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The Microfossil Record of Early Land Plants: Advances in Understanding of Early Terrestrialization, 1970-1984 [and Discussion]

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The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970–1984

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[Plates 1–2]

The plant spore record indicates two major phases of adaptive radiation of land plants before the Devonian; these can be interpreted to correspond to different reproductive, vegetative, and ecophysiological strategies of these early terrestrial plants. The first major adaptive radiation by plants onto land occurred in the mid Ordovician. These early plants are represented by abundant obligate spore tetrads; this assemblage persists from the mid Ordovician to about the mid-late Early Silurian. The fossil spore records indicate that these primary producers were widespread by the end of the Ordovician and the beginning of the Silurian. The close similarity of the fossil tetrads with obligate spore tetrads produced by some hepatics and mosses suggests a non-vascular vegetative grade of organization for plants of this interval. The second major adaptive radiation begins with the replacement of the monotonous spore tetrad assemblage by single trilete spores in the mid-late Early Silurian. These trilete spores find morphological counterpart with spores produced by vascular cryptogams; they suggest a vegetative grade of organization at the vascular level for plants of this interval. The initially smooth-walled trilete spores of this radiation are followed by diverse assemblages of trilete spores with variously ornamented spore coat patterns and varied laesurae morphologies by the mid-Late Silurian.

The interval from the mid Ordovician to the mid-late Early Silurian is hypothesized on the basis of the abundant and widespread spore records to be one of rapid colonization by founder populations with limited genetic diversity and with life-history strategies that included an ecophysiological tolerance to desiccation and a short vegetative life cycle. The interval from the mid-late Early Silurian to the Přídolí largely coincides with the appearance of vascular plant megafossils. It is hypothesized on the basis of the spore assemblages to be one of major establishment of large populations of genetically diverse plants exploiting a broad spectrum of ecological sites that have escaped representation in the meagre megafossil record.

1. Introduction

Almost 15 years ago Harlan Banks organized a symposium concerned with the major evolutionary events of plant life during the past 3000 million years. Chaloner was responsible for reviewing the early evolution of the land plants; his paper on the rise of the first land plants, dealt only with 'vascular land plants'. He placed their major adaptive radiation in a time span of approximately 30 million years from 'the appearance of vascular plants late in the Silurian, to the end of the Lower Devonian' (Chaloner 1970, p. 353). The limited plant microfossil record from the latest Silurian–Early Devonian was of little evolutionary concern, but was seen as a biostratigraphic resource for dating the megafossils, and as a means of confirming trends in vascular plant evolution recognized by megapalaeobotanists (Banks 1968*a*, 1973; Chaloner 1970). With regard to the plant microfossil record Chaloner wrote (1970, pp. 367–368):

> '...the palynological data suggest that the microfossil evidence represents an approximation to the true sequence of evolution of the vascular land plants. There are spores of rather limited diversity pre-dating the earliest known Silurian vascular plants. Diversification of both morphology...and of various types of sculptural elements...seems to parallel the morphological diversity of the vascular plants of the late Silurian and Lower Devonian, which must have been producing the majority of these spores. It is of course conceivable that there was a long pre-Silurian history of vascular plants living on land and producing spores which either lacked an exine, or which had a simple, conservative morphology. If this were the case, it would be hard to understand why the spores 'waited' until the Lower Devonian to undergo their main diversification. There is an economy of hypotheses in concluding that the spores were merely keeping pace in their rate of evolutionary change with the plants which were producing them...'

In 1970, Silurian records of 'proven' vascular megafossils were confined to Britain (North Atlantic Region of the North Silurian Realm) (Banks 1968*b*, 1972; Chaloner 1970) where they were represented by the rhyniophytes that many palaeobotanists have perceived to be 'truly simple plants' and the 'starting point in the comparative morphology of vascular plants' (Banks 1968*b*, p. 73, 1975*a*, *c*) although their assumed prototype position has been questioned (Scott 1920; Berry 1945; Leclercq 1954; Axelrod 1959; Jeffrey 1962; Schopf *et al.* 1966; Krassilov 1981; Gray *et al.* 1982). The 'confirmatory' spore record came from the same biogeographical province and was based largely on records from the British sequence.

In 1970, the only previously recognized pre-Devonian assemblage of vascular plants outside the North Atlantic Region was the Australian (Uralian–Cordilleran Region) *Baragwanathia* flora, assigned to the Ludlovian by Lang & Cookson (1935) but later redated on the basis of associated graptolites (Jaeger 1966, 1967) as Siegenian–Emsian (Early Devonian). By 1970 a tidy picture of the early evolution of vascular plants had emerged which subsequently became accepted textbook dogma. The evolutionary derivation of vascular plants invariably begins with a simple rhyniophyte of *Cooksonia* morphology in a seminal phylogenetic position just below the Silurian–Devonian boundary, and continues across it with the adaptive radiation leading to phyletic diversification occurring in the Lower Devonian (Banks 1977; Chaloner & Sheerin 1979).

Channelling of thinking about early land and vascular plant evolution into a Late Silurian–Early Devonian time frame, which continues unabated (cf. Chaloner & Sheerin 1979; Banks 1980; Edwards 1980), has inhibited inquiry into, and acceptance of, information that does not conform to the model. It parallels traditional dogma about Precambrian life that similarly inhibited inquiry into the palaeobiology of that interval until the 1960s, despite the pioneering efforts of Walcott and others in the late 19th and early 20th centuries (Schopf 1970).

The purpose of this paper is to review some of the newer, and what is seen by some to be more controversial, plant microfossil data. These data can be interpreted to indicate: (i) the availability of widespread primary producers on land at least by the end of the Ordovician or the beginning of the Silurian; (ii) a continental environment inhabited in the mid Ordovician by spore-producing plants whose vegetative morphology can be inferred to be at the hepatic level of organization; (iii) the establishment of vascular plants by at least the mid Llandovery (Early Silurian) paralleling the early hepatic-like plants with which they may or may not have shared a common ancestry; (iv) the availability of well-established, widespread, and ecologically diverse vascular plants by the mid-Late Silurian when the earliest rhyniophytes are found in the North Atlantic Region; and (v) two 'adaptive radiations' documented by the microfossil record that can be interpreted to correspond to different life strategy adjustments of early plants to terrestrial life.

2. The value and limitations of the plant microfossil record

The now controversial pre-Devonian microfossil record was an acceptable source of evolutionary information as long as it appeared only supplementary (additive) to the megafossil data (Chaloner 1970; Banks 1973). Banks wrote in 1969 (published in 1973, p. 231) that 'the sequence of isolated spores from a series of successively younger strata yields an unmistakable evolutionary progression. Hence the spore data seem to be reliable'. In the same paper he accepted spore evidence from North Africa to indicate 'that vascular plants arose even earlier than the first acceptable macrofossils... Late Llandovery as opposed to Přídolí–Downtonian...'. Only when it began to appear that there was a large 'discrepancy between the number of spore genera and the number of genera of megafossils' (Banks 1975*b*, p. 736) such that spore-producing plants must have vastly exceeded available vascular plants, did it seem appropriate to suggest that algae, bryophytes, and vascular plants all produced 'spores with triradiate marks' and to dismiss the spore data as irrelevant to the course of vascular plant evolution.

Because the mega- and microfossil records are seen through a series of differentially distorting mirrors due to a variety of taphonomic variables, they are truly complementary, rather than merely supplementary (or additive). Evolutionary theories should take advantage of that fact, rather than assuming parallelism in the records. The value of the spore record lies in largely decoupling it from the evolutionary expectations raised by the pre-Devonian megafossil record and appraising it on its own merits. I agree with Banks – the sequence of isolated spores from a series of successively younger strata *does* yield an unmistakable evolutionary progression. Whether that sequence duplicates the meagre vascular megafossil record from the North Atlantic Region is immaterial.

The mega- and microfossil records deal with different aspects of the evolution of early land plants: one, with recognition of the oldest organism that incorporates requisite features that define vascular plants; the other, with the origin of structures – terrestrial adaptations that collectively define vascular plants – that may have evolved at different rates and at different geological times. These are structures whose relation to any one plant group is necessarily uncertain because they are found dispersed in the rock. We have yet to learn how many terrestrial plants may have evolved characters that 'simulate' those of vascular plants; a few are known. A certain amount of convergence in morphological structures of plants adapting to land life is reasonable within the concepts of the functional utility of these structures to land plants. Some of the dispersed structures may belong to terrestrial plants for which there is no other existing evidence. There is no evidence that the cardinal features defining vascular plants all independently evolved in unrelated groups of plants and are merely combined into a single organism in the latest Silurian as Banks suggests (1972, 1975*c*, p. 80). Some may assume that *all* dispersed remains necessarily have come from terrestrial phyletic sidebranches, unrelated or remotely related to existing or fossil systematic groups just because records of fully demonstrable pre-Devonian vascular plants are out of phase with the microfossil record. This thesis overlooks the obvious potential of the microfossil record for providing a better understanding of vascular plant evolution, even though it is an admission that the microfossil record provides a better guide to the vegetation than megafossils. By the time the 'purist' finds acceptable vascular plant fossils, the transitional stages, which may be recognizable in terms of discrete morphological adaptations, are complete. Thus no known plant with terrestrial adaptive characters has ever found acceptance as being morphologically, or until recently, even environmentally 'transitional'. The microfossil record would seem to have the better potential for contributing to an understanding of the morphologically transitional stages in the evolutionary continuum leading (possibly more than once) from green algae to vascular plants, and the time frame in which they occurred. This is true even if we are dealing with terrestrial plants that only parallel land vascular plants in time and adaptations. The microfossil remains provide a viable model against which to assess the sequence of adaptations by which the evolution of vascular plants may have been accomplished. Pre-Devonian trilete spores and spore tetrads are abundant and occur in stratigraphic sequences that can be sampled continuously over time. They are a far better guide to the diversity, and changes in diversity, of the spore-producing vegetation than the limited number of coeval megafossils whose records are isolated in time and space.

When assessing spore diversity it should be borne in mind that there is not necessarily a one-to-one correlation between population diversity that might be recognizable from other character states and the number of taxa recognizable from spore assemblages. The phrase 'morphological pollen species' has been used (Faegri & Iversen 1975, p. 46) to indicate that pollen and spore 'taxa' are of greatly varying taxonomic values, representing anything from several collective families or parts of families to species or subspecies. Some spore and pollen taxa undoubtedly represent more than one plant taxon. But even palaeobotanists commend the disparity in the two records as a valuable ecological clue to the contemporary vegetation by 'throwing...light on plants which grew too far away from...sites where they would stand a chance of being incorporated in accruing sediments' (Chaloner 1970, p. 366). Chaloner (1970, p. 366) suggests that it is '...reasonable to suppose that Devonian and pre-Devonian spores represent an analogous cross section of the contemporaneous flora'. Edwards (1980, p. 75) notes that the variety of spores and dispersed cuticular fragments in the Lower Devonian 'is a further indication of the incompleteness of the macrofossil record'. Because the megafossil record *is* incomplete there is no factual basis for concluding that plants represented by megafossils were wholly typical or atypical of the evolutionary pool of plants available for incorporation into the fossil record.

Spores and pollen behave as mineral or rock particles in depositional environments, sedimenting with their mineral hydraulic equivalents. It is essential when suggesting that the spore record approximates the 'true sequence of evolution of the vascular land plants' (Chaloner 1970, p. 367) to be certain that changes in spore abundance and diversity are not related in part or entirely to ecological factors and biofacies control rather than evolutionary factors. Tabulations of numbers of pre-Devonian genera for the North Atlantic Region purported to show 'a rather slow diversification of spore characters through the Silurian, with a more rapid appearance of new types in the [Lower Devonian]' (Chaloner 1970, table 1) are based on changing depositional environments that late in the sequence favour the incorporation of greater numbers of spores than earlier when spore rarity can be correlated with deeper water, more off-shore marine deposits (Gray & Boucot 1972; Gray *et al.* 1974).

3. MICROFOSSIL STRUCTURES

The megapalaeobotanist is accustomed to dealing with systematic groups and taxa, even though most plants are known from fragmented remains which represent only some of the most common or durable structures. The plant microfossil record also depends on the most common or durable characters. In some parts of the geological column, cell types and tissue fragments are adequate to identify the systematic groups involved. In the Palaeozoic, where modern morphological analogues may be unknown, structures may not always be systematically definitive and the microfossil record is thus less useful for marking the advent of a taxon than for recognizing levels of organization compatible with specific habitats. Because structures may mark transitional states of organization between groups, it is inevitable that some structures fulfil the morphological expectations for some specific habitat or environment, but not assignment to any systematic group. The more rigorous and uncompromising the morphological data necessary to define a systematic group, the more difficult it will be to recognize transitional states that may bridge the evolutionary gap between long-separated, well-defined groups of organisms. Structures preserved in the fossil record may not be definitive for a systematic group; it does not follow that they cannot represent that group or immediately preceding forms. A tissue system, the vascular system, is the *only* evidence that some will accept for the presence of vascular plants. Because only vascular plants will have a vascular system there is no way to recognize early stages in the evolution of vascular plants unless we also make use of available structures that are evolutionarily closely correlated with the vascular system in vascular plants but not necessarily restricted to them.

It is unfortunate that some have come to believe that dispersed spores provide *no direct information* about the taxonomy or the levels of organization of the parent plants. In broader usage, the term 'spore' has no explicit taxonomic meaning (cf. Chaloner & Orbell 1971, p. 275), but some have gone so far as to suggest that 'we have as yet no certain criteria to discriminate between the spores of major plant groups' (Chaloner & Orbell 1971, pp. 280–281; Banks 1975*a*, p. 21) and that 'spores by themselves are not diagnostic of the higher categories of plants' (Banks 1977, p. 299). This is inaccurate. Morphological similarity based on actualistic models generally permits assignment of dispersed pollen and spores throughout geological time to groups at the Division (Phylum) level and commonly at the Class, or even lower levels. Pollen produced by angiosperms is distinguishable from that produced by gymnosperms. Neither in turn can be confused with the spores produced by pteridophytes or bryophytes. No one has suggested on the basis of actualistic models that pollen and spores of plants within any of the above groups cannot be distinguished from structures, reproductive or otherwise, produced by algae and fungi or by blue-green algae (cyanobacteria) and true bacteria. Indeed remains of algae, bacteria and fungi have been convincingly identified in the Precambrian based on their comparative morphology in relation to modern taxa (Schopf 1970). We are not dealing with unidentifiable microfossils. Comparative morphology suggests that meiospores essentially identical to the pre-Devonian spores are restricted to land vascular plants and bryophytes. This fact carries taxonomic implications as well as broader implications about the morphology, physiology, biochemistry, ecology, and evolution of the parent spore-producing plants.

In the early Palaeozoic, there are clearly more challenges to the use of actualistic models than in the post-Palaeozoic because of the large number of now-extinct organisms within each Division. The fact that Carboniferous palynologists recognize a category such as 'prepollen' for Palaeozoic *sporae dispersae*, whose organization is not clearly that of pollen grains or cryptogamic spores indicates that reliable morphological distinctions of the post-Palaeozoic may be less clear earlier, although few such examples are known where palynologists feel uncomfortable in making a more specific morphological–taxonomic attribution.

In the Silurian and Devonian systematically anomalous land-dwelling plants are known with morphologically convergent structures that simulate those of vascular plants. Since evolution does not operate in an ecological vacuum, we feel secure in suggesting that 'land adaptive morphology' implies specific information about the habitat and functioning of such organisms, irrespective of their phylogenetic affinities. The fact that a few taxonomically anomalous, land-dwelling plants are known reinforces the possibility that many more *may* have existed for which we have no fossil records. But examples of such plants have shown no steady increase in numbers over the past 50 years; the small handful has only been increasingly restudied and reinterpreted with refined techniques.

(*a*) *Tetrahedral spore tetrads*

Obligate tetrads, all in tetrahedral tetrad form, dominate spore assemblages from the Middle Ordovician to the mid-late Early Silurian (plates 1, 2). Many obligate tetrads (all in some assemblages) are smooth-walled, without spore coat ornamentation (plate 2, figure 18). Similar, essentially smooth-walled tetrahedral tetrads have been found within sporangia of some early vascular plants of the North Silurian Realm (North Atlantic Province), but their state of maturation is uncertain and it cannot be determined if they would have been dispersed in that condition.

Other smooth-walled tetrads, possibly under conditions of better preservation, occur within a *single* common wall formed around the tetrad and in some cases easily detached from it (plate 1, figures 2–16; plate 2, figures 17, 19–22). Such spore tetrads have never been found within sporangia of any fossil plant, nor have they a fossil record that postdates the Early Silurian. On rare occasions when such obligate tetrads are split apart, the proximal face of the individual spores display prominent trilete laesurae (plate 1, figure 1). The earliest tetrads are very small; they progressively increase in size, although they are no larger at maximum size before the time they disappear from the record than most of the single trilete spores that replace them.

Spores dispersed in obligate tetrads are unknown among modern vascular cryptogams, even though tetrads are sometimes found in early vascular plant sporangia. Obligate spore tetrads occur in a number of bryophytes, including Hepaticae and Musci. None, to my knowledge, is found in the Anthocerotae which is commonly regarded as an isolated group sometimes put in a separate Division (Stotler & Crandall-Stotler 1977). However, obligate tetrads have been reported as normal in species of the liverwort genera *Sphaerocarpos*, *Cryptothallus* and *Riccia*, and in the moss *Andreaea*, and members of at least six families of both hepatics (including taxa in the Calobryales, Jungermanniales, Marchantiales and Metzgeriales) and mosses occasionally disperse spores in tetrads (Campbell 1959; Erdtman 1965; Schuster 1967; Boros & Járai-Komlódi 1975). In the latter category, obligate tetrads may be specific to a species, or they may

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occur commonly in a taxon whose spores also come apart. For example, spores of at least one species of *Haplomitrium* (Calobryales) show a common tendency to adhere in both tetrads and dyads (Campbell 1959; Schuster 1967) although the relationship is apparently casual with tetrads sometimes separating into single spores before dispersal. Obligate tetrads are common only in the liverwort *Sphaerocarpos* (Sphaerocarpales) where they are found among most species (Siler 1934; Proskauer 1954; Doyle 1975). In addition to similarity in basic form of the dispersal unit, many *Sphaerocarpos* tetrads also share with the Palaeozoic fossils the character of a common outer wall or 'perisporal' membrane. A similar common wall occurs in *Jungermannia hodgsoniae* Grolle (Jungermanniales), and so obscures the contact areas between the individual spores, as it does in some of the fossil specimens, that the basic tetrad character of the unit was unrecognized by Taylor *et al.* (1974) who illustrated them (figures 47, 48 and 50) as abnormal single spores. Spore tetrads found in *Sphaerocarpos*, and in *Riccia* (Marchantiales) where they do *not* appear to have a common wall are far larger than those of the Palaeozoic fossil specimens; tetrads in *Jungermannia hodgsoniae* are smaller than many of the fossils; those of *Cryptothallus* (Metzgeriales) are similar in size to many of the fossils (Schuster 1981). The basic similarity in morphology of the modern and fossil spore tetrads is not negated by the size disparities.

The fossil specimens, *as obligate tetrads*, find close morphological counterpart among living members of the hepatics, including at least one taxon in the Calobryales, a small 'ancient complex' with many primitive features often placed in 'a central position in phylogenetic speculation' (Schuster 1967, pp. 1, 2; Schuster 1979), as well as in other taxa in both branches of the major dichotomy, that is, Jungermanniidae (Jungermanniales, Metzgeriales) and Marchantiidae (Marchantiales, Sphaerocarpales) that some see as occurring early in hepatic evolution (Schuster 1966, 1979, pp. 64–78, figure 2; R. E. Longton, personal communication).

For years hepatics figured prominently into the thinking of morphologists as models for what the earliest archegoniate land plants looked like. They include the simplest living terrestrial plants, some scarcely more differentiated than some green algae. Watson (1968, p. 19) suggests that the male plant thallus of *Sphaerocarpos* 'comes as near as any to an undifferentiated expanse of green cells that might have characterized a hypothetical algal ancestor'. Schuster (1979, p. 43) describes the challenge of recognizing that plants he originally believed to be 'ramified strands of a...delicate...filamentous, green alga' were in fact 'a major new type of liverwort!' Genera such as *Riccia* and *Sphaerocarpos* have fuelled speculation regarding the origin of the alternation of heteromorphic generations. This phenomenon has played a prominent part in discussions on land plant phylogeny, because such alternation is a universal character among the embryo-forming, sexually reproducing bryophytes and vascular plants. *Riccia* and *Sphaerocarpos* (immortalized in Lotsy's hypothetical prototype genus *Sphaero–Riccia*) have been alternately seen as primitively simple and closest to the hypothetical early land plant or as simple end members of an evolutionary reduction series, depending on whether one favours the interpolation (antithetic) or the transformation (homologous) theory as the basis for explaining alternation of generations. Although the interpolation theory as stated by Bower (1908, 1959) and others has lost favour in recent years with seemingly increased understanding of the varied types of life cycles in the algae, recent investigations of the freshwater *Coleochaete* and other green algae may have reopened the issue of the *de novo* origin of the sporophyte in land plant evolution by a delay in zygotic meiosis as suggested by Bower (Graham 1984). Bower himself (1959) appears, however, to have repudiated the idea that either *Riccia* or *Sphaerocarpos* were primitively simple hepatics.

