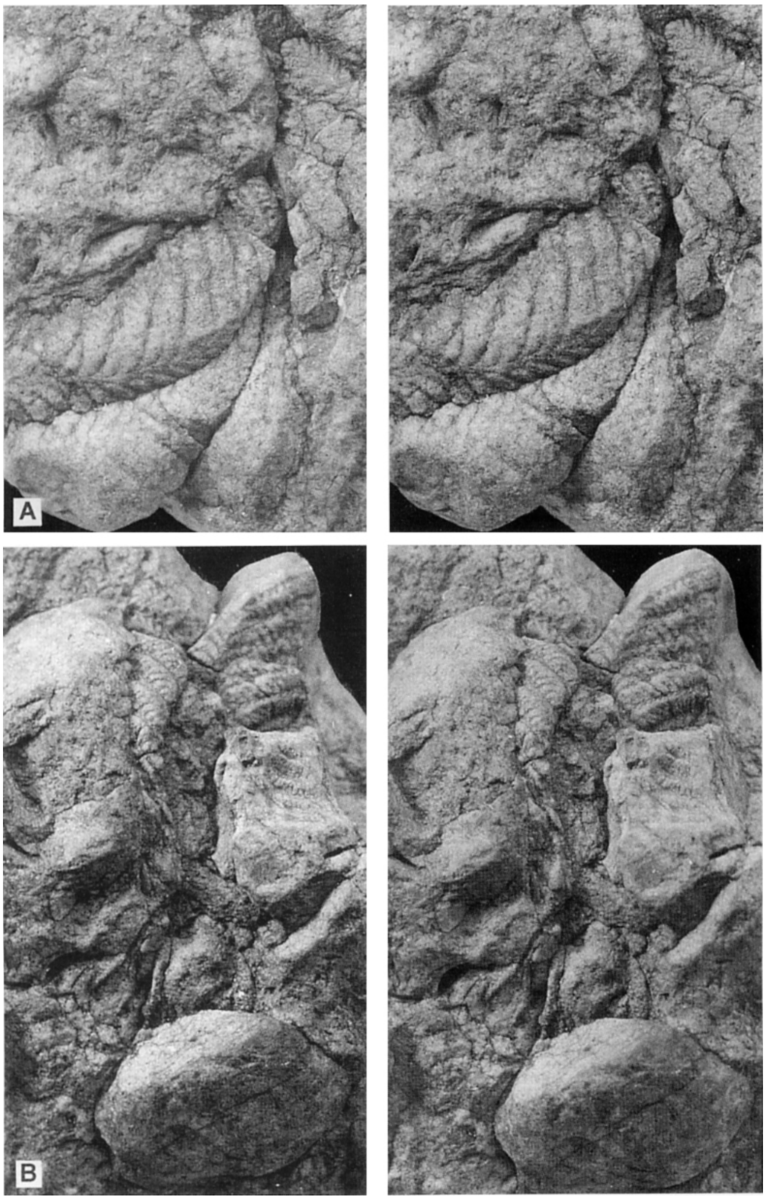

Fig. 2. Stereophotographs of the basal surface of sandstone block GU Pf 247 (illustrated also in Pflug, 1970b, pl. 34:3, 5, 35:1–2 and Jenkins, 1985, fig. 2C, F, 7A) with several *Rangea schneiderhoehni* Gürich, 1930, fronds from the Kliphoek Member of the Dabis Formation, Nama Group of Namibia. **A**: Tip of the frond (bottom) of specimen II and rachis of specimen IV with petaloid bases (right). Note the empty cavity between the petaloid tips. **B**: Basal bulb, rachis and basal part of the frond of specimen V, the most complete in the block; all ×1.

were no more accessible to sand particles (Dzik and Krumbiegel, 1989). To achieve this state of preservation it was presumably enough for the axis to be hollow and open at one end.

Whether the sand filling of the axis developed in vivo or postmortem, the most likely way for this to be achieved was either: 1) rupture of the rachis (in the case of a dead animal), or 2) development of an opening at the base of the bulb. Perhaps the basal bulbs of other frond-like fossils will offer evidence to decide between these conflicting interpretations.

The anatomical feature specific to *Rangea* is that a few vanes radiate from the axis. To know their number and disposition may help in detecting the anatomical symmetry pattern in this organism.

Number of Vanes

Jenkins (1985, fig. 4) identified four vanes in specimen GU Pf 247 V, extending laterally from the sediment-filled cavity of the rachis. According to Jenkins (1992, p. 149) some vanes may be missing at the exposed surface of the specimen, so that the original number could be even higher. This does not seem likely, as in all other specimens complete enough to show all sides of the frond I am able to confirm only four vanes. The specimens in block GU Pf 247 (Fig. 2A) were strongly deformed by the sediment mass flow and, if the direction of this deformation is taken into account, the original arrangement of the vanes appears radial around the shaft. This implies a tetrameric symmetry of the frond.

Jenkins (1985) proposed that a thin membrane extended from each of the vane margins in *Rangea*. This may find some support in specimen GU Pf 523, where the bases of four petaloids are exposed across the bedding plane (Fig. 1B). Despite their being extended flat, there are free membranes that penetrate the rock vertically. This fossil may represent an exfoliated and spread-out basal lining of the petaloids. If so, this is consistent with the idea that there were four petaloids, that their basement membrane was relatively stiff, and that the membranes terminating the vanes were rather narrow.

Original Relief of the Petaloids

The possible in situ position of the basal bulb in block GU Pf 247 implies that the specimens were almost intact while sand covered them. Their deformation is a result of collapse of the soft tissue. If so, the existing space between the axial cavity filling and the petaloid surface is the only remnant of an original body volume. Usually, the petaloid surface only touches the surface of the axial filling in a narrow area. Even here some space (Fig. 2A), probably filled with an easily weathering material, originally separated those surfaces. The free space between neighboring petaloids was relatively voluminous, which allows the centers of petaloids to arch parabolically instead of being tightly attached to the axis. The sand was thus allowed to move only between the vanes. This concurs with the preservation of the frond tip in the block GU Pf 247, which shows flat petaloid surfaces at their contact with the rachis and angular contact of these surfaces with vanes (Fig. 1A). There are two possibilities: either 1) the original body volume was not great and the body had a Maltese cross-shaped transverse section, or 2) the petaloid walls were originally more distant from the axis and subsequently collapsed, being supported only by a rigid radial membrane in the center of the vanes.

Specimen GU Pf 534, with compressed petaloids (Fig. 1A), may be helpful in deciding which of those interpretations is closer to reality. The imprints of petaloids form a multilayered structure, being separated by sand layers penetrating relatively close to the body axis. This shows that the body, or at least its organic skeleton, truly had an iron cross-shaped cross-section. In this case, unlike the equidimensional specimens, the specimen compression was apparently directed only vertically, without any prior lateral collapse. The sand had to fill spaces between vanes before their collapse.

In specimens preserved along bedding planes, particular units tend to be oriented almost transverse to the petaloid axis (Fig. 1C). The indistinct representation of the petaloid structure in the exfoliated specimen GU Pf 523 (Fig. 1B), as well as the much more inclined and dense distribution of metameric units of the petaloid in specimens preserved within the sediment, indicate some elasticity of the petaloid basal skeleton. These differences may have partially resulted from a postmortem contraction of suddenly killed specimens entrapped in the sediment flow, instead of the relaxing of slowly decaying bodies on the sea-bed.

In some petaloids showing a convex relief, a reticulate pattern can be discerned, as if pinnately arranged minute furrows on each terminal unit (petal) are crossed by perpendicular furrows of the same size. This may be a kind of palimpsest, collapsing petals from both sides of the vane being overprinted by the pressure of sand. They were apparently distributed alternately on sides of the vane.

All this suggests that the preserved petaloid structures represent an organic membranous skeleton underlying a soft structure. The topology of such a skeleton is represented in several Vendian fossils, replicated in the rock after the less resistant tissues were removed by decay (as was probably the case with *Xenusion* and *Ernietta*; Dzik and Krumbiegel, 1989; Dzik, 1999) or collapsed completely under the sand load. The effect in both cases would be the same: the membranous skeleton of the petaloids shows, in negative, the basal morphology of the soft organs that were supported by it.

