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Exceptional Preservation of Photosynthetic Organisms in Silicified Carbonates and Silicified Peats

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Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats

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[Plates 1 and 2]

Carbonaceous cherts in Proterozoic carbonate sequences provide an exceptionally clear record of early microbial life, but one that is significantly biased with respect to the range of environments inhabited by contemporary organisms. Many of the best preserved Proterozoic microfossil assemblages come from microbial mats and organic-rich muds that accumulated in protected coastal areas where a combination of high productivity, limited water circulation, and, often, hypersalinity limited *post mortem* degradation. The close distributional relationship between early diagenetic silica and organic matter can be explained in terms of a model developed by Leo and Barghoorn for the silicification of wood. Three factors appear to control the distribution of early diagenetic chert in Proterozoic sequences: sediment permeability, availability of silica in ground water solution, and locally high concentrations of organic matter in near-surface sediments. Of these, organic content appears to impose the major environmental bias.

In terms of their excellent preservation, geochemistry of formation, and limited environmental coverage, Phanerozoic silicified peats bear comparison with their Proterozoic counterparts. Swamp dwellers may be the plants most likely to be preserved exceptionally well, but they may also be the plants least likely to give rise to new populations that will become ecologically widespread and evolutionarily important in subsequent periods. Allochthonous elements in permineralized peats may be unusually important to palaeobotany because they combine the exceptional preservation conferred by peat permineralization with ecological representation of floodplain and upland evolutionary cradles rather than swampland museums.

1. Introduction

Plant tissues and the remains of organic-walled microorganisms continually rain onto surface sediments, but because they are easily destroyed by microbial oxidation, few of these potential fossils become incorporated into the sedimentary record. Materials that survive this pre-burial to earliest diagenetic gauntlet of fungi and bacteria remain vulnerable to obliteration or profound alteration by abiotic oxidation and compression during later stages of diagenesis. Relative to other sedimentary rocks, chert is extremely impermeable, incompressible, and difficult to recrystallize or shear; therefore, early diagenetic silicification can protect microbial populations and plant tissues from subsequent diagenetic destruction.

It is difficult to overstate the importance of silicified fossils in efforts to elucidate the evolutionary history of photosynthetic life. The description by Kidston & Lang (1917–1921) of silicified peats from a Lower Devonian succession near Rhynie, Scotland, redirected thinking about the nature of early vascular plants and the pathways of morphological evolution in tracheophytes. The discovery of fossil prokaryotes in cherts from the 2000 Ma old Gunflint Iron Formation (Tyler & Barghoorn 1954; Barghoorn & Tyler 1965) profoundly changed scientific estimates of the antiquity of life on Earth. More recently, the discovery of silicified peats in Antarctica and Australia has provided for the first time anatomical information on glossopterid gymnosperms, the dominant plants of Gondwana during the late Palaeozoic era (Schopf 1971; Gould & Delevoryas 1977).

In this paper, I will look first at the silicification of Proterozoic microfossils, asking in particular whether the conditions necessary for silica permineralization impose any environmental bias on silicified assemblages. Conclusions drawn from the Proterozoic record will then be tested for their applicability to Phanerozoic silicified peats.

2. Silicification and the Proterozoic fossil record

In his classic text *Plant life through the ages*, A. C. Seward (1931) summarized much contemporary opinion with the statement that 'we can hardly expect to find in Pre-cambrian rocks any actual proof of the existence of bacteria though it would be foolish to deny the possibility'. Beginning with the Gunflint Iron Formation, numerous discoveries of microfossils in Precambrian rocks have demonstrated that Seward's expectations were far too low. Of the more than 180 Proterozoic microbiotas known at present, only about a third occur in cherts; however, silicified biotas dominate the subset of Proterozoic microfossil assemblages characterized by exceptional preservation of biological information.

Cherts in the Gunflint and other iron formations may be primary sedimentary rocks precipitated directly from sea water, but the cherts in most other Proterozoic formations are diagenetic replacements of carbonates or sulphates, or permineralizations of microbial peats (Horodyski & Donaldson 1983). Field evidence overwhelmingly supports this viewpoint. Chert is a volumetrically minor constituent of most Proterozoic successions, occurring for the most part as nodules, lenses, and irregularly discontinuous or locally continuous beds in carbonate or, less often, fine-grained siliciclastic units. Bedding features can often be traced across lithological boundaries from carbonate to chert (see, for example, Donaldson & Delaney 1975; Muir 1976; Horodyski & Donaldson 1980, 1983; Knoll 1982, 1984; and figure 1, plate 1). Surrounding sediments may be compacted around chert patches, indicating that silicification took place early in the diagenetic history of the bed. The occasional discovery of ripped-up and redeposited chert clasts also suggests that in such cases silicification occurred while sediments were near enough to the surface to be reworked during storms (see, for example, Knoll 1984). Petrographic observations (see, for example, Horodyski & Donaldson 1983; Swett & Knoll 1984) corroborate these observations. Etched carbonate grains may be common near the edges of silicified zones, and carbonate or evaporite textures may be faithfully preserved. Fossils are often essentially uncompressed, and filament populations may retain vertical orientations (figures 8–17), further underscoring the earliness of silicification.

