

Were the Ediacaran fossils lichens?

Gregory J. Retallack

Abstract.—Ediacaran fossils are taphonomically similar to impressions of fossil plants common in quartz sandstones, and the relief of the fossils suggests that they were as resistant to compaction during burial as some kinds of Pennsylvanian tree trunks. Fossils of jellyfish are known from siderite nodules and fine-grained limestone, and even in these compaction-resistant media were more compressed during burial than were the Vendobionta. Vendobionta were constructed of materials that responded to burial compaction in a way intermediate between conifer and lycopsid logs. This comparative taphonomic study thus falsifies the concept of Vendobionta as thin soft-bodied creatures such as worms and jellyfish.

Lichens, with their structural chitin, present a viable model for the observed preservational style of Vendobionta, as well as for a variety of other features that now can be reassessed from this new perspective. The diversity of Ediacaran body plans can be compared with the variety of form in fungi, algae, and lichens. The large size (ca. 1 m) of some Ediacaran fossils is reasonable for sessile photosynthetic symbioses, and much bigger than associated burrows of metazoans not preserved. Microscopic tubular structures and darkly pigmented cells in permineralized late Precambrian fossils from Namibia and China are also compatible with interpretation as lichens. The presumed marine habitat of Ediacaran fossils is not crucial to interpretation as lichens, because fungi and lichens live in the sea as well as on land.

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They are ill discoverers that think there is no land, when they can see nothing but sea. Francis Bacon

Introduction

An outstanding anomaly of Ediacaran fossils is the surprising relief of their impressions in quartz-rich sandstones buried to depths of about 5 km (Wade 1968; Fedonkin 1992). Fossil logs are common nonskeletonized fossils also found in deeply buried quartz sandstones. Burial compaction can be measured from fossil logs as the ratio of thickness to width. The former thickness of fossil logs is equal to their width, because the lateral spread of these cylindrical objects is checked by lithostatic pressure at the sides (Briggs and Williams 1981; Rex and Chaloner 1983). Fossil logs also vary in strength depending on the proportion of bark and wood compared with parenchymatous tissue of the pith and cortex. As is well known from studies of Pennsylvanian coal balls, fossil trees varied considerably in the relative proportions of these tissues (Taylor and Taylor 1993). Many gymnosperms such as cordaites and seed ferns had solid woody stems like those of modern pines, whereas tree lycopsids had a thin cyl-

inder of wood that included both tracheids and parenchyma. In this paper I aim to quantify a scale of resistance to burial compaction in quartz sandstones, ranging from moderately resistant logs rich in woody tissues to poorly resistant logs rich in soft tissues. Even though Ediacaran fossils may not have been cylindrical, their mass and strength is reflected in their response to processes of flattening during burial. A surprising result is that Ediacaran fossils were as compaction resistant as some kinds of fossil tree trunks!

Similarly, Norris (1989) has shown that Ediacaran fossils were much stiffer and less easily torn than the jellyfish and sea pens with which they have been compared in the past. Others of this distinctive assemblage of late Precambrian fossils have been interpreted as echinoderms and arthropods (Glaessner 1984; Runnegar and Fedonkin 1992; Valentine 1992). Less widely accepted interpretations of these fossils include algae (Ford 1958), large foraminifera (Zhuralev 1992), or an extinct group intermediate between plants and

animals (Pflug 1973). The adoption of a form taxonomic approach to the classification of these fossils as problematica (Fedonkin 1981) did not diminish enthusiasm for interpretation of these fossils as a variety of early metazoans (Runnegar 1982, 1992; Jenkins 1985; Gehling 1988). Nevertheless, there remain nagging doubts about the true nature of these strange worms without guts, jellyfish without marginal musculature, echinoderms without plates, and arthropods with alternating (rather than opposed) appendages. These concerns led Seilacher (1984, 1985, 1989) to suggest that these fossils be called "Vendozoa", or preferably Vendobionta (Seilacher 1992), and that they be regarded as an extinct early experiment in the evolution of life: a view that has gained some support (Gould 1984; Lewin 1984; Bergström 1990). This view has been embellished to suggest that these extinct organisms—without obvious mouth, gut, or other means of subsistence—may have housed chemosynthetic or photosynthetic symbiotic microbes (McMenamin 1986).

Comparative taphonomic evidence for Vendobiont toughness presented herein and by Norris (1989) allows comparison with another kind of symbiosis that is common and widespread; the photosynthetic algae and fungi of lichens (Retallack 1992c). Lichens have structural chitin (Herrera 1992), and would be more resistant to burial compaction than soft-bodied metazoans, foraminifera, or algae. A lichen interpretation may also explain a variety of other aspects of Vendobiont form, anatomy, size, and habitats, as well as other problematic fossils. These other potential tests of the idea that Vendobionts were lichens are also discussed in this paper.

Comparative Taphonomy of Vendobionts

The preservation of Ediacaran fossils has long been recognized as problematic, because Phanerozoic jellyfish and worms are not preserved in quartz sandstones (Seilacher 1989; Bruton 1991). A persistent notion, first proposed by Wade (1968) and still argued by Fedonkin (1992), is that Ediacaran fossils were cemented early during burial by silica or siderite that subsequently disappeared without

a trace. Until some possible tracer of former cements can be identified, this proposal remains untestable. A more popular explanation for the unique preservation of Vendobionts is that they predated the advent of herbivores, predators, or microbial decomposers (Seilacher 1989). However, fossil burrows found along with Vendobionta were probably made by metazoans, whose body fossils have never been found and presumably decayed (Fedonkin and Runnegar 1992). Furthermore, all the potential destroyers of fossils have not precluded a fossil record of unskeletonized organisms in Phanerozoic quartz sandstones, in the form of fossil leaves, fruits, seeds, and logs (for examples see Jennings 1974; White 1986; Rowe 1988; Burns 1991). A fundamental assumption of this study is that Vendobionta and fossil plants were subject to the same burial constraints.

This paper aims to compare quantitatively the preservation of Vendobionta and fossil plants, particularly fossil logs. Unlike Vendobionta, fossil plants of Pennsylvanian age are well known biologically (Taylor and Taylor 1993) and their preservation is well understood in a variety of matrices, including quartz sandstone (Schopf 1975; Rex and Chaloner 1983). This is an isotaphonomic study, in which material was deliberately selected for comparability of preservational style, matrix type, and burial history to those of Vendobionta. By keeping these variables constant, Vendobionta can be ranked in their strength to resist burial compaction using a scale derived from study of fossil logs.

Beyond the Ediacaran fossils identified as jellyfish, I know of no well-accepted fossil medusae preserved in quartz sandstone. However, some constraints can be placed on the preservation of such creatures by study of the Pennsylvanian fossil jellyfish *Essexella asherae* in siderite nodules. This species has the additional advantage of being preserved sideways (fig. 1), so that the umbrella was flattened from a spherical outline in the same way as the fossil logs studied (Foster 1979).

Here, as in all previous interpretations of Vendobionta, they are assumed to have been unskeletonized. As is well known, skeletonized fossils can be preserved with little com-

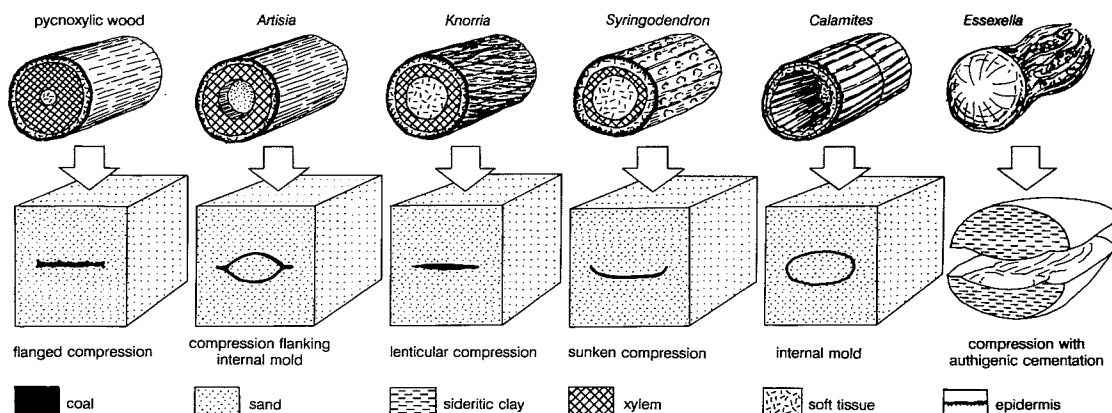


FIGURE 1. Paleobotanical terminology for compaction of Pennsylvanian logs and jellyfish.

paction in deeply buried quartzites, e.g., brachiopod shells and fish exoskeletons of the Mulga Downs and Lambie groups of Australia (Mackay 1964; Ritchie 1973) and trilobite cephalae of the House Range of Utah (Robison and Hintze 1972).

An obvious missing element in this comparative study is measurement of undoubted fossil lichens buried some 5–6 km in quartz sandstones. Nematophytes and other fossils that could plausibly be interpreted as lichens are discussed in a later section of this paper, but cannot yet be considered sufficiently well understood to constitute evidence for lichen preservation in quartz sandstone.

Materials and Methods.—This paper includes new measurements of a variety of fossil Vendobionta, logs, and jellyfish (tables 1, 2). The Pennsylvanian logs were identified as decorticated sigillarian lycopod (*Syringodendron*), decorticated lepidodendroid lycopod (*Knorria*), calamite (*Calamites*), chambered-pith cordaite (*Artisia*), and undifferentiated woody gymnosperm (pycnoxylic) based on the nature of surface ridges, leaf scars, and texture (following Gillespie et al. 1978).

Compression and impression fossils were cut with a diamond saw to expose a cross section perpendicular to the long axis of the fossils. Width and thickness of the specimens were then measured using vernier calipers accurate to 0.1 mm. This was not feasible for the Ediacaran fossils which are preserved as negative impressions. These and several of

the Paleozoic fossils were measured using a vernier depth micrometer accurate to 0.025 mm. The depth micrometer was designed for mechanical engineering applications, and has a rod that penetrates a measured distance down from a level base. Some 12–50 measurements at 1-mm intervals were made of widths, thicknesses, and depths of each specimen (table 2).