PRESERVED ANATOMICAL STRUCTURES OF *RANGEA*

There is not enough evidence to confirm that the structures preserved in the Namibian fossils of *Rangea* truly represent its soft body. Instead, it seems likely that the sandstone imprints replicate the morphology of an internal organic skeleton of the organism. This skeleton was apparently membranous and the most probable interpretation of its nature which can be offered on the available limited evidence is that it was some kind of basement membrane, similar to *Ernietta* and *Pteridinium* (Dzik, 1999). The complete anatomy of *Rangea* can, therefore, be restored only if certain additional assumptions are accepted. Before phylogenetic comparisons are proposed, I will restrict speculations to more direct inferences on the morphology of the proposed basement membranes, on the assumption that they underlie some internal body organs.

Gastric Cavity

The sand-filling of the *Rangea* rachis is tubular and, at least in the part extending beyond the petaloids, does not show any surface structures. It is rather unlikely that its surface corresponds to the surface of a stem. Instead, it seems to be simply the cavity, expanded close to its end, located within a possibly more voluminous body (Fig. 7B). Its tentative interpretation as a kind of gastric cavity (e.g., Jenkins, 1992) does not necessarily involve any precise taxonomic affiliation.

Structure of the Petaloids

The pinnate units of the petaloids (petals) are deeply concave from outside of the specimen (from where the sand load pressed on it). The structures held by such membranous skeletons are thus likely to be bulbous, with internal fluid pressure controlling their original shape. Their arrangement (Figs. 1A, 2A), with a central furrow, is suggestive of a system of sacs joining together in a medial canal and then leading to the base of the petaloid. As there is no need for the medial canal of each of the units to be duplicated, the external surface could have been of a basically different morphology than its interior (Fig. 7B). It is difficult to infer from the existing specimens of *Rangea* whether the "collecting" canal of each of the four petaloids opened to the outside of the body or into the axial cavity.

Not much of anatomical importance, therefore, can be inferred from the fossils of *Rangea*. Fortunately, there is a way of reasoning which may help in restoring the complete picture of its body organization; this is by identifying possibly homologous structures in other Precambrian and Cambrian fossils and then supplementing the anatomical data available for them but not known in *Rangea*.

VENDIAN RELATIVES OF *RANGEA*

Most of the Ediacaran fossils are preserved as positive or negative imprints on the lower surface of sandstone beds (Wade, 1968; Gehling, 1991). They originated as a result of sudden deposition of a sand layer on the muddy sea bed covered with a cyanobacterial mat. This could lead to different preservational styles of the anatomical structures (Dzik and Ivantsov, 1999) that are usually different from that typical of the Namibian fossils (Dzik, 1999). Although frond-like organisms are well represented and diverse among the Ediacaran fossils, few of them show a feathery, fractal (Seilacher, 1995) organization of petaloids so characteristic for *Rangea*. Actually, outside Namibia (and rare cases at Ediacara; Gehling, 1991, pl. 3:1) this kind of petaloid morphology characterizes only the fossils of the Mistaken Point assemblage of Newfoundland (Seilacher, 1989, 1992). This similarity may be of a taphonomic nature. In Mistaken Point fossils, catastrophically buried under a volcanic ash layer, the soft organs of the body collapsed, similar to those of Namibia, and only the rachises, with bulbs, are preserved as elevated structures. One may thus argue that in both these localities the fractal organization resulted from collapse of the petaloids, whereas in other Ediacaran assemblages impressions of their external surfaces are usually represented. The fractal structure may thus reproduce their inner surfaces, which were reached by the sand load. This can be tested by comparing differently preserved fossils of the same, or at least related, species.

In such a way, specimens of frond-like fossils known from various localities of the Vendian may thus help in restoring the original anatomy and understanding the taphonomic processes which led to its representation in various ways. Of special importance are those fossils which were preserved in different kinds of sediment. The closest to the Namibian specimens of *Rangea* in this respect are three-dimensional fossils from the Russian White Sea assemblage, the least similar are the Chinese *Paracharnia*, preserved in limestone. Below, the most informative of these fossils are reviewed.

Bomakellia

Two fossils from the Vendian of the White Sea, originally described by Fedonkin (1985, 1992, 1998) as arthropods belonging to his new class Paratrilobita, show several features in common with *Rangea* and may even be congeneric with it. These are *Bomakellia kelleri* Fedonkin, 1985 and *Mialsemia semichatovi* Fedonkin, 1985. Both are represented only by their type specimens, *B. kelleri* coming from the Suzma Member of the Ust-Pinega Formation (Stankovsky et al., 1990), and *M. semikhatovi* being collected as a float specimen. These strata have been radiometrically dated as being 555 Ma old (Martin

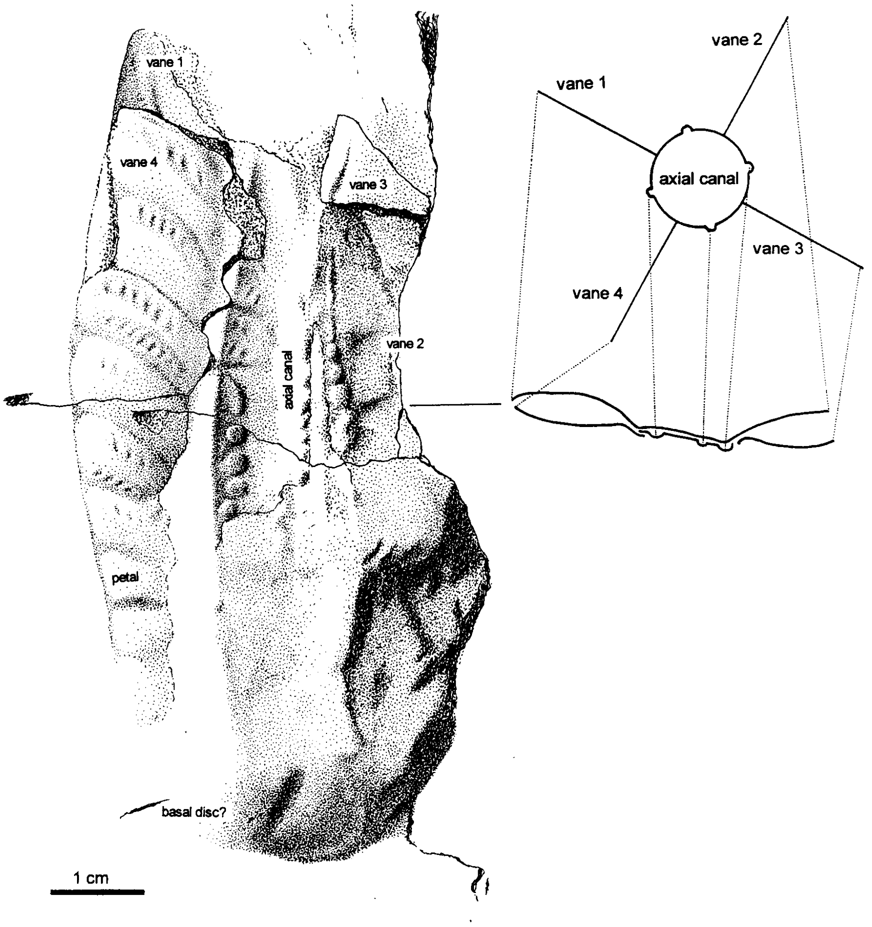

Fig. 3. *Bomakellia kelleri* Fedonkin, 1985, from the Suzma Member of the Vendian Ust-Pinega Formation, collected at the right side of the Syuzma River 5 km from its mouth on the Onega Peninsula, Summer Coast of the White Sea. Interpretive drawing of the holotype PIN 3992/508, arrangement of the preserved imprints within the rock in cross section and inferred arrangement of the vanes in respect to the axial canal prior to its collapse and compression.

et al., 2000). According to Fedonkin (in Sokolov, 1997, p. 144) *Bomakellia* was a "large arthropod, with separate head shield, a thin dorsal carapace covering double-pinnate lateral appendages which may have served at the same time respiratory and locomotory functions (as gills and fins)."

The Russian fossils thus indirectly support the restoration of *Rangea* with four vanes. The part PIN 3992/508a of the holotype of *Bomakellia* (Fig. 3; Fedonkin, 1985, pl. 21:6, 1992, fig. 41; Sokolov, 1997, pl. 23:5) shows the frond in apparently basal view, strongly convex and with the petaloids partially displaced in respect to the axis, which was pushed deeper into the sediment. Nine feathery units (petals) of the petaloid are preserved on the left side (vane 4 on Fig. 3). The petals are in low positive relief and clearly connected together by a continuous membrane. The specimen is exfoliated, showing below this petaloid membrane other membranes separated by a thin sandstone layer. Four vanes with petaloid units are preserved. The axial organ is completely collapsed, with no evidence of any sediment infill. In the middle of it, three rows of small oval tubercles are represented. They may represent either weaker areas on the axial organ wall, penetrated and swollen by the sand load, or (less likely) these are bases of canals radiating from the axis and filled with sand. A strongly convex oval structure with central depression is recognizable at the basal end of the specimen but its morphology is too poorly replicated in the coarse sandstone to allow interpretation. Its shape and location suggest that this is a basal bulb, similar to that in *Rangea*. The only specimen of *Mialsemia* (PIN 3993/401; Fedonkin, 1985, pl. 21:2–3) does not show any features which would substantiate its taxonomic separation from *Bomakellia*. The differences between *Bomakellia* and *Mialsemia* are mostly preservational.