Thallus-like structures attributed to the hepatics, suggest that extant subclasses and orders go back to the Late Devonian (Schuster 1966, 1979) with '*types superficially approaching some existing families*' (Schuster 1966, p. 351). These records are now supplemented by others from the lowermost Middle Devonian and possibly the Late Silurian (Ishchenko & Shlyakov 1979). One may agree with Schuster (1966, p. 351) that a probable origin for the hepatics 'well before the Devonian' may be assumed. These megafossils, together with the Ordovician and Early Silurian spore records, should provoke thinking anew about the seminal position of hepatics or of hepatic-like organisms in the phylogeny and evolution of land plants.

(*b*) *Trilete spores*

Single trilete spores are dispersed at maturity as single units derived from tetrahedral tetrads. Spore tetrads in the process of breaking apart are a common configuration in pre-Devonian assemblages. These spores have distinct triradiate laesurae on the proximal (inner) face of the spore. They are identical in morphology and size to contemporary vascular plant spores.

The remark has been made about spores produced by vascular plants and bryophytes that 'we have no simple criterion to distinguish the spores of one group from the other' (Banks 1975*c*, p. 78). In fact among *living* bryophytes, trilete spores are rare compared with inaperturate and other morphologies (see, for example, Erdtman 1965; Taylor *et al.* 1974; Boros & Járai-Komlódi 1975; Clarke 1979; Horton 1983) since, in most mosses and many hepatics, disintegration of the tetrad occurs very early in sporogenesis (Mogensen 1981). They are found mainly among the Anthocerotales (Anthocerotae), the Sphagnales and some of the Andreaeales (Musci) (Erdtman 1965; Boros & Járai-Komlódi 1975). In some of these (*Andreaea*, for example), the 'aperture system' is referred to as 'cryptotrilete' or as a 'trifid streak' (Erdtman 1965). Recent studies by Brown & Lemmon (1984, pp. 412, 414, figures 13–15) have confirmed that the spore of *Andreaea rothii* Web. is not only inaperturate but in fact 'distinct from all other bryophyte spores'. The angular proximal faces of the spore that mimic the trilete configuration of the typical trilaesurate spore merely reflect contact with other members of the tetrad or as Brown & Lemmon (1984, p. 419) remark 'physical constraints imposed on the enlarging spores by the common sporocyte wall'. These data, together with the occasional shedding of *Andreaea* spores in tetrads (Erdtman 1965; Boros & Járai-Komlódi 1975, p. 100), suggest that the tetrad unit comes apart very late in sporogenesis and point toward the possibility of the obligate tetrad as having been a more common configuration in the subclass of mosses (Andreaeidae) that some see as possessing more of the characters (in *Andreaeobryum*) that can be attributed to a common ancestor of the mosses than other Musci (Crosby 1980). Only four other orders, Marchantiales (Hepaticae), and Pottiales, Funariales and Isobryales (Musci) have any taxa with trilete spores, all being less common than inaperturate spores and in some cases (Pottiales and Funariales) of very restricted or rare occurrence (Erdtman 1965). Possibly 25 from among an estimated 900–1000 bryophyte genera are known with trilete or cryptotrilete spores.

Thus it is clear that the trilete configuration is not typical of extant bryophytes as it is of extant vascular cryptogams. If the obligate tetrahedral tetrad was a more common configuration among bryophytes in the past, however, it is also possible that trilete spores may have been more common among now extinct groups of bryophytes and among the ancestral forms of extant taxa whose spores now have other morphologies. This would imply an evolutionary trend in bryophytes toward decrease in the time of tetrad disintegration in sporogenesis. These possibilities could be seen to raise the question whether trilete spores of the late Early Silurian and Late Silurian could have equally well belonged to bryophytes as to vascular plants. Varied aspects of the reproductive biology of bryophytes suggest to me that their spores have always been less apt to have had significant representation in the atmospheric 'spore rain' than vascular plant spores despite the huge numbers of spores produced per capsule by some bryophytes (see for example Longton 1976; Longton & Miles 1982, p. 225, table 3). Among dioecious bryophytes, for example, sporophyte production may be limited (Longton 1976; Longton & Miles 1982; Longton & Schuster 1983) owing to the restrictions of spatial separation of the sexes at both local and regional levels and by other factors such as unequal sex ratios. While these limit spore abundance, different emphasis on the sporophytic aspects of the life cycle in bryophytes and vascular plants is potentially even more limiting with regard to the amounts of atmospheric spores. Thus as Longton & Schuster point out (1983, p. 387) '...each fertilization potentially gives rise to a single sporangium producing...a single "crop" of spores....in other land plants...a single successful fertilization can potentially give rise to an indefinitely perennial sporophyte that forms immense clones by vegetative spread and which, in turn, can produce thousands of sporangia over many decades'. Thus even if trilete spores were more common among bryophytes in the past, there are valid reasons for believing that once vascular plants were also contributing spores to the atmosphere that they would tend to 'swamp out' the atmospheric and depositional representation of bryophyte spores just as they appear to do in 'spore rains' at the present time.

A few smooth-walled single trilete spores appear in Llandovery assemblages dominated by obligate tetrahedral tetrads. Trilete spores dominate assemblages in the post-mid Late Llandovery. They are indistinguishable from Devonian spores, with a number of taxa passing from the Silurian into the Devonian. By the mid-Late Silurian (Ludlovian) trilete spores have a diversity of spore-coat patterns and features associated with the laesurae, and represent a large number of taxa for which there are no co-occurring megafossils.

The occurrence of trilete spores (in fact dispersed *obligate spore tetrads*) in *Protosalvinia* has provided the basis for speculating that a plethora of hypothetical pre-Devonian marine or continental algae, pelagic marine organisms of unknown affinities to which Smith (1979) attributed trilete spores in the Irish Silurian, or unknown non-vascular continental plants, have produced spores that 'may simulate spores of vascular plants' (Banks 1975*a*, p. 21). Review of all morphological and biochemical evidence with regard to *Protosalvinia* (Gray & Boucot 1979) leaves little doubt that this biogeographically and stratigraphically restricted late Upper Devonian taxon was a continental organism that can as easily be viewed as related to bryophytes as to algae to which some assign it. Some see the resemblance between *Protosalvinia* and certain Riccias as only a matter of similar 'life-form' (Lundblad 1954). Others (Lacey 1969, pp. 197–198) see *Protosalvinia* 'as probably bryophytic' representing the 'terminal branches of a rosette-forming liverwort in which large tetrads of spores were produced in simple sporophytes sunk in the gametophyte thallus, much as in the living genus *Riccia*'.

To speculate about the affinities of *all* fossil trilete spores based on the *single* example provided by *Protosalvinia* in which the spores, united into obligate tetrads, are more analogous to those of bryophytes than vascular plants, obviously puts dispute about spore affinities beyond the possibility for direct investigation. Unknown, long extinct algae, bryophytes and anomalous plants may have produced spores 'that appear to demonstrate the existence of early Palaeozoic vascular plants...' (Banks 1975*a*, p. 22), but the availability of actualistic models for direct comparison suggests that it is less speculative to conclude that trilete spores represent vascular plants. Referring to the pre-Devonian dispersed spore record, Banks (1973, p. 231) wrote:

> 'although it is not possible usually to determine the plant from which these dispersed spores were derived, some of them have been compared with those found in situ in attached sporangia...and the degree of similarity is much too great to be due to chance.'

I agree there is an 'economy of hypothesis' in an interpretation which derives Silurian trilete spores from vascular plants, before advancing to more speculative hypotheses which call upon a nonexistent fossil record.

(*c*) *Sheets of cells*

A variety of cellular scraps are dispersed in many of the spore-bearing preparations. These scraps first appear in the mid Ordovician. Most are imperforate; others perforate. None possesses evidence of stomata of the type known in epidermal cells of post-Gedinnian vascular plants in the North Atlantic Region, or of the type found on some bryophyte capsules. The scraps were singled out (Gray & Boucot 1971, 1977), because of their co-occurrence with other microfossils (spores and tracheid-like tubes) as evidence for the presence of land, that is, terrestrial plants, and 'possibly' for vascular plants as well, and not as has been incorrectly stated as evidence for the presence of pre-Pridolian vascular plants (Banks 1975*a*, *b*). Edwards' detailed work on dispersed Ludlovian-age scraps, which find morphological analogues with fragments isolated elsewhere and in other time intervals, has demonstrated that they are 'cuticles rather than sheets of thick-walled cells...', that the 'general organization...parallels that in vascular plants' (Edwards 1982, p. 225), and that their 'resilience...suggests that they were composed of complex polymers at least comparable...with cutin of higher vascular plants' (Edwards 1982, p. 254). Despite the continued absence of any knowledge of the botanical affinities of the cuticles, the environmental and possible systematic interpretations originally suggested by Gray & Boucot (1971, 1977) have been strengthened by detailed study. The suggestion that such cuticle scraps might be those of bryophyte or bryophyte-like organisms has not been considered in detail. Hepatics are often said to lack cuticles although Lacey

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Description of plate 1

Nomarski interference photographs of obligate tetrahedral tetrads typical of Microfossil Assemblage Zone I. Magn. ×1000. Photographs taken by J. Gray.

Figure 1. Single spore physically broken from a tetrahedral tetrad, showing remnants of other spores in the tetrad and clear triradiate mark. Medina Formation, New York State (Gray no. 1197).

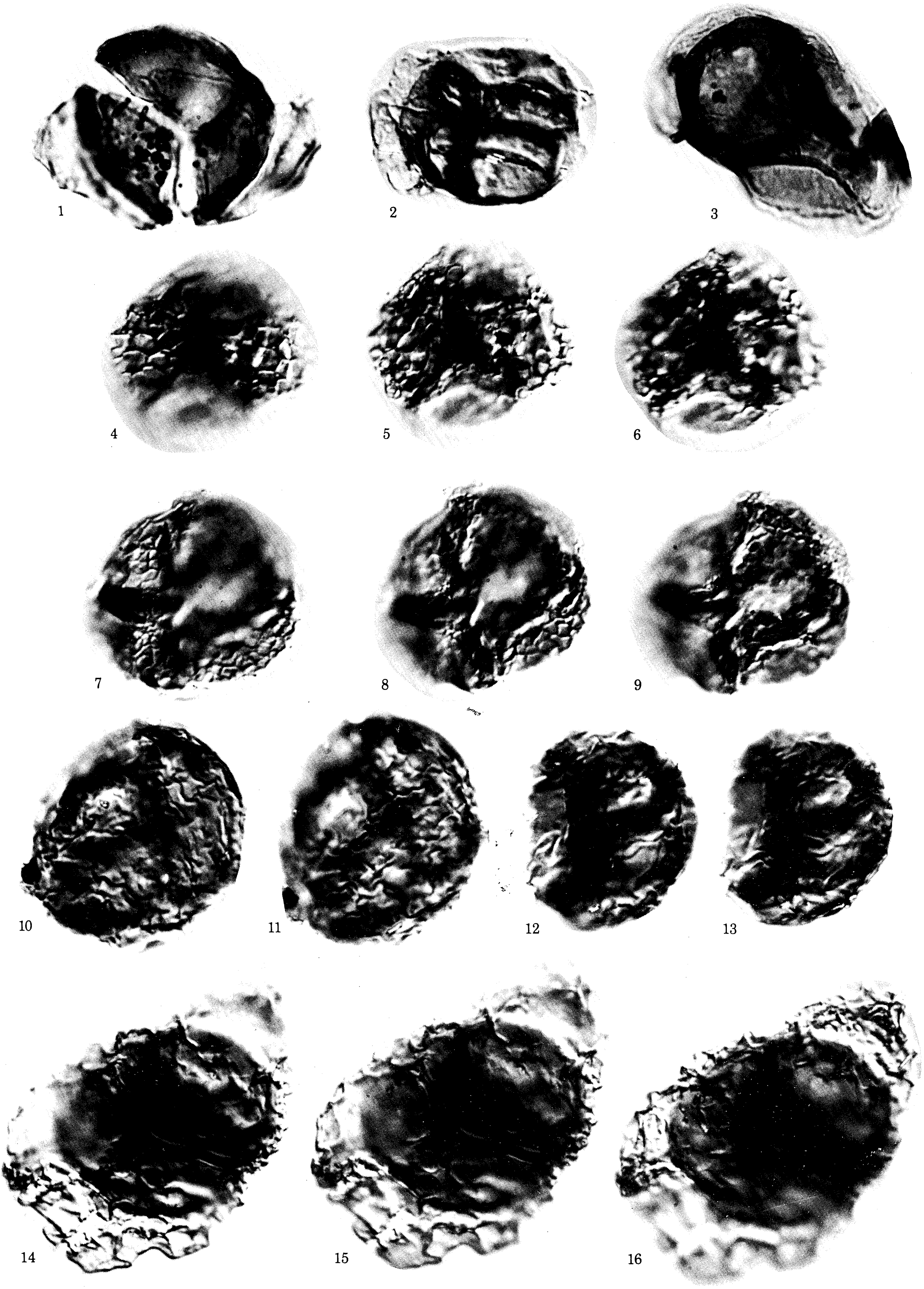
Figure 2. Obligate tetrad with smooth, or possibly degraded reticulate perispore. Elkhorn Formation, Kentucky (Gray no. 1285).

Figure 3. Obligate tetrad with smooth perispore. Elkhorn Formation, Kentucky (Gray no. 1285).

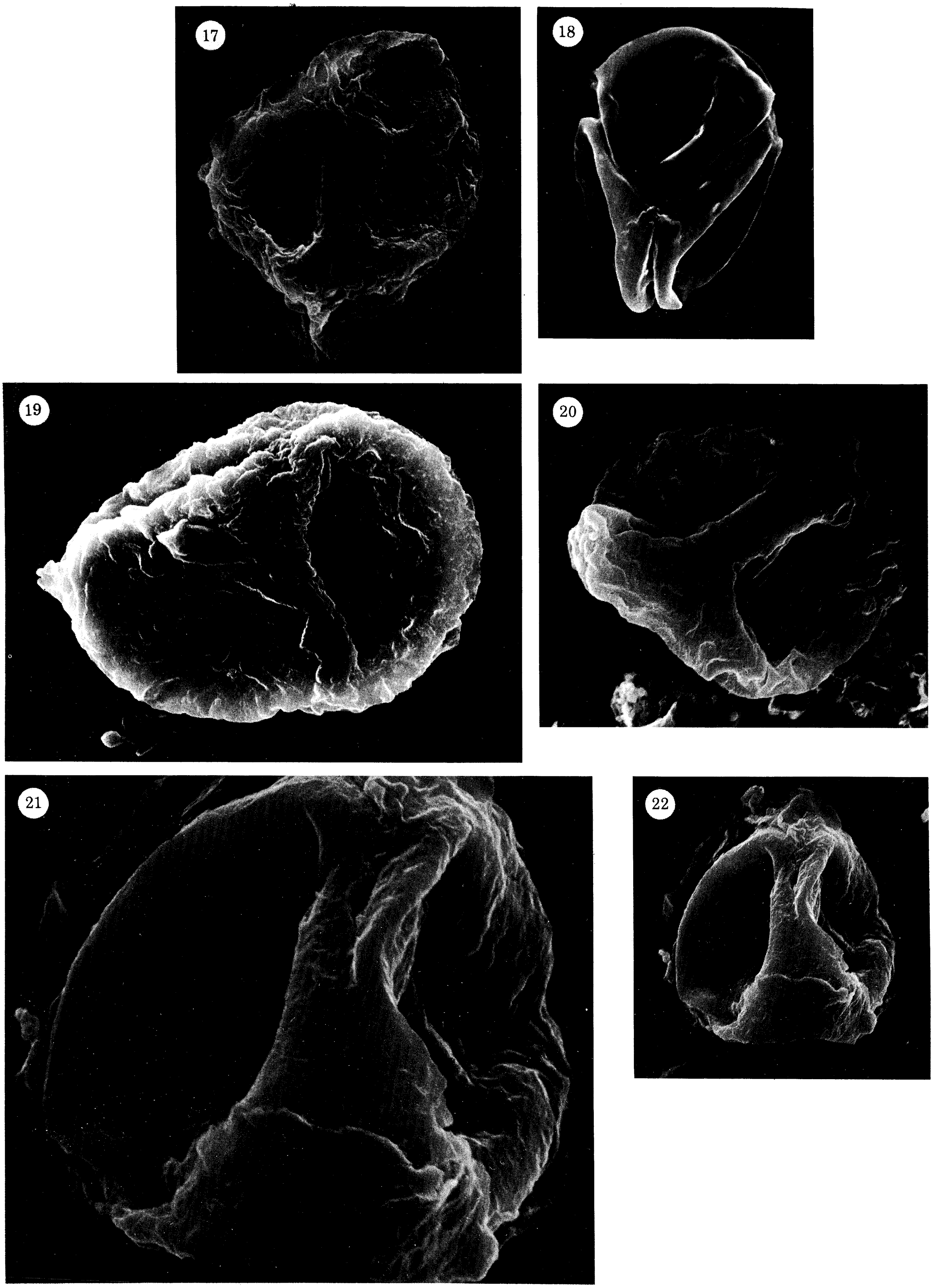
Figures 4–9. Two specimens of obligate tetrads with reticulate perispore in different focal planes. Elkhorn Formation, Kentucky (Gray no. 1285). Note loose attachment of perispore and smooth-walled tetrad beneath.

Figures 10–13. Two specimens of obligate tetrads with firmly adherent rugose perispore. Jupiter Formation, Quebec (Gray no. 1350). Note that the suture lines between the individual spores in the tetrad are obscured by the enclosing perispore with the walls of the tetrad showing as 'shadows' beneath the perispore.

Figures 14–16. Obligate tetrad with very loose reticulate perispore in the process of being lost from the smooth-walled tetrad beneath. Elkhorn Formation, Kentucky (Gray no. 1285).



FIGURES 1–16. For description see opposite.



FIGURES 17–22. For description see opposite.

(1969, p. 191) notes that 'acetolysis of certain *Riccia* L. (*Ricciella* (Braun) Boulay) gametophytes releases a very thin and delicate membrane from the surface of the thallus which may represent a cuticle'. He refers to this (1969, p. 197) as an 'acetolysis-resistant cuticle-like outer layer'.

(*d*) *Tracheid-like tubes*

Gray & Boucot (1971, 1977) reported on the occurrence of abundant tubes that simulate tracheids in spore-bearing samples. Such tubes have yet to be found in samples of Ordovician age, nor are they found before the late Early Silurian (based on redating of Massanutten Mountain material: J. Gray & A. J. Boucot, unpublished data). They compared their morphology with tubes found associated with *Nematothallus*, and used the term 'tracheid-like' to describe the gross aspect of these tubes. Following the lead of other palaeobotanists (Lang 1937, Høeg 1942; Lyon 1962), they suggested that these tubes may have functioned in terrestrial plants in a manner similar to the tracheids that they simulate. The term tracheid-like was used in deference to morphological similarity and functional possibilities and not with the intention of implying phylogenetic relationship between the plant or plants in which they occur and vascular plants.

Most tracheid-like tubes dispersed in palynological samples are short lengths of unbranched tubes a few tens of micrometres long and 15–30 μm in diameter (see Gray & Boucot 1977) that display helical thickenings. Dichotomous branching and tapering occasionally reported by some investigators, as well as clusters of tubes (Pratt *et al.* 1978; Edwards 1982), are not features that occur with any regularity in dispersed examples.

Morphologically identical structures are found *in situ* in Lang's (1937) *Nematothallus*, land plants that apparently became extinct without leaving terrestrial descendants, and whose affinities are obscure. However, the wide geographical dispersal and abundance of the tracheid-like tubes in pre-Devonian spore-bearing residues has no parallel in Silurian age megafossils attributed to *Nematothallus*. Before 1978 the one or two records of this genus were restricted to the European section of the North Atlantic Province. At that time Pratt *et al.* (1978) reported on a single, possible North American occurrence. Like trilete spores that some see as 'simulating' spores of vascular plants, it may be that these widely dispersed helically thickened tubes are simulating tubes found *in situ* in *Nematothallus* but have come from a variety of

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DESCRIPTION OF PLATE 2

Scanning electron micrographs of obligate tetrahedral tetrads typical of Microfossil Assemblage Zone I. Micrographs by G. Kent Colbath.

FIGURE 17. Obligate tetrad with a strongly reticulate perispore, magn. ×2000. Elkhorn Formation, Kentucky (Gray no. 1285).