Petrographic thin sections were cut from billets of sandstone oriented vertical to bedding and point counted using a Swift model F automatic point counter. Each count was of 500 points, which is known to have a standard deviation of $\pm 2\%$ (Van der Plas and Tobi 1965). Three petrographic characteristics were measured: the proportions of grains showing different numbers of contacting grains as a measure of compaction (Taylor 1950), the proportions of sand, silt, and clay as a measure of grain size, and the proportions of quartz and other minerals as a measure of mineral composition (Retallack 1990).

Similarity of Preservation.—Preservational states of fossil logs and Pennsylvanian jellyfish are well understood (Schopf 1975, 1979; Foster 1979). The coalified remains of log is conventionally called a compression, and its image in the surrounding matrix is an impression (fig. 1). Hollows in logs, such as the chambered pith of some cordaites and the hollow pith of calamites, can be filled with sediment to create three-dimensional internal molds that are more resistant to compac-

TABLE 1. Localities of fossil Vendobionta, logs, and jellyfish.

Locality number	Description	Taxa	Formation & Age	References
UO2808	Quartzites 60 cm stratigraphically above and to west of red beds (Jenkins et al. 1983: fig. 4), on hillside south of Brachina Gorge, South Australia	<i>Dickinsonia costata</i> , <i>Tribrachidium heraldicum</i>	Ediacara Member, Rawnsley Quartzite, Late Precambrian	Jenkins et al. 1983
UO2809	Quartzites 2 m stratigraphically above and to west of red beds in same area as UO2808	<i>Dickinsonia costata</i>	as above	as above
UO2810	Thin quartzite interbed to red beds in same area as UO2808	<i>Medusinites mawsoni</i>	as above	as above
UO2811	Quartzites of low ridge, Elands-vlei, South West Cape Province, South Africa	<i>Haplostigma irregulare</i>	Blinkberg Sandst. Witteberg Group, Late Devonian	Anderson and Anderson 1985
UO2812	Quartzites below limestone and coal in hillside quarry 2 km NE of Stanhope, Durham Co., England	<i>Stigmaria ficoides</i>	Rogerly paleosol, Firestone Sill, mid-Carboniferous	Percival 1986; Retallack 1990, 1992a
UO2813	Lower sandstone paleochannel in roadcut on highway I48 through Big Savage Mountain, 3 km W of Frostburg, Maryland	<i>Syringodendron</i>	New River Formation. Early Pennsylvanian	Cardwell et al. 1986; B. Cecil, personal communication 1992
UO2814	Upper sandstone paleochannel in roadcut of UO2813	<i>Syringodendron</i> , <i>Gymnospermae</i>	as above	as above
UO2815	Creek bank boulders in Dry Branch of Cabin Creek, 3 km SE Cabin Creek village, West Virginia	<i>Syringodendron</i> , <i>Knorria</i> , <i>Gymnospermae</i>	as above	as above
UO2816	Road cut inside SW entrance ramp at Bragg Corner Exit from highway I64, Raleigh Co., West Virginia	<i>Syringodendron</i> , <i>Knorria</i> , <i>Calamites</i>	as above	as above
UO2817	Upper sandstone paleochannel in road cut on Highland Scenic Highway (WV150), 16 km N Cranberry Visitor Center, Monongahela National Forest, West Virginia	<i>Syringodendron</i> , <i>Knorria</i> , <i>Gymnospermae</i>	as above	Burns 1991
UO2818	Lower sandstone paleochannel in road cut of UO2817	<i>Syringodendron</i> , <i>Stigmaria</i> , <i>Artisia</i>	as above	as above
UO2819	Old mine workings on Joliet Sports Club, 4 km NE Essex, Kankakee Co., Illinois	<i>Essexella asherae</i>	Francis Creek Shale, mid-Pennsylvanian	Foster 1979

Note: Specimens and locality information are stored in the Condon Collection of the University of Oregon.

tion than the woody tissue of the plant. Some logs and other plant parts such as fleshy pinules (Walton 1936) are compacted to the extent that the upper surface is deformed downward below the level of the edges of the log: a form of preservation here referred to as a sunken compression. The lunate cross section of such compressions was seen to be convex-down in outcrop and in loose blocks whose orientation could be determined from truncated ripple marks (as in specimen UO34293).

Fossil jellyfish, *E. asherae*, also are presumed to be examples of sunken compressions, although the siderite nodules were recovered from coal dumps and their original orientation in enclosing strata is not known. Sunken compressions yield a convex impression of the upper surface and a concave impression of the lower surface.

Modes of preservation of Ediacaran fossils have been described using an alternative nonpaleobotanical terminology by Wade

TABLE 2. Measurements of compressed thickness and depth of fossil Vendobionta, logs, and jellyfish.

Taxon	Specimen	Locality	Width (mm)					Depth (mm)					Thickness (mm)				
			n	Avg.	σ_n	Min.	Max.	n	Avg.	σ_n	Min.	Max.	n	Avg.	σ_n	Min.	Max.
<i>Dickinsonia</i>	F34285	2808	20	140	24.9	88.7	161	50	2.4	0.96	0.7	4.0	—	—	—	—	—
<i>Tribrachidium</i>	F34286	2808	26	31.9	5.8	20.5	37.6	50	1.8	0.69	0.4	3.3	—	—	—	—	—
<i>Dickinsonia</i>	F34287	2809	12	36.7	4.5	30.2	44.9	38	1.4	0.56	0.7	2.6	—	—	—	—	—
<i>Medusinites</i>	F34288	2810	28	25.9	4.5	14.8	31.4	37	0.8	0.58	0.3	1.8	—	—	—	—	—
<i>Haplostigma</i>	F34289	2811	11	35.1	1.0	33.2	36.7	50	1.2	0.31	0.3	1.7	50	1.6	0.2	1.1	1.9
<i>Stigmaria</i>	F34290	2812	5	23.9	0.7	23.1	24.8	—	—	—	—	—	25	0.8	0.2	0.5	1.3
<i>Syringodendron</i>	F34291	2813	10	20.6	0.5	19.5	21.2	—	—	—	—	—	30	1.1	0.3	0.5	1.6
<i>Syringodendron</i>	F34292	2813	16	25.1	0.4	24.0	25.4	—	—	—	—	—	30	0.9	0.2	0.4	1.2
<i>Syringodendron</i>	F34293	2813	16	101	1.4	100	106	60	5.4	1.0	1.7	6.4	60	3.2	0.6	1.6	4.1
<i>Syringodendron</i>	F34294	2813	1	109	—	—	—	—	—	—	—	—	35	1.1	0.5	0.6	2.5
<i>Syringodendron</i>	F34295	2814	11	23.8	0.4	23.3	24.6	—	—	—	—	—	50	1.7	0.2	1.2	2.1
<i>Gymnospermae</i>	F34297	2814	6	14.4	1.8	12.9	18.3	—	—	—	—	—	25	1.7	0.8	0.5	3.1
<i>Syringodendron</i>	F34298	2815	11	14.8	0.5	13.8	15.4	—	—	—	—	—	30	1.3	0.2	0.7	1.7
<i>Knorria</i>	F34299	2815	16	13.9	0.4	13.2	15.1	—	—	—	—	—	30	1.3	0.1	1.1	1.5
<i>Syringodendron</i>	F34300	2815	11	7.3	0.1	7.1	7.5	—	—	—	—	—	15	0.8	0.2	0.5	1.0
<i>Gymnospermae</i>	F34301	2815	16	6.4	0.6	5.6	7.1	—	—	—	—	—	18	0.8	0.1	0.5	1.1
<i>Syringodendron</i>	F34302	2816	11	19.3	0.7	18.5	20.9	—	—	—	—	—	34	1.3	1.2	0.4	1.7
<i>Calamites</i>	F34303	2816	16	12.3	0.4	11.2	12.7	—	—	—	—	—	15	0.6	0.1	0.4	0.8
<i>Knorria</i>	F34304	2816	16	11.2	0.5	10.5	12.0	—	—	—	—	—	25	1.1	0.5	0.3	1.9
<i>Syringodendron</i>	F34305	2816	21	17.2	0.7	16.0	18.6	—	—	—	—	—	25	0.5	0.1	0.3	0.8
<i>Knorria</i>	F34306	2816	11	14.3	0.5	13.3	15.0	—	—	—	—	—	25	0.8	0.1	0.5	0.9
<i>Syringodendron</i>	F34307	2817	11	77.4	1.1	74.5	78.6	—	—	—	—	—	50	1.4	0.6	0.7	3.6
<i>Gymnospermae</i>	F34308	2817	11	23.4	0.4	22.9	24.1	—	—	—	—	—	25	1.9	0.5	1.1	2.8
<i>Syringodendron</i>	F34309	2817	11	24.9	0.2	24.7	25.3	—	—	—	—	—	25	0.9	0.2	0.6	1.7
<i>Knorria</i>	F34310	2817	11	16.1	0.2	15.8	16.6	—	—	—	—	—	25	0.8	0.1	0.6	1.1
<i>Syringodendron</i>	F34311	2818	16	18.9	0.7	17.5	19.8	—	—	—	—	—	20	0.8	0.1	0.6	1.1
<i>Artisia</i>	F34312	2818	11	20.9	0.5	20.1	21.8	—	—	—	—	—	30	0.9	0.3	0.6	1.7
<i>Stigmaria</i>	F34313	2818	26	23.2	1.0	21.7	24.8	—	—	—	—	—	25	1.3	0.4	0.9	2.2
<i>Essexella</i>	F34314	2819	32	41.2	5.2	31.3	46.8	50	1.3	0.7	0.1	2.3	50	0.8	0.1	0.6	1.0
<i>Essexella</i>	F34315	2819	26	25.5	2.2	22.8	29.8	50	1.0	0.5	0.1	1.9	35	0.7	0.1	0.5	0.9
<i>Essexella</i>	F34316	2819	26	19.5	1.5	17.2	22.5	50	0.9	0.3	0.3	1.5	35	0.7	0.1	0.4	0.9
<i>Essexella</i>	F34317	2819	26	20.5	1.5	17.2	21.9	49	1.6	0.3	0.3	2.2	30	0.7	0.1	0.4	0.8