(a) *The state of preservation and timing of silicification*

Although silicification took place early on a geological timescale, the preservational state of Proterozoic microfossils indicates that microbial remains were subject to pervasive, if incomplete, decomposition before permineralization. In terms of preservation potential, the degradation-resistant cell walls and external sheaths or envelopes of many plants and microorganisms are analogous to the mineralized skeletons of animals. Cells that lack recalcitrant walls or sheaths stand little chance of becoming fossilized, while remains such as the robust sheaths of cyanobacteria and the reproductive cysts of protists may accumulate in large numbers in sediments.

Microfossils in Proterozoic stromatolites do not resemble the surface populations of modern mats so much as they do partly degraded remains a few millimetres or more beneath mat surfaces (Golubic & Barghoorn 1977; Horodyski *et al.* 1977; Knoll & Golubic 1979; Aizenshtat *et al.* 1984). Sheaths, envelopes, and walls constitute the most abundant Proterozoic remains. These materials are often empty, but may contain cell remnants in various stages of decomposition (figures 8–17). Well preserved cellular trichomes, best known from the Bitter Springs Formation (Schopf 1968; Schopf & Blacic 1971), are rare elements of most assemblages. (The interpretation of selected organic granules as preserved organelles remains controversial (Taylor 1981; Knoll 1983; Nyberg & Schopf 1984).) One need not grieve unduly for the incomplete preservation of silicified microfossils. Even the empty sheaths of cyanobacteria often retain much biological information, including patterns of cell division and growth (see, for example, Knoll *et al.* 1975; Golubic & Hofmann 1976; Golubic & Campbell 1979; Knoll & Calder 1983; and figures 13, 14). More problematic is the complete absence of bacterial or protist groups that lacked degradationally resistant walls or sheaths. Their presence can be inferred, if at all, only on the basis of geochemical information or comparative studies of recent microbial communities.

Golubic (1976) has described 8000 year old microbial peats from Abu Dhabi that contain structurally preserved cyanobacterial remains. Coupled with taphonomic data showing the rapidity of early degradation, such observations define the probable range of timescales for the silicification of Proterozoic fossils. Permineralization could have occurred shortly after initial degradation, on a timescale of 10^0–10^1 years; the Abu Dhabi example demonstrates that scales of 10^3–10^4 years are also permissible. On the other hand, it seems unlikely that exceptional preservation of the type found in the Bitter Springs and Draken assemblages could occur if the time between burial and silicification were much greater than that.

(*b*) *Requirements for silicification*

The obvious first requirement for silicification is a source of SiO_2. Volcanoes and hydrothermal ridge systems provide ready sources, but many richly fossiliferous Proterozoic sequences contain no evidence for nearby volcanism. Knauth (1979) has presented a model for the origin of chert in coastal Phanerozoic carbonates in which the simultaneous dissolution of calcium carbonate and precipitation of silica take place in the subsurface mixing zone where meteoritic and marine ground waters meet. This model can explain a number of geochemical and sedimentological features of chert formation, in particular, oxygen isotope ratios which indicate the presence of meteoritic water at sites of silicification (Knauth & Epstein 1976; Kolodny *et al.* 1980).

In Knauth's model, the source of silica is diatom frustules, radiolarian tests, or sponge spicules in subaerially exposed sediments. These remains dissolve in meteoritic ground waters which may build up concentrations of dissolved silica that approach saturation with respect to opal-A. Biogenic silica sources were not available through most of Proterozoic time, but a substitute source appears reasonable. In the absence of silica precipitating organisms, the concentrations of dissolved SiO_2 in sea water must have been much higher than today. In open marine waters, reactions with clay minerals would have kept concentrations below saturation with respect to amorphous silica (Siever & Woodford 1973), but at the edges of the ocean, along broad tidal flats or in restricted lagoons, evaporation would have caused precipitation of silica along with carbonates and evaporites. The percentage of silica in such sediments would have been small, but like the biogenic silica in Phanerozoic coastal deposits, this material would dissolve readily in meteoritic ground waters.