FIGURE 18. Obligate tetrad without perispore, magn. ×1000. Rockwood Formation, Georgia (Colbath ND 105).

FIGURE 19. Obligate tetrad with rugose perispore, magn. ×2000. Poor Valley Ridge Member, Virginia (Colbath HG II-118).

FIGURE 20. Obligate tetrad with weakly reticulate perispore, magn. ×2000. Elkhorn Formation, Kentucky (Gray no. 1285).

FIGURES 21 AND 22. Obligate tetrad loosing smooth? perispore, magn. ×5000, ×2000. Elkhorn Formation, Kentucky (Gray no. 1285).

Note that in all but figure 18, the perispore covers and obscures the suture between the individual spores of the tetrad. In figures 21 and 22 the suture is beginning to appear between the individual spores as the perispore is peeled off.

Formal taxonomy for the taxa illustrated will be presented by J. Gray, A. J. Boucot and G. K. Colbath in a later publication.

unrelated plants that represent a similar grade of evolution. On the other hand, they may provide a far more reliable guide to the pre-Devonian biogeography of *Nematothallus* than the limited Silurian megafossils.

There have been attempts to attribute these helically thickened tubes to marine animals such as graptolites or to problematic fossil marine groups such as chitinozoans, and to suggest that the substance of which they are composed is chitinous (Banks 1975*a*, *b* and references therein). Detailed studies, morphological and biochemical, have only tended to reinforce and strengthen earlier conclusions about the functional and environmental significance of tracheid-like tubes based on comparative morphology and fossil analogues. Niklas & Pratt (1980, pp. 396, 397) who have isolated 'lignin-like constituents' from tube-containing samples suggest that the tubes 'fulfill most of the morphological and chemical criteria for cell types that could have functioned as water-conducting cells', and that similarity to tracheids 'suggest the probability of their being evolutionary separate solutions to similar physiological or structural problems'. Edwards (1982, p. 254), who unhesitatingly refers dispersed tracheid-like tubes to *Nematothallus*, notes that their resilience' suggests that they were composed of complex polymers at least comparable with lignin...of higher vascular plants'. She further states, somewhat enigmatically, '...I am now more hesitant to state categorically that the banded tubes are quite different from xylem conducting elements...'. Functional and environmental interpretations of these tracheid-like tubes have thus come basically full cycle to the original interpretation of Lang (1937) who seems to have correctly deduced their significance in at least one terrestrial plant.

(*e*) *Fungal spores and hyphae*

Although uncommon, fungal remains are an important part of the early land plant story because of their present importance in continental environments. Their earliest well-documented occurrence comprising fungal remains of probable ascomycete affinities found in the Ludlow age, Burgsvik Sandstone (Gotland) (Sherwood-Pike & Gray 1985), is coincident with the early vascular plants. Similar but less well-preserved material also occurs in the Late Llandovery (late Early Silurian) Massanutten Mountain assemblage from eastern North America (Pratt *et al.* 1978). The ascomycetes are a predominantly terrestrial group; the occurrence of probable conidia, ascospores and hyphal remains in the Burgsvik closely parallels the occurrence of trilete spores, spore tetrads and other evidence of land plants, that is, both are largely absent from biofacies dominated by normal marine microfossils. Remains in the Massanutten come from a non-marine, probably fluvial, facies that also includes a few trilete spores, abundant spore tetrads (J. Gray, unpublished data), tracheid-like tubes and sheets of cuticle. This occurrence provides evidence that fungi had entered the non-marine environment by the Early Silurian. The data provided by Sherwood-Pike & Gray (1985) can be interpreted as geological evidence for the earliest stage in evolution of the terrestrial decomposer niche that is occupied by higher fungi and saprophagic microarthropods, and thus indirectly as the earliest evidence for the microbiological degradation processes involved in litter and soil formation.

4. Microfossil assemblage zones

(*a*) *Microfossil Assemblage Zone I* (*mid Ordovician to mid-late Early Silurian*)

This interval provides evidence for the first adaptive radiation of plants onto land. Tetrahedral spore tetrads are found first in North Africa in the mid Ordovician (Gray *et al.* 1982) with additional records in Saudi Arabia (J. Gray, H. C. McClure and A. J. Boucot, unpublished data). By the late Ordovician, spore tetrads are found in Ghana (Bär & Riegel 1980), Czechoslovakia (Vavrdova 1982), throughout the Appalachian regions of the south-eastern U.S., and in the continental interior of North America (Gray & Boucot 1972), as well as in Libya (Boucot & Gray 1982). By the earlier Llandovery, spore tetrads are known from North Africa, South Africa (J. Gray, J. H. Theron and A. J. Boucot, unpublished data), from the Paraná Basin of southern Brazil (J. Gray, G. K. Colbath, Alvaro de Faria, A. J. Boucot and D. H. Rohr, unpublished data), and throughout the Appalachian region from Georgia, north to Nova Scotia (Gray & Boucot 1971 and unpublished data; Pratt *et al.* 1978; Strother & Traverse 1979; Miller & Eames 1982).

Where preservation is good, three or four genera are recognized by J. Gray, A. J. Boucot and G. K. Colbath (unpublished) based on variation in the often loosely attached perisporal membrane that surrounds each tetrad to obscure the suture lines of the individual spores. Two of these genera have overlapping, but largely independent stratigraphic ranges, where they are best observed throughout the Appalachian Region. Tetrads with loose, reticulate perispores are found as early as the late Ordovician and persist until the mid-Late Llandovery. By the mid Llandovery and persisting to the mid-Late Llandovery, they are joined by tetrads of a second type with rugose ornamentation rather more firmly attached to the spore tetrads. Loose, smooth-walled perispores characterize other tetrads during this interval; this third type is uncommon and its stratigraphic range poorly defined. Abundant smooth-walled tetrads without an outer wall may be those from which loosely attached perispores have been removed; alternatively they may have always lacked perispores, thus representing a fourth type. Throughout Zone I there is a marked increase in tetrad size.

At some time in the Early Silurian (sampling is not adequate to indicate the first occurrence) smooth-walled, single trilete spores that have separated from the tetrad at maturation begin to appear. Cuticle fragments occur throughout Zone I; tracheid-like tubes appear late in Zone I (late Early Silurian).

(*b*) *Microfossil Assemblage Zone II* (*post-mid-Late Llandovery to late? Wenlock*)

Assemblage Zone II is set apart by the dominance of smooth-walled trilete spores, a change from spore tetrads which fixes the lower boundary of Zone II in the mid-late Early Silurian at approximately the C_2–C_3 boundary. The top of Zone II is poorly defined because of sampling limitations. Spore assemblages of Zone II are morphologically monotonous like those of Zone I, but the change from tetrads to single spores marks a major change in the diaspore and in the reproductive strategies of the organisms involved. The lineage or lineages of spore-producing plants post-dating the change may or may not be related to the lineage or lineages of Microfossil Assemblage Zone I. Cuticle scraps and tracheid-like tubes are common. Zone II assemblages are found in the Appalachian region, western Europe and North Africa.

(*c*) *Microfossil Assemblage Zone III* (*late? Wenlock to Pridoli*)

In the late Wenlock or early Ludlovian there is a marked increase in diversity of single trilete spores that correlates with, but exceeds, evidence of increase in numbers and diversity of vascular plant megafossils in the North Atlantic and Uralian–Cordilleran Regions. Spore diversity coupled with the wide distribution of spores in comparison with vascular megafossils suggests that the environments (biofacies) being tapped exceed those represented by megafossils. Mid-Late Silurian spore assemblages have many novelties in spore-coat morphology and other new morphological features (Richardson & Lister 1969; Richardson & Ioannides 1973; J. Gray and A. J. Boucot, unpublished data). Tetrahedral tetrads remain conspicuous in some assemblages but none have an enclosing perisporal membrane of the type found in Zone I tetrads. Zone III assemblages are found in eastern North America, Arctic Canada, western Europe, North Africa and South America.

5. Discussion

Land plants have undergone two major pre-Devonian periods of adaptive radiation, involving plants with different evolutionary levels of organization; these may only partly correlate with existing well-defined systematic groups of land plants. The first adaptive radiation corresponds to Microfossil Assemblage Zone I: it is termed the *period of non-vascular level of organization*. This period predates the recognition of vascular plant megafossils, yet the abundance of spores and occasional cuticle scraps provide a firm basis for recognizing the presence of land plants. Absence of other structures may be an artefact or it may relate to the occurrence of land plants that largely lacked preservable structures except spores and cuticle. Similarity in organization of the fossil spores, their exclusive occurrence in obligate tetrads (found among hepatics and mosses), together with the enclosing perisporal membrane or outer retaining wall (found today only in tetrads of hepatics), provides the basis for speculating about the level or grade of vegetative organization of the spore-producing plants and their systematic relationship. The precise phylogenetic and systematic relationship of the parent plants is, of course, indeterminable in part because nothing is known of the relationship between gametophytes and sporophytes, a feature that provides one of the major distinctions between extant bryophytes and other land plants. Gray (1985) suggested that the spore tetrads should be considered within the context of primitive 'vascular' plants that lacked the full complement of morphological and biochemical adaptations that characterize extant members of the group. This implied the possibility of a more or less linear succession of spore-producing plants. This now seems too narrow a model because the fossil tetrads have no counterpart with spores produced by extant vascular plants (although smooth-walled spore tetrads lacking perisporal membranes are similar to tetrads found in sporangia of early vascular plants) and the spore producers may have had limited relationship with vascular plants. The suggestion (Gray & Boucot 1977, p. 168) that the parent spore-producers might represent plants morphologically but not necessarily phylogenetically intermediate between green algae and vascular plants at a bryophyte or pre-bryophyte grade of evolution in terms of vegetative structure is probably more compatible with the complex of plants represented in Microfossil Assemblage Zone I. This complex could include any one or any combination of the following: (i) protobryophytes, protohepatics or hepatics unrelated to the later trilete spore producers; (ii) a common ancestor for vascular plants and bryophytes for those who believe that the similarities between them, or some of them, are too great to be due to parallel evolution (Schuster 1966; Crum 1972, p. 279; Hébant 1977): one could then envisage some bryophytes as reduced from organisms similar, or ancestral, to the rhyniophytes or the rhyniophytes as having evolved from a group of organisms similar, or ancestral, to some bryophytes; or (iii) multiple lineages, some hepatic-like and some related to the vascular plants, which may or may not have shared a common ancestral form.

The second adaptive radiation, termed the *period of vascular level of organization*, corresponds to Microfossil Assemblage Zones II and III, and the dominance of single trilete spores which find morphological counterparts among spores of extant spore-producing vascular plants. Vascular plant or probable vascular plant megafossils of this age are known from New York, Britain, Czechoslovakia, Podolia, North Africa and Australia. The indicated level of organization implies the presence of vascular plants in the traditional sense (with 'true' morphological tracheids) as well as other plants, based on the common and widespread incidence of 'tracheid-like' tubes, experimenting with internal transport of water: a level of vegetative organization compatible with the evolution of the capacity for internal water conduction, irrespective of the phylogenetic relationship of the plants involved.

The fossil record demonstrates that spores were the first land plant structures capable of widespread preservation. There are additional reasons to believe that durable-walled spores would have been optimal structures to predate other characters that define vascular plants. For spore-producing land plants, an anhydrobiotic and aerially dispersed spore is a potentially crucial morphological and ecophysiological adaptation: it can withstand harsh conditions during transport to arrive in a viable state; it permits the plant to survive in intervals between the often vulnerable gametophytic vegetative and sexual reproductive stages dependent on moisture; it carries the genetic potential, including possible new gene combinations, for the development of both gametophyte and sporophyte. It is thus a cardinal structure which provided the minimal preadaptation necessary to the radiation of aquatic plants onto the land.

Because they are based on fossil structures and on actualistic models, suggestions about evolutionary trends in spore morphology and in reproductive strategies of early land plants related to spore morphology are provided for the first time with a fossil-based biostratigraphic framework. Because distinctions in level of vegetative organization are based on only one structure of the life cycle, they provide a more speculative basis for arriving at broad-based systematic conclusions as well as for postulating varied life-history strategies of the spore-producing plants.

Period of non-vascular level of organization

(*a*) *Vegetative and ecophysiological strategies*

'...however well adapted the sporophyte may be to a terrestrial existence, it is nevertheless restricted to those habitats where the prothallus can grow and become fertilised. The ecology of homosporous pteridophytes is to a large extent, therefore, that of their prothalli' (Sporne 1965, p. 16). Sporne's comment is basically an ecological restatement of Bower's (1908) evolutionary assessment of the seminal position of the gametophyte with regard to the evolution of land plants. Bower perceived the gametophyte to be as ultimately dependent on an external water supply as an alga, while the sporophyte was a characteristically subaerial body, an evolutionary by-product of the terrestrial environment. Among spore-producing vascular plants, selection pressures on the independent sporophyte have been different from those on the independent gametophyte, particularly as they diverged morphologically in time in response to different life styles, a position also taken by Jeffrey (1962). While selection has led to different life styles, both phases are still limited by the mode of life of the gametophyte in sexually reproducing vascular cryptogams. This is even truer for bryophytes, where selection pressures on the dependent sporophyte are necessarily subordinated to those operating on the gametophyte (Vitt 1981). Selection acting on free-living gametophytes of spore-producing vascular plants and on bryophyte gametophytes, whose ecology is largely constrained by similar environmental variables, has led to some remarkable parallelisms in life styles; both, for example, have evolved subterranean gametophytes (in the hepatic *Cryptothallus* (Schuster 1981) and in *Lycopodium*). Life history strategies of early land plants must have involved life styles that would have permitted terrestrial life, *until* selection by the land environment itself led to increased morphological, physiological and biochemical specialization in the vascular sporophyte (as stressed by Gray & Boucot 1977) that ultimately eliminated the free-living gametophyte and allowed full exploitation of terrestrial habitats. The gametophyte can be assessed as more likely than the sporophyte to embody in its fundamental morphology and physiology primitive characteristics closely akin to those of the earliest land plants. Thus, as a basis for resolving life history strategies of the earliest land plants whose spore tetrads are so abundant in the fossil record, we should look to the more evolutionarily conservative gametophytes that have probably always occupied relatively unchanged microhabitats (cf. Crum 1972), rather than to the vascular sporophyte with its land-stimulated modifications.

For early land plants non-biological stresses related to physical aspects of their environment must have been critical; biological stresses related to population density and competitive interaction with other organisms were initially non-existent or minimal. In a landscape unvegetated with higher forms of plant life, environmental factors contributing to the sum of abiotic stresses would doubtless be similar to many of those found today in arid and semiarid regions, irrespective of amounts and frequency of rainfall in early Palaeozoic environments. These stresses would include, among others, maximum levels of solar radiation, high temperatures, maximum temperature extremes and rapid temperature changes, maximum evaporation rates, full exposure to winds and to surface run-off that would have contributed to constant disturbance and erosion of the substrate, and bare, litter-free soil and rocky substrates with limited water retention capacity. Shumm (1968) has cogently discussed some of the hydrological aspects that, in the absence of vegetation, would have contributed to substrate mobility as the result of greatly accelerated surface run-off and the higher incidence of floods. Such habitats would be marked by extreme moisture variability and subject to periodic and complete desiccation at the microhabitat level of small plants, even in environments of constantly high humidity, and especially in seasonally dry tropical, temperate and cold regions which would have been at least as common as environments of constant and regular water supply. Water is commonly the most limiting environmental variable for land plants since it is essential for metabolic activities and uptake of mineral nutrients. In the harsh environments of early land plants, water deficits must have been a constant threat to tiny plants whose microenvironments were bounded by the upper few millimetres of substrate surface below and the few millimetres of air above.

Among extant land plants, vascular sporophytes largely avoid water deficits even in xeric habitats, through morphological and biochemical adaptations (cutin, lignin). Free-living gametophytes without such adaptations cope with environmental limitations, including limited water supply, by alternate strategies: evading them through an ephemeral life style or tolerating them through physiological adaptations (During 1979; Bewley 1979). Gametophytes of vascular plants have an ephemeral, transient life style, normally terminated by fertilization and the independent sporophyte phase. Bryophytes can evade environmental stress by greatly telescoped life cycles with gametophytic and sporophytic phases limited to attain spore production in a few weeks. Riccias of the Mediterranean deserts, for example, have life cycles shortened to two to three weeks with the spores ripening before the sandy substrate dries out (Bischler & Jovet-Ast 1981). Survival is then limited to desiccation-tolerant thalli or to spores;

viability in a dry state for such thalli and spores can be reckoned in years (Crum 1972; During 1979; Bischler & Jovet-Ast 1981; Scott 1982, p. 117). Such strategies that take advantage of temporary habitats, whether the habitats are predictably temporary owing to a set of locally re-occurring environmental circumstances, or unpredictably temporary owing to locally non-recurring circumstances, are characteristic of 'annual shuttle' and 'fugitive' species (During 1979; see also Slack (1982) who includes During's 'shuttle species' within the 'fugitive' category). Fugitive species have rapid, successful dispersal mechanisms, typically small spores and are rapidly established in a series of locally non-recurring temporary habitats. 'They become extinct in one habitat not because of competition of closely related species...but because the habitat itself becomes extinct' (Slack 1982, p. 201). Annual shuttle species, whose life cycle is often determined by periodic events that impose severe stresses, often avoid stresses by survival as spores. Under pressure of extreme desiccation, for example, annual shuttle species 'can disappear overnight...only to reappear...days later with a shower of rain or heavy dew...' (Scott 1982, p. 106).

Tolerance strategies are physiological and related to cytoplasmic capacity to survive severe dehydration and rapidly resume normal activities when rehydrated. Desiccation tolerance among mosses and hepatics is well documented. Among hepatics, groups such as the terricolous Marchantiales are especially well-represented as species and individuals in semiarid climate, and can withstand wide ranges of temperature (0–50 °C) and high light intensities (see, for example, Bischler & Jovet-Ast 1981) in minerogenic substrates. Desiccation tolerance is less well documented among gametophytes of vascular plants but in examples where it is known, cytoplasmic tolerance is similar to that encountered in mosses and hepatics (Page 1979 and references therein; Bower 1908, pp. 26–27). According to Page (1979, p. 569) drought tolerance in fern gametophytes '...may be far more widespread...than has been generally appreciated...'.

I suggest that both these strategies (evading stress through an ephemeral life style or tolerating stress through physiological adaptations) would have been highly adaptive in early land plants exploiting temporary environments of inconstant water supply; that early land plants at the hepatic grade of vegetative organization solved varied environmental stresses by alternate life history strategies that involved a minimum of morphological and biochemical adaptations, and that were in part physiological as in bryophytes; and that these alternate strategies were primitive features in early land plants. With regard to desiccation tolerance Bewley (1979, p. 227) reached a similar conclusion.

> 'In many respects desiccation tolerance is a primitive feature, being more prevalent in procaryotes than in eucaryotes.... Desiccation tolerance also is more common in lower plants than in higher ones, and the ability of the former to act as primary colonizers in uncompromising habitats is intimately linked to their tolerance of severe environments. The evolution of higher plants seems, to varying extents, to have been at the expense of their capacity to withstand severe water stress conditions. Adaptations to avoid or to resist drought are more common....'

(*b*) *Reproductive strategies*

Biostratigraphic information and the morphological analogy with spore tetrads of hepatics provide the basis for speculations about functional aspects of fossil spores, evolutionary trends in spore morphology, and reproductive strategies of early spore producers.

For spore-producing land plants the obligate spore tetrad appears to be the primitive reproductive unit; the single spore split from the tetrad at maturity, derivative. In obligate tetrads of living hepatics the sporeling emerges or 'dehisces' from the distal (free) surface of the tetrad (Duthie & Garside 1936; Proskauer 1954; Schuster 1981); it is reasonable to conclude that this was also the case for the fossil tetrads. This suggests that distal dehiscence is primitive among spore-producing land plants, proximal dehiscence derivative. Inoue (1960) had previously postulated the primitiveness of permanent tetrads and distal dehiscence for living hepatics; others (Schuster 1966, p. 186) regard both features and the hepatic groups in which they occur as derivative. The fossil record supports the retention of primitive spore characters in otherwise *possibly* derivative groups of hepatics. Germination from the outer, distal face occurs in a number of single bryophyte spores (Proskauer 1961), including single trilete spores of most species of *Riccia* (Duthie & Garside 1936), the endemic Indian *Stephensoniella* (Mehra & Kachroo 1952) and other taxa, and implies as Proskauer (1961) suggests '...an ancestry of forms with permanently united tetrads', and the possibility that the obligate tetrad in bryophytes and perhaps in vascular plants was a more common configuration in the past. In living hepatics with obligate spore tetrads such as *Riccia* (Duthie & Garside 1936), *Sphaerocarpos* (Proskauer 1954; Doyle 1970, 1975), and *Cryptothallus* (Schuster 1981), the sexes of the gametophytes developed from the tetrad are cytogenetically controlled by male and female chromosomes (although this has only been proven for *Sphaerocarpos*) such that two male and two female gametophytes are developed from each tetrad. The gametophytes are thus dioecious and unisexual. Although other models are possible, it seems reasonable to suggest that spore tetrads of early land plants also gave rise to unisexual gametophytes. Dioeciousness and unisexuality would thus appear primitive in spore-producing plants; monoeciousness and bisexuality derivative. Many consider dioeciousness and unisexual gametophytes primitive among living bryophytes (Schuster 1966; Wyatt 1982) in part because it is widespread and prevalent among taxa considered primitive. Whether dioecy or monoecy is primitive in vascular spore-producers could depend on the affinities of some of the spore tetrads, and on whether the gametophytes arising from them were at least potentially functionally monoecious as are the majority of extant vascular cryptogam prothalli. The monoecious, bisexual condition in spore-producing land plants would have been necessary once spores were dispersed as individual units *if* sexual reproduction, as opposed to vegetative cloning, were to be a factor in the life history of such plants especially in low population density communities.