Charniodiscus

This model may apply also to the Vendian frond-like fossil most commonly referred to *Charniodiscus concentricus* Ford, 1958, from Charnwood Forest, England (Ford, 1958). There is an aspect of the preservation of its frond which is suggestive of more than two vanes being preserved. This refers to the part which was interpreted by Jenkins and Gehling (1977, figs. 2, 4) as overfolded. The actual relationship between vanes is not so apparent on the casts studied by these authors, but it is somewhat more visible in the original specimen belonging to the Geological Museum of Leicester University. Some differences in coloration between the rock forming the bedding surface on which the body of *Charniodiscus* is preserved and the underlying mudstone (tuffite?) allows one to see that the petals on the left side are uniformly distributed along the frond, with no disturbance in the proximity of the seemingly overfolded part. The series of metameric units covering the rachis, preserved in positive relief and well above the negative imprints of lateral series, does not seem to be in continuation with the left lateral series. It is likely that the central series represents the third vane, attached to the middle of the rachis. It may thus represent one of the four radial blades, collapsed and partially preserved over the rachis.

Available evidence from *Charniodiscus* is compatible with the four-vane model of *Rangea* anatomy. The English specimen of *Charniodiscus*, although complete, is too crudely preserved to allow more precise restoration of the anatomy because of the rock cleavage. In this respect the specimens from Ediacara are more informative.

Arborea

The genus *Arborea* was proposed by Glaessner and Wade (1966) for stalked frond-like organisms from Ediacara, but Jenkins and Gehling (1977) synonymized *Arborea* with *Charniodiscus*. Still, the Australian species may deserve taxonomic separation from its English relative, at least on a subgeneric level. There is a great variety of preservation styles among the Ediacaran frond-like fossils. This seems to reflect different stages in the collapse and decay of the soft tissue and can be used to restore the spatial relationship between organs which emerged in successive stages of decay.

The Australian material provides evidence that the external body surface of the frond-like Ediacaran organisms was smooth, with only the sutures between compressed metameric units being visible. This is shown by the holotype of *Charniodiscus (Arborea) oppositus* Jenkins and Gehling, 1977, which is preserved as an external imprint of the body (Jenkins and Gehling, 1977, fig. 6). Jenkins and Gehling (1977) proposed to classify *C. (A.) oppositus* specimens with strictly symmetrical, not alternate, distribution of the metameric units. Among specimens housed at the South Australian Museum (SAM), some, like SAM F16712, show a smooth and gently convex external surface of the serial units (Fig. 4A). The axial area, separating series of metameric units, is there much narrower than the rachis visible in other specimens. Another mode of preservation is represented by specimen SAM T93-2016 (Fig. 4B; also Glaessner and Daily, 1959, pl. 44:3). There, the serial units developed parallel wrinkles that extend to the axial belt. The units are no longer convex but depressed with respect to their boundaries. This may indicate a lowered pressure of internal fluids and initiation of collapse of the body. The lowering of central parts of the serial units is much more advanced in yet another specimen, SAM F16718 (Fig. 4C; also Glaessner and Wade, 1966, fig. 2), preserved in the same way as the holotype of *Charniodiscus (Arborea) arboreus* (Glaessner, 1959; Glaessner and Daily, 1959). In some of the units, fusiform series of bulbs emerge from under the basement membrane cover. This indicates that the fusiform bodies were internal organs. To be impressed in the sediment, the tissues external to them had to wither and collapse. The fusiform bodies were thus embedded in box-like chambers, presumably with basement membrane walls and filled with a liquid under pressure.

Equally mysterious as the petaloids is the nature of the basal bulb ("disc") in the Vendian "sea-pens." Its shape and internal fill vary in differently preserved specimens. In *Charnia masoni* Ford, 1958, the rachis was restored with a fusiform structure behind the petaloids (Jenkins, 1992). This was also the case with the Middle Cambrian *Thaumaptilon*, in which the extension was rather short (Conway Morris, 1993). The *Thaumaptilon* basal bulb ("holdfast") and axis are filled with dark matter, so originally the axial cavity content was organic-rich (Conway Morris, 1993). The nonmineral nature of such fill, or its complete lack, is apparent in many cases of the frond-like Ediacaran fossils. The basal disc of *Charniodiscus* from Charnwood Forest is completely

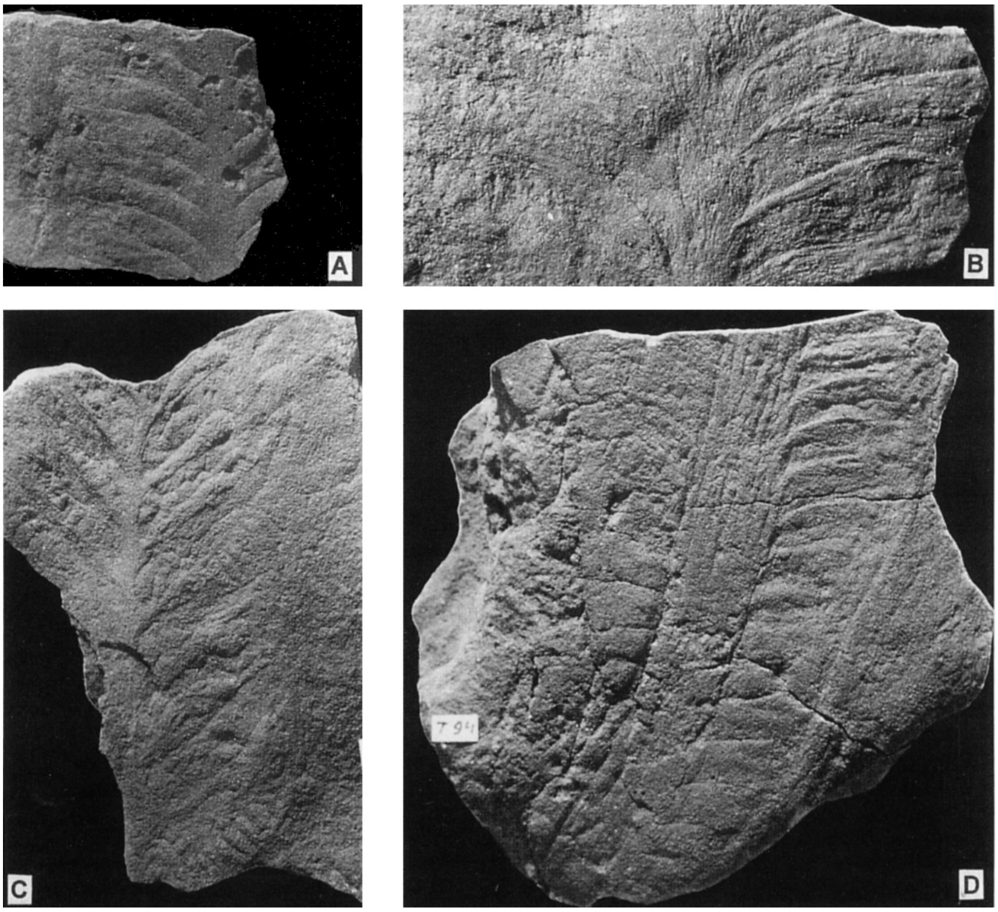

Fig. 4. Specimens of *Charniodiscus (Arborea) arboreus* (Glaessner, 1959) from the Rawnsley Quartzite at Ediacara, Flinders Range of South Australia showing different stages of collapse of the soft tissues; all ×1. **A**: Specimen SAM T 93-2016 (illustrated also in Glaessner and Daily, 1959, pl. 44:3) showing probably the original morphology of the external surface of the body prior to collapse. **B**: Specimen SAM F16712 representing a slightly withered frond with collapsing fluid-filled chambers. **C**: Even more withered specimen SAM F16718 with annulated fusiform organs emerging from under withered chambers in their centers (illustrated also in Glaessner and Wade, 1966, pl. 102:2 as P17018). **D**: Specimen SAM T 94-2015 (illustrated also in Glaessner and Daily, 1959, pl. 44:2), a case of composite preservation style with the distal part showing the external body surface (slightly withered) and the proximal part three-dimensionally preserved with internal fill of the rachis.

collapsed (Jenkins and Gehling, 1977, fig. 2). In the Australian specimens preserved on the upper surfaces of rock slabs, the basal discs are sometimes represented as collapse craters (Jenkins and Gehling, 1977, p. 351, fig. 3). It seems, therefore, that the rachis of the frond of *Rangea* and related forms was originally a hollow structure or contained an easily decomposed organic substance. The axial cavity and the bulb may thus represent the digestive zone, only occasionally filled with sediment, perhaps originally rich in organic matter. This does not necessarily contradict the idea that the basal bulb could function as an anchor, loaded with sand. The way in which the sediment entered the rachials cavity remains unknown, as there is no evidence of any opening in the basal disc.