(1968) and by Runnegar and Fedonkin (1992), but are here reconsidered in paleobotanical terms. The measured specimens of *Dickinsonia* and *Tribrachidium* are negative impressions (hollows) in the rock collected in place from the underside of outcrop ledges (fig. 2). The measured specimen of *Medusinites* is also a negative impression, but was found loose in scree so that its original orientation is not known. According to Wade (1968), Vendobionta like *Medusinites* are most commonly preserved as sunken compressions (fig. 2B), whereas *Dickinsonia* is mostly preserved as raised compressions (fig. 2D). Raised compressions have an upper concave impression very different in appearance from the relatively featureless lower convex impression. This implies a rigid tentlike structure for *Dickinsonia*, and has been controversial be-

cause it is unique among non-skeletonized organisms to Vendobionta (Runnegar and Fedonkin, 1992). An alternative interpretation for preservation of *Dickinsonia* is simple compression (fig. 2). Other styles of preservation known from fossil plants in quartz sandstones, including molds and casts, also are known in Vendobionta (Pflug 1973; Glaesner 1984), but are not considered here.

Similarity of Matrix.—The fossil logs studied were all selected for matrix as similar as possible in grain size and composition to that of Vendobionta. These aspects of the matrix were quantified by point counting the proportion of grain size classes and the proportion of different minerals in the fossiliferous sandstones (fig. 3). All are dominantly sandy and quartz-rich, with the South African *Haplostigma* preserved in matrix most like that of Ven-

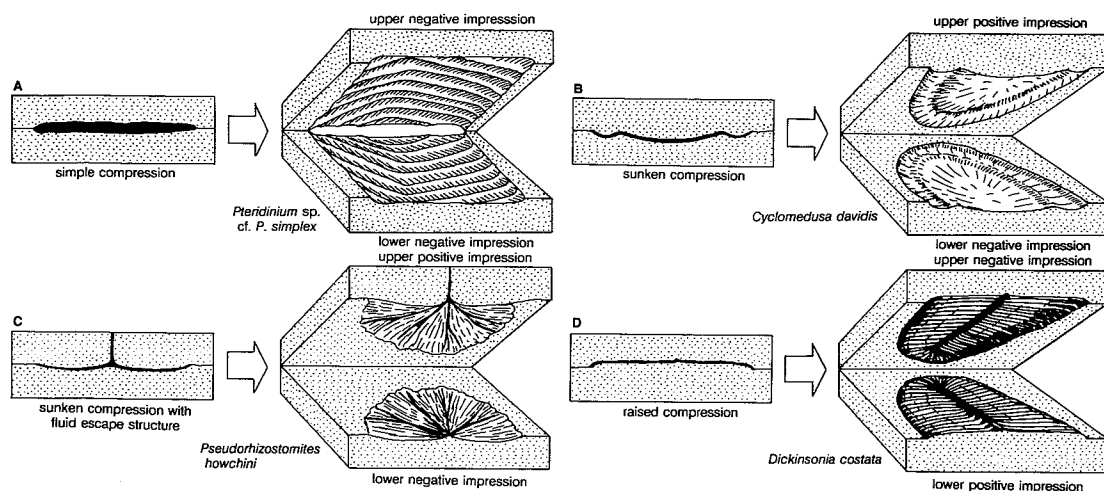


FIGURE 2. Preservational styles of Ediacaran fossils (adapted from Wade, 1968). A, Simple compression. B, Sunken compression. C, Sunken compression with fluid escape structure. D, Raised compression. Raised compressions, and particularly their lower positive impressions, have not been convincingly demonstrated.

dobionts. The Pennsylvanian logs were preserved in slightly more lithic sandstones. The fossil logs and Vendobionts can be considered similar in matrix. On the other hand, the fossil jellyfishes studied were in siderite nodules of silt to clay grain size.

Similarity of Burial Environment.—The horizon yielding Ediacaran fossils in Brachina Gorge, South Australia, is buried by 568 m of late Precambrian sandstones (Jenkins et al. 1983), and the overlying Cambrian sequence is 5258 m thick (Daily 1957): a total of about 5.8 km.

Haplostigma stems from the Early Devonian Blinkberg Sandstone of South Africa were buried by some 2570 m of Witteberg Group, 750 m of Dwyka Group, 1740 m of Ecca Group and 605 m of Abrahamskraal and Teekloof formations (Anderson 1977; Kent 1980): a total of about 5.7 km.

Fossil logs from the New River Formation of West Virginia are overlain by about 1306 m of additional Pennsylvanian strata and 137 m of largely Permian Dunkard Group (Cardwell et al. 1986): a total of only about 1.4 km. Additional loading by 3000 m of subsequently eroded Permian rocks has been postulated to satisfy structural, sedimentological, coal-metamorphic, and moisture and fission track data (Beaumont et al. 1987), giving a total burial of the fossil logs of about 4.4 km. Depth of burial of the Pennsylvanian jellyfish stud-

ied is less well constrained, but probably comparable to that of Pennsylvanian logs from West Virginia.

Depth of burial also was evaluated by estimating the number of contacting grains around each grain, which averages 3 at 1000 m but increases to 5 by 2500 m as grains are forced together by compaction (Taylor 1950). My point counts of the matrices of Vendobiont fossils and Devonian and Pennsylvanian logs show that most of the quartz grains have seven or more contacting grains (fig. 3), values compatible with geological estimates of burial by 5–6 km of overburden as given above.

From these data the Devonian lycopod logs are most comparable in burial depth with the Ediacaran fossils, and the Pennsylvanian logs were not buried quite so deeply.

Comparative Compaction Resistance of Vendobionta.—The measured widths and thicknesses of Paleozoic logs in orthoquartzites demonstrate that they have been flattened during burial to one eighth to one fiftieth of their former thickness (table 2, fig. 4). Although a population of widths and thicknesses was measured and averages and standard deviations calculated to demonstrate variation, the maximum values most likely reflect compaction according to Walton's (1936) compaction theory. This is because the maximum thickness of the compression rep-

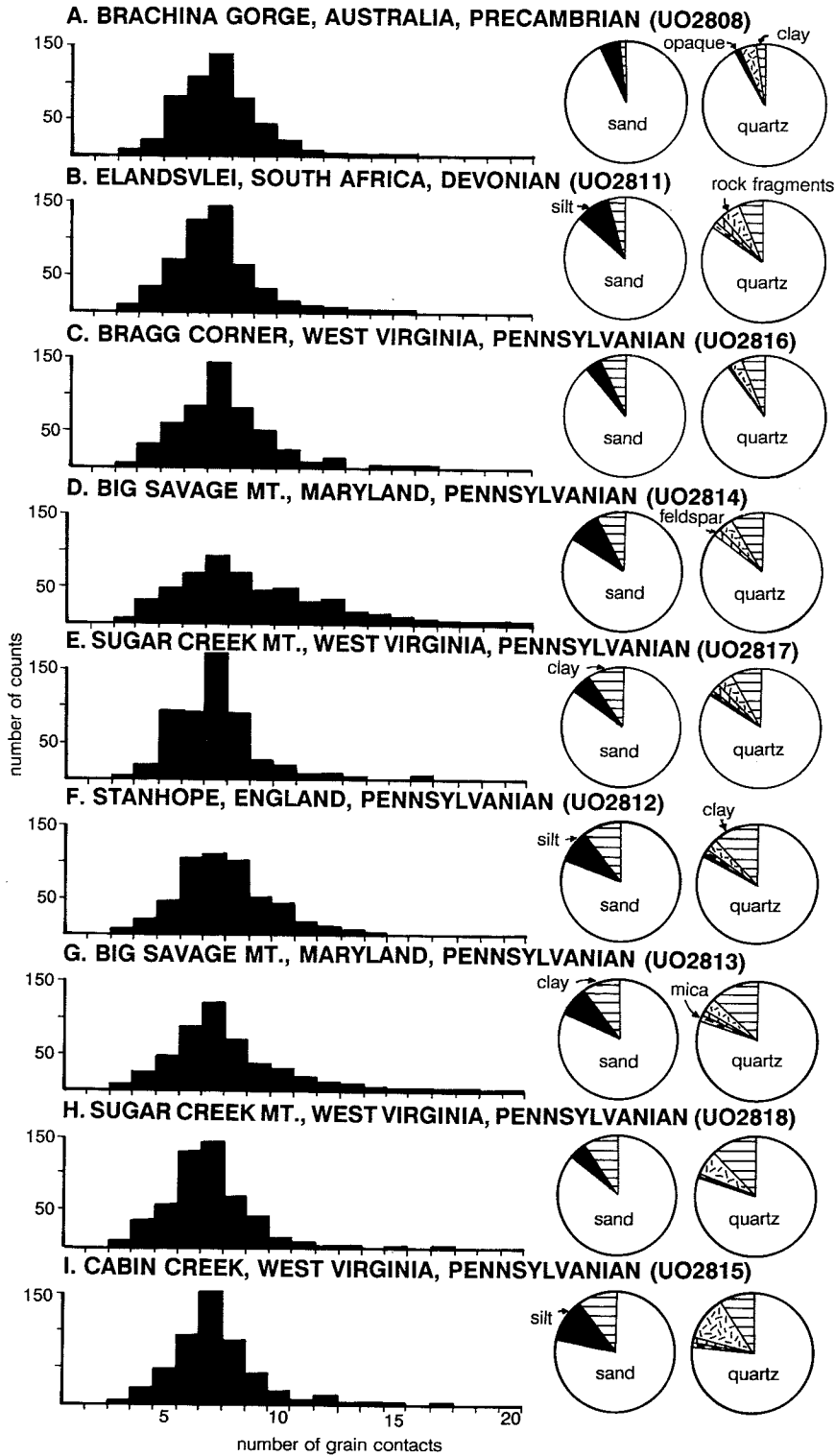


FIGURE 3. Petrographic data on matrices of Precambrian Vendozoa and Pennsylvanian fossil logs, illustrating comparable burial compaction (grain contacts per grain), grain size, and mineral composition (pie diagrams).