Dioeciousness allows the accumulation or maintenance of heterozygosity. But in the colonization of uninhabited or temporary habitats the necessity for two spores having the capacity for maleness and femaleness to arrive concurrently may well have led to the adaptive advantages of vegetative reproduction that often accompanies the dioecious habit in living bryophytes. The advantages of a diaspore that assured juxtaposition of male and female plants in a pioneer colonist exploiting distant and otherwise uninhabited sites is obvious. It has the ecological advantage of monoecy where the potential for fertilization between separate gametophytes would be inhibited by limited moisture and low population density (Wyatt 1982, p. 183), as well as obvious evolutionary advantages. Selfing in homosporous spore-producing plants is equivalent to asexual reproduction. It leads to complete homozygosity in a single generation with a sporophyte homozygous for every gene in the genome (Klekowski 1979; Walker 1979). Sexual reproduction between male–female gametophytes from a single tetrad produced by one sporophyte is not the out-crossing level of a seed plant, nor is it equivalent to selfing on a homosporous gametophyte since it involves sibling gametophytes rather than single gametophytes. It does not lead to the immediate genetic consequences of self-fertilization but to the maintenance of low-level heterozygosity, although the consequence even in such a breeding system is ultimate homozygosity (R. E. Longton, personal communication; R. M. Lloyd, personal communication).

The small size of the fossil spore tetrads (average tetrad size is comparable to small isospores of homosporous vascular cryptogams) is compatible with both their ecological and evolutionary significance as dispersal units. Number and size of spores plays an obvious part in the reproductive strategies of spore-producing plants with spore size usually a trade-off against spore number and dispersal potential. Size increase limits potential dispersal distances, with the correlation between size and distribution following an exponential function (Mogensen 1981): the bulk are deposited near the plant source, some are carried for very great distances. Computed dispersal probabilities (Schmidt 1918, cited in Crum 1972; During 1979; Mogensen 1981) indicate that spores 25 μm or smaller are most suited to wind dispersal, with the carrying capacity of spores in the 8–12 μm size range almost 20000 km in a moderate wind. Although the problems of getting even small spores airborne from small plants can be formidable, as D. M. Lane, A. Stoneburner and L. E. Anderson (unpublished) (as cited in Wyatt 1982) have demonstrated with spore-trapping experiments, the distribution patterns of bryophytes (cf. van Zanten 1978) and ferns (cf. Tryon 1970), often on isolated ocean islands, seem to establish the possibility of successful colonization from distant sources, most probably through spore dispersal.

For an opportunistic colonist presented with the unique combination of physical and biological environments of the mid Ordovician and Early Silurian, the spore tetrad clearly was an ecologically and evolutionarily optimal reproductive unit. The wide biogeographical distribution of fossil spores attests to extensive colonization and dispersal potential of the spores. The limited variation in spore tetrad morphology suggests low taxonomic diversity consistent with sexual reproduction between members of a tetrad which would not introduce genetic variability (Crum 1972, p. 283) but would maintain, at least temporarily, a very low level of heterozygosity.

Period of vascular level of organization

Reproductive strategies

Biostratigraphic information and morphological analogues between single trilete spores produced by homosporous vascular plants and fossil isospores provide the basis for speculation about the functional aspects of the fossils, the reproductive strategies of the spore-producing plants, and possible evolutionary trends in spore morphology. The trilete configuration is only common among spore-producing vascular plants: I consider this group to be the source of all or most of these spores, although either they or plants vegetatively at the hepatic grade of evolution may be the source of the uncommon spore tetrads that co-occur with the single spores.

For spore-producing land plants as a group, the single spore split from the tetrad at maturity is a derived condition. Loss of the retaining wall may have been a factor. In genetic races of the hepatic *Sphaerocarpos donnellii*, spores that split apart are held together 'tenuously' by strands of the retaining wall such that the spores are easily broken apart by mechanical pressure (Doyle 1975).

In modern spore-producing vascular plants, the sporeling emerges from the proximal spore surface along the well-marked laesurae, as it does in some trilete or otherwise polar bryophyte spores (Inoue 1960; Schuster 1966). But, since bryophyte spores with triradiate marks and distal dehiscence are known, the dehiscence patterns of these fossil trilete spores is uncertain, although proximal dehiscence is a consequence of tetrad break-up, and thus derivative.

In homosporous vascular plants, unlike dioecious bryophytes where morphologically similar spores may differ in sex, the spore gives rise to gametophytes that carry the genetic potential for maleness and femaleness: gametophytes of homosporous vascular plants are all potentially hermaphroditic. The ecological advantages of monoeciousness in opportunistic colonists have been spelled out. The evolutionary consequences of obligate inbreeding (homozygosity) may also be advantageous for pioneer taxa in restrictive habitats where variation or the introduction of variability may be disadvantageous. Smith (1982, p. 192), for example, notes that among obligate epilithic and epiphylous bryophytes monoeciousness is prevalent; dioecy is prevalent among facultative epilithic and epiphylous taxa 'suggesting that...heterozygosity...is advantageous in species...catholic in their choice of habitat'. Lloyd (in Holbrook-Walker & Lloyd 1973, p. 173) also notes examples of inbred fern taxa where genetic uniformity provides a genotype highly selected for colonization and survival in a narrow range of particularly harsh environments. The long term consequences of monogametophytic reproduction are loss of genetic variability and the potential for evolutionary success measured in terms of large populations and the capability for occupying diverse habitats. But the gametophytic expression of sexuality which determines the nature of gamete exchange in monoecious spore-producers is extremely labile with degrees of bisexuality and unisexuality influenced by factors such as population density, niche diversity, habitat preferences and gametophyte longevity in both vascular plants and bryophytes (Cousens & Horner 1970; Holbrook-Walker & Lloyd 1973; Cousens 1979, 1981; Klekowski 1979; Duckett & Duckett 1980; Longton & Miles 1982; Ramsay & Berrie 1982). Different patterns of sex expression leading to different breeding system syndromes may be adaptive by permitting different balances of selfing and outbreeding in different environments (Holbrook-Walker & Lloyd 1973; Duckett & Duckett 1980): dense populations of 'mature', more stable habitats may have outbreeding mating systems and correspondingly higher levels of heterozygosity; 'weedy' pioneer species may have inbred mating systems and corresponding homozygosity. Monoecious vascular cryptogams potentially have the best of two worlds: because unisexuality in a normally hermaphroditic system can apparently arise according to 'need', the evolutionary consequences of homospory in spore-producing plants can lead to high probability for outbreeding as population densities increase. The full genetic and evolutionary consequences of outbreeding, which allows accumulation of heterozygosity in spore-producing plants, can only occur where spores are derived from *different* sporophytes. This can occur as a result of the monoecious state as it occurs in most vascular cryptogams or as the result of the dioecious state as it occurs in many extant bryophytes, but not as a consequence of the level of outbreeding that can occur among male and female members of a single tetrad. Given the reproductive strategies available to gametophytes arising from the spore tetrad and those arising from the single spore, it seems that gametophytic reproduction mechanisms that increased heterozygosity had greater selective advantages as plant populations increased in density and environments became more stable, than a mechanism that only permitted maintenance of low-level existing heterozygosity and that would lead ultimately to homozygosity.

By the time that single trilete spores dominate assemblages their sizes are compatible with spores of the majority of extant homosporous vascular cryptogams, that is, they are in the 30–60 μm size range and often larger than entire tetrads. The evolutionary trend towards larger spore size correlated with production in smaller numbers culminated for homosporous spore-producing plants very early in time. Larger size and smaller numbers suggests more limited dispersal potential than that of the smaller tetrads. Computed dispersal probabilities (Schmidt 1918, cited in Crum 1972; During 1979; Mogensen 1981) for spores in the size range of those of the late Silurian suggests dispersal of a few tens or a few hundred kilometres rather than thousands of kilometres, as pertains to diaspores in the 25 μm and under size range. Increase in spore size in both bryophytes and vascular plants can be seen as an adaptation to reduction in dispersal potential (Carlquist 1966; Mogensen 1981) with apparently small differences in size being biologically significant. The loss of dispersal potential would contribute to the build-up of populations exploiting a wider variety of local habitats than the earlier spore producers, particularly as the number of adaptations for terrestrial life increased in the vascular sporophyte.

Fossil spores of the Late Silurian display many individual morphological novelties in sculpture patterns and in aspects of the laesurae. There is also less uniformity in spore assemblages: assemblages from North Africa are distinct from those of Gotland, suggesting the beginnings of biogeographical differentiation.

Vascular sporophytes of this interval have some of the morphological adaptations on which selection could begin to act. Competitive interaction due to increasing density stress as populations increased in size would be a powerful selective force on those sporophytes with the developing capacity to exploit drier, more marginal environments.

The adaptations of the earliest land plants had to do with selection pressures related to non-biological environmental stresses. For them dispersal and establishment were more critical than adaptability to a wide variety of habitats. Later populations were beginning to have adaptations related to selection pressures correlated with competition and biological interactions. As these came to play an increasing part in the selective forces affecting the vascular plant sporophyte, an increasing number of finer adaptations to land life became necessary. Competitive interaction made advantageous adaptation to new habitats.

6. Summary

The first adaptive radiation of plants onto the land occurred in the mid Ordovician. During the interval from the mid Ordovician to the mid-late Early Silurian, land plants are represented by distinctive spore assemblages consisting of obligate tetrahedral spore tetrads, some smooth-walled, others enveloped in a perisporal membrane or sac; minor numbers of smooth-walled, single trilete spores (in the post-Ordovician); cuticle fragments, and towards the end of the interval, tracheid-like tubes. The spore tetrads find morphological analogues in spore tetrads produced by some extant hepatics and to a much lesser extent extant mosses; the tetrad configuration may have been more common, however, among earlier bryophytes as previously noted. No living vascular plants produce spores with the morphologies of the fossil specimens, although smooth-walled tetrahedral tetrads found in sporangia of early vascular plants may indicate that the tetrad configuration was also common in early vascular plants.

These land plants appear to have had a number of reproductive strategies adaptive for pioneer, opportunistic colonists. These include: (i) the extremely small size of the spore tetrads:

close to the computed optimal dispersal size for wind-dispersed spores; (ii) production of spore tetrads in large numbers, as a corollary to small size; (iii) development of male and female gametophytes from the same spore tetrad, which provided the distributional and ecological advantage of monoeciousness, but the evolutionary advantages of dioeciousness.

Other life history strategies deduced for these organisms from analogy with hepatics, also advantageous for opportunistic colonists, include varied adaptations for dealing with environmental stresses, which would have been more limiting than minimal biological stresses. I see these as including a greatly abbreviated vegetative cycle from spore to spore, telescoped to take advantage of ephemeral water supply, similar to the life style found among the so-called 'annual shuttle' and 'fugitive' species of bryophytes of temporary habitats and the potential for extreme desiccation tolerance, a major ecophysiological adaptation in bryophytes. Desiccation tolerance and an ephemeral life style would appear to be valuable primitive life history strategies: both retained by gametophytes of some bryophytes and vascular plants.

The wide dispersal of the fossil spores suggests that these plants were optimal founder populations. The limited variability in spore morphologies suggests low taxonomic diversity. Reproductive strategies involving sibling gametophytes are consistent with low genetic variability.

The second adaptive radiation began in the mid-late Early Silurian with the dominance of single trilete spore assemblages. The first such assemblages had limited morphological variability, being mostly smooth-walled spores. Later, in the Upper Silurian, more elaborate spore coat and laesurae morphologies appeared. These assemblages included spore tetrads morphologically distinct from earlier forms, plus cuticle scraps, and common tracheid-like tubes. Single trilete spore assemblages find morphological counterparts in spores produced by vascular plants, and only to a minor extent with those produced by living bryophytes.

Single spores had sizes comparable to spores of modern homosporous vascular plants; most were considerably larger than the earlier tetrads. Increase in spore tetrad size, which culminated in single trilete spores in the 30–60 μm size range is believed to be an adaptation to overall decreased dispersal potential and production of spores in smaller numbers. Gametophytes developed from these single spores probably had the potential for bisexuality, but like gametophytes of extant vascular cryptogams (and bryophytes) were probably also sexually opportunistic in relation to habitat, population density stresses and longevity. Population size increased as a consequence of more limited spore dispersal in conjunction with greater ecological adaptability of the vascular sporophyte. As habitats became more stable with increase in vegetation cover, outbreeding doubtless became a more common phenomenon, with fuller expression of heterozygosity, although selfing would still have prevailed where population density was low.

As population sizes increased at available, colonizable habitats, competitive interaction due to increasing density stress would have provided a powerful selective force on vascular sporophytes with the developing capacity to exploit more marginal and drier habitats.

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REFERENCES

Axelrod, D. I. 1959 Evolution of the psilophyte paleoflora. *Evolution* **13**, 264–275.

Banks, H. P. 1968*a* The stratigraphic occurrence of early land plants and its bearing on their origin. In *International symposium on the Devonian System, Calgary 1967*, vol. II (ed. D. H. Oswald), pp. 721–730. Calgary, Canada: Alberta Society of Petroleum Geologists.

Banks, H. P. 1968*b* The early history of land plants. In *Evolution and environment* (ed. E. T. Drake), pp. 73–107. New Haven and London: Yale University Press.

Banks, H. P. 1972 The stratigraphic occurrence of early land plants. *Palaeontology* **15**, 363–375.

Banks, H. P. 1973 Occurrence of *Cooksonia*, the oldest vascular land plant macrofossil, in the Upper Silurian of New York State. *J. Indian Bot. Soc. Golden Jubilee Volume* **50A**, 227–235.

Banks, H. P. 1975*a* The oldest vascular land plants: a note of caution. *Rev. Palaeobot. Palynology* **20**, 13–25.

Banks, H. P. 1975*b* Early vascular land plants: proof and conjecture. *BioScience* **25**, 730–737.

Banks, H. P. 1975*c* Palaeographic implications of some Silurian–Early Devonian floras. In *Gondwana geology* (Papers Presented at the Third Gondwana Symposium, Canberra, Australia 1973) (ed. K. S. W. Campbell), pp. 75–97. Canberra: Australian National University Press.

Banks, H. P. 1977 Plant macrofossils. In *The Silurian–Devonian boundary* (Final Report of the Committee on the Silurian–Devonian Boundary within IUGS Commission on Stratigraphy and a state of the art report for Project Ecostratigraphy) (ed. A. Martinsson), pp. 298–300. International Union of Geol. Sci., Series A, no. 5. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Banks, H. P. 1980 Floral assemblages in the Siluro–Devonian. In *Biostratigraphy of fossil plants* (*successional and paleoecological analyses*) (ed. D. L. Dilcher & T. N. Taylor), pp. 1–24. Stroudsburg, Pennsylvania: Dowden, Hutchinson & Ross, Inc.

Bär, P. & Riegel, W. 1980 Mikrofloren des höchsten Ordovizium bis tiefen Silurs aus der Unteren Sekondi-Serie von Ghana (Westafrika) und ihre Beziehung zu dem Itaim-Schichten des Maranhao-Beckens in NE-Brasilien. *N. Jb. Geol. Paläont. Abh.* **160**, 42–60.

Berry, E. W. 1945 The beginnings and history of land plants. *Johns Hopkins Univ. Stud. Geol.* **14**, 9–91.

Bewley, J. D. 1979 Physiological aspects of desiccation tolerance. *Ann. Rev. Pl. Physiol.* **30**, 195–238.

Bischler, H. & Jovet-Ast, S. 1981 The biological significance of morphological characters in Marchantiales (Hepaticae). *The Bryologist* **84**, 208–215.

Boros, Á. & Járai-Komlódi, M. 1975 *An atlas of Recent European moss spores*. Budapest: Akademiai Kiado. 466 pages.

Boucot, A. J. & Gray, J. 1982 Geologic correlates of early land plant evolution. *Third North American Paleontological Convention, Proceedings*, vol. 1, August, 1982, pp. 61–66.

Bower, F. O. 1908 *The origin of a land flora*. London: Macmillan and Co., Limited. 727 pages.

Bower, F. O. 1959 *Primitive land plants, also known as the Archegoniatae*. New York: Hafner Publishing Co. 658 pages. (Originally published in 1935.)

Brown, R. C. & Lemmon, B. E. 1984 Spore wall development in *Andreaea* (Musci: Andreaeopsida). *Am. J. Bot.* **71**, 412–420.

Campbell, E. O. 1959 The structure and development of *Calobryum gibbsiae* Steph. *Trans. R. Soc. New Zealand* **87**, 243–254.

Carlquist, S. 1966 The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. *Brittonia* **18**, 310–335.

Chaloner, W. G. 1970 The rise of the first land plants. *Biol. Rev.* **45**, 353–377.

Chaloner, W. G. & Orbell, G. 1971 A palaeobiological definition of sporopollenin. In *Sporopollenin* (ed. J. Brooks, P. R. Grant, M. Muir, P. van Gijzel & G. Shaw), pp. 273–294. London and New York: Academic Press.

Chaloner, W. G. & Sheerin, A. 1979 Devonian macrofloras. In *The Devonian System* (ed. M. R. House, C. T. Scrutton & M. G. Bassett), Special Papers in Palaeontology no. 23, pp. 145–161. London: The Palaeontological Association.

Clarke, G. C. S. 1979 Spore morphology and bryophyte systematics. In *Bryophyte systematics* (ed. G. C. S. Clarke & J. G. Duckett), The Systematics Association special volume no. 14, pp. 231–250. London and New York: Academic Press.

Cousens, M. I. 1979 Gametophyte ontogeny, sex expression, and genetic load as measures of population divergence in *Blechnum spicant*. *Am. J. Bot.* **66**, 116–132.

Cousens, M. I. 1981 *Blechnum spicant*: habitat and vigor of optimal, marginal, and disjunct populations, and field observations of gametophytes. *Bot. Gaz.* **142**, 251–258.

Cousens, M. I. & Horner, H. T., Jr. 1970 Gametophyte ontogeny and sex expression in *Dryopteris ludoviciana*. *Am. Fern J.* **60**, 13–27.

Crosby, M. R. 1980 The diversity and relationships of mosses. In *The mosses of North America* (ed. R. J. Taylor & A. E. Leviton), pp. 115–129. San Francisco, California: Pacific Division/American Association for the Advancement of Science.

Crum, H. 1972 The geographic origins of the mosses of North America's eastern deciduous forest. *J. Hattori Bot. Lab.* no. **35**, 269–298.

Doyle, W. T. 1970 *The biology of higher cryptogams*. London: The Macmillan Company, Collier-Macmillan Limited. 163 pages.

Doyle, W. T. 1975 Spores of *Sphaerocarpos donnellii*. *The Bryologist* **78**, 80–84.

Duckett, J. G. & Duckett, A. R. 1980 Reproductive biology and population dynamics of wild gametophytes of *Equisetum*. *Bot. J. Linn. Soc.* **80**, 1–40.

During, H. J. 1979 Life strategies of bryophytes: a preliminary review. *Lindbergia* **5**, 2–18.

Duthie, A. V. & Garside, S. 1936 Studies in South African Ricciaceae. I. Three annual species: *R. plana* Taylor, *R. cupilifera* sp.nov., and *R. curtisii* T. P. James. *Trans. R. Soc. S. Afr.* **24**, 93–133.

Edwards, D. 1980 Early land floras. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), The Systematics Association special volume no. 15, pp. 55–85. London and New York: Academic Press.

Edwards, D. 1982 Fragmentary non-vascular plant microfossils from the late Silurian of Wales. *Bot. J. Linn. Soc.* **84**, 223–256.

Erdtman, G. 1965 *Pollen and spore morphology/plant taxonomy: Gymnospermae, Bryophyta* (*text*) (*An introduction to palynology, III*). Stockholm: Almqvist & Wiksell. 191 pages.

Faegri, K. & Iversen, J. 1975 *Textbook of pollen analysis*. 3rd edn. New York: Hafner Press, A Division of Macmillan Publishing Co., Inc. 295 pages.

Graham, L. E. 1984 Coleochaete and the origin of land plants. *Am. J. Bot.* **71**, 603–608.