If the indistinct structure at the proximal end of *Bomakellia* also represents a basal bulb, it was in close proximity to the frond, unlike the other frond-like organisms which had a distinct stalk. A similar relationship between the basal disc and frond was proposed by Sun (1986) for *Paracharnia*, the most unusually preserved Vendian frond-like fossil.

Paracharnia

Paracharnia dengyingensis (Ding and Chen, 1981) (Sun, 1986) from the Dengying Formation of the Yangtze Gorge of southern China is the only Vendian frond-like fossil with the Cambrian style of preservation, that is, with mineralized soft tissues (Steiner and Reitner, 1999). Its earlier descriptions have been based mostly on photographs (Sun, 1986; Steiner, 1994), the single known original specimen being permanently encased in the museum exhibition of the Wuhan Geological Museum, China (WGM ZnF0011; Fig. 5). I have examined the specimen. The rock is a black laminated limestone with lighter bands representing purely calcitic laminae; the darker bands are rich in clay minerals. The fossil is much less informative than claimed in previous descriptions. Contrary to earlier assumptions (Steiner, 1994), the tissues are not preserved as carbonized remnants. The fossil is not similar in this respect to the algae known from coeval strata. Instead, the frond is partially covered with a crust of a dark mineral (presumably pyrite). The surface of the slab is etched as an effect of weathering in the soil. The etching is quite deep in some areas, exposing various levels of the specimen, which is three-dimensionally preserved within the rock. The mineral crust was resistant to etching and is exposed in some areas well above the surrounding matrix. Apparently, it originally formed a continuous sheet over the whole fossil.

In lateral parts of the fossil, the mineral sheet underlies fusiform depressions, in places it is still filled with remnants of the limestone lamina that originally covered the frond (Fig. 5). The depressions are separated from each other by elevated ridges which, being more resistant then the rest of the sheet, usually extend closer to the axis. They were erroneously interpreted as 'stalks' by Sun (1986). The actual picture of the distribution of 'leaves' (petals) is thus opposite to that restored by that author; they were located between the 'stalks.'

In the axial part of the fossil, the limestone matrix fills a wide depression in the crust. Its bottom is exposed by etching near the tip of the frond. There the crust forms indistinct fusiform elevations, oblique in disposition.

In most of the specimen the crust is not preserved, but there are patches of darker sediment, slightly more resistant to etching than the surrounding limestone (Fig. 5). Presumably, it is cemented there with the same dark mineral which forms the crust. A series of them clearly represent metameric petals (Sun, 1986). Nevertheless, there is no 'disc-like marking' at the base of the frond, and cannot be, as the limestone surface there is deeply etched, which precludes preservation of any bedding plane imprints.

Paracharnia is thus similar to *Rangea* in frond-like appearance but differs in its much greater elongation. In this respect it may be similar to incompletely preserved *Bomakellia*. There is a possibility that the fusiform elevations at the bottom of the rachis represent the third vane, the forth one, originally facing the slab, being completely removed, but this evidence is weak. Particular petals are too poorly preserved to show convincingly that their organization was pinnate or not, but the apparent concavity of the crust suggests that only the smooth surface of metameric chambers is represented there.

It may thus be concluded from the above review that variously preserved fossils of the frond-like Ediacaran organisms represent three different levels of their anatomy: 1) a smooth external surface of the petaloid units preserved only in external imprints produced before the loss of its internal fluid pressure, 2) boundaries between chambers emerging in partially collapsed specimens, and 3) a complex pattern of connections between the petaloid units at their inner surface, which can be seen in the completely collapsed specimens from Namibia and Newfoundland. The smooth external surface and the radial membranes arming the edges of vanes make the Precambrian frond-like organisms unlike Recent pennatularians and, in fact, all colonial organisms with filter-feeding lifestyles. Filtration requires a basket-like or feather-like network that was definitely not present there. No zooids extended from the body surface, as it was smooth and without any perforations. The sea-pen model is thus not applicable to them.

Whatever were the anatomical details of the Vendian frond-like organisms, they were different from anything known from the present seas. To interpret their anatomy in zoological terms one has to show their phylogenetic connection with members of Recent phyla. This can be done only by using Paleozoic fossil organisms as intermediates. Some of the Cambrian fossils of soft-bodied organisms may help in this.

EARLY CAMBRIAN CTENOPHORE *MAOTIANOASCUS* AND ITS RELATIVES

No fossils closely related to *Rangea* are known from post-Vendian strata, but the Middle Cambrian *Thaumaptilon* from the Burgess Shale (Conway Morris, 1993) and an undescribed organism from the Chengjiang fauna (Zhang and Babcock, 1996) have been proposed to be members of the same clade. *Thaumaptilon* specimens are preserved in a typical manner for the Burgess Shale, that is, with a mineral staining reflecting original organic matter contents in the soft tissues (Conway Morris, 1993). In its general shape, the presence of pinnately ar-