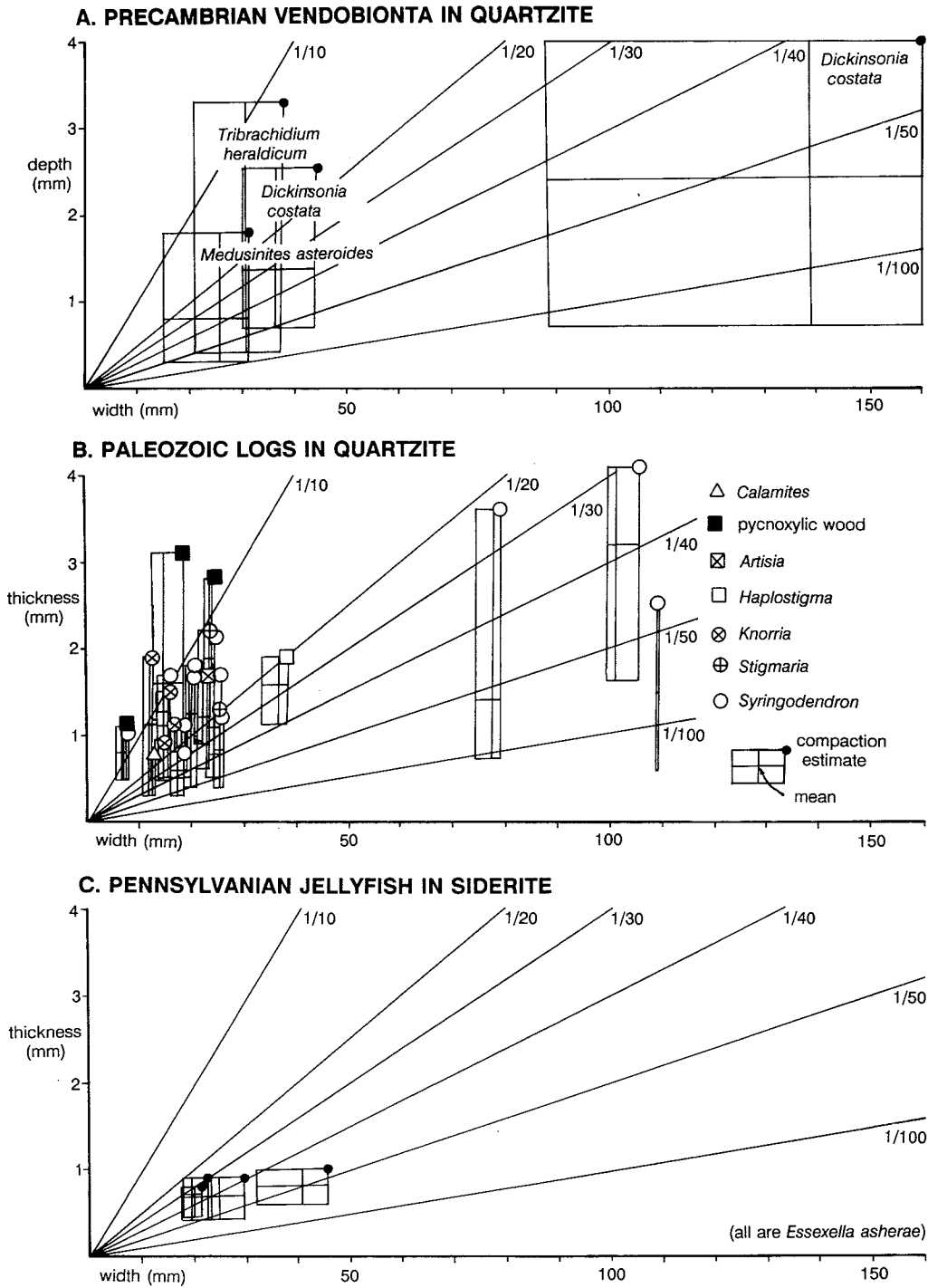


FIGURE 4. Relative compaction of Pennsylvanian logs and Vendobionts in quartzite and of jellyfish in siderite nodules. Means and ranges are shown, but maximal values indicated by symbols are best used for comparison.

resents that part of the log where the full diameter was perpendicular to bedding. Thus, maximum values were used here, and are indicated by symbols in figure 4, although means and ranges give comparable results.

Woody logs of gymnosperms were consistently the least compacted, compared with lycopsid axes, which showed extreme compaction. Lycopsid trunks are known to have had a higher proportion of soft parenchymatous tissue to hard xylem, or are manoxylic, compared with gymnosperms, which are pycnoxylic (Taylor and Taylor 1993).

Fossil jellyfishes (*E. asherae*) were found to be even more flattened than the fossil logs (fig. 4C). This is surprising considering their preservation in siderite nodules within which authigenic cementation and permineralization have been documented to preserve little-compacted woody stems (Schopf 1979). The sunken compressions of jellyfish have a much greater relief than the thickness of the jellyfish, whereas the sunken compressions of logs tend to have relief comparable with their compressed thickness (table 2), suggesting that jellyfish are much weaker than logs.

Considered from this perspective, Ediacaran fossils make a much better impression than do jellyfish in siderite or many lycopod logs in sandstone, but not as deep an impression as that of pycnoxylic gymnosperm wood. Unlike the fossil logs and jellyfish in which thicknesses and sometimes also depths could be measured, only depths could be measured on the available Ediacaran fossils (fig. 4A). If all were simple compressions (fig. 2A), then the compacted thickness of the fossils would be twice the measured depths and Vendobionts would have been tough and thick like conifer logs, rather than like lycopsid logs. Even if the compression of *Medusinites* were half as thick as the preserved hollow, its compaction would still compare with that of lycopsid logs. Similarly, an interpretation of *Dickinsonia* as raised compressions also yields compaction similar to that of lycopsid logs. This is much more compaction resistant than fossil jellyfish, suggesting that Vendobionta were tougher, thicker, or both. From data presented (fig. 4), the following scale of relative

compaction can be proposed: jellyfish (most compacted), sigillarian wood, lepidodendroid wood—which is roughly equal to Vendobionta—and gymnosperm wood (least compacted).

Interpretation of Vendobiont Toughness.—This study shows that Vendobionta were thicker, tougher, or differently organized, than the kinds of creatures with which they have been compared. Their observed compactional thickness is comparable with lepidodendroid logs, but they could only have had comparable strength to resist compaction if they were also as thick as they were wide, as were the logs. If Vendobionta were in life as thin as they are as fossils, then they must have been made of much stronger stuff than logs. Fossil shell and bone are known to maintain their thickness and curvature under 5 km or so of lithostatic compaction in quartz sandstones (Mackay 1964; Ritchie 1973; Robison and Hintze 1972). Such thickness and toughness constraints rule out interpretation of Vendobionta as soft-bodied animals such as jellyfish or worms, or as extinct creatures with a mattresslike or "pneu-structure" (Seilacher 1989).

Interpretation of Vendobionta as lichens offers an escape from these constraints because the fungal hyphae of lichens are strengthened by structural chitin fibrils (Galun et al. 1976; Herrera 1992). Chitin is a prominent component of trilobite exoskeletons, which can be preserved with considerable relief in deeply-buried quartz sandstone, e.g., ollellids in quartzites of the House Range, Utah (Robison and Hintze 1972). In addition, many lichens are thick and bushy (Hale 1983), and could have made deep impressions by means of mass as well as strength. At least a few Ediacaran fossils are known to have been massive and thick, especially *Rangea* and *Ernettia* from Namibia (Glaessner 1984; Jenkins 1985). Even *Dickinsonia* and *Spriggina*, conventionally interpreted as flat annelids, are seldom preserved with perfect symmetry, but usually curve as if they rolled slightly during burial (Jenkins 1992). Another possibility for raised compressions of *Dickinsonia* is a tentlike structure, as found in some crustose lichens,