Gray, J. 1985 Ordovician–Silurian land plants: the interdependence of ecology and evolution. *Spec. pap. Palaeont.* (In the press.)

Gray, J. & Boucot, A. J. 1971 Early Silurian spore tetrads from New York: earliest New World evidence for vascular plants? *Science, Wash.* **173**, 918–921.

Gray, J. & Boucot, A. J. 1972 Palynological evidence bearing on the Ordovician–Silurian paraconformity in Ohio. *Geol. Soc. Am. Bull.* **83**, 1299–1314.

Gray, J. & Boucot, A. J. 1977 Early vascular land plants: proof and conjecture. *Lethaia* **10**, 145–174.

Gray, J. & Boucot, A. J. 1979 The Devonian land plant *Protosalvinia*. *Lethaia* **12**, 57–63.

Gray, J., Laufeld, S. & Boucot, A. J. 1974 Silurian trilete spores and spore tetrads from Gotland: their implications for land plant evolution. *Science, Wash.* **185**, 260–263.

Gray, J., Massa, D. & Boucot, A. J. 1982 Caradocian land plant microfossils from Libya. *Geology* **10**, 197–201.

Hébant, C. 1977 *The conducting tissues of bryophytes*. Vaduz: J. Cramer. 157 pages.

Høeg, O. A. 1942 The Downtonian and Devonian flora of Spitsbergen. *Norges Svalbard- og Ishavs-Undersøk.* **83**, 1–228.

Holbrook-Walker, S. G. & Lloyd, R. M. 1973 Reproductive biology and gametophyte morphology of the Hawaiian fern genus *Sadleria* (Blechnaceae) relative to habitat diversity and propensity for colonization. *Bot. J. Linn. Soc.* **67**, 157–174.

Horton, D. G. 1983 A revision of the Encalyptaceae (Musci), with particular reference to the North American taxa. Part II. *J. Hattori Bot. Lab. no.* **54**, 353–532.

Inoue, H. 1960 Studies in spore germination and the earlier stages of gametophyte development in the Marchantiales. *J. Hattori Bot. Lab. no.* **23**, 148–191.

Ishchenko, T. A. & Shlyakov, R. N. 1979 Middle Devonian liverworts (Marchantiidae) from Podolia. *Paleont. J.* **13**, 369–380.

Jaeger, H. 1966 Two late *Monograptus* species from Victoria, Australia, and their significance for dating the *Baragwanathia* flora. *Proc. R. Soc. Victoria* **79**, 393–413.

Jaeger, H. 1967 Preliminary stratigraphical results from graptolite studies in the Upper Silurian and Lower Devonian of southeastern Australia. *J. geol. Soc. Australia* **14**, 281–286.

Jeffrey, C. 1962 The origin and differentiation of the archegoniate land-plants. *Bot. Notiser* **115**, 446–454.

Klekowski, E. J., Jr 1979 The genetics and reproductive biology of ferns. In *The experimental biology of ferns* (ed. A. F. Dyer), pp. 133–170. London and New York: Academic Press.

Krassilov, V. 1981 *Orestovia* and the origin of vascular plants. *Lethaia* **14**, 235–250.

Lacey, W. S. 1969 Fossil bryophytes. *Biol. Rev.* **44**, 189–205.

Lang, W. H. 1937 On the plant-remains from the Downtonian of England and Wales. *Phil. Trans. R. Soc. Lond.* B **227**, 245–291.

Lang, W. H. & Cookson, I. C. 1935 On a flora, including vascular land plants, associated with *Monograptus*, in rocks of Silurian age, from Victoria, Australia. *Phil. Trans. R. Soc. Lond.* B **224**, 421–449.

Leclercq, S. 1954 Are the Psilophytales a starting or a resulting point? *Svensk bot. Tidskr.* **48**, 301–315.

Longton, R. E. 1976 Reproductive biology and evolutionary potential in bryophytes. *J. Hattori Bot. Lab. no.* **41**, 205–223.

Longton, R. E. & Miles, C. J. 1982 Studies on the reproductive biology of mosses. *J. Hattori Bot. Lab. no.* **52**, 219–240.

Longton, R. E. & Schuster, R. M. 1983 Reproductive biology. In *New manual of bryology* (ed. R. M. Schuster), vol. 1, pp. 386–462. Japan: The Hattori Botanical Laboratory.

Lundblad, B. 1954 Contributions to the geological history of the Hepaticae. Fossil Marchantiales from the Rhaetic–Liassic coal mines of Skromberga (Prov. of Scania), Sweden. *Svensk. bot. Tidskr.* **48**, 381–417.

Lyon, A. G. 1962 On the fragmentary remains of an organism referable to the Nematophytales, from the Rhynie Chert, *Nematoplexus rhyniensis* gen.et sp.nov. *Trans. R. Soc. Edinb.* **65**, 79–87.

Mehra, P. N. & Kachroo, P. 1952 Sporeling germination studies in Marchantiales II. *Stephensoniella brevipedunculata* Kash. *The Bryologist* **55**, 59–64.

Miller, M. A. & Eames, L. E. 1982 Palynomorphs from the Silurian Medina Group (lower Llandovery) of the Niagara Gorge, Lewiston, New York, U.S.A. *Palynology* **6**, 221–254.

Mogensen, G. S. 1981 The biological significance of morphological characters in bryophytes: the spore. *The Bryologist* **84**, 187–207.

Niklas, K. J. & Pratt, L. M. 1980 Evidence for lignin-like constituents in early Silurian (Llandoverian) plant fossils. *Science, Wash.* **209**, 396–397.

Page, C. N. 1979 Experimental aspects of fern ecology. In *The experimental biology of ferns* (ed. A. F. Dyer), pp. 552–589. London and New York: Academic Press.

Pratt, L. M., Phillips, T. L. & Dennison, J. M. 1978 Evidence of non-vascular land plants from the early Silurian (Llandoverian) of Virginia, U.S.A. *Rev. Palaeobot. Palynology* **25**, 121–149.

Proskauer, J. 1954 On *Sphaerocarpos stipitatus* and the genus *Sphaerocarpos*. *J. Linn. Soc. Bot.* **55**, 143–157.

Proskauer, J. 1961 On *Carrpos* I. *Phytomorphology* **11**, 359–378.

Ramsay, H. P. & Berrie, G. K. 1982 Sex determination in bryophytes. *J. Hattori Bot. Lab. no.* **52**, 255–274.

Richardson, J. B. & Ioannides, N. 1973 Silurian palynomorphs from the Tanezzuft and Acacus Formations, Tripolitania, North Africa. *Micropaleontology* **19**, 257–307.

Richardson, J. B. & Lister, T. R. 1969 Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology* **12**, 201–252.

Schopf, J. M., Mencher, E., Boucot, A. J. & Andrews, H. N. 1966 Erect plants in the early Silurian of Maine. *Prof. Paper U.S. Geol. Surv.* **550-D**, D69–D75.

Schopf, J. W. 1970 Precambrian micro-organisms and evolutionary events prior to the origin of vascular plants. *Biol. Rev.* **45**, 319–352.

Schuster, R. M. 1966 *The Hepaticae and Anthocerotae of North America*, vol. 1. New York and London: Columbia University Press. 802 pages.

Schuster, R. M. 1967 Studies on Hepaticae XV. Calobryales. *Nova Hedwigia* **13**, 1–76.

Schuster, R. M. 1979 The phylogeny of the Hepaticae. In *Bryophyte systematics* (ed. G. C. S. Clarke & J. G. Duckett), The Systematics Association special volume no. 14, pp. 41–82. London and New York: Academic Press.

Schuster, R. M. 1981 Paleoecology, origin, distribution through time, and evolution of Hepaticae and Anthocerotae. In *Paleobotany, paleoecology, and evolution* (ed. K. J. Niklas), pp. 129–191. New York: Praeger.

Scott, D. H. 1920 *Studies in fossil botany*, vol. 1 (*Pteridophyta*), 3rd edn. London: A. and C. Black Ltd. 434 pages.

Scott, G. A. M. 1982 Desert bryophytes. In *Bryophyte ecology* (ed. A. J. E. Smith), pp. 105–122. London and New York: Chapman and Hall.

Sherwood-Pike, M. A. & Gray, J. 1985 Silurian fungal remains: Oldest records of the Class Ascomycetes? *Lethaia*. (In the press.)

Shumm, S. A. 1968 Speculations concerning paleohydrologic controls of terrestrial sedimentation. *Geol. Soc. Am. Bull.* **79**, 1573–1588.

Siler, M. B. 1934 Development of spore walls in *Sphaerocarpos donnellii*. *Bot. Gaz.* **95**, 563–591.

Slack, N. G. 1982 Bryophytes in relation to ecological niche theory. *J. Hattori Bot. Lab. no.* **52**, 199–217.

Smith, A. J. E. 1982 Epiphytes and epiliths. In *Bryophyte ecology* (ed. A. J. E. Smith), pp. 191–227. London and New York: Chapman and Hall.

Smith, D. G. 1979 The distribution of trilete spores in Irish Silurian rocks. In *The Caledonides of the British Isles – reviewed* (ed. A. L. Harris, C. H. Holland & B. E. Leake), pp. 423–431. London: Geological Society of London.

Sporne, K. R. 1965 *The morphology of gymnosperms: the structure and evolution of primitive seed-plants*. London: Hutchinson University Library. 216 pages.

Stotler, R. & Crandall-Stotler, B. 1977 A checklist of the liverworts and hornworts of North America. *The Bryologist* **80**, 405–428.

Strother, P. K. & Traverse, A. 1979 Plant microfossils from Llandoverian and Wenlockian rocks of Pennsylvania. *Palynology* **3**, 1–21.

Taylor, J., Hollingsworth, P. J. & Bigelow, W. C. 1974 Scanning electron microscopy of liverwort spores and elaters. *The Bryologist* **77**, 281–327.

Tryon, R. 1970 Development and evolution of fern floras of oceanic islands. *Biotropica* **2**, 76–84.

Van Zanten, B. O. 1978 Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern Hemisphere. *J. Hattori Bot. Lab. no.* **44**, 455–482.

Vavrdova, M. 1982 Recycled acritarchs in the uppermost Ordovician of Bohemia. *Casopis pro mineralogii a geologii* **27**, 337–345.

Vitt, D. H. 1981 Adaptive modes of the moss sporophyte. *The Bryologist* **84**, 166–186.

Walker, T. G. 1979 The cytogenetics of ferns. In *The experimental biology of ferns* (ed. A. F. Dyer), pp. 87–132. London and New York: Academic Press.

Watson, E. V. 1968 *The structure and life of bryophytes*. 2nd edn. London: Hutchinson University Library. 192 pages.

Wyatt, R. 1982 Population ecology of bryophytes. *J. Hattori Bot. Lab. no.* **52**, 179–198.

Discussion

W. G. CHALONER, F.R.S. (*Department of Botany, Royal Holloway and Bedford Colleges, Huntersdale, Virginia Water, Surrey, U.K.*). It seems to me important in this context to emphasize that resistant spores formed in tetrads are not necessarily indicative of a land plant (vascular plant or bryophyte). The Devonian fossil, *Protosalvinia* (*Foerstia* of many authors) has spores formed in tetrads and showing clear triradiate marks; yet despite the view expressed by Dr Gray, several other recent authors (Niklas & Phillips 1976; Schopf & Schwietering 1970) agree in regarding it, on good grounds, as an aquatic plant (regardless of its affinity).

I think there is also a hazard in seeing the adhesion of spore tetrads as an indicator of hepatic affinity. The spores of a number of vascular plants, of diverse relationship, also occur in cohering tetrads, no doubt in response to equally diverse selective pressures (for example, in the flowering plants, in the Ericaceae and Droseraceae). We should be cautious in seeing hepatic affinity on the basis of this feature alone.

References

Niklas, K. J. & Phillips, T. L. 1976 Morphology of *Protosalvinia* from the Upper Devonian of Ohio and Kentucky. *Am. J. Bot.* **63**, 9–29.

Schopf, J. M. & Schwietering, J. F. 1970 The *Foerstia* Zone of the Ohio and Chattanooga Shales. *U.S. Geol. Surv. Bull.* **1294-H**, 1–15.

J. GRAY. Professor Chaloner uses one plant, the anomalous late Devonian *Protosalvinia* as the basis for a sweeping generalization that 'resistant spores formed in tetrads are not necessarily indicative of a land plant...'. The affinities of *Protosalvinia* (which Chaloner does not discuss) and the environmental implications of this plant have been considered in detail by Gray & Boucot (1979; see also Gray & Boucot 1977, pp. 158–162) after reviewing all evidence and all the literature related to this enigmatic plant. They conclude that *Protosalvinia* could only have been a land plant for reasons related to its morphology, anatomy, biochemistry, type of preservation plus evidence that its remains had been transported before deposition from what many investigators have seen as a littoral habitat, but from what Gray & Boucot suggested was a supralittoral position. Gray & Boucot (1979) point out that, apart from Schopf & Schwietering's (1970) 'advocacy of a fully marine pelagic environment for *Protosalvinia*, the paleoecology of this organism has long been in less contention than its taxonomic position. Few have failed to suggest at least an amphibious shoreline habitat for *Protosalvinia*, in which extended desiccation was a distinct environmental factor, if not in fact a terrestrial existence'. As for Chaloner's statement that there is agreement between Schopf & Schwietering (1970) and Niklas & Phillips (1976) that *Protosalvinia* was aquatic, I offer in rebuttal the following quotation from papers published by Niklas in 1976 including one coauthored with Chaloner the same year, in the hope that the reader may draw his own conclusions about whether Niklas sees *Protosalvinia* 'as an aquatic plant'.

(i) 'The clustering demonstrated in the chemical compositions of plants showing thick 'cuticle'-like stages of preservation (*Nematothallus*...*Protosalvinia* and possibly *Prototaxites*), cutinized or exined spores (?*Nematothallus*, *Parka* and *Protosalvinia*)...suggest morphological evidence for terrestrial adaptation of taxonomically diverse plants during the Paleozoic' (Niklas 1976*a*, p. 127).

(ii) 'Chemical comparisons between various fossil genera indicates that *Prototaxites* parallels plants thought to have adapted to a terrestrial habit (*Protosalvinia*), as well as the known vascular plant *Taeniocrada*...' (*Niklas* 1976*b*, p. 15).

(iii) '...*Protosalvinia*, *Taeniocrada* and *Prototaxites* appear to have paralleled one another in their adaptation to a terrestrial habit' (Niklas 1976*b*, p. 1).

(iv) '*Taeniocrada* (a known vascular plant), *Protosalvinia* (a proposed brown alga showing adaptation to the land), and *Prototaxites* are similar in the organic constituents isolated from their fossil remains...' (Niklas 1976*b*, p. 15).

(v) 'The isolation of lignin-like residues from *Solenites* [a Jurassic gymnosperm] and *Protosalvinia* and *Taeniocrada* suggests they were associated with land plant metabolism' (Niklas & Chaloner 1976, p. 91).

As Gray & Boucot wrote (1979, p. 60) 'The biochemical data...provided by Niklas (1976*a*, *b*, *c*, *d*); Niklas & Chaloner (1976); and Niklas & Gensel (1976) for *Protosalvinia* appear to be unique. This taxon is isolated from forms that cluster at the algal end of the chemical spectrum as well as from those that cluster at the vascular end of the chemical spectrum, being consistently nearest genera, such as the terrestrial *Prototaxites* and *Nematothallus*, that are intermediate in their chemistries, but not clustering with them. Taken at face value, the data suggest that these and other Early Paleozoic nonvascular plants of diverse affinities were simultaneously exploiting terrestrial habitats'.

Chaloner suggests that because hepatic spores and angiosperm pollen may occur in tetrads that this character provides no evidence for relationships of fossil specimens to hepatics. I find this equivalent to suggesting that because all algae have chlorophylls (and accessory pigments) that the presence of chlorophyll *a* and *b* provides no basis for indicating that a plant is a member of the green algae. A tetrad stage is characteristic of all bryophytes and vascular plants that undergo meiosis at the time of formation of meiospores. The vast majority of meiospores occur as tetrahedral tetrads; the vast majority also do not remain in the tetrad configuration at maturity (none are known for vascular cryptogams or any of the gymnosperms). Obligate tetrads in angiosperms are morphologically wholly unlike obligate tetrads in bryophytes apart from the fact that both are tetrads. In each case their distinctive morphology is an acceptable basis for identifying them as belonging to either angiosperms or bryophytes. In each case, the spore and pollen morphology, including adherence in obligate tetrads, is also a perfectly valid basis for suggesting relationship with other taxa having spores or pollen grains with similar morphology.

Adherence of spores in tetrahedral tetrads is clearly a primitive character among spore-producing land plants judged from the fossil record. As I have elaborated in my paper, I also see the tetrad as a primitive character among hepatics (as indeed have a number of bryologists), and I suggest that the obligate tetrahedral tetrad may have been a more common configuration among both bryophytes and early vascular plants. Obligate smooth-walled tetrahedral tetrads cannot be seen as necessarily providing indication of hepatic affinity. Obligate spore tetrads with a perisporal membrane enclosing the tetrad have a direct morphological analogue among some hepatic spore tetrads and it is on this basis that I suggest the possibility of hepatic affinity for many of the tetrads, not merely on the basis of their occurrence as obligate tetrahedral tetrads.

References

Gray, J. & Boucot, A. J. 1977 Early vascular land plants: proof and conjecture. *Lethaia* **10**, 145–174.

Gray, J. & Boucot, A. J. 1979 The Devonian land plant *Protosalvinia*. *Lethaia* **12**, 57–63.

Niklas, K. J. 1976*a* Chemical examinations of some non-vascular Paleozoic plants. *Brittonia* **28**, 113–137.

Niklas, K. J. 1976*b* Chemotaxonomy of *Prototaxites* and evidence for possible terrestrial adaptation. *Rev. Palaeobot. Palynology* **22**, 1–17.

Niklas, K. J. & Chaloner, W. G. 1976 Chemotaxonomy of some problematic Paleozoic plants. *Rev. Palaeobot. Palynology* **22**, 81–104.

Niklas, K. J. & Phillips, T. L. 1976 Morphology of *Protosalvinia* from the Upper Devonian of Ohio and Kentucky. *Am. J. Bot.* **63**, 9–29.

Schopf, J. M. & Schwietering, J. F. 1970 The *Foerstia* zone of the Ohio and Chattanooga Shales. *U.S. Geol. Surv. Bull.* **1294H**, H1–H15.

Addendum

Although I have stated above that no obligate tetrahedral tetrads are known in modern vascular cryptogams, that statement is not wholly correct. The microspores of a number of species of *Selaginella* may occur as obligate tetrahedral tetrads, although apparently in all cases the relationship is a casual one with the same species also occurring as single spores as well as tetrahedral tetrads (Erdtman & Sorsa 1971; Tryon & Tryon 1982). Tryon & Tryon (1982) note the tendency for adherence of tetrads of spores in *Pteris mutilata* L. and in the monotypic tropical *Hypoderris Brownii* Hook., also apparently casual relationships. In reporting on the presence of tetrads in such morphological studies, it is not certain whether *occurrence* as tetrads necessarily means *dispersal* as tetrads. For example, Selling (1946) notes that the microspores of *Selaginella deflexa* Brack. are 'united in tetrads' but that in 'the fossil state the spores generally occur separated'.

References

Erdtman, G. & Sorsa, P. 1971 *Pollen and spore morphology/plant taxonomy: Pteridophyta* (*text and additional illustrations*) (*An Introduction to Palynology, IV*). Stockholm: Almqvist & Wiksell. 302 pages.

Selling, O. H. 1946 *Studies in Hawaiian pollen statistics. Part I of the Hawaiian pteridophytes*. Honolulu, Hawaii: Bernice P. Bishop Museum, special publication 37.

Tryon, R. M. & Tryon, A. F. 1982 *Ferns and allied plants: with special reference to tropical America*. New York and Heidelberg: Springer-Verlag. 856 pages.