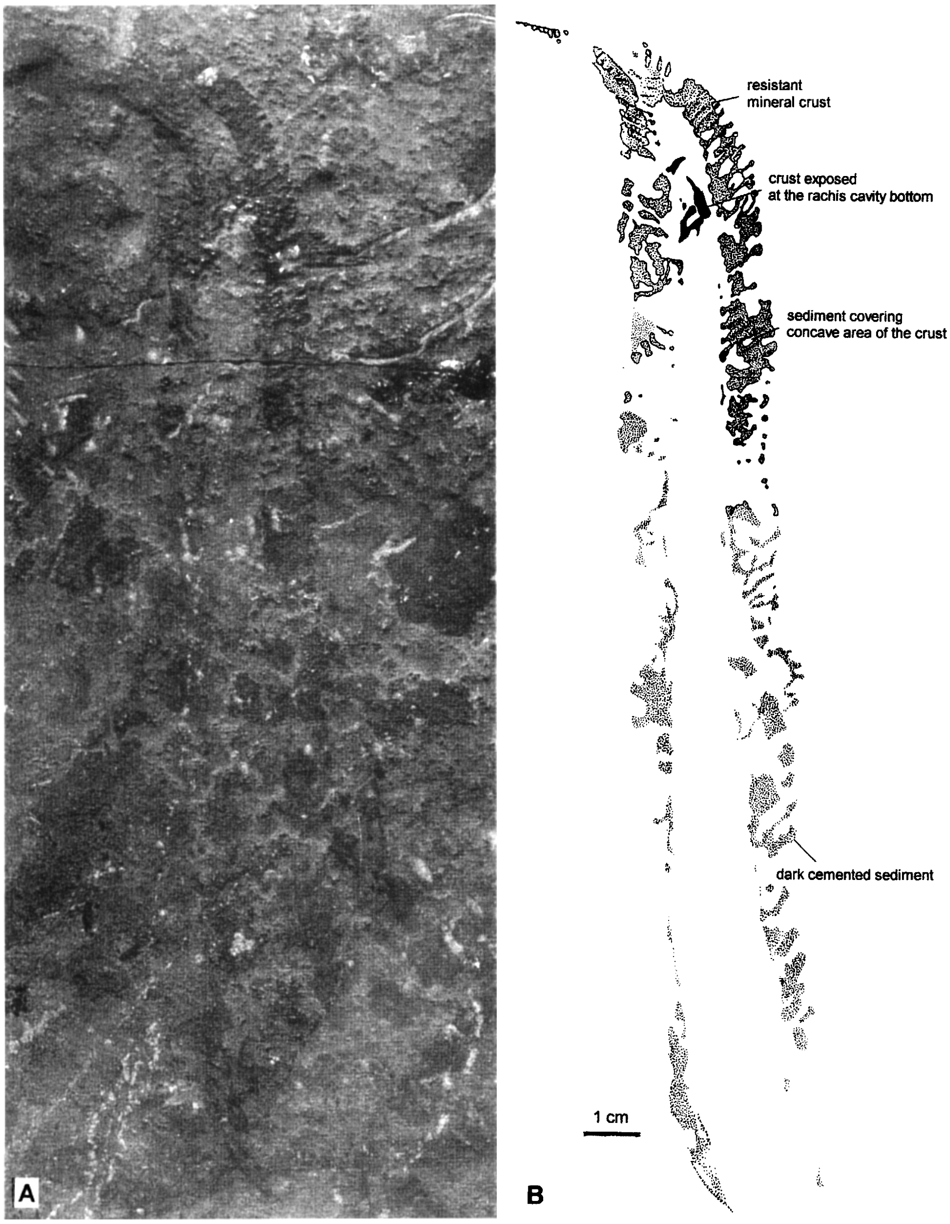

Fig. 5. *Paracharnia dengyingensis* (Ding and Chen, 1981) from the Dengying Formation in Hubei, China; photograph and interpretive drawing of the holotype WGM ZnF0011 (illustrated also in Sun, 1986, fig. 1); note that the dark mineral crust is preserved in positive relief in effect of etching of surrounding limestone matrix.

ranged metameric units on both sides of an axial rachis, and a marginal membrane ("folded margin" of Conway Morris 1993, text-fig. 2), it truly resembles the Ediacaran frond-like organisms. The fusiform darker organs that are serially distributed on both sides of the body seem homologous to petaloids of the Vendian frond-like organisms. If so, the Burgess Shale specimens preserve different details of these organs than do specimens from Ediacara or Namibia.

The fusiform serial organs of *Thaumaptilon* do not show any clear segmentation or fractal structure. Instead, there are bands of irregularly distributed dark spots ("pustules," interpreted as zooids by Conway Morris, 1993). Some minute organs, rich in organic matter, were thus present there. Their nonrandom but uniform distribution suggests that they occurred on the surface of the fusiform organ. As such, they cannot be homologous to anything known in the Vendian frond-like organisms, as their preservation in coarse-grained sediments precludes identification of so fine details. There is a possibility, however, that the spots are homologous to some more regularly distributed structures in coeval organisms.

Among other Burgess Shale fossils, metameric fusiform organs pinnately arranged in respect to the central body axis occur in *Fasciculus*. These have been interpreted as comb organs and the organism has been interpreted as a ctenophore (Conway Morris and Collins, 1996), with numerous comb rows arranged in four longitudinal series, two of them in a feather-like disposition (Figs. 7D, 8; Simonetta and Delle Cave, 1978; Conway Morris and Collins, 1996). The body symmetry is clearly biradial, the kind of symmetry probably transitional to bilaterality (Martindale and Henry, 1998). I propose that the lateral pinnately arranged fusiform organs of *Thaumaptilon* are homologous to those of *Fasciculus*. If so, one may wonder whether there is anything in the morphology of *Thaumaptilon* which could correspond to the medial series of comb organs in *Fasciculus*. In fact, there are such structures. These are minute areas with dark spots serially distributed in proximity to the rachis on both sides. These may represent homologs of the medial comb organs series in *Fasciculus*, but also of the third and fourth vane in *Rangea*. They were much less prominent than the other two vanes, so *Thaumaptilon* may differ from *Rangea* in being biradial, not tetraradial.

The fundamental difference between the fusiform organs of *Thaumaptilon* and the comb organs of *Fasciculus* is that they do not show transverse dark bands of ciliated cells. This disparity may appear not so important if the irregularly distributed dark spots (pustules) represent macrocilia. This would mean that in the Vendian the surface ciliation was not yet organized in any regular pattern which could be identified in fossils of Ediacaran-style preservation. If true, the complex serial organs within the petaloids of the frond-like organisms were thus not directly homologous with the comb organs but rather were homologous with structures underlying them. The macrocilia and comb organs developed above the chamber-like units encapsulating the petaloids.

There seems thus to be a possibility to connect the Ediacaran frond-like organisms via a series of Cambrian problematic fossils with organisms of a rather well-established zoological affinity. Somewhat unexpectedly, some of the basic features of *Rangea* and *Thaumaptilon* are represented by *Maotianoascus* from the Early Cambrian Chengjiang fauna of South China (Chen and Zhou, 1998). This fossil is the closest in geological age to the Vendian frond-like organisms. It is also the oldest known ctenophore, and thus deserves a discussion in some detail.

While visiting the Nanjing Institute of Geology and Paleontology in 1993, I was permitted to study two specimens of seemingly tentacle-bearing "anthozoans." As typical for the Chengjiang fossils, despite compaction of the mudstone, they show some relief. Particular parts of the compressed bodies occupy different levels, some being separated by a thin sediment layer. In both specimens the sediment did not enter the central part of the body, as could be expected if there were truly a ring of tentacles surrounding the mouth. Instead, only a few sediment wedges separated the external parts of the supposedly tentacle-like structures (Fig. 6). This enabled restoration of the original (precompaction) three-dimensional appearance of the organism (included with permission from Chen Jun-yuan in Dzik, 1996, fig. 5.9F). It appeared that it had an octaradial symmetry, with 16 fusiform double bands of transverse dark lines running along the body; thus, the body plan of a ctenophore. The formal description of the fossil, named *Maotianoascus*, was published subsequently by Chen and Zhou (1998).

Only those two specimens of *Maotianoascus* are known. The holotype (ELRC 06301; Fig. 6A; Chen and Zhou, 1998, fig. 147) is represented in the collection only by the part, but the paratype is represented by both part (06302a) and counterpart (06302b) (Fig. 6B,C; Chen and Zhou, 1998, fig. 148). The body is different in shape from that of other ctenophores. It is composed of a geometrically complex region with comb organs, almost circular in lateral view, with a black apical organ at the top, and a large visceral sac. Because of the vaned organization of the main part of the body and bulbous appearance of the visceral sac, I will use the same terms for them as for the proposed homologous parts of *Rangea* (i.e., the frond and basal bulb).

"Frond" of *Maotianoascus*

The frond of *Maotianoascus* is composed of eight units radially arranged around the axis (Figs. 6, 7I; Dzik, 1996, fig. 5.9F; Chen and Zhou, 1998, fig. 28).