One might expect that all carbonates passing through the mixing zone would have an equal likelihood of becoming silicified, but in fact sites of silicification are not randomly distributed within sequences. Relative permeability certainly affects chert distribution (Knauth 1979), but permeability alone cannot explain observed patterns of silicification in Proterozoic successions. In the thick Upper Proterozoic carbonates of East Greenland and Svalbard, which I have examined in some detail, the distribution of chert correlates well with that of one other feature: organic matter. Silicification occurred preferentially in facies where relatively high concentrations of organic matter were present in near-surface sediments. The relation between silica and organic matter can be seen clearly in intraformational gravelstones and fine-grained conglomerates from the 700–800 Ma old Draken Conglomerate Formation, Spitsbergen (Wilson 1961; Knoll 1982). In these rocks, microbial mat fragments and clasts of organic-rich mud have been silicified, but adjacent organic-poor clasts remain carbonate (figures 2, 4). Figure 3 shows preferential silicification on a fine scale within a late Proterozoic stromatolite from East Greenland. One further sample, from the partly correlative Ryssö Formation, Nordaustlandet (Knoll & Calder 1983), illustrates strikingly how exact the silica–organic matter relationship can be. The rock in question is a dolostone that contains organic matter distributed in a series of wisps a few to several tens of micrometres thick. The organic wisps

DESCRIPTION OF PLATE 1

FIGURE 1. Fossiliferous chert nodules in microbially laminated dolostone from the *ca*. 850 Ma old Bitter Springs Formation, Australia. Arrows point to nodules; note also thin stringers of chert. Pocketknife provides scale.

FIGURE 2. Fossiliferous chert in 700–800 Ma old Draken Conglomerate Formation, Spitsbergen. Black clasts are chert; lighter 'matrix' is dolomite. 15 cm ruler provides scale.

FIGURE 3. Lamina-by-lamina silicification in a stromatolitic dolostone from the 700–800 Ma Limestone–Dolomite Series, central East Greenland. Note pocketknife for scale.

FIGURE 4. Petrographic view of Draken flake conglomerate shown in figure 2. Light clast is silicified; darker clasts are carbonate. Small white patches are quartz sand grains. Bar in figure 17 is 500 μm for this figure.

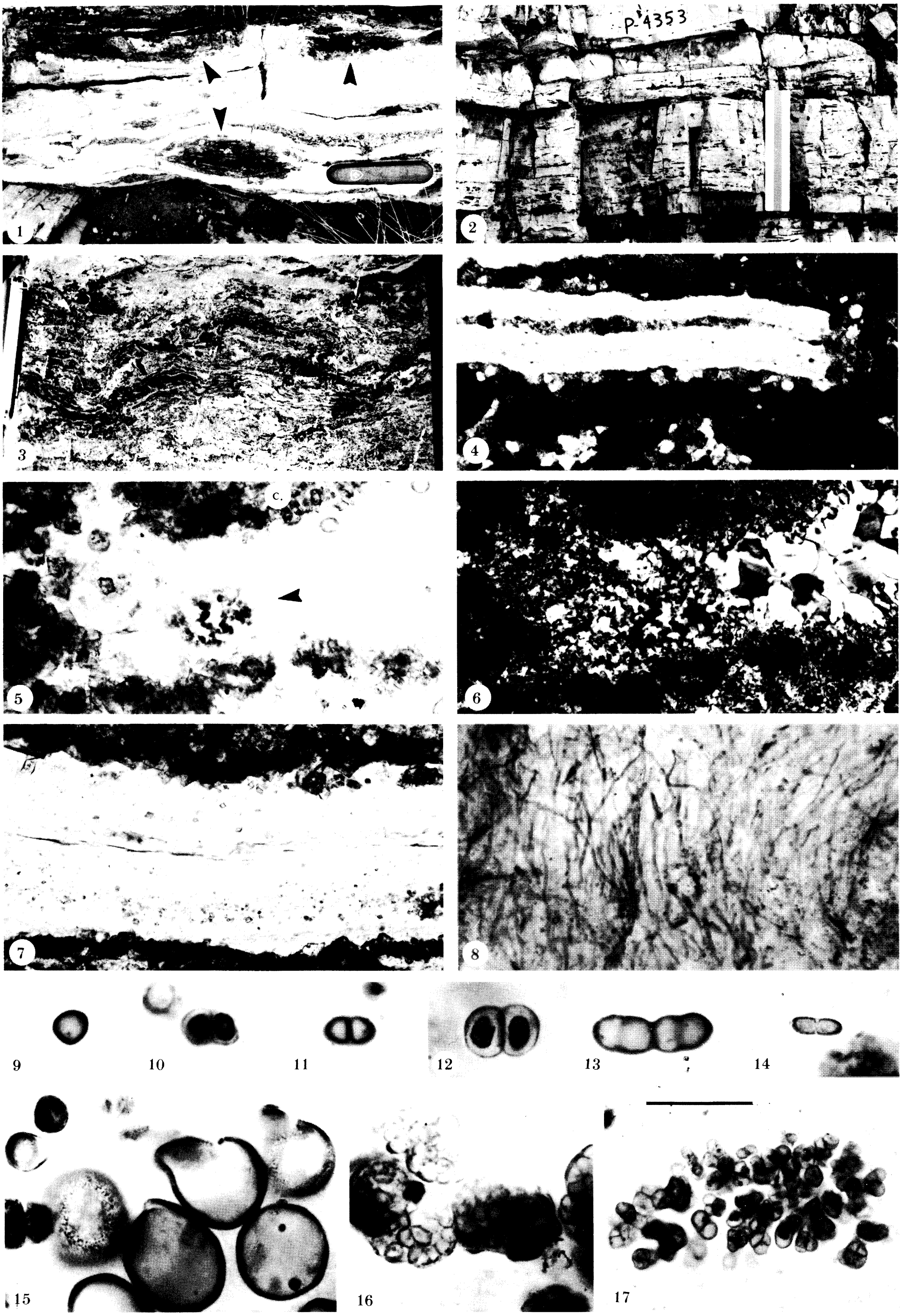
FIGURES 5 AND 6. Plane- and cross-polarized views of locally silicified areas within a dolostone from the 700–800 Ma old Ryssö Formation, Nordaustlandet, Svalbard. In figure 5, dark areas marked 'C' are carbonate, while the lighter area is chert. Arrow points to rim of fine-grained silica around a colony of small, prokaryotic microfossils. Light area outside the rim consists of large quartz crystals visible in figure 6. Bar in figure 17 is 200 μm for these figures.