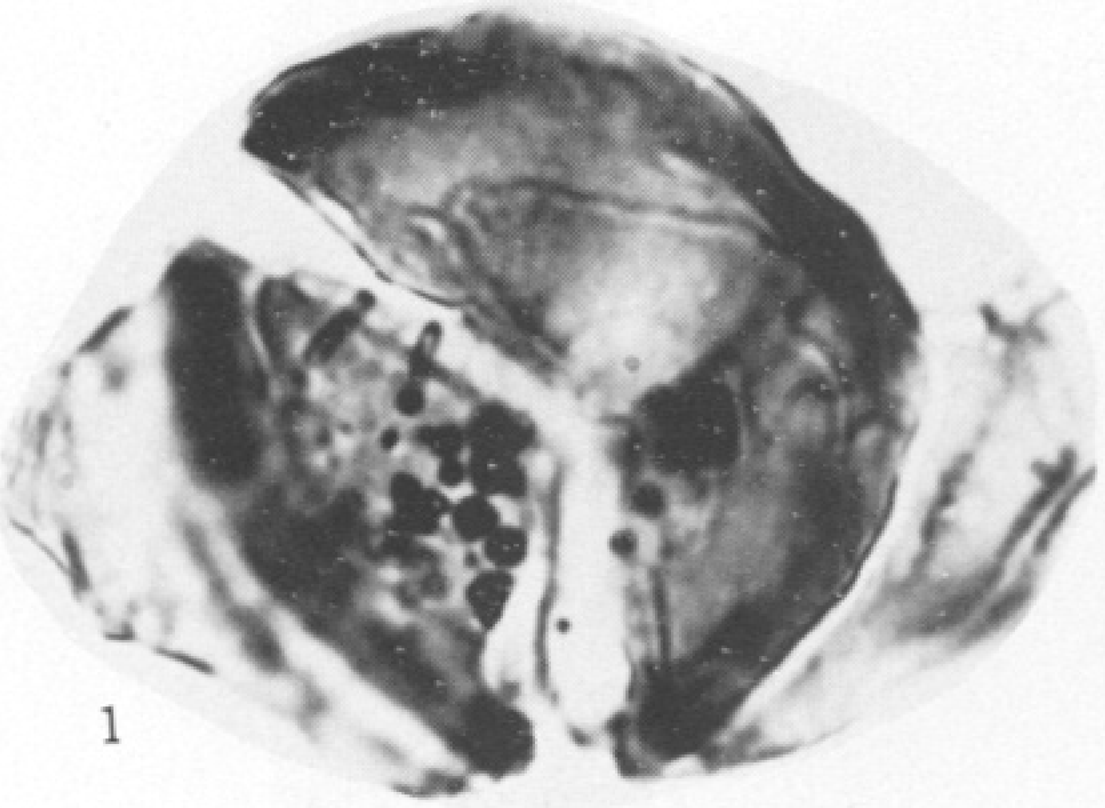
T. S. Westoll, F.R.S. (*Department of Geology, University of Newcastle upon Tyne, Newcastle upon Tyne, NE1 7RU, U.K.*). What is the likelihood that some trilete spores may not belong to land plants? For example, what is the nature of the spores of the rather enigmatic *Parka*?

J. Gray. There is no evidence that trilete spores, now or in the past, belong to plants that do not live on the land. The spores of *Parka* are inaperturate. There 'is no evidence, though this has been repeatedly looked for, that they developed in tetrads' (Lang 1945, p. 544). The evidence with regard to the affinities of durable-walled spores with triradiate marks has been reviewed in detail by Gray & Boucot (1977), after consultation with many algologists. The durable wall in land plant spores is a desiccation resistant adaptation. Land plants that have secondarily returned to the aquatic environment and flower beneath the water lose the durable wall. There is no need for such an adaptation in the spores of aquatic plants. The timing on the break-up of the tetrad unit determines the presence or absence of the triradiate mark. Many bryophyte spores disintegrate from the tetrad early in sporogenesis and have inaperturate spores. Others that stay in contact till late in sporogenesis may have a triradiate mark or a cryptotrilete mark due to the extended pressure of the enlarging spores against one another within a common sporocyte wall. The triradiate spores of vascular cryptogams stay together long enough for the 'scar' (juncture between individual grains) to be impressed in the durable wall. A durable wall is essential for this to happen. There is no evidence for this among aquatic plants (as reviewed by Gray & Boucot 1977) such as algae, even those with tetrad stages. Among algae with a tetrad stage there is either no durable wall on which the 'scar' can be impressed, or the spores split from the tetrad early and round up (leaving no marks on the surface), or the tetrads are not tetrahedral tetrads (a requirement for the presence of the triradiate scar). I refer Professor Westoll to Gray & Boucot (1977, p. 157) where comments are provided by algologists Harold C. Bold, George F. Papenfuss, Walter H. Adey and John L. Wray, with regard to these questions.

References

Gray, J. & Boucot, A. J. 1977 Early vascular land plants: proof and conjecture. *Lethaia* **10**, 145–174.