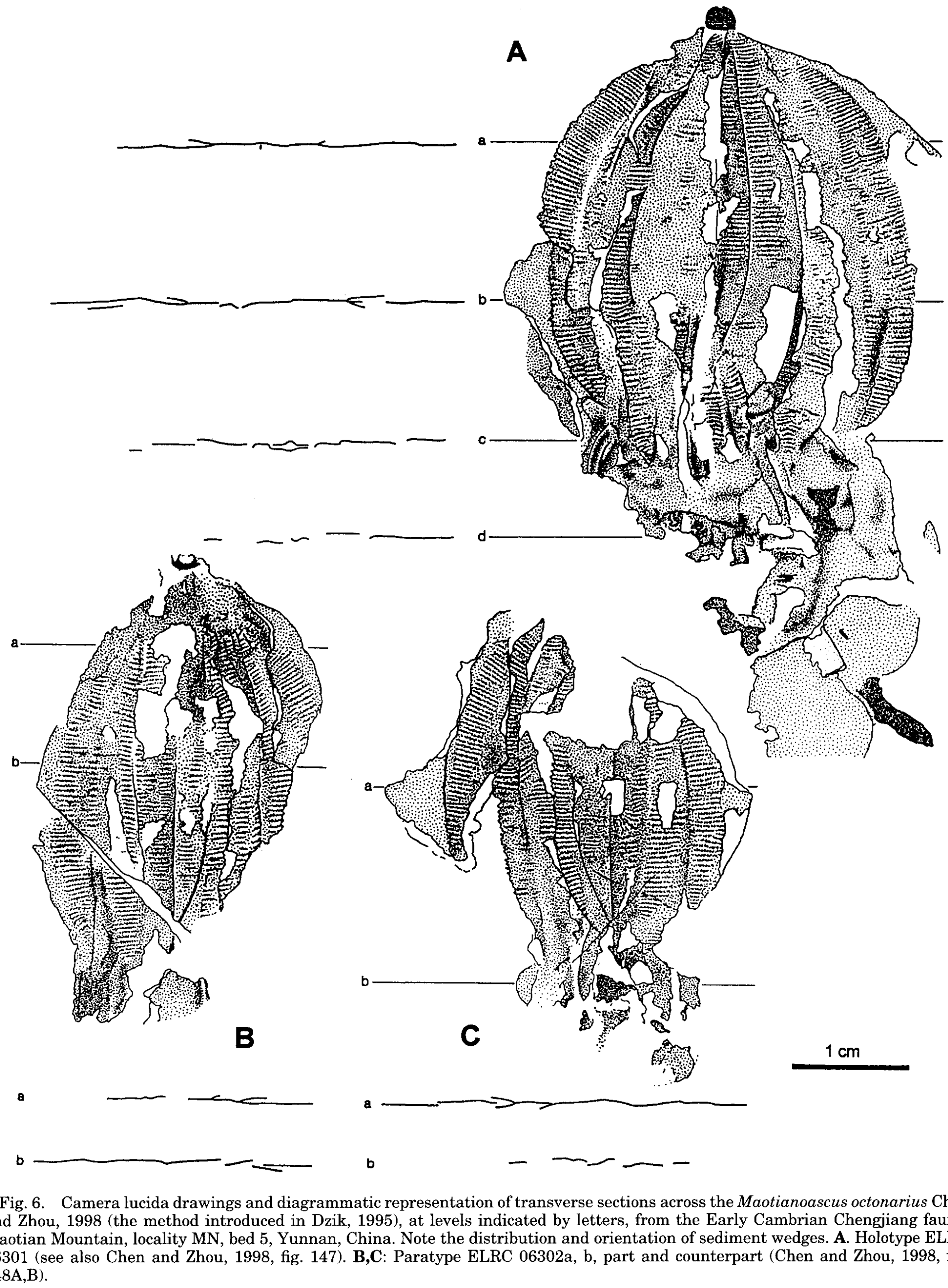

Fig. 6. Camera lucida drawings and diagrammatic representation of transverse sections across the *Maotianoascus octonarius* Chen and Zhou, 1998 (the method introduced in Dzik, 1995), at levels indicated by letters, from the Early Cambrian Chengjiang fauna, Maotian Mountain, locality MN, bed 5, Yunnan, China. Note the distribution and orientation of sediment wedges. **A**. Holotype ELRC 06301 (see also Chen and Zhou, 1998, fig. 147). **B,C**: Paratype ELRC 06302a, b, part and counterpart (Chen and Zhou, 1998, fig. 148A,B).

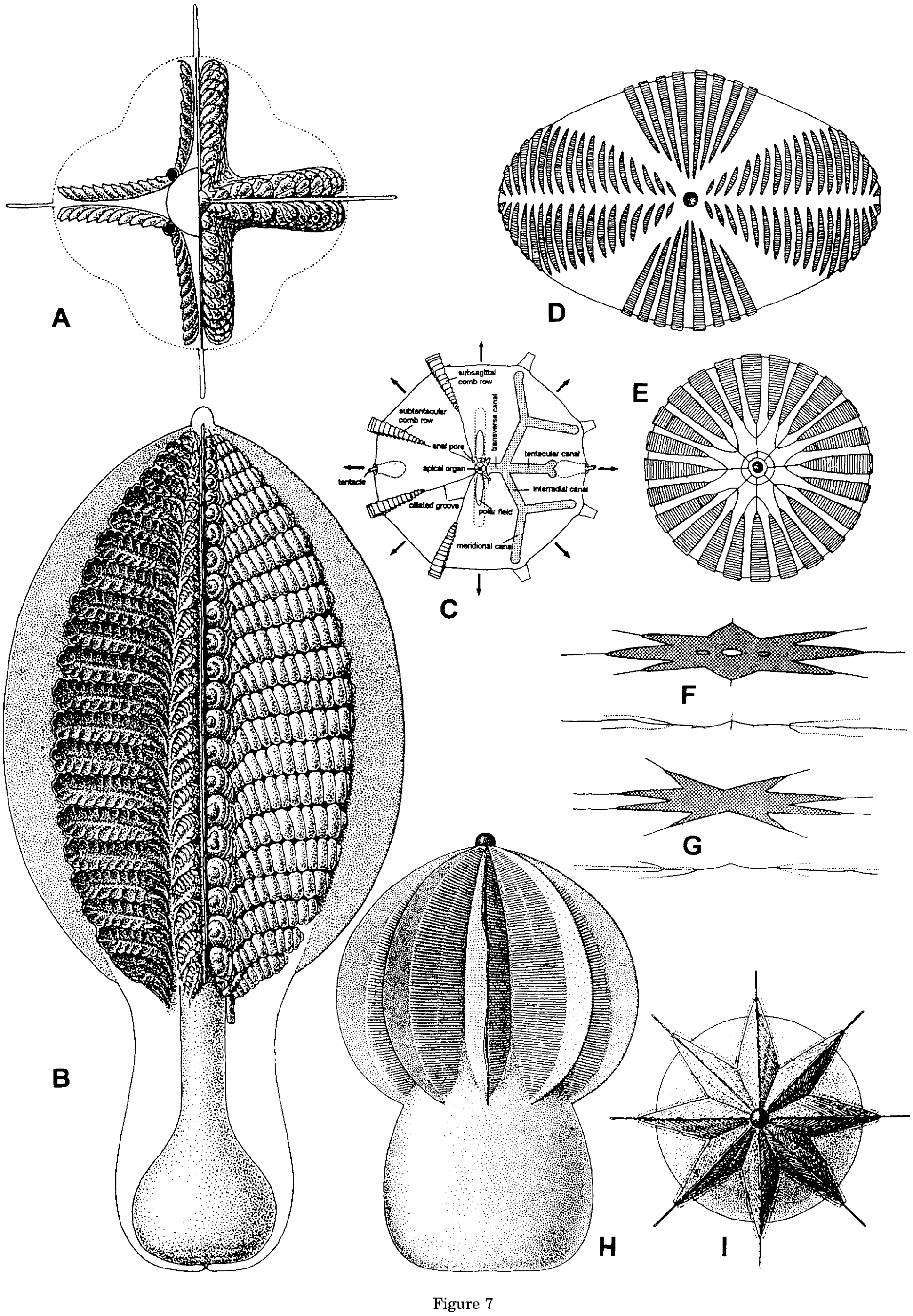
A
D
subsagittal comb row
subtentacular comb row
anal pore
transverse canal
apical organ
tentacle
tentacular canal
interradial canal
ciliated groove
polar field
meridional canal
C
E
F
G
B
H
I

Figure 7

The comb organs are represented in *Maotianoascus* fossils by fusiform belts, darker than the surrounding remnants of the soft tissue, and so presumably with a higher organic content. The transverse bands, which total about 90, are not only darker but are also expressed by smooth undulations (alternating narrow depressions and elevations) of the sediment surface. These are apparently the basal cushions of the comb rows; perhaps they had a dense cytoskeleton, similarly to fibrous cells and macrocilia of Recent beroid ctenophores (Hernandez-Nicaise, 1991, p. 377), which provided sufficient carbon.

Outside the comb organs the margin of the frond is completely smooth and lacks any stain. At the left side of the holotype two such smooth areas are represented at different levels. The sediment between these levels apparently penetrated towards the frond axis. This is one of the mudstone wedges, with the sharp margins pointing towards the center on both sides of the specimens (Fig. 6). It can be inferred from this peculiar distribution of the compacted sediment and completely collapsed soft body that there were strongly concave areas running along the main part of the body (Fig. 7I). The mud originally located in those concavities now forms the wedges. Assuming that the mud was not able to compress the soft body laterally, its extent delimits the depth of furrows and the diameter of the central part of the body. The marginal smooth bands thus represent marginal membranes extending radially from the elevated ridges of the frond.