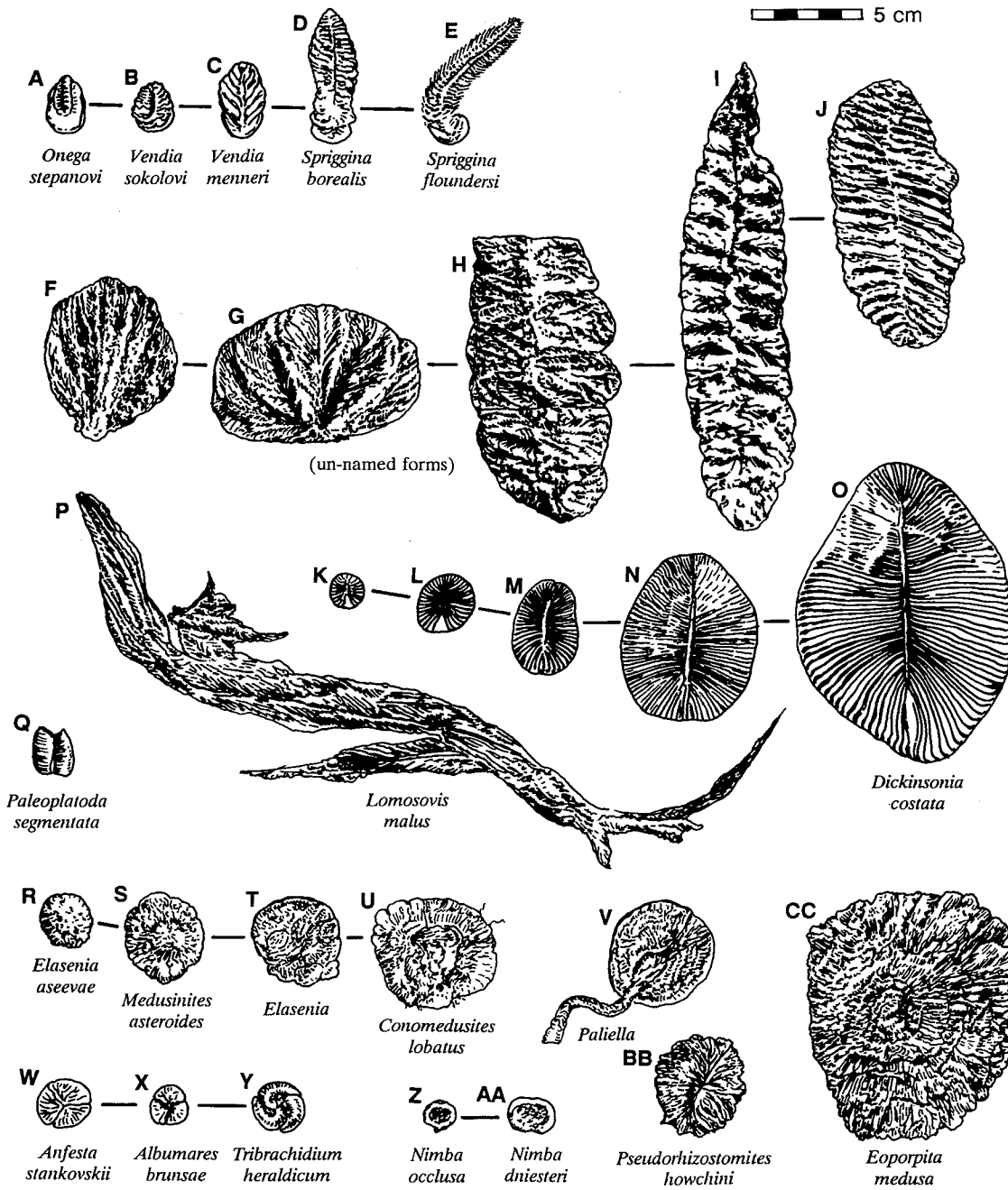


FIGURE 5. Body forms of selected Vendobionta. Redrawn to same scale (upper right) from Anderson and Conway Morris (1982), Sokolov and Iwanowski (1990), and Runnegar and Fedonkin (1992).

where sand is held under the lichen but eroded around it. In this way strength to withstand compaction is gained from sand originally beneath the fossil. The concept of "Psammocorallia" proposed by Seilacher

(1992) similarly involves sediment incorporated within the body, but that model for sessile cnidaria explains molds and casts rather than raised compressions. In conclusion, a lichen model offers a range of strength, thick-

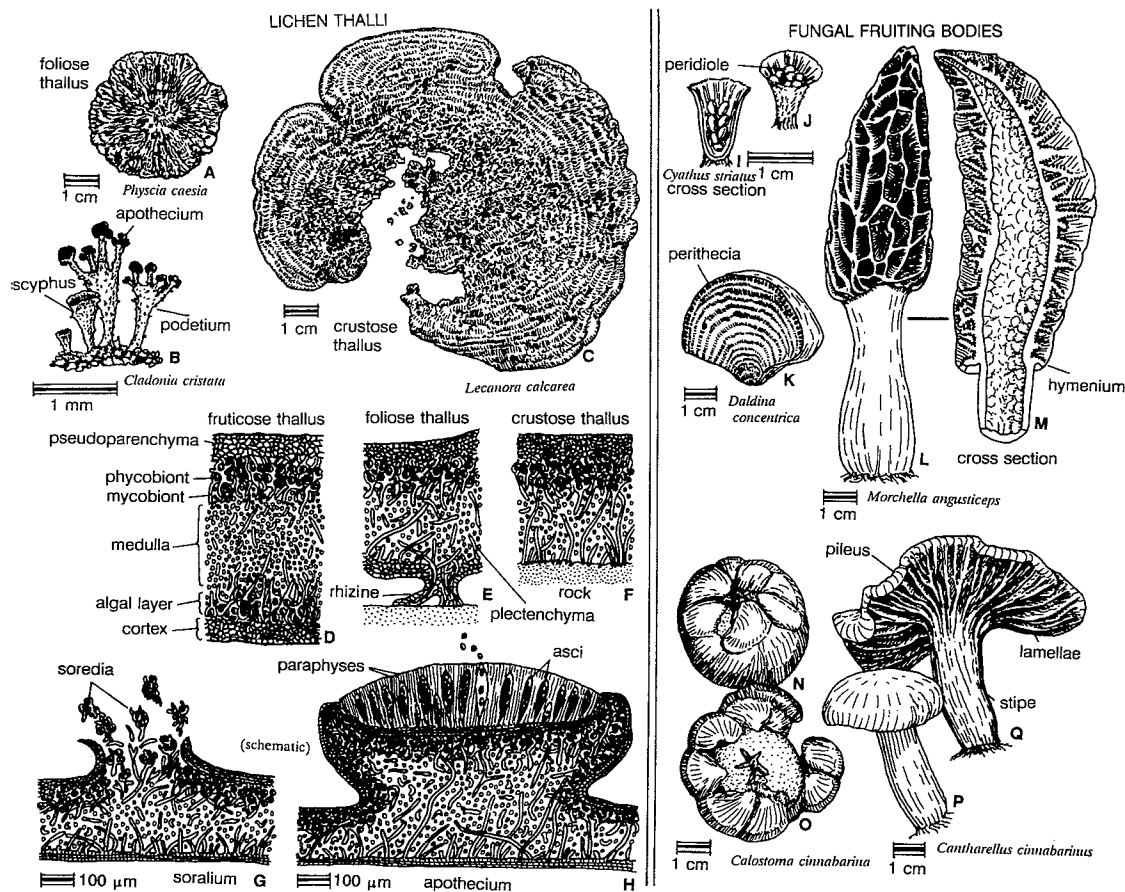


FIGURE 6. Morphological and anatomical features of living fungi and lichens (adapted from Scagel et al. 1965; Phillips 1980; Margulis and Schwartz 1982; Hale 1983; Katsaros 1990).

ness, and structure to explain the puzzling preservation of Vendobionta in the same way as fossil plants.

Reassessment of Other Features of Vendobionts

Taphonomic indications that Vendobionta were as tough or thick as tree trunks is compatible with the idea that they were lichens. Fungi should also be considered as plausible models for Vendobionta, because in many lichens, particularly the basidiolichens, the fungal component (mycobiont) reproduces like an unlichenized fungus (Hale 1983). This new fungal-lichen model for Vendobionta is used in the following paragraphs to reassess traditional interpretations and to suggest further tests of the biological affinities of Vendobionta and other problematic fossils.

Vendobiont Body Plans.—The diversity and degree of organization of Vendobiontan body plans (fig. 5) have been suggested as definitive of animals (Glaessner 1984; Sokolov and Iwanowski 1990). Modern lichens also show an impressive diversity of form ranging from radially or concentrically zoned crusts to clumps, skeins, and lobes of fruticose lichens (fig. 6A–C). Fertile structures of fungi also show considerable variety, including mushrooms, stinkhorns, morels, puff balls, and pixie cups (fig. 6J–Q). As is the case for the Vendobionta, lichens and fungi include both bilateral (frondose) and radial symmetry.

Also found with Vendobionts are a variety of less distinctive bed markings, such as “old-elephant-skin texture,” which has been interpreted as a cyanobacterial crust that promoted fissility and exposure of the fossils (Fedonkin

TABLE 3. Alternative interpretations of Vendobiontan structures.

Vendobionta	Metazoan body	Fertile fungus	Lichen thallus
<i>Charniodiscus</i> , <i>Spriggina</i> , <i>Parvancorina</i>	holdfast, prostomium, carapace	veil remains, bulbous base	holdfast
<i>Cyclomedusa</i> , <i>Ovatoscutum</i>	umbrella, float	pileus, veil remains	veined and zoned placoid
<i>Charniodiscus</i> , <i>Eoporpita</i>	polyps	morel wrinkles, coral fungus	podetia, pseudopodetia
<i>Charniodiscus</i>	rachis, stalk	stem, pileus	pseudopodetium
<i>Dickinsonia</i>	segments	lamellae	areole, podetia
<i>Dickinsonia</i>	intestine	bracket base	central stipe
<i>Spriggina</i>	parapodia	extruded asci	rhizines, cilia
<i>Tribrachidium</i>	ambulacra	peridiole margins	soralia margins
<i>Tribrachidium</i>	marginal plates	wrinkled cup	effigurate margin
<i>Brachina</i> , <i>Spriggina</i>	tentacles	rhizines	rhizines, cilia

1992; Runnegar and Fedonkin 1992). These indistinct markings could equally be interpreted as fungal hyphal mats, lichen rhizines, or fibrous fruticose lichens similar to living *Usnea subfloridana* (see e.g., Phillips 1980).

The complex form of lichens and fungi is reflected in a complex biological terminology that can be applied to Vendobiontans in the same superficial way as has zoological terminology in the past (table 3). There do not appear to be living fungi or lichens exactly like the Vendobiontans, just as there do not appear to be living animals exactly like them (Runnegar and Fedonkin 1992). This is not the place to pursue the myriad structural and taxonomic reassignments that would follow reinterpretation of Vendobiontans as lichens, fungi, or both. Suffice it to say that morphological comparisons with any living creatures are superficial at best given the poor preservation of most Vendobionta.

Vendobiont Size.—The large size of some Ediacaran fossils has long been a puzzle for interpreting them as multicellular animals. *Dickinsonia* has been found up to 1 m long (Glaessner 1984). This is not large for an animal these days, but Vendobionta are associated with burrows of animals no more than 4 mm in diameter (Fedonkin and Runnegar 1992; Runnegar and Fedonkin 1992) and the earliest convincing animal fossils are also only a few millimeters in size (Bengston 1992). In their large size and other peculiar features, Vendobiontans appear unrelated to the earliest metazoan body and trace fossils (Seilacher 1989, 1992; Runnegar and Fedonkin

1992; see also Glaessner 1984 and Conway Morris 1993 for a contrary view). However, large size is not unusual in sessile photosynthetic organisms such as lichens.