FIGURE 7. As in preceding figures, this shows a locally silicified horizon within dolostone from the Ryssö Formation. Scale as for figure 5.

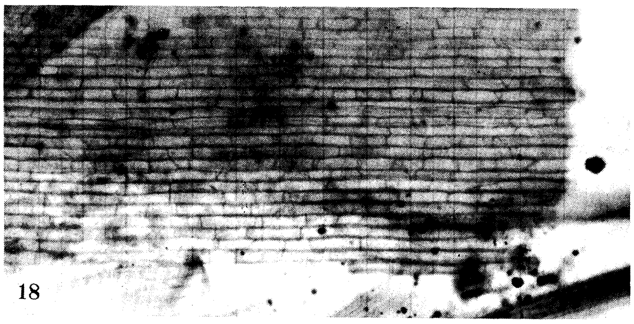
FIGURE 8. Vertically aligned filamentous sheaths of mat-building cyanobacteria preserved in chert from the 700–800 Ma old Limestone–Dolomite Series, central East Greenland. Bar in figure 17 is 200 μm in this figure.

FIGURES 9–16. Silicified microfossils from the 700–800 Ma old Draken Conglomerate Formation, Spitsbergen. Figures 9–13 show cell division pattern evident in a population of chroococcalean cyanobacteria; figure 14 shows binary fission in a rod-shaped prokaryote; figure 15 shows the granular texture of vesicle walls in problematic unicells; figure 16 shows colonies of pleurocapsalean cyanobacteria. Note that cell contents are partly preserved only in figures 10 and 12. Bar in figure 17 is 20 μm for figures 9–15 and 33 μm for figure 16.

FIGURE 17. Endolithic microorganisms preserved in silicified pisolites from the Limestone–Dolomite Series, Greenland. Bar is 80 μm.