Fig. 7. Morphological gradient connecting the anatomies of the Vendian petalonamean *Rangea* and the Early Cambrian ctenophore *Maotianoascus*. Note that the Namibian and Newfoundland style of preservation gives only information on deeply located petaloid base (perhaps corresponding to the ctenophoran meridional canals), whereas the Cambrian fossils show only the superficially located comb organs. Some Newfoundland petalonameans show biradial symmetry (e.g., Seilacher, 1995). **A,B**: Restoration of preserved skeletal structures of *Rangea schneiderhoehni* Gürich, 1930, from the Kliphoek Member, Namibia (left half of the specimen) and conjectural appearance of the chambers (right half) in apical (**A**) and lateral (**B**) views. The external body covers (dotted) are not represented in the Namibian material. Presumably, they were of chambered organization, similar to that of *Ernietta* (see Dzik, 1999), *Pteridinium*, and *Swartpuntia* (see Narbonne et al., 1997). **C**: Body plan of a generalized Recent ctenophore (modified after Hernandez-Nicaise, 1991). **D,E**: Apical views of the Middle Cambrian Burgess Shale ctenophore *Fasciculus vesanus* Simonetta and Delle Cave, 1978 (**D**) and *Ctenorhabdotus capulus* Conway Morris and Collins, 1996 (**E**: both based on restorations in Conway Morris and Collins, 1996). **F–I**: The Early Cambrian Chengjiang ctenophore *Maotianoascus octonarius* Chen and Zhou, 1998; interpretation of the origin of the present arrangement of compressed parts of the body in the holotype (**F**) and paratype (**G**) with interpreted transverse section of the actual fossils (see Fig. 6) and a transitional step in the 'retrodiction' leading to the original status before the soft body collapse and compaction; restoration of the body in lateral (**H**) and apical (**I**) views.

Apical Organ of *Maotianoascus*

The hemispherical apical organ is black in both known specimens of *Maotianoascus* and built of a rather thick carbonaceous film (Figs. 6, 7H). It was, therefore, originally rich in organic matter. Basally the organ shows densely arranged wrinkles and possibly had a short cylindrical base of the same diameter as the main hemispherical part. The carbon film ends at the top of the frond in both the holotype and paratype. No organic-rich stiff axis was observed.

Apical organs of Recent ctenophores are not dense enough to provide enough carbon to produce such a dark stain as observed on the Cambrian *Maotianoascus*. Hence, this was definitely much more than just a couple of cells with a statolith covered by cilia (Aronova, 1986). The apex of the rachis of *Thaumaptilon* corresponds closely to the apical organ of *Maotianoascus*, being separated morphologically from the frond and basally annulated. The nature of these apical organs in *Thaumaptilon, Maotiaanoascus*, and other Cambrian ctenophores remains to be identified.

"Basal Bulb" of *Maotianoascus*

In *Maotianoascus* there is a slight constriction at the base of the frond separating it from the large bulb (Fig. 6A). This part of the body is poorly preserved in both specimens, but it was apparently as large as the frond. Its surface is smooth and almost without any stain. It is preserved in a way similar to the marginal membrane and was equally poor in organic matter. The exact shape of the bulb is difficult to restore because of the incompleteness of both specimens (Fig. 6A–C), but it is clear that it was swollen, and originally probably of subspherical appearance (Fig. 7H). Some darker areas are seen in the holotype. They may belong either to the specimen itself or represent superimposed organisms. It cannot be excluded that some of these darker bands that extend radially from the main part of the bulb (Fig. 6A) are some sort of tentacle, but there is no unequivocal evidence for this. Around the basal bulb some smooth areas with poorly delimited boundaries occur, but those have unclear relationships to the remaining parts of the fossil. They may represent fragments of the bulb, decomposed or cut by a predator or, equally likely, parts of other specimens. Membrane-like partings at the lower end of the holotype, located at a different level than the rest of the bulb, may represent exfoliated anterior wall derived from the decomposed body of the bulb.

Immediately below the frond in the axial part of the holotype a sediment-filled axial cavity is delimited by two layers of organic film. Its cross section is roughly rhombic (Fig. 6A, level c). Below, in the center of the basal bulb, small pellet-like objects occur (Fig. 6A, level d). Their precise nature and position in respect to the bulb wall are not clear.

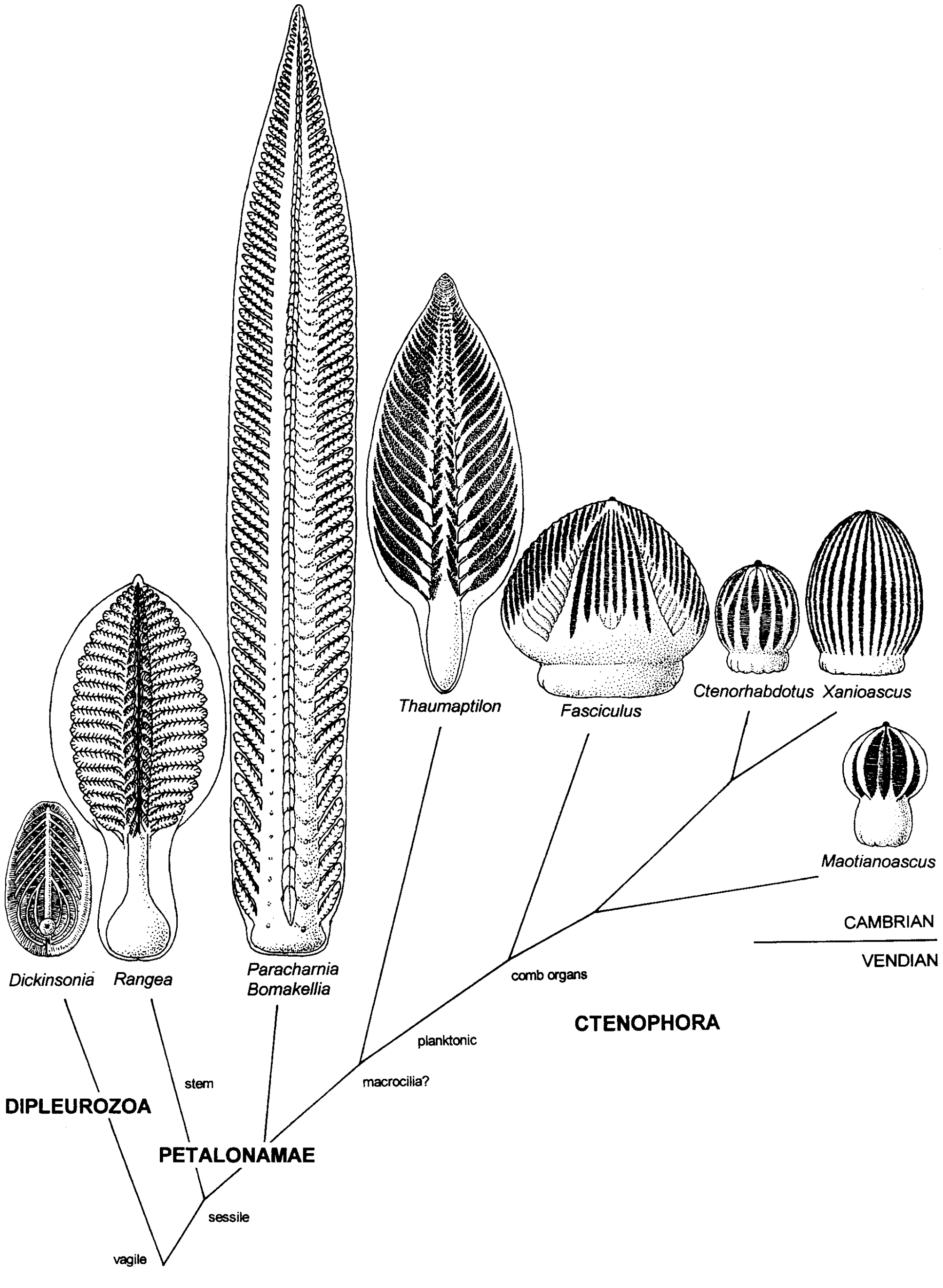

Fig. 8. Diagram showing possible relationships between the Vendian petalonameans and the Cambrian ctenophores. The restoration of *Paracharnia* is highly conjectural, partially based on its similarity to *Bomakellia*; the restoration of *Dickinsonia* is taken from Dzik and Ivantsov (2001).

TABLE 1. Assumed homologies

Rangeids	Ctenophores
1. Tetraradial or biradial (unnamed 'spindle shaped organism') symmetry with vanes	1. Octaradial (*Maotianoascus*) or biradial (*Fasciculus*) symmetry with vanes
2. Axial cavity expanding distally into a 'basal bulb' or disc	2. Variously developed oral expansion ('bulb')
3. Pinnate internal (glandular?) organs (petaloids) with their ducts opening to the axial cavity	3. Pinnate organization (only in *Fasciculus*) transformed into longitudinal arrangement of units
4. Above the petaloids fusiform organs of irregular organization	4. Comb organs with regular transverse rows of ciliated cells

Longitudinal structures with low relief are associated with the central sediment-filled canal on its both sides. They are a little darker than their background. This refers especially to the left structure that shows a prominent relief, but only a small part of it is preserved. The boundaries and internal organization of the right structure are obliterated by the bulb wall but it extends for a somewhat longer distance. These were probably longitudinal canals with thin organic walls but it remains unclear whether or not they were filled with sediment.