Another distinctive feature of Vendobiontans is their wide range in size. These variations in size and segment number, for example in *Dickinsonia*, have been interpreted as growth series (Runnegar 1982). It is not difficult to imagine similar growth in length of unnamed leaflike forms from Newfoundland (fig. 5F–J), in diameter of circular forms such as *Cyclomedusa* (fig. 5R–U), or increased definition of the leaflike blades of *Tribrachidium* (fig. 5W–Y). Seilacher (1989) has suggested that Vendobionta show three different modes of growth: bipolar, unipolar, and radial. These modes of growth are known among animals, particularly colonial animals. Such indeterminate growth is also widespread in plants, lichens, and fungi. Population studies of the size range of Vendobiontans should incorporate tests of lichen as well as other affinities.

Vendobiont Anatomy.—Most Vendobiont fossils are poorly preserved impressions in sandstones, lacking anatomical details that could flesh out their biological interpretation. There are, however, possible structurally preserved Vendobiontans from the late Precambrian, Nama Group of Namibia (fig. 7), described in some detail by Pflug (1973). There is no doubt that many of these fossils are Vendobionta, but the preservation of internal structures has not been widely accepted.

Glaessner (1984) dismissed Pflug's micro-

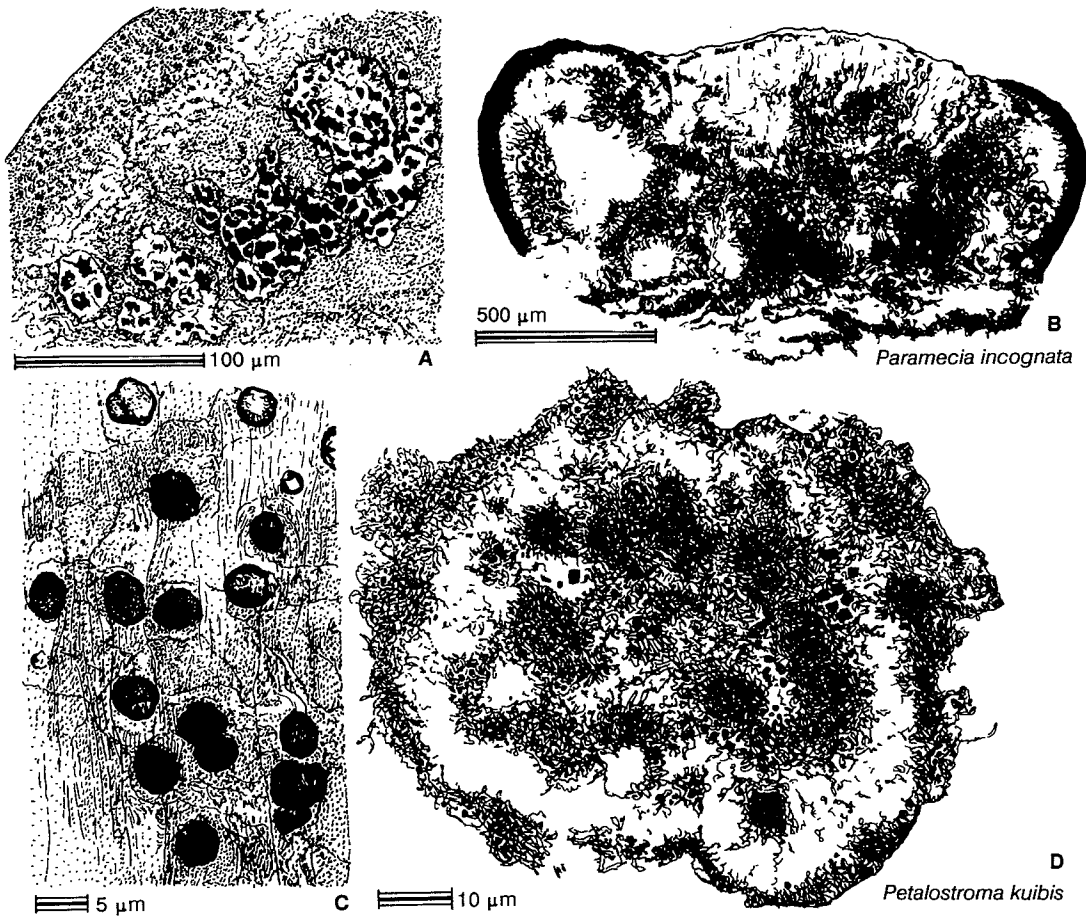


FIGURE 7. Microstructures of late Precambrian fossils from China (A, B, *Paramecia incognata*) and Namibia (C, D, *Petalostroma kuibis*) interpreted here as lichens: A, detail of pseudoparenchymatous cortex and dark aggregates of phycobionts; B, apothecium in crustose thallus; C, dark phycobionts in plectenchymatous cortex; D, cross-section of podetium with soredia and some pyrite cubes (drawn from light photomicrographs of Pflug 1973; Zhang and Yuan 1992).

scopic structures as related to Tertiary silcretization of these outcrops. Tertiary silcretites are thought to form either in desert soils or during deep burial (Summerfield 1983; Milnes and Thiry 1992). Either way it is difficult to see how geologically younger biological structures could be introduced. Structurally preserved Cretaceous and Tertiary fossil plants in silcretites appear to be the same age and reflect similar paleoclimates as the enclosing sediments and paleosols (Lange 1978; Peters and Christophel 1978). Furthermore, Pflug (1973) described a chalcedony matrix of Vendobionta that postdates organic matter, as well as partly pyritized cell lumina and surface efflorescences of tiny crystals. These

crystals were identified as carbonate, but could be oxalate crystals, which are common on lichens (Hale 1983). I am unaware of any case of pyrite, carbonate, or oxalate in Tertiary silcretites, whereas such minerals are not unusual in permineralized plants and peats formed in reducing alkaline bogs (Knoll 1985). Identification of the fossils as organic by differential thermal analysis, as well as from appearance under plain and fluorescent light (Pflug 1973) is also convincing.

One of the reasons for rejection of Pflug's microstructure as preserved Vendobiont anatomy is that they were difficult to understand (Runnegar 1992). By the lichen hypothesis, it is possible to make sense of the

TABLE 4. Lichen interpretation of Vendobiont microstructures.

Terms of Pflug 1973	Lichenological terms
Gewebe Springbrunnen-Verzweigung (tissue multiaxial ramification)	Periclinal and fastigiate prosoplectenchyma and pseudoparenchyma
Endogewebe (endotissue)	Plectenchymatous medulla
Ectogewebe (ectotissue)	Pseudoparenchymatous cortex
Endozellen (endocells)	Phycobiont cell (alga)
Filament (filament)	Mycobiont cell (fungus)
Tubae (tubes)	Podetia
Globulus (globule)	Soredium
Cupulus (cupule)	Soredium
Cupulae-Aggregat (cupule aggregate)	Soralium
Karbonat-Kristalle (carbonate crystal)	Pruina (of calcium oxalate?)
Basis-Lamelle (basal lamella)	Crustose thallus
Petalon (petal)	Foliose thallus
Trichter (funnels)	Scyphi
Gelenke (articulation)	Lobule base
Kriechende Sprosse (creeping shoot)	Stipitate apothecium? or cephalodium? (not known to contain ascospores or phycobionts, respectively)

meshwork of tubular cells as a fungal plectenchyma and the darkly pigmented spherical cells as a cyanobacterial or algal symbiont (fig. 7C). An alternative explanation could be as a saprophytic fungus invading animal or plant tissues, but no trace of host tissues are preserved, unlike well documented cases of fungally degraded plant fossils (Stubblefield and Taylor 1988). The terminology of lichenology works as well as Pflug's invented terminology in characterizing the various microstructures seen (table 4). From this perspective, the structurally preserved Nama fossils are most similar to fruticose lichens. The models developed by Pflug (1973) for the organization of podetia into dense bundles and frondlike organs offer a plausible biological model for a variety of Vendobionta.

Other late Precambrian fossils with lichen-like microstructure include phosphatized remains referred to *Paramecia incognata* from Ghizhou Province, China (fig. 7A, B; Zhang and Yuan 1992) and organic impressions of *Vendotaenia antiqua* from the Russian Platform (Sokolov and Iwankowski 1990). Both show

a microscopic tubular structure with interspersed darkly pigmented cells that is typical of lichens. Some of the *Vendotaenia* are covered in dark ellipsoidal stalked sporangia of actinobacteria identified as a fossil decomposer, *Primoflagella speciosa* (Sokolov and Iwanowski 1990). These could be modern contaminants, although they appear carbonized to the same extent as their substrate. Actinobacterial affinities for the Chinese and Namibian fossils are suggested by their cell size (1–5 μm), which is small for fungi (1–170 μm , usually 5–10 μm : Hickman 1965). These fossils could have been lichens of actinobacteria with cyanobacterial phycobionts: a lichen combination currently rare (Hawksworth 1988a). Detailed study of these microstructures should be a high priority for future research on Vendobionta. The main point here is that they make biological sense as lichens but not as animals.

Vendobiont Habitats.—Apparent obstacles to interpreting Vendobionta as lichens are the widespread assumptions that lichens live only on land and that Vendobionts lived only in the sea. Neither assumption is warranted. There is a great diversity of fungi and lichens in the sea, lakes, and streams, as well as on land (Ramkaer 1977; Kohlmeyer and Kohlmeyer 1979; Hale 1983).