FIGURES 1–17. For description see opposite.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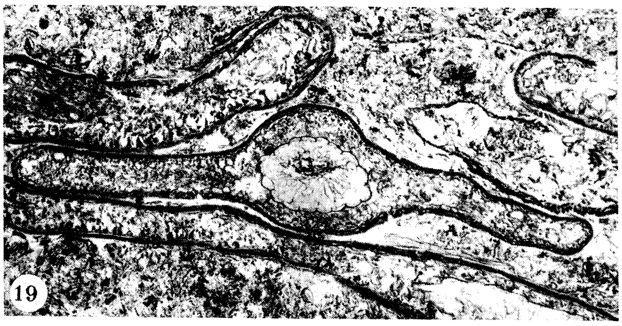
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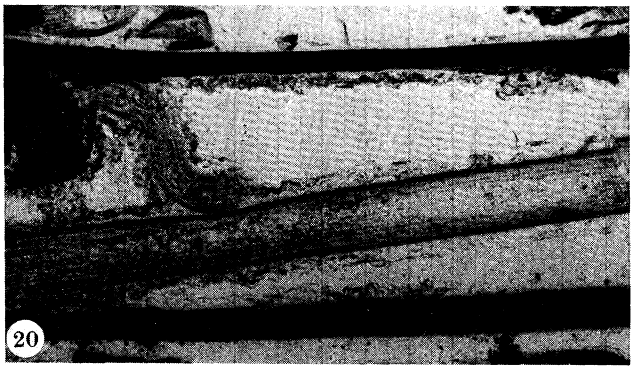
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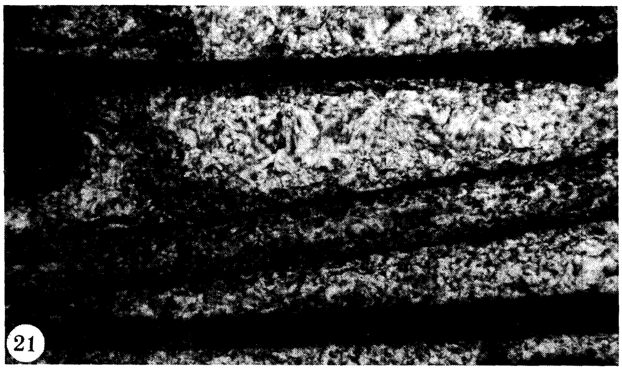
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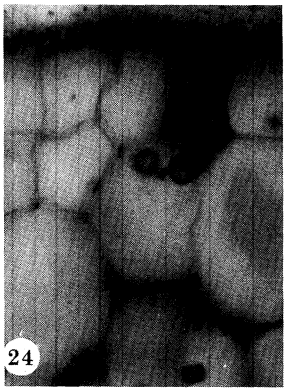
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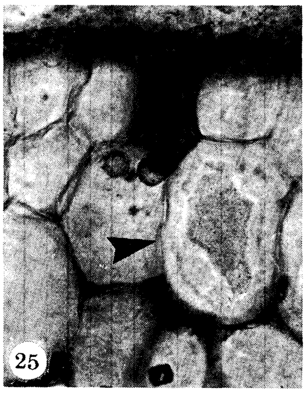
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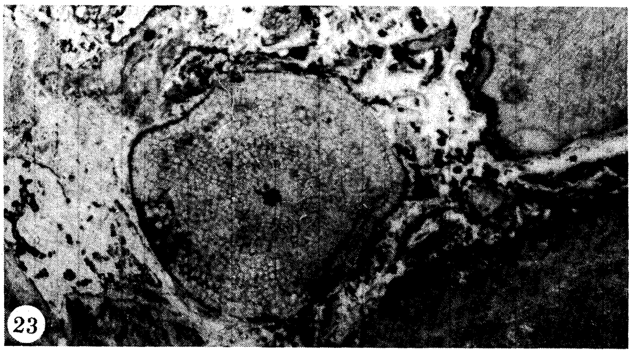
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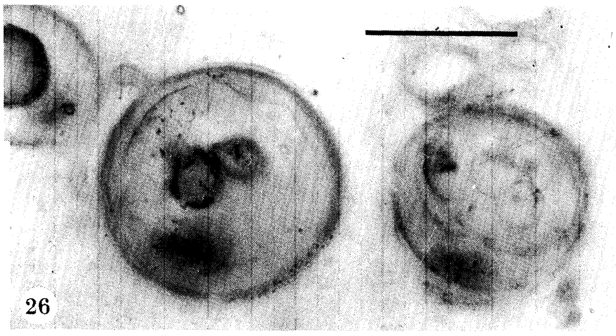
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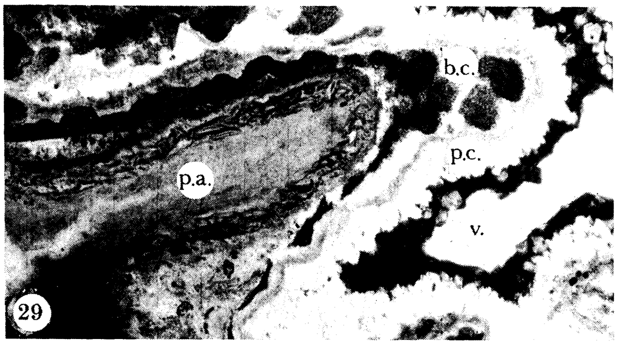
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FIGURES 18–29. For description see opposite.

are silicified, and chert extends a few micrometres beyond the organic material, but the rest of the rock shows no evidence of silicification (figures 5–7).