There was thus a kind of axial canal (although its exact shape remains unknown) in the body of *Maotianoascus* which was accessible to sediment and connected with the cavity inside the basal bulb which contains possible fecal pellets or ingested foreign objects. There is also weak evidence that the axial canal was backed laterally by (at least) two longitudinal canals.

POSSIBLE *RANGEA-MAOTIANOASCUS* HOMOLOGIES

The presence of radially arranged vanes and the subdivision of the body into vaned frond and bulbous visceral cavity make *Maotianoascus* to some degree transitional between the other Cambrian ctenophores and the Ediacaran frond-like organisms. There are also some differences. The number of radii is double that in *Rangea*. The frond organization is also different in that instead of complex petaloids there are just 16 comb rows. The morphologic gap can be filled, at least partially, with the evidence from the only Cambrian probable rangeid *Thaumaptilon* and *Fasciculus*, the most complex of the Middle Cambrian ctenophores.

Interestingly enough, in *Fasciculus* there are deeply located metamerically arranged internal organs with "a feathery appearance" (lobate organs of Conway Morris and Collins, 1996, p. 291). Although they are rather different in appearance, it is tempting to suggest that these were homologs with the petaloids of *Rangea*. They occupied a position on the frond roughly corresponding to that of the paired meridional canals in the ctenophores (see Hernandez-Nicaise, 1991). The common canal, from which all the petaloid units originate (or to which they merge) would then correspond to the interradial canal. Along with their digestive function, the meridional canals of the Ctenophora also hold gonads. The comb rows in the Recent ctenophores are arranged in pairs (Fig. 7C; Hernandez-Nicaise, 1991, p. 361), which suggests their original tetrameric organization.

The proposed petaloid-meridional canal homology implies that in the course of evolution from *Rangea*-like Vendian organisms to Cambrian ctenophores (with *Fasciculus* being derived from transitional forms) the complexity of meridional canals decreased but, instead, the macrocilia-like units scattered over the fields associated with petaloid units were ordered into transverse combs. This may be connected with a transition from benthic to pelagic mode of life (Fig. 8). The Recent Ctenophora are highly advanced in this respect and even if some among them are benthic, these certainly developed their mode of life secondarily from pelagic ancestors. The most parsimonious interpretation of the ctenophoran phylogeny by Harbison (1985) implies that the ancestral pelagic ctenophore had a radially symmetrical arrangement of canals with anastomosing diverticula in large specimens, a spacious gastric cavity, and a large mouth. The beroid ctenophores, active predators lacking tentacles but searching for prey, may be close to the ancestor of all Recent ctenophores. The Cambrian forms were probably similar to beroids in their mode of life as they lacked tentacles and generally had more or less elongated body shapes (Conway Morris and Collins, 1996). A passive feeding with tentacles is a secondary adaptation of the ctenophores. The Recent ctenophores are transparent pelagic animals of lightly built bodies. Their epithelial covers are underlined only by a thin two-layered basal lamina (Hernandez-Nicaise, 1991) of a low fossilization potential. The only exception is the deep-sea *Aulacoctena*, with its mesoglea of cartilaginous consistence and penetrated by numerous muscle fibers (Mortensen, 1932; Harbison and Madin, 1982). There is no special reason, however, to consider this ctenophore, with its unusually deeply sunk statocyst, as especially primitive.

Rangea is thus proposed to be interpreted as an ancient benthic ctenophore (Fig. 7A,B). This is based on the assumed homologies in Table 1.

The petaloid modules of *Rangea* are a clear case of serial homology. It seems reasonable to assume that they developed phylogenetically from a less complex ancestral organization by fractal branching of units. Among the known Vendian metazoans, the dickinsoniid Dipleurozoa are likely to offer possible homologies in their body plan (see Dzik and Ivantsov, 1999; Dzik, 2000). Phylogenies based on the nucleotide sequences of 18S rRNA suggest that the Ctenophora branched off the main stock of the Metazoa earlier even than the cnidarians (Kobayashi et al., 1993; Wainright et al., 1993).

Although unavoidably speculative, the proposed petalonamean-ctenophoran relationship is at least consistent with the available fossil evidence. It removes most of the difficulties with interpretation of the fossil structures which immediately emerge if the long-held concept of their colonial nature, filter-feeding lifestyle, and pennatularian affinities is applied.

CLASSIFICATION OF *RANGEA*

All the complex Vendian organisms are usually referred to as Petalonamae or Vendozoa (Vendobionta). In both concepts, a hidden assumption is that they represent a monophyletic unit. The concept of Vendobionta implies also a lack of relationship to later animals. In fact, the early attempts to compare Ediacaran fossils with Recent cnidarians or members of other phyla were based on a quite superficial similarity and poor understanding of their formation (Dzik, 1991). No convincing evidence for the presence of any separate zooids has ever been offered for the alleged Precambrian pennatulaceans. However, there is growing evidence that organisms of this kind are not restricted to the Precambrian (Conway Morris, 1993; Geyer and Uchman, 1995; Grotzinger et al., 1995; Narbonne et al., 1997; Jensen et al., 1998). The occurrences of both the Petalonamae and earliest skeletal fossils were controlled mainly by taphonomic factors (Dzik, 1994, 1999; Gehling, 1999) and their ranges strongly overlap. It is thus an open question whether to classify the Vendian and Cambrian frond-like organisms in a group of their own, or to attribute them to high-rank taxa invented for Recent organisms, as advocated by Gehling (1991).

The main argument forwarded by Seilacher (1989) to support the monophyly of most of the Vendian organisms is the serial arrangement of transverse units in their bodies. This metamery alone does not seem to be a strong argument in favor of their close relationship. Instead, it seems safer to separately classify the frond-like forms, with pinnately arranged internal organs, well exemplified by *Rangea*. The name Petalonamae seems the most appropriate for them. *Charniodiscus* from Charnwood Forest (Ford, 1958; Jenkins and Gehling, 1977), *Rangea* from Namibia, and some other fossils from the Mistaken Point Formation of Newfoundland, the White Sea assemblage from Russia, and from Ediacara would fit this concept. This requires some restriction of the original meaning of the Petalonamae.

Metameric units of *Ernietta* and *Pteridinium* are not necessarily related to the pinnate organs of *Rangea*; they were more likely linings of muscular chambers close to the body surface (Dzik, 1999). Similar and possibly homologous muscular chambers, arranged in a flat, presumably dorsal structure, characterize *Dickinsonia* and related organisms, for which the name Dipleurozoa is already available (Dzik, 1995; Dzik and Ivantsov, 1999). Each of these clades may be of different zoological affinities. It has to be kept in mind that attribution of particular groups of the Vendian organisms to different phyla does not contradict their monophyly (that is, paraphyly in terms of cladistics). No other reasonably preserved metazoan fossils are so close in time to the common ancestor of all animals.

If the ctenophoran affinities of *Rangea* are accepted, the taxon Petalonamae Pflug, 1970, can be included in the Ctenophora Eschscholz, 1829, possibly as a class. The petalonameans would then comprise frond-like benthic ctenophores with cilia not arranged in combs and with pinnate arrangement of internal units connected with meridional canals. Regarding lower rank taxonomic units for *Rangea*, Jenkins (1985, p. 351) proposed to use the class-rank name Rangeomorpha Pflug, 1972, as an ordinal name (Pflug, 1972). This was, in fact, erection of a new taxon, for which the emended form would be Rangeida Jenkins, 1985. The family Rangeidae Glaessner, 1979, seems to differ from other members of the class (and order) in tetraradial symmetry of the frond, with most petalonameans showing probably biradial or even bilateral symmetry. It includes only the genus *Rangea* Gürich, 1930, with the only species *Rangea schneiderhoehni* Gürich, 1930. The other petalonameans are too poorly known for a differential diagnosis for low-rank taxa to be offered. It also remains to be decided whether the Cambrian pelagic ctenophores deserve a special class-rank taxon to be established.

The hypothesis of relationship between the benthic rangeid Petalonamae and Recent pelagic ctenophores implies a correspondence between the petalonamean petaloids and the ctenophoran meridional canals and possible origin of the locomotory comb organs from ciliary bands on the surface of vanes. Recent discoveries of new Cambrian and Vendian localities of extraordinarily preserved fossils may allow testing of this hypothesis in the not too distant future.

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