Lang, W. H. 1945 *Pachytheca* and some anomalous early plants (*Prototaxites*, *Nematothallus*, *Parka*, *Foerstia*, *Orvillea* n.g.). *Bot. J. Linn. Soc.* **52**, 535–552.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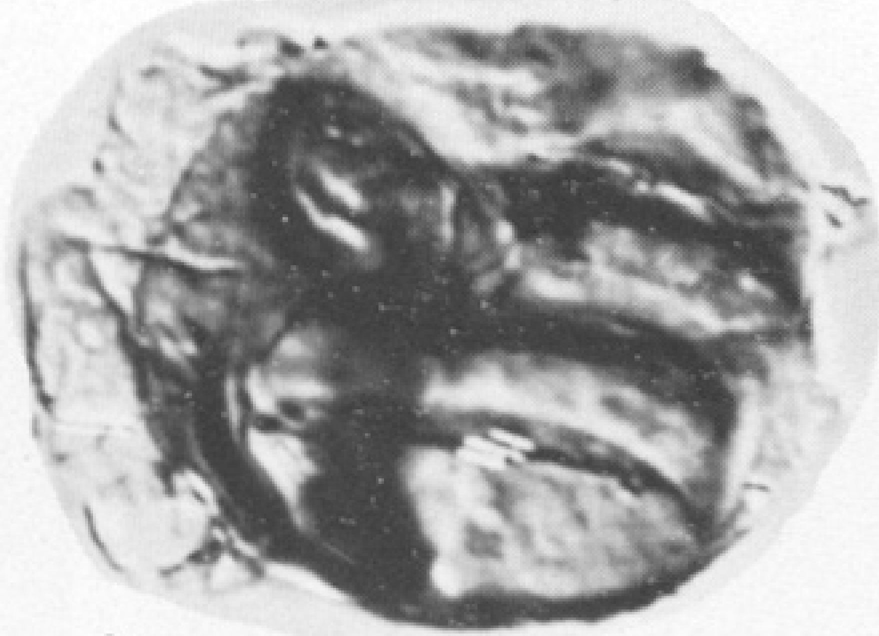
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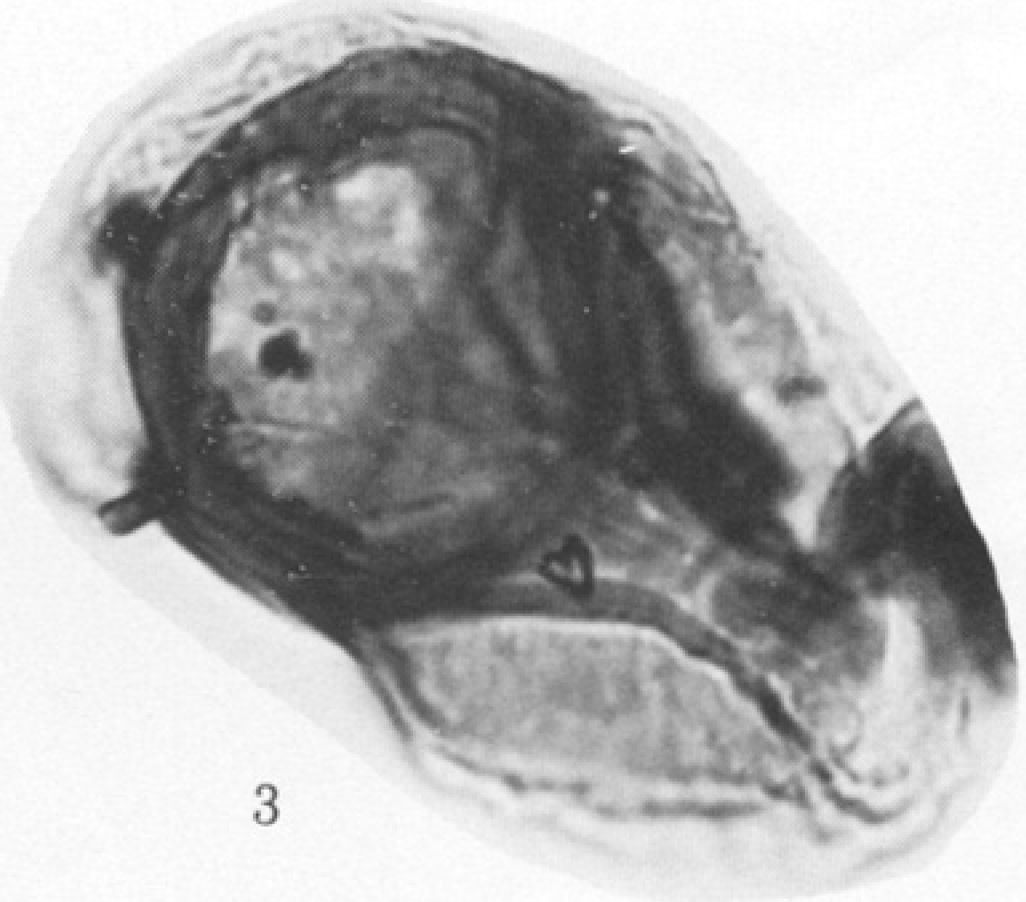
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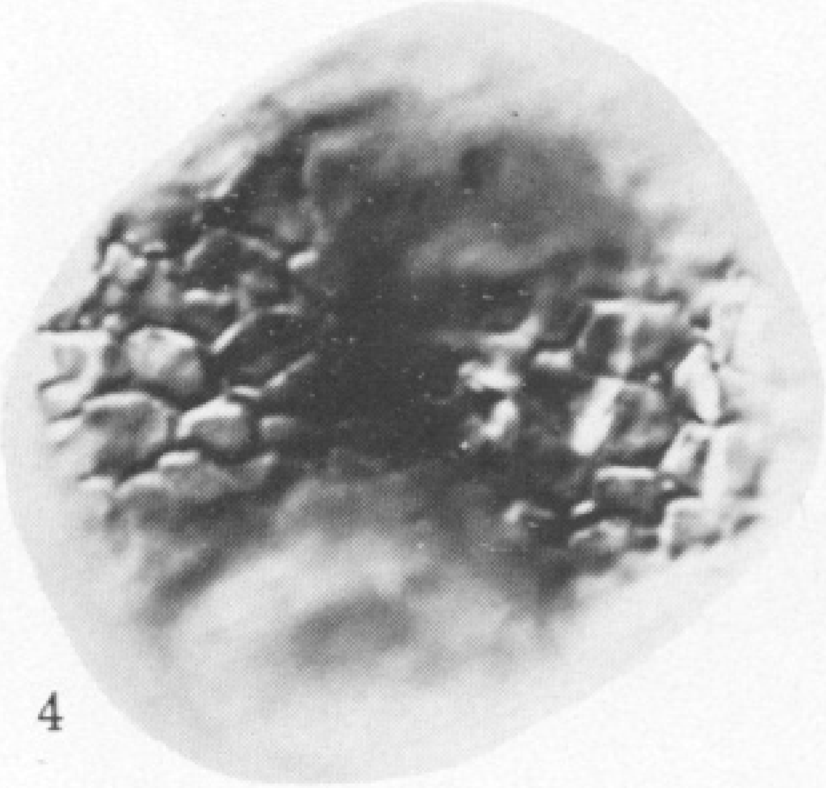
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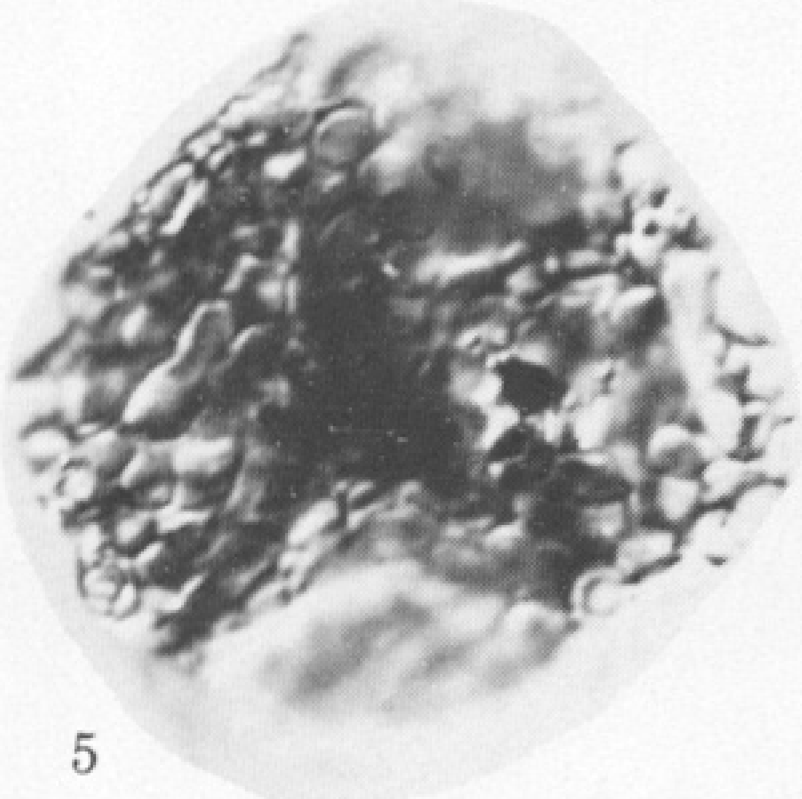
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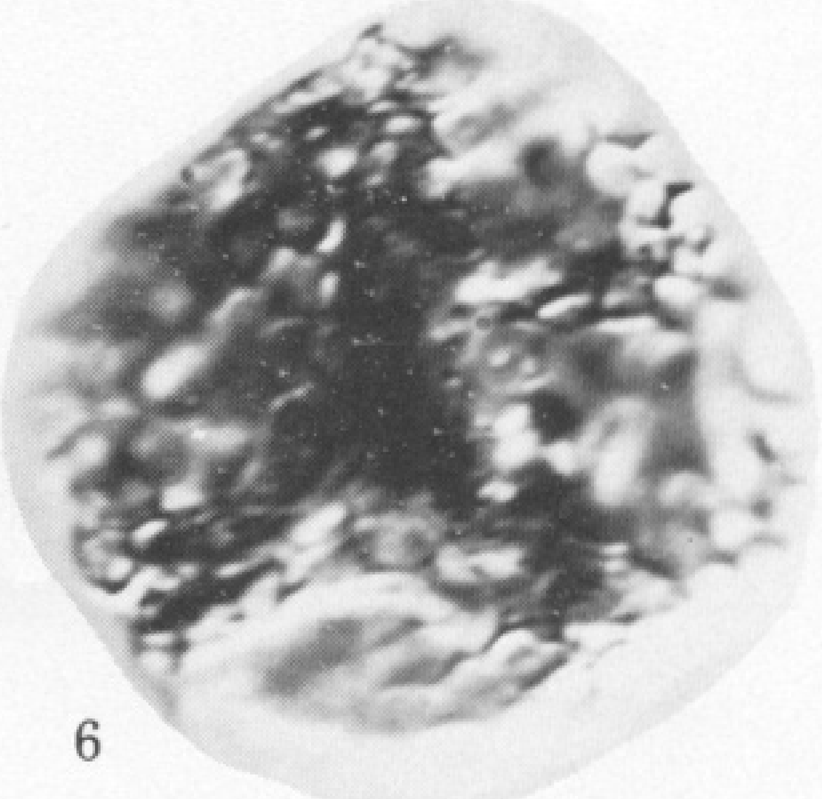
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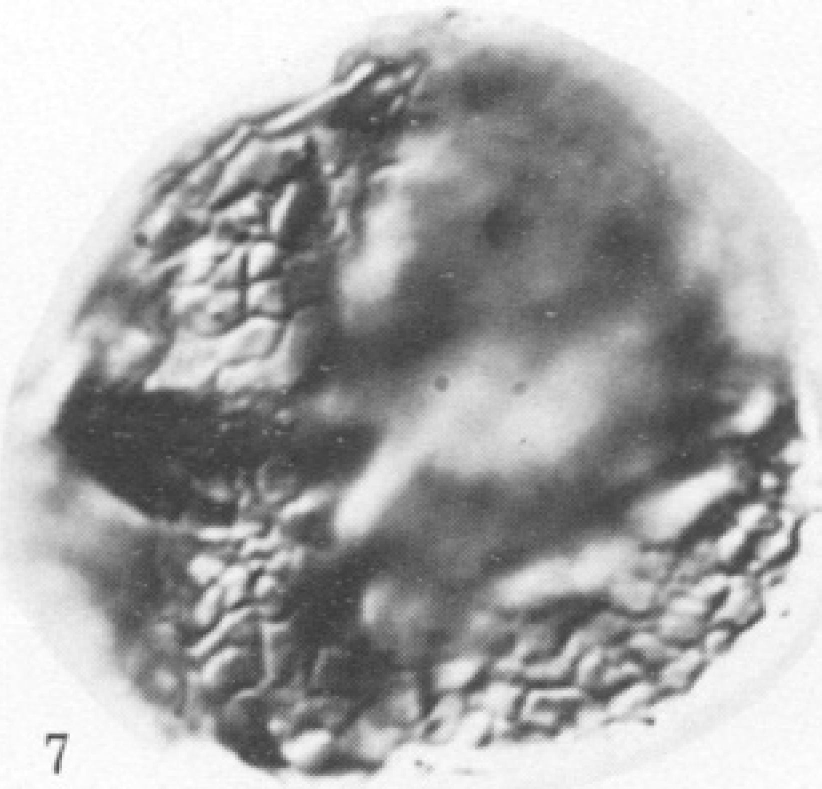
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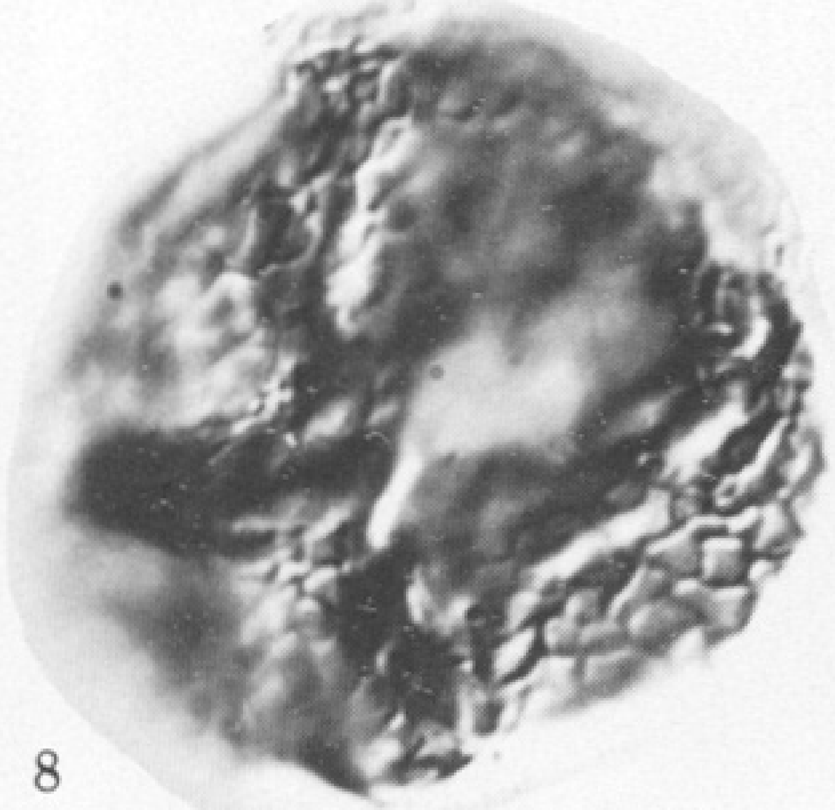
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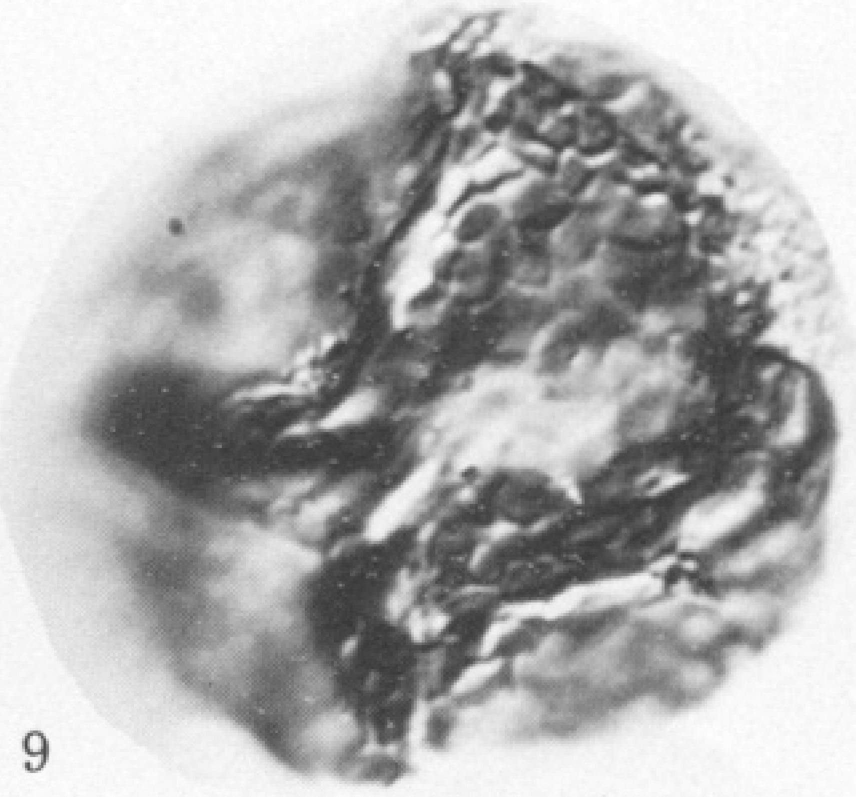
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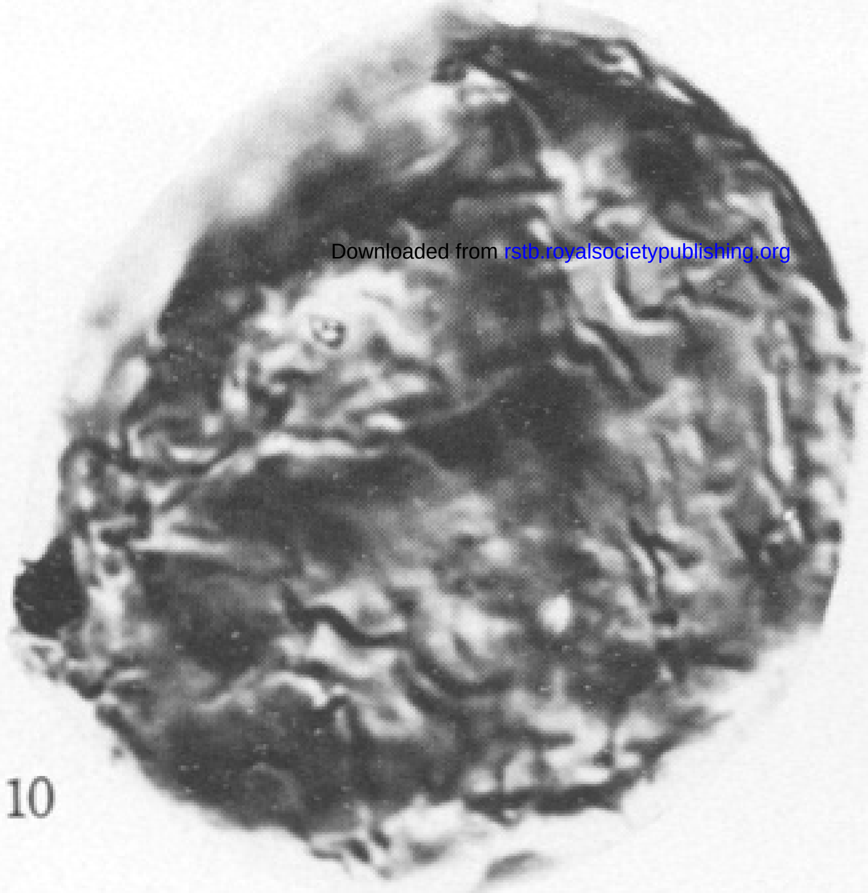
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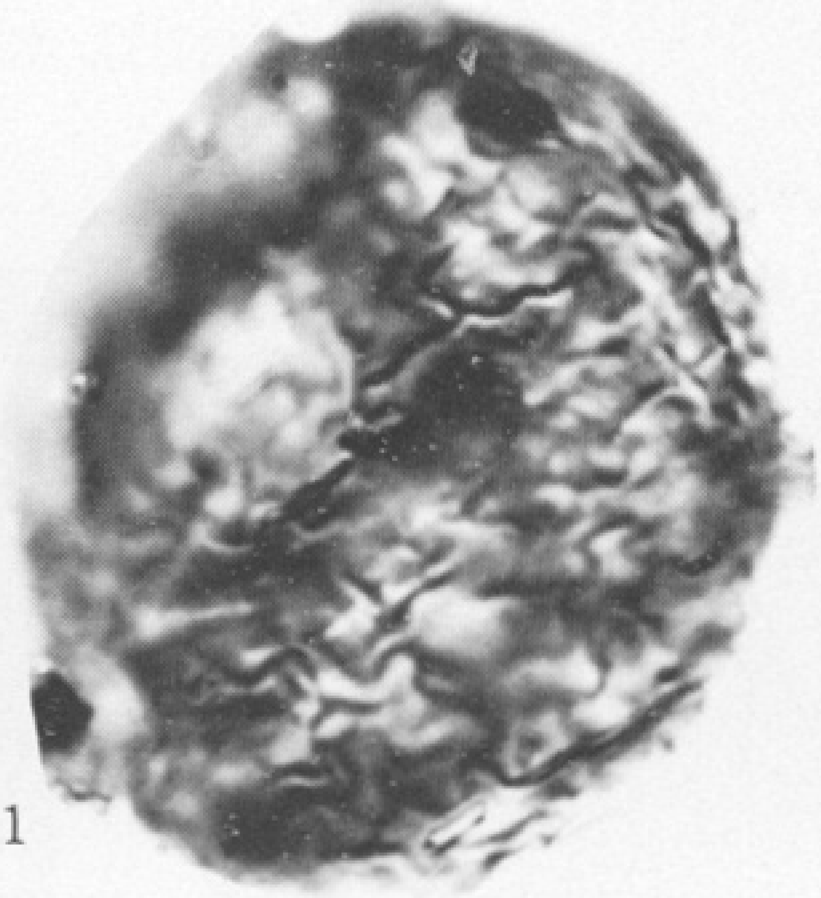
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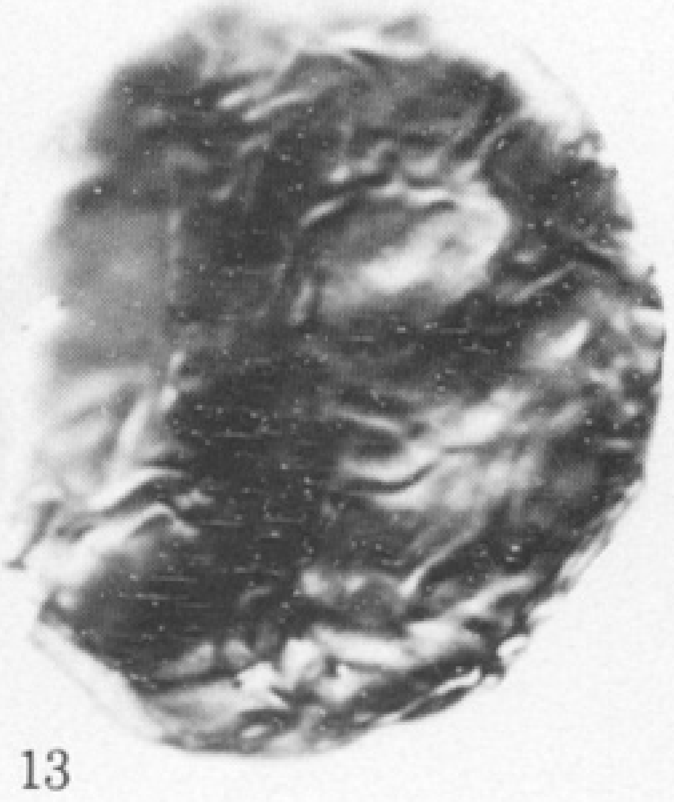
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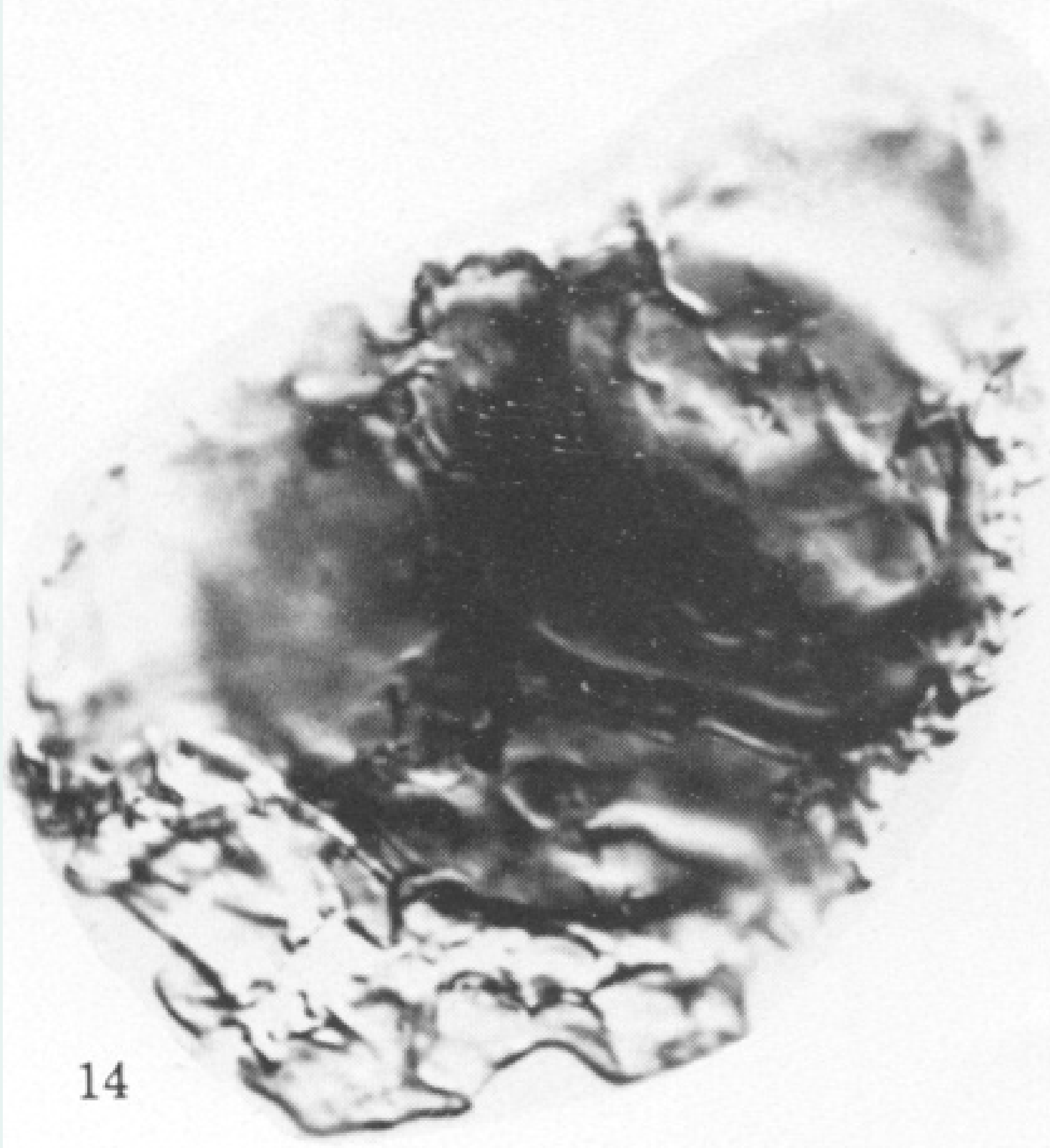
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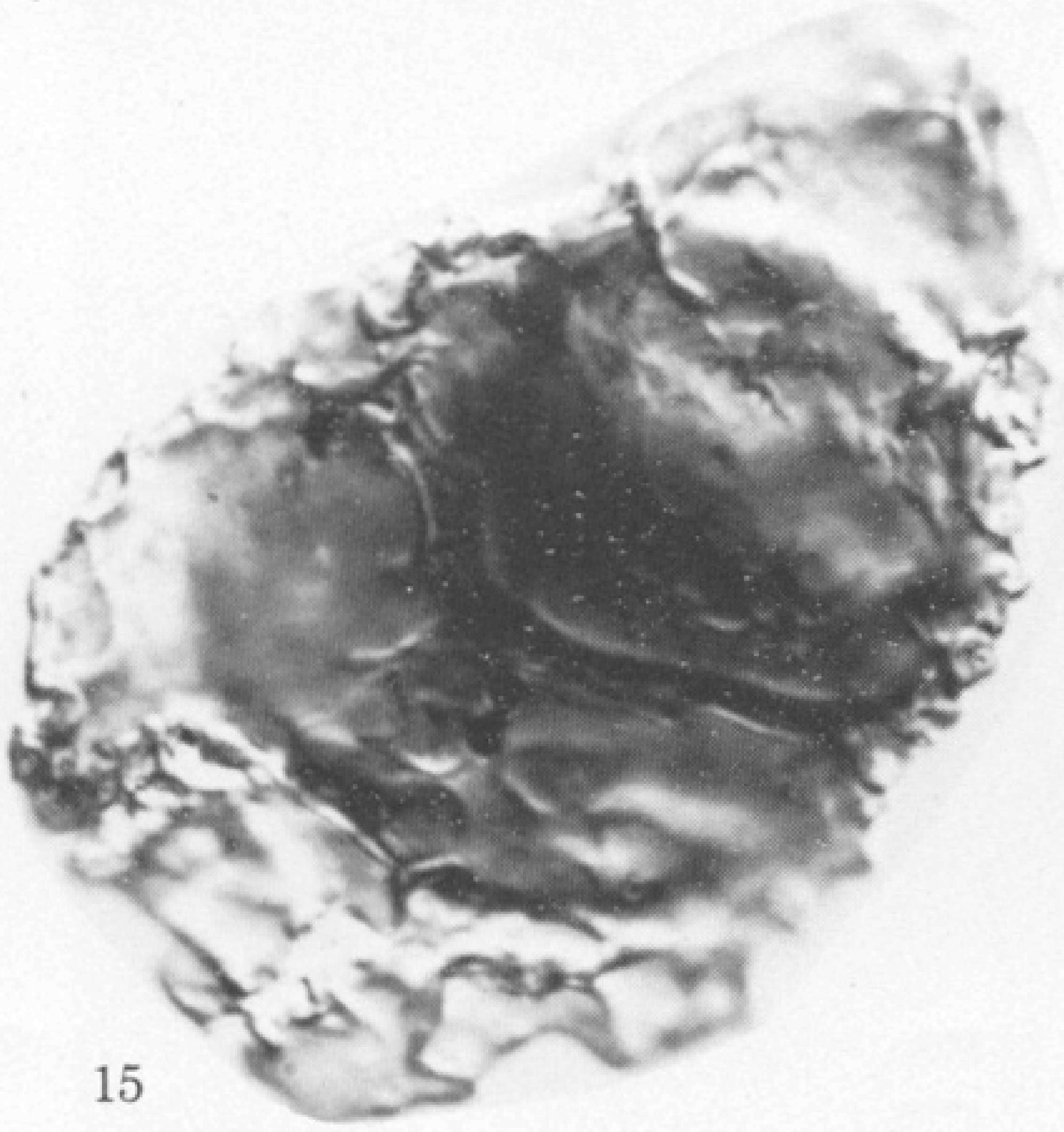
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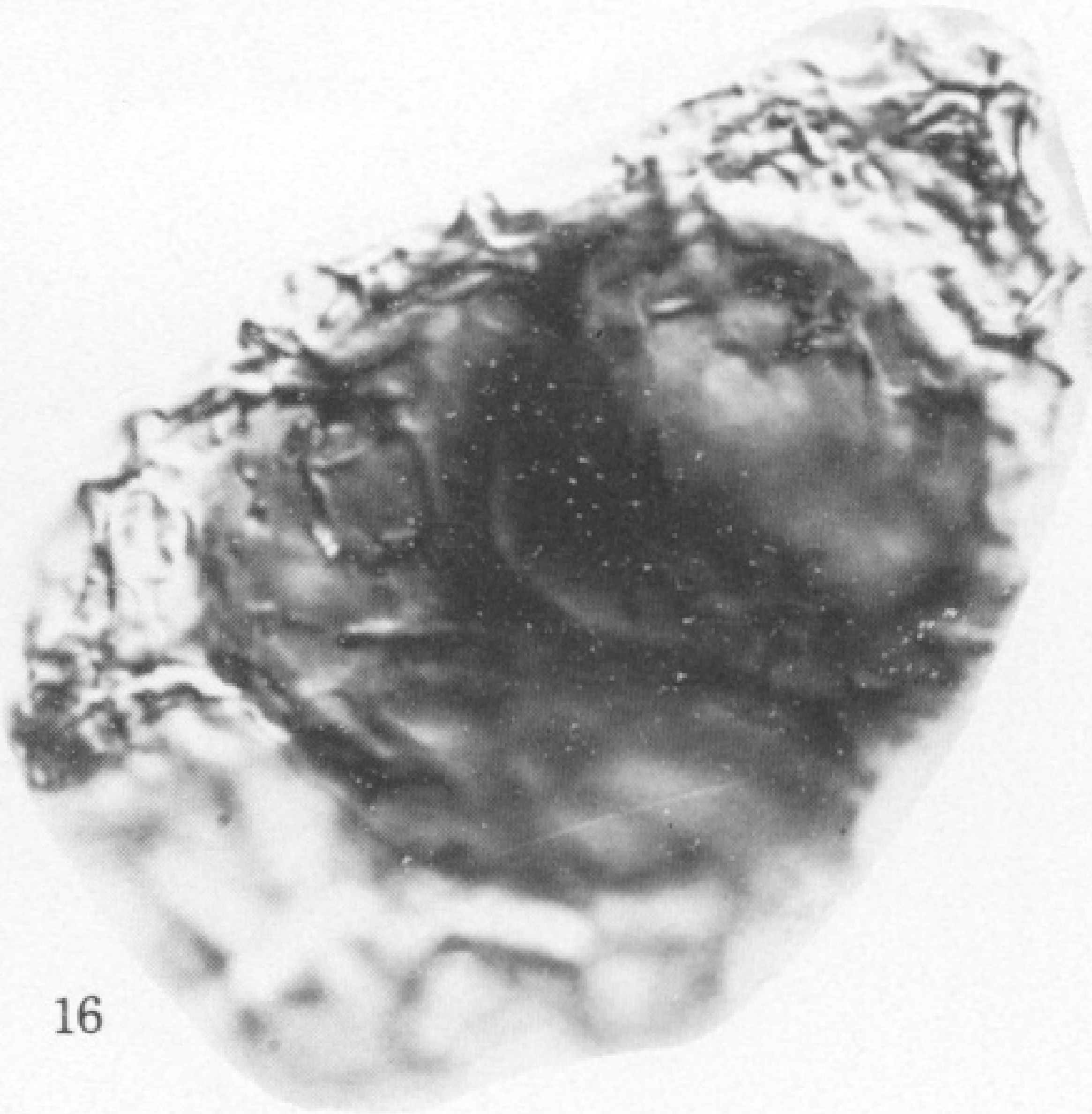
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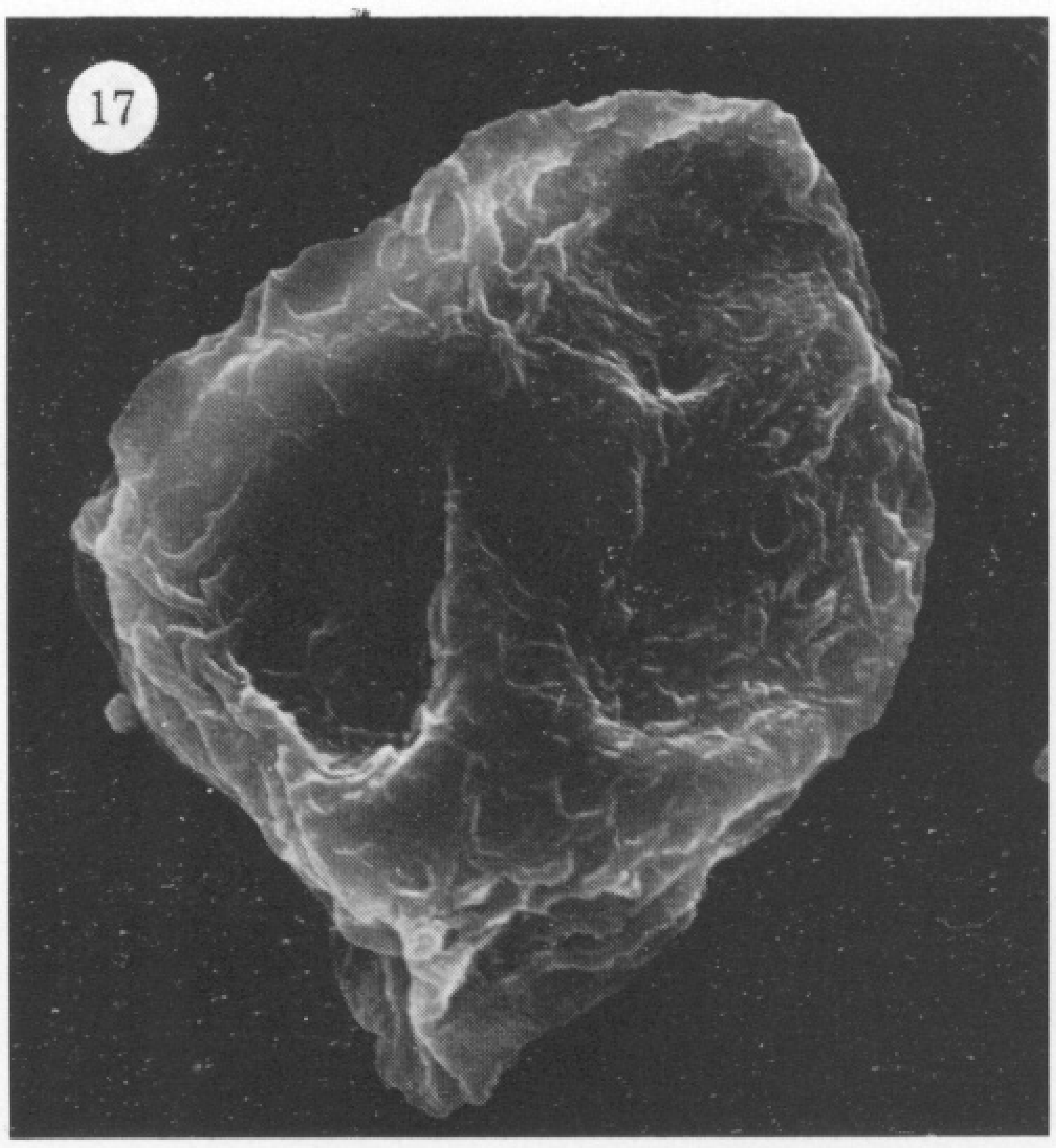
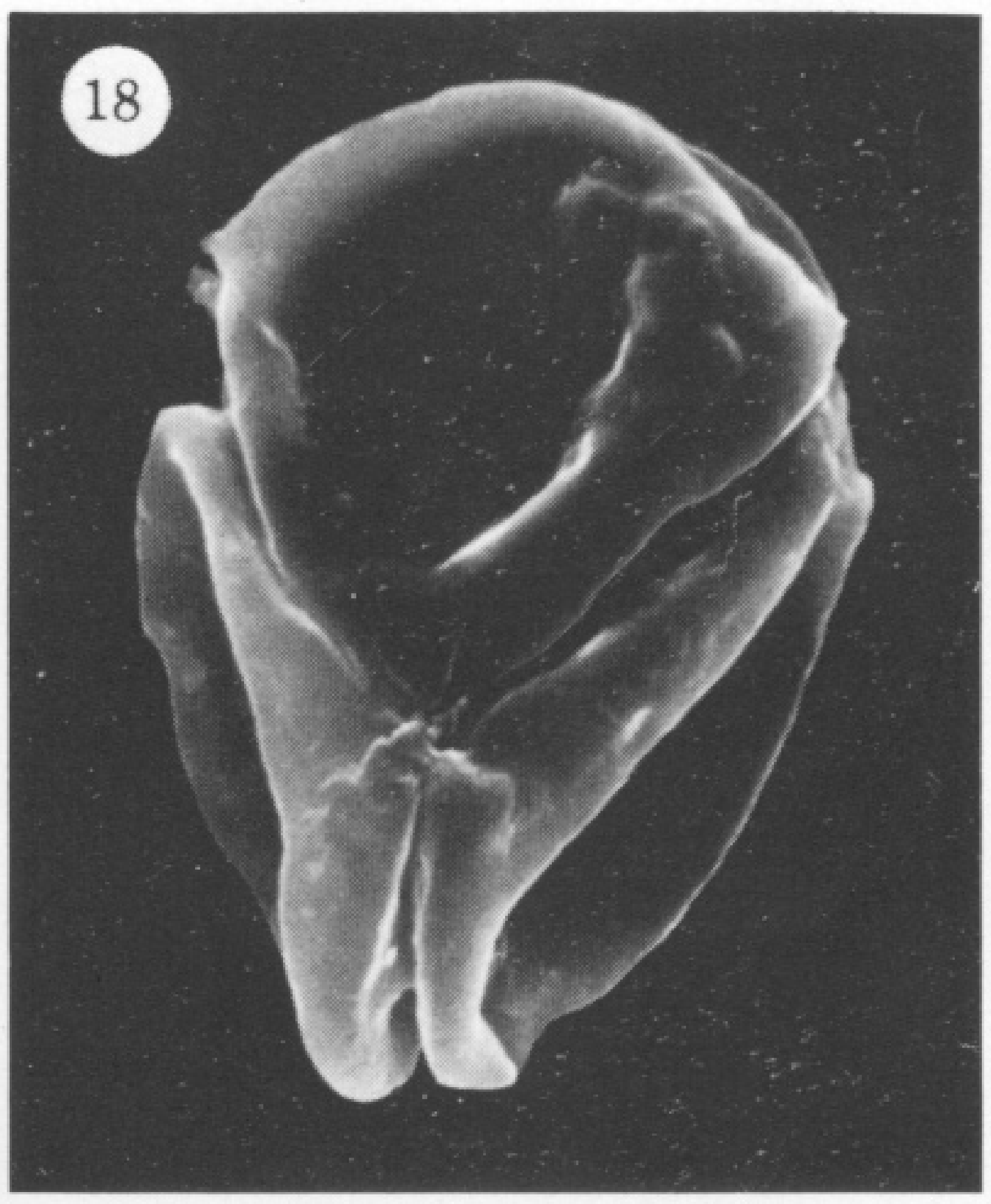
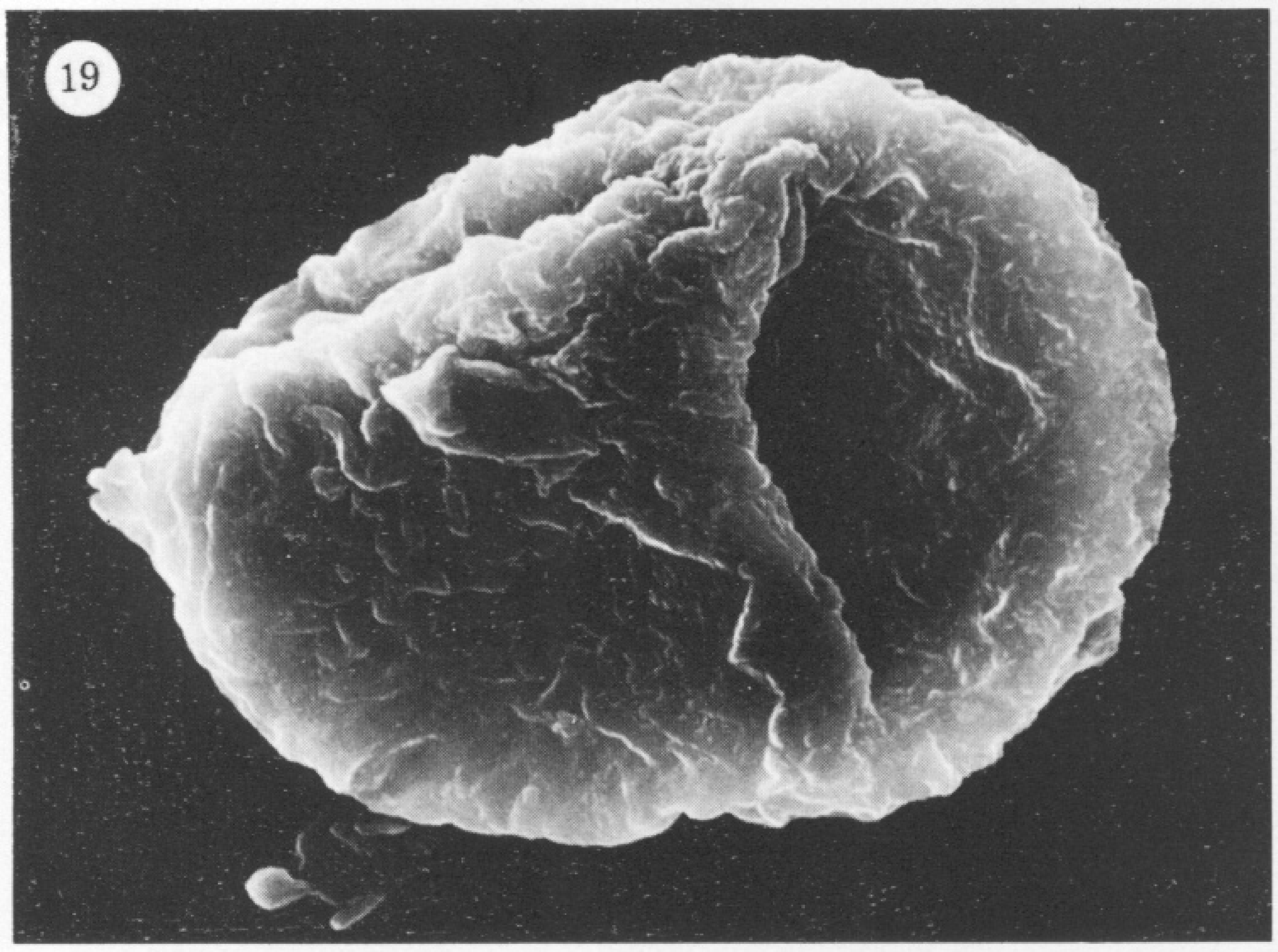
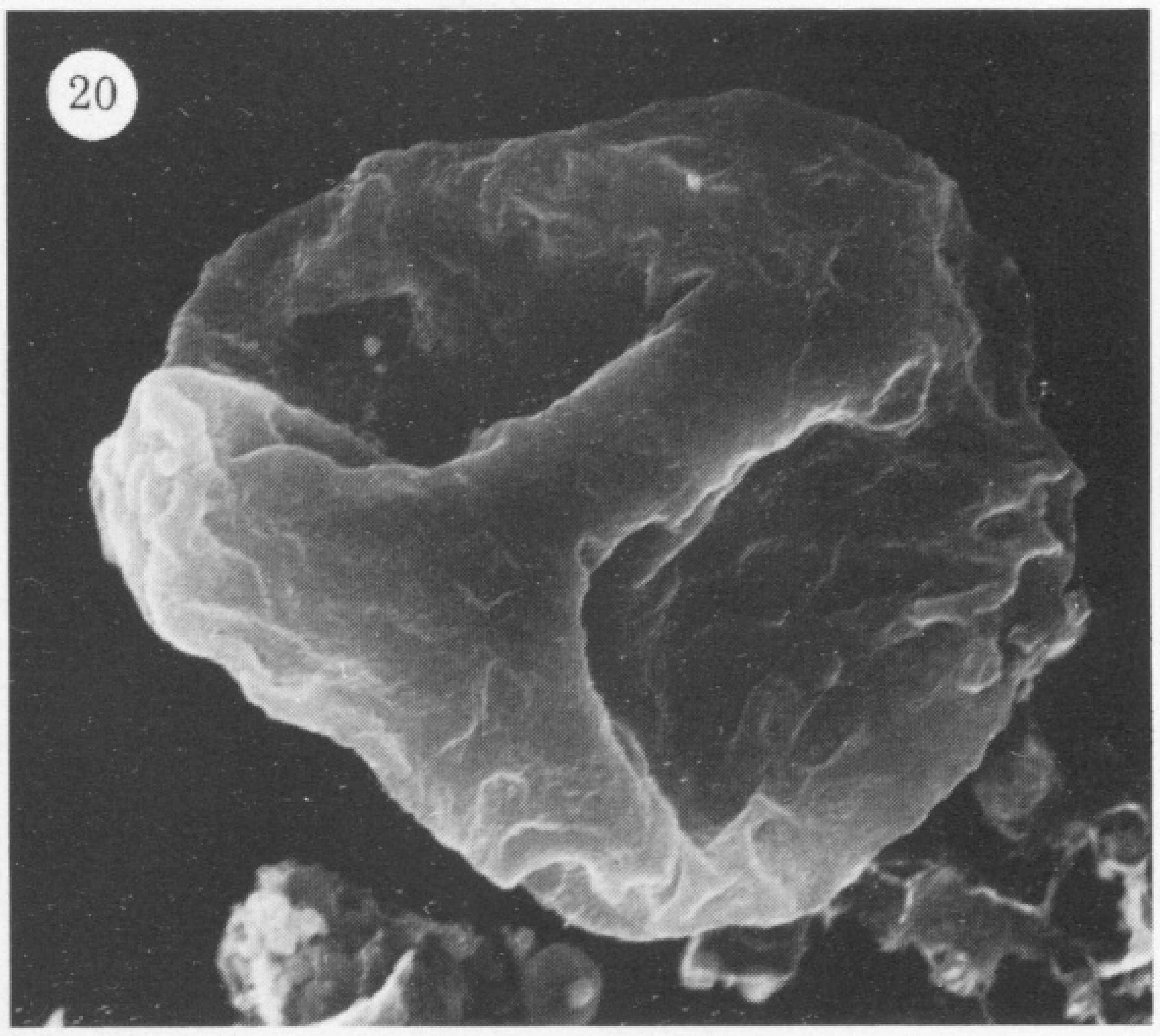
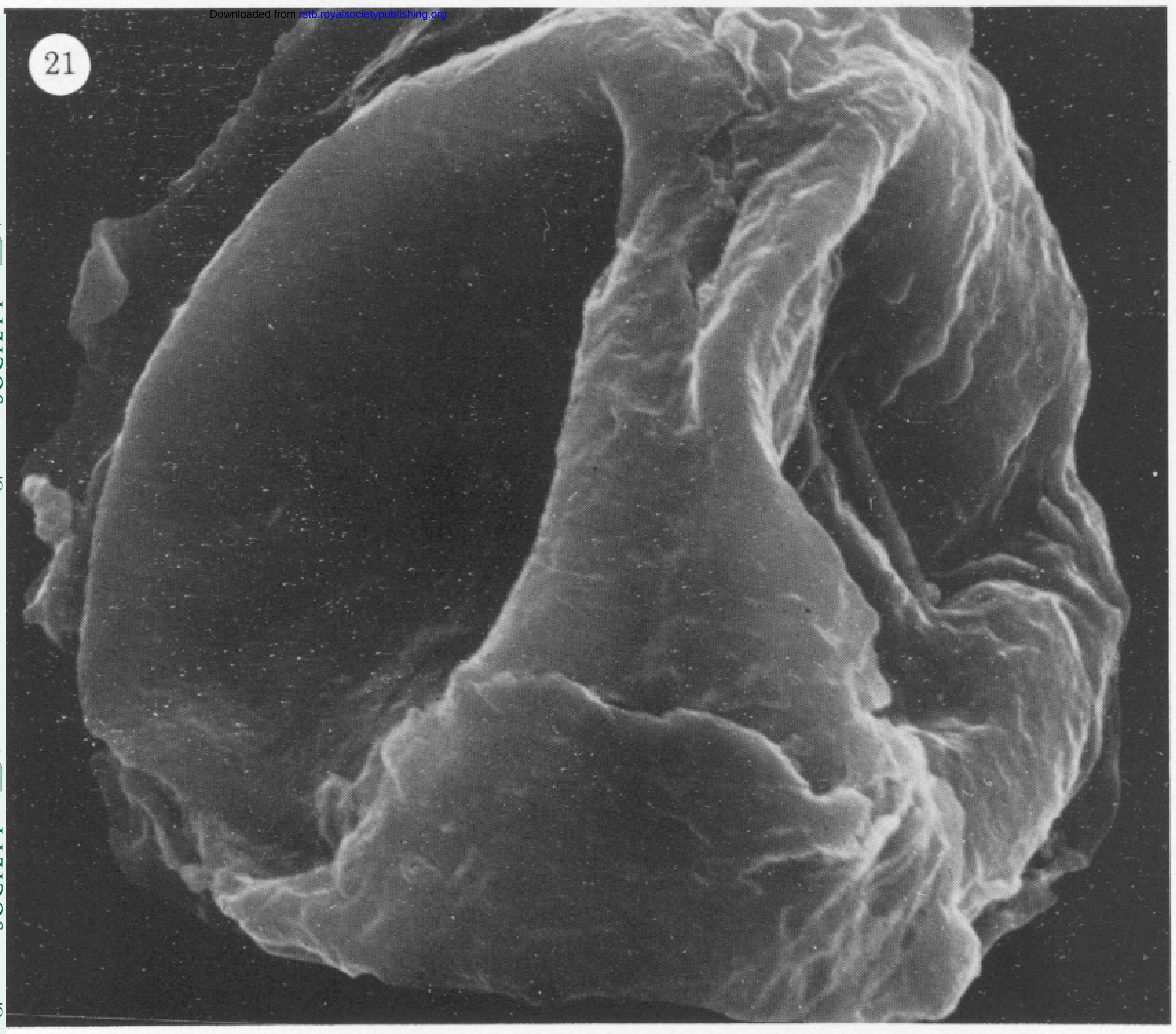
FIGURES 1–16. For description see opposite.