The observation that early diagenetic chert tracks organic matter is not new (Siever 1962). The precise localization of silica in petrified wood has long been appreciated (see, for example, Leo & Barghoorn 1976), and Wetzel (1957) attributed the preferential silicification of shells in limestones to the presence of organic matter in shell matrices. It may be that organic matter somehow affects the solubility of silica or the kinetics of its precipitation. Leo & Barghoorn (1976) presented a model for the silicification of wood which seems applicable to silica permineralization of Precambrian organic matter. In brief, Leo & Barghoorn suggested that hydroxyl and other functional groups present in partly degraded plant tissues form multiple hydrogen bonds with mono- or polysilicic acid in ground water solution. The organic matter serves as a template for initial silica deposition, after which further silica precipitation occurs by silicic acid polymerization. Buurman *et al.* (1973) have described thin silica replicates of tracheid walls in one- to several-hundred-year-old acidic soils from Thailand and the Netherlands; A. Karowe and T. H. Jefferson (unpublished) have noted similar thin coatings of silica in xylem cells of wood buried during a 19th century eruption of Mt St Helens. In the Leo–Barghoorn model, such coatings are to be expected in preference to silica growth that is independent of organic matter distribution.

If silicification occurs in the manner hypothesized by Leo & Barghoorn (1976), a limited degree of decomposition may actually increase chances for long term preservation by providing abundant sites for hydrogen bond formation as well as microcracks and holes through which ground water can percolate. It is worth noting in this context that silicified Proterozoic fossils often exhibit a markedly granular texture (Knoll & Golubic 1979; Horodyski & Donaldson 1980; Nyberg & Schopf 1984) that is resolvable upon close examination into individual points of organic matter (figure 15). Degradation of organic matter in carbonate sediments may further promote silicification by causing a local increase in CO_2 activity and, hence, a drop in pH that in the absence of ambient reducible iron, will cause carbonate dissolution (Siever 1962; Gardner 1973); pH profiles in modern microbial mats show a marked lowering in subsurface zones of active bacterial sulfate reduction (Javor & Castenholz 1980; Jørgensen *et al.* 1983). In some cases the growth of early diagenetic chert nodules may be limited by the degree to which pre-existing carbonate minerals can be removed by dissolution.

Description of plate 2

Figures 18–22. Late Miocene to Pliocene silicified peat, Lost Chicken Creek, Alaska. Figure 18, epidermis of rhizomatous monocot. Figure 19, transverse section of a conifer needle. Figures 20 and 21, plane- and cross-polarized views of a silicified rhizome showing the close relationship between organic matter and fine-grained early diagenetic chert; interareas contain radiating fibrous chalcedony. Figure 22, fungal spores. Bar in figure 26 is 200 μm for figure 18, 500 μm for figures 19–21, and 33 μm for figure 22.

Figures 23–26, 29. Early Devonian silicified peat from Rhynie, Scotland. Figure 23, transverse section through axis of *Rhynia* sp. Figures 24 and 25, higher magnification views of same, showing preservation of cortical and epidermal cells as empty walls (with fungi) and, in figure 25, showing growth of silica inward from walls with later filling of central cavity (arrow). Figure 26, fungi in partly decomposed *Rhynia* axis. Figure 29, organically preserved plant axis (p.a.) from which a botryoidal silicification front extends outward (b.c.); late diagenetic prismatic quartz crystals (p.c.) grew into void space (v.) from the silicification front. Bar in figure 26 is 2 mm for figure 23, 80 μm for figures 24 and 25, 33 μm for figure 26, and 500 μm for figure 29.

Figures 27 and 28. Late Carboniferous silicified peat from St Étienne, France, showing distribution of fine-grained chert and radiating fibrous chalcedony in plane- and cross-polarized light. Bar in figure 26 is 500 μm.