Although many Vendobionta have been found within probable marine strata (Sokolov and Iwanowski 1990; Runnegar and Fedonkin 1992), there are occurrences that could be interpreted as non-marine. A classical explanation for forms found in tidal flat facies such as those of the Australian Flinders Ranges is that they were thrown up from the sea by storms (Jenkins et al. 1983; Glaessner 1984). They could equally have been washed down from the land, or more likely, lived where they are found. The idea that they lived where they are found is supported especially by the common recognition of growth series in Vendobionts (fig. 5). In my own observations of jellyfish swarms and mass strandings on the coast of New South Wales, Australia, there was impressive uniformity in the size of fully grown individuals (see also Bruton 1991), unlike my observations of Vendobionta.

These general suspicions were confirmed

by my observations in Brachina Gorge, South Australia (fig. 8). Here Vendobiont fossils can be found on thin (8–15 mm) sandy beds within a red mud-cracked shale. Large *Dickinsonia* and other Vendobionts are most common on the soles of quartz-sandstone flags overlying the red shale. Vendobiont fossils become both rarer and smaller up section, and could not be found more than 3 m above the red shale. The fossiliferous sandstone flags have been interpreted as lower intertidal to subtidal deposits of tidal channels or flood-tidal deltas and the red shales and siltstone as deposits of intertidal flats (Jenkins et al. 1983). The red color, mud cracks and local bioturbation of these red shales are all characteristics of paleosols, which in these conspicuously bedded red shales would have been very weakly developed (Retallack 1988, 1990). Vendobionts were preserved in the red oxidized shale only when buried by sand, as would be expected from general models for preservation of organic fossils (Retallack 1984). These intermittently exposed muds could well have been their habitat, with abundance and diversity declining markedly offshore into fully marine sands. Vendobionta are also found in association with red beds in Newfoundland, Namibia, and Podolia (Glaessner 1984; Sokolov and Iwanowski 1990). Reexamination of sediments and fossil occurrences in all these places is needed.

A difficulty for the lichen or any photosynthetic interpretation of Vendobionta is their supposed occurrence in deep-water deposits well beyond the photic zone, in Newfoundland (Jenkins 1992), northwest Canada (Narbonne and Aitken 1990) and North Carolina (Gibson et al. 1984). One could make a parallel argument to that of McMenamin (1986) that the phycobiont was a chemosynthetic microbe, but that would not be a lichen as commonly understood, and is a life form yet to be discovered, as far as I am aware. Seilacher (1992) has instead addressed this issue by questioning the evidence for deep water. He argues that the beds of Newfoundland interpreted as turbidites are not conclusive evidence of depth. Benus (1988) notes features of the Newfoundland beds atypical of turbidites: sharp tops to the sandy basal

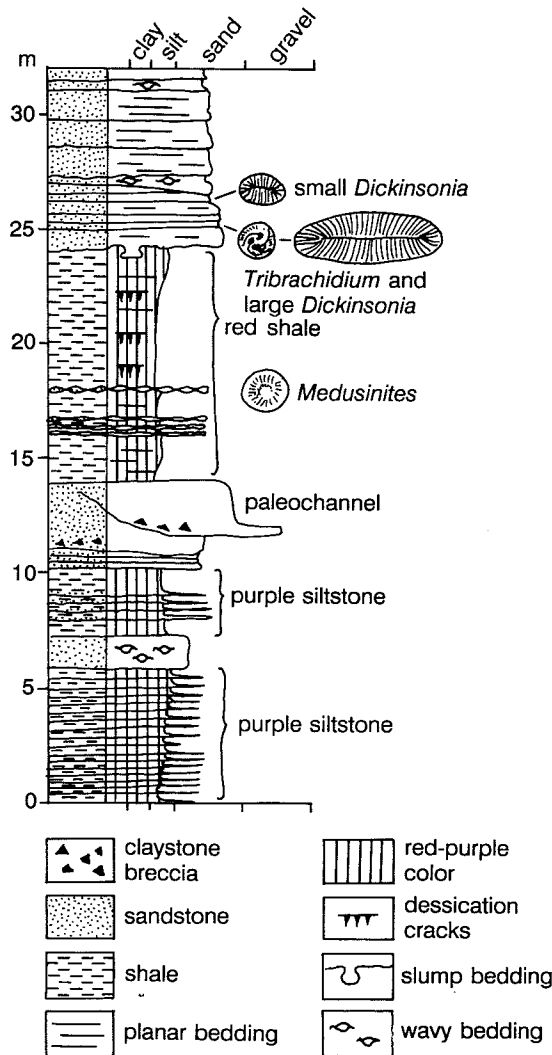


FIGURE 8. Stratigraphic section of the Ediacara Member of the Rawnsley Quartzite on the south side of Brachina Gorge, South Australia (from Jenkins et al. 1983, augmented by personal observations).

part of the beds, rarity of sole markings, and lack of bundling (thickening and coarsening upwards sequences of beds that reflect migration of submarine fan lobes). Association of northwest Canadian Vendobionta with meandrine trace fossils now typical of deep water also loses force considering documentation of such traces in shallow water deposits of Cambrian age (Crimes and Anderson 1985). Also troubling is the calcareous composition of the northwest Canadian "turbidites," indicating deposition above carbonate compen-

sation depth, and the maroon to purple color of the Newfoundland "turbidites" indicating well oxygenated waters. In addition it is uncertain whether the Canadian and Carolinian fossils were in place or redeposited, although Jenkins (1992) makes a case that the Newfoundland fossils were in place of growth. Here is further cause to reconsider the taphonomy and sedimentology of Vendobiont localities.

Another peculiarity of the geological occurrence of Vendobionta is that particular taxa appear to be found only in a limited array of rock types. This is particularly striking in Namibia where calcareous sandstone and shale contain *Petalostroma*, and are interbedded with shales containing *Ernettia* and arkosic sandstones containing *Pteridinium* and *Rangaea* (Pflug 1973). This is the kind of distribution one would expect from sessile organisms, and such substrate specificity is characteristic of lichens (Hale 1983). It is not a distribution expected from stranding of swimming creatures.

The idea of Vendobionta living in place and on land raises new problems, but these are not insurmountable when one considers the hardiness of living lichens. Quartz sand would have been a very low fertility substrate for fungi, but is commonly now colonized by oligotrophic lichens (Smith 1921; Hale 1983). Desiccation and high fluxes of ultraviolet light could also have been limiting, but desert and montane lichens are adapted to such difficult conditions. In the driest of modern deserts in coastal Peru and Namibia, lichens locally cover 40%–60% of the soil surface with a dry weight of up to 267 g/m² (Walter 1985). Both deserts support "window lichens," whose thallus is buried in the soil beneath diaphanous grains so that only the discus-shaped and sand-sized apothecia emerge, and "rolling lichens" which are dispersed by wind like tumbleweeds (Rauh 1985; Walter 1985). These modern models offer new ways of reassessing Vendobiont fossils that are near spherical or preserved as three-dimensional molds and casts (discussed by Horodyski 1991; Runnegar and Fedonkin 1992; Seilacher 1992). Lichens are among the hardiest of living organisms

and grow in environments where little else survives.

Other Possible Fossil Lichens.—There has not been any question about the authenticity of fossil fungi among Silurian palynomorphs or in the Devonian Rhynie Chert (Sherwood-Pike and Gray 1985; Stubblefield and Taylor 1988) or of lichens on Eocene leaves (Sherwood-Pike 1985) or in Oligocene Baltic amber (Smith 1921), but published claims of Precambrian fungi and Paleozoic lichens have all been disputed as contaminants, artifacts of preparation, or abiogenic structures (Smith 1921; Mendelson and Schopf 1992).

This commendable skepticism has not prevented a few of these records from finding some degree of acceptance via inclusion in paleobotanical textbooks (Stewart 1983; Taylor and Taylor, 1993) and paleoenvironmental reconstructions (Hartmann and Miller 1991). These include an ellipsoidal structure containing small spherical bodies similar to the ascus and spores of ascomycete fungi from the 770 Ma Skillogalee Dolomite of South Australia (Schopf and Barghoorn 1969). This single specimen could be interpreted as unusually preserved cyanobacteria. Nevertheless, there is another fossil from the Skillogalee Dolomite (Schopf 1992: fig. 39A₁–A₃) showing filaments that swell and curl before septae like the croziers of ascogenous hyphae of Ascomycetes.

Also in the textbooks is *Witwatermomyces conidiophorus*, a possible fungal mycelium, and *Thucomyces lichenoides* (fig. 9), a possible fruticose lichen in the 2.4 Ga Carbon Leader Reef of the Witwatersrand Supergroup of South Africa (Hallbauer and van Warmelo 1974; Hallbauer et al. 1977). As indicated in a sympathetic discussion of these fossils by Barghoorn (1981), a photosynthetic interpretation is supported by the isotopically light carbon of these fossils, their pentose/hexose ratio of 1, presence of chlorophyll derivatives such as pristane and phytane, and their fluvial depositional environment. There remains the problem that these acid-etched fossils could be artifacts of preparation (Cloud 1976).