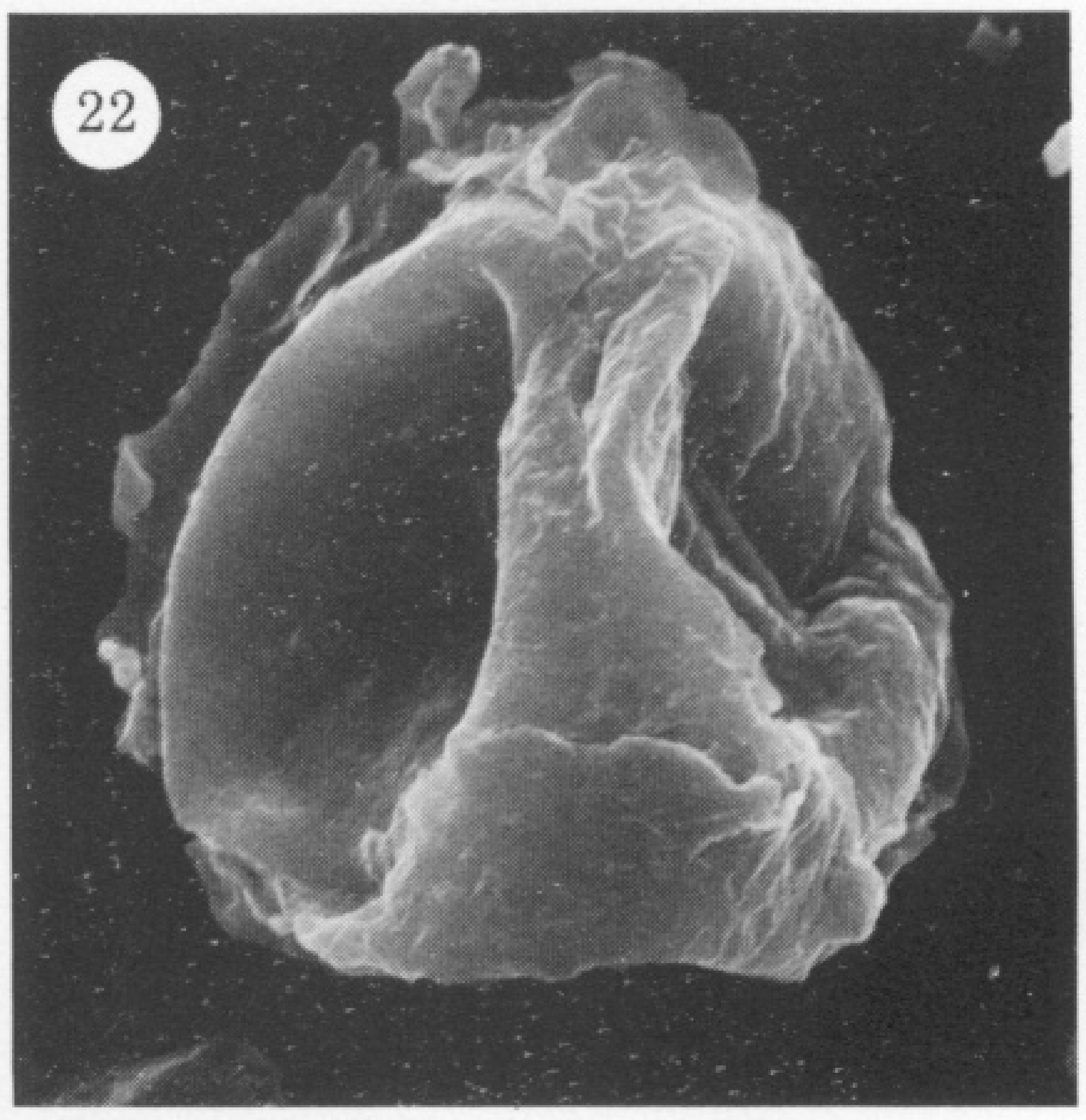












Figures 17–22. For description see opposite.