(c) The environmental distribution of fossiliferous cherts

The details of silica emplacement in Proterozoic (and Phanerozoic) sediments remain poorly known, but a significant role for organic matter seems assured. Field observations suggest that silicification can occur in rocks deposited under conditions ranging from supratidal to basinal (see, for example, Knoll 1985). Differential availability of dissolved silica in different environments does not seem to be a principal source of preservational bias. On the other hand, the availability of sedimentary organic matter does. Silicified assemblages are markedly skewed toward microbial mats and organic-rich muds that accumulated in restricted or protected coastal environments. Under such conditions, high productivity is combined with limited (surface) water circulation, and anaerobic conditions become established just below the surface. Hypersaline conditions, for which there is evidence in some of these restricted coastal rocks, further limit decomposition by excluding some anaerobic decomposers (Knoll & Golubic 1979; Horodyski & Donaldson 1983). Many of the best known Proterozoic microfossil assemblages come from such environments. Examples include the biotas of the Bitter Springs (Schopf 1968; Schopf & Blacic 1971; Knoll & Golubic 1979), Draken (Knoll 1982), Belcher Islands (Hofmann 1976), Amelia (Muir 1976), Balbirini (Oehler 1978), Gaoyuzhuang (Zhang 1981), Dismal Lakes (Horodyski & Donaldson 1980, 1983), Narssârssuk (Strother *et al.* 1983), Min'Yar (Nyberg & Schopf 1984), Shorikha (Mendelson & Schopf 1982), and Ryssö (*partim*, Knoll & Calder 1983) cherts. In all these examples, prokaryotic remains predominate, even though, in the Middle and Late Proterozoic examples at least, large and in some cases morphologically complex eukaryotic cells are abundant in contemporary shelf shales. Few well preserved microfossil assemblages are known from columnar stromatolites that accreted in zones of active current activity. It may not be coincidental that the complex stromatolites best known for well preserved microfossils are *Conophytons* that accumulated in quiet waters below wave base.

In summary, the widely held view that many exceptionally preserved Precambrian microfossil assemblages owe their preservation to early diagenetic silicification is correct, but conceptually incomplete in that it links preservation principally to silica precipitation. Certainly, the long term preservation of delicate prokaryotic and protistan remains may be ensured by silicification, but the silica itself owes its presence, at least in part, to the short-term preservation of the organic matter. In this view, exceptional preservation stems first from the early abortion of microbial degradation in organic-rich sediments. Silicified microfossil assemblages provide our clearest view of Proterozoic life, but it is a view that is, on the whole, environmentally limited. Augmentation from other sources is necessary to achieve a balanced view of early microbial evolution.

3. PHANEROZOIC SILICIFIED PEATS

The preceding brief discussion of Proterozoic silicification suggests three generalizations: sites of early diagenetic silicification are determined jointly by the availability of silica, sediment permeability, and the presence of locally high concentrations of sedimentary organic matter. Silica availability does not in itself appear to be a principal palaeoecological biasing factor; sites of organic accumulation, in particular the accumulation of structurally intact microbial remains, can impose a significant environmental bias on silicified assemblages that must be considered in evolutionary interpretations of the Precambrian fossil record.

To what extent are these generalizations applicable to silicified peats found in Phanerozoic sequences? The question of possible palaeoecological bias is particularly important because palaeobotanists rely heavily on silicified and other permineralized peats for anatomical knowledge of extinct plants.

Geochemically, the Leo–Barghoorn model appears to work as well for peats as it does for isolated logs or microbial mats. Petrographic examination of silicified peats from five localities (table 1) shows a common pattern of silicification that is predicted by the model (figures 20, 21, 24, 25, 27–29, plate 2). Silica precipitation did not begin at a single point and then move concentrically outward, passively encompassing plant materials as it went. On the contrary, silicification clearly followed a template provided by the walls of partly decomposed plant cells and other organic debris. Spaces that were originally empty (water-filled) generally contain radiating fibrous chalcedony or large anhedral crystals that document later stages of silica deposition. In the Rhynie Chert, some areas between adjacent plant axes remain unmineralized, bordered by botryoidal silicification fronts or euhedral crystals that grew unimpeded into cavities (figure 29). Schopf (1971) similarly noted that lysigenous cavities in silicified *Vertebraria* roots from Antarctica were filled by prismatic quartz crystals that precipitated relatively late in diagenesis.