Rhysonetron lahti from the 2.2 Ga Huronian Supergroup of Canada (fig. 9I; see also color

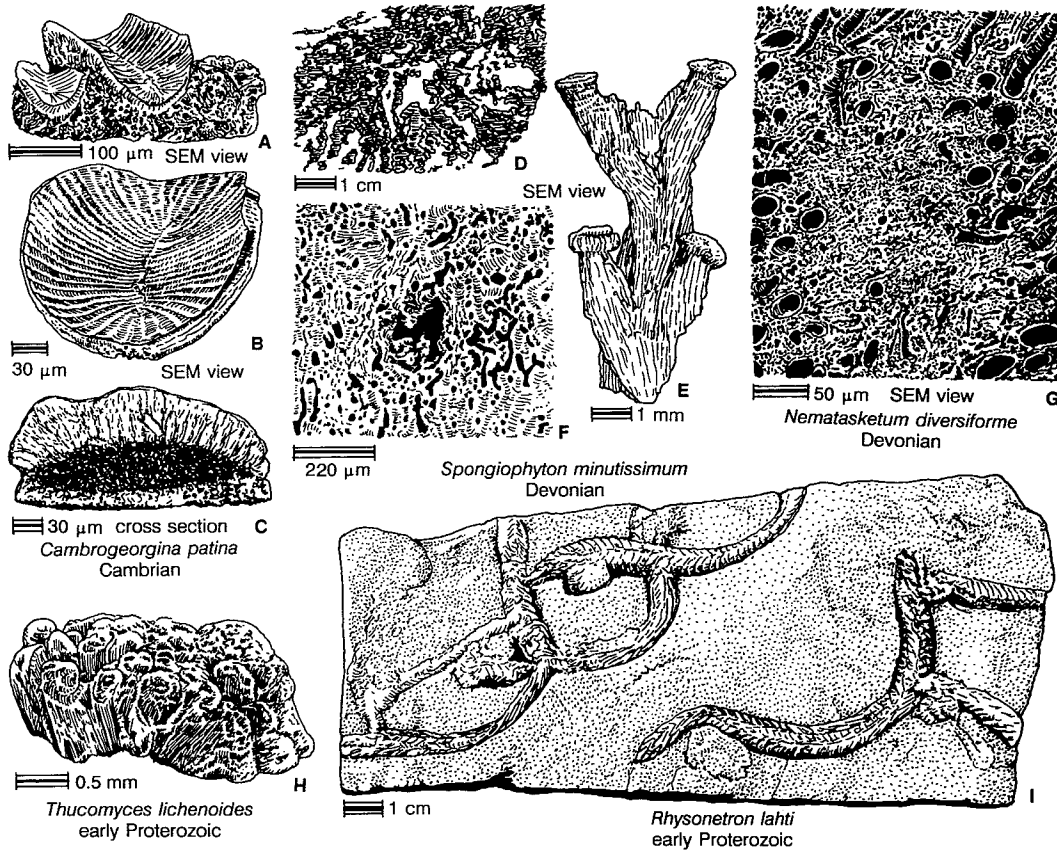


FIGURE 9. Problematic fossils that may be fossil lichens (redrawn from Hallbauer et al. 1977; Burgess and Edwards 1988; Eldredge 1991; Gensel et al. 1991; Müller and Hinz 1992).

photo of Eldredge, 1991: pl. 35) is problematic largely because it is preserved on slabs of quartz sandstone associated with red beds, very like late Precambrian Vendobionta. Hofmann (1971, 1992) has interpreted them as mud-cracks, but it is difficult to see how this explains apparent overlapping specimens, their lateral lobation oriented in opposed directions in some specimens, and the appearance that they are molds of hollow structures (Frarey and McLaren 1963; Hofmann 1967). They could alternatively be viewed as fruticose lichens with squamules or isidia.

Runnegar and Fedonkin (1992) have reviewed the variety of fossils similar to Vendobionta in Paleozoic rocks. To these may be added *Cambrogeorgina* (fig. 9A-C), a *Dickinsonia*-like fossil preserved on hardgrounds in Middle Cambrian phosphorites of Queensland (Müller and Hinz 1992). These and sev-

eral other similar fossils show internal structures ranging from plectenchymatous to pseudoparenchymatous and palisade-like tissues, and are generally reminiscent of the apothecia of lichens. Other fossils from these same phosphorites show cortical-medullary tissue differentiation, monopodial branching, and external striation (Fleming and Rigby 1972). These were identified as possible plants, but are also similar to fruticose lichens.

Nematophytes such as *Prototaxites*, *Nematothallus*, and *Nematasketum* are lichen-like in their internal structure of tubules, often of two markedly different size classes (fig. 9G; Strother 1988; Burgess and Edwards 1988). It is tempting to regard the small tubules as the mycobiont and the large ones as the phycobiont. However, the uniformity of wall ultrastructure suggests that all the tubes are

fungal, and perhaps other structures such as the "medullary spots" (fig. 9G) of Burgess and Edwards (1988) were clusters of phycobionts. Thus, these fossils may be similar to modern lichens known to include two mycobionts and one phycobiont (Hawksworth 1988b). Septal pores in the fine tubules of *Prototaxites* are most like those of basidiomycete fungal hyphae, and less like the pores of red algae (Schmid 1976). Biochemically, *Prototaxites* is more like land plants than algae (Niklas 1976a). Nematophytes have commonly been referred to red or brown algae (Jonker 1979; Schweitzer 1983) or to parataxa of problematica (Strother 1988), and their tubes have been compared with tracheids of land plants (Niklas and Smocovitis 1983). Nematophytes are known from the Siluro-Devonian strata of Britain, United States, Europe and Arabia (Jonker 1979; Schweitzer 1983). Isolated tubular elements similar to those of nematophytes in bulk macerations may extend their stratigraphic range to Ordovician (Gray et al. 1982), and perhaps late Precambrian (McMenamin 1992).

Protosalvinia is yet another enigmatic thaloid plant resistant to compaction and maceration, found in Late Devonian marine shales of Brazil and the eastern United States. Its pristane, phytane, and porphyrins mark it as a photosynthetic organism (Niklas 1976b). The cell walls of its large spores show a coarse fibrillar wall ultrastructure, with an outer layer becoming more electron dense toward the interior of the spore and an inner electron transparent layer (Taylor and Taylor 1987). Such a wall ultrastructure is also found in spores of ascomycete fungi (Beckett et al. 1974, figs. 325, 328; Herrera 1992). Some ascomycete spores, such as those of *Daldinia concentrica* also show a germination slit through the inner wall layer, terminating as a furrow in the outer wall layer (Hawker and Madelin 1976, pl. 3, fig. 15), again as in *Protosalvinia* (Taylor and Taylor 1987). *Protosalvinia* has traditionally been compared with red and brown algae, but the wall ultrastructure of algal spores is very different (Taylor and Taylor 1987). A problem with an ascolichen interpretation of *Protosalvinia* is that lichens usually produce ascospores in linear tetrads or groups of eight

or more, and only rarely in tetrahedral tetrads like those of *Protosalvinia* (Niklas and Phillips 1976).

Spongiophytes are another problematic thallose group of fossils from Devonian non-marine rocks of the Americas, Africa, Poland, and Russia (Gensel et al. 1991). Their compaction-resistant, thick cortex has a spongy texture (fig. 9F) that has been regarded as a product of overmaceration, but is similar to the prosoplectenchymatous cortex of fused filaments and epicortical pores found in lichens such as *Parmelia croceopustulata* (Hale 1983). The external morphology of some spongiophytes is like that of a fruticose lichen with apothecia (fig. 9D,E). As this manuscript was in preparation, notice came to hand that others also now regard *Spongiophyton* as a lichen (Stein et al. 1993). All these problematica deserve reconsideration from this new perspective.

Wider Implications.—Vendobionta have been regarded as a totally extinct evolutionary experiment (Seilacher 1989), or an early phase in the adaptive radiation of metazoa (Glaesner 1984; Sepkoski 1992; Conway Morris 1993). As lichens, however, they may have evolved with fungi during the eukaryote adaptive radiation of 1700–1900 Ma, well before the radiation of coelomate animals some 560–540 Ma (Knoll 1992). Phylogenetic arguments have long been used to argue for the geological antiquity of lichens (Dawson 1970; Cain 1972). Although unrelated to Metazoa, Vendobionta may have played a role sheltering and nurturing the diversification of animals and plants and crowding out preexisting stromatolitic ecosystems.

Vendobionts have also been thought useful in understanding oxygenation of the atmosphere (Runnegar 1982; Kasting 1987), when considered as animals that required a certain level of oxygen and assuming diffusion limited transport of oxygen in thin organisms without apparent circulatory systems. By the lichen model, Vendobionts were producers, not consumers of oxygen, and they were thick, bushy, and firm, rather than thin and soft-bodied. Modern lichen formations are restricted to polar, montane, and desert regions where they attain a biomass of 51–950 g/m²

of dry weight and a productivity of 21–250 g/m²/yr, whereas microbial earths and stromatolitic ecosystems attain a biomass of 19–363 g/m² and productivity of 2–357 g/m²/yr (Retallack 1992b). The biomass of both lichen and microbial ecosystems could have been much greater in less extreme habitats than those they have been forced to occupy by the subsequent evolution of land plants. Nevertheless, the advent of lichens in a world of microbes could have been a significant sink of atmospheric carbon dioxide and source of oxygen. An early Proterozoic (2.5–1.8 Ga) origin of lichens and late Proterozoic (1.3–0.6 Ga) diversification could explain both glaciations and pronounced atmospheric oxygenation at these times, evident from study of glaciogene strata (Harland 1983), of Precambrian paleosols (Retallack 1990; Holland 1992) and of carbon isotopes in sedimentary rocks (Des Marais et al. 1992). These speculations suggest further tests of the lichen model from the timing and diversification of Vendobionta relative to evidence for glaciation and marine stable isotopic shifts.

Conclusions

A case can be made from the morphology, growth, internal structure, habitats, and preservation of Vendobionts and other problematic fossils for a previously unrecognized fossil record of lichens. The compaction-resistance of Vendobionta and the microscopic structure of permineralized specimens are so compelling that it is surprising that lichens have never before been considered as biological models for these fossils. Much better evidence for the lichen hypothesis, or perhaps against it, could have been gathered by the original discoverers and describers of these fossils if they had considered a lichen model. Much better evidence will now be needed to dispel the idea that Vendobionta were soft-bodied animals. Each of these fossils is controversial in its own way, but each deserves more serious attention from the new perspective of paleolichenology.

Interpretation of Vendobionta as lichens offers new vistas for the interpretation of land environments during the late Precambrian. The "Garden of Ediacara" may have been an apt description, not just the metaphor in-

tended by McMenamin (1986). Undulating transparent films of *Dickinsonia* and pulsating bells of *Ediacaria* depicted in reconstructions and dioramas of the "Ediacaran fauna" (see e.g., Glaessner 1984: frontispiece), may have instead been low green bushy tufts between taller blades of *Charniodiscus*. The idea of the late Precambrian as the "Age of Lichens" is at the very least a fascinating new way to reevaluate these fossils, which may not have been so extraordinary after all.

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