Table 1. Silicified peats examined petrographically

Formation	location	age	reference
Rhynie Chert	Scotland	early Devonian	Kidston & Lang (1917–1921)
Rive de Gier Formation	France	late Carboniferous	Renault (1878)
Formation unknown	Sarawak	Triassic	Gastony (1969)
Allenby Formation	British Columbia	Eocene	Basinger & Rothwell (1977)
Lost Chicken Creek Chert	Alaska	Neogene	unpublished material

Silicification is the most common form of plant permineralization; it can result in impressively good preservation of plant tissues and associated fungi, usually as empty or resin-filled cell walls (Schopf 1975; and figures 18, 19, 22, 23, 24, 26). A major source of silica is the weathering of volcanic ash and lava flows (see, for example, Murata 1940; Sahni 1941), but it is also apparent that SiO_2-rich ground water solutions can be generated by the deep weathering of exposed cratonic rocks (see, for example, Schopf 1971). Wood provides the best measure of the environmental distribution of silica availability. Allochthonous logs commonly occur as silica petrifactions in Mesozoic and Cainozoic non-marine successions, and *in situ* silicified tree trunks are also well known (see, for example, Dorf 1964; Jefferson 1982). Wood that is transported into marine basins may become silicified as well, as shown by *Callixylon* in Upper Devonian black shales of midcontinent North America (Arnold 1931). From this, one may fairly conclude that subject to the availability of weatherable source materials and suitable sediment permeability, silicification is possible in a wide range of environments extending from montane valleys to coastal flats.

While there may be no identifiable environmental bias associated with silica availability or processes of silicification, there is certainly a bias connected to silicified peats. This obtains because swampy habitats comprise an extremely limited and nutritionally unusual subset of the environments available to terrestrial plants. It has long been known that swampy environments of the late Carboniferous Euramerican realm hosted plant communities that differed substantially from those of nearby floodplains (Havlena 1970; Oshurkova 1974; Scott 1977, 1979; Phillips 1980), and the same appears to have been true for other periods. For example, if current age estimates for the Rhynie Chert are correct, rhyniophytes dominated swamp floras well after they were displaced on floodplains by zosterophyllophytes, lycopods, and trimerophytes (see, for example, Edwards 1980). The few data available for the late Devonian suggest that *Rhacophyton* formed almost monospecific stands in swamps, while arborescent lycopods and progymnosperms dominated the wetter and drier parts of adjacent floodplains, respectively (Gillespie *et al.* 1981). By the early Carboniferous, arborescent lycopods (*Lepidodendropsis*) populated the swamps while pteridosperms (and, perhaps, late progymnosperms) thrived on the floodplains. According to Krasilov (1975), Jurassic wetlands in northern Eurasia were populated by large *Equisetites* and associated specialized ferns and benettitites; taxodiaceous conifers formed the canopy in associated delta-plain forests. By the late Cretaceous, angiosperms had radiated to dominate many floodplains, but taxodiaceous conifers continued to be significant elements of wet environments (see, for example, Parker 1975).

It appears that swamp plants of the past were not only different from contemporary floodplain taxa, but often they were also relictual in the sense that they belong to higher taxa which were significant elements of floodplain floras in earlier epochs. Ecological models for community differentiation along resource gradients provide the basis for an explanation of this phenomenon (Tilman 1982 and references cited therein). Following the initial colonization of a previously unexploited habitat, plant populations would be expected to become differentiated along gradients of nutrient, water, and light availability. One would expect new adaptations capable of conferring widespread competitive superiority to arise more often in floodplains or 'uplands' than in swamps. This is statistically likely because for most of plant history swamp habitats have constituted an areally limited subset of the vegetated Earth; it is ecologically likely in that plants that have become architecturally or physiologically specialized for wet, acidic, oxygen-poor, and nutrient-poor swamp environments must surmount several hurdles to radiate in non-swamp environments. Many features of the fossil record verify this expectation; I know of none that contradict it.

New innovations that result in ecological success on the floodplain have often involved increased abilities to harvest sunlight (taller habit, more efficient distribution of photosynthetic surfaces) or to maximize growth when ground water availability is limited or seasonally variable. Such features are unlikely to confer competitive superiority in the swamps, and so, well adapted swamp biotas may be relatively resistant to invasion from other environments. Thus, as new plants become dominant on the floodplain, persisting swamp biotas take on something of a relictual character. Extinction of swamp taxa may be primarily a function of habitat disruption as swamps periodically decrease in areal extent. Indeed, the degree to which swamp biotas develop their own within-swamp patterns of evolution and relictual character may depend on the extent and persistence of swampy environments in different epochs. As new swamps expand after drier periods of swamp plant extinction, adjacent populations again differentiate along resource gradients to produce new swamp dominants, and this pattern is repeated again and again through time. A fine example of this phenomenon in the fossil record is provided by the detailed history of Pennsylvanian coal swamps in midcontinent North America presented by DiMichele *et al.* (1985).

The model presented in the preceding paragraphs is impressionistic, but it is amenable to detailed analysis by carefully coupled palaeoecological and evolutionary studies such as those typified by the work of Phillips & DiMichele (1981; Phillips 1980, 1981; DiMichele 1983, DiMichele *et al.* 1985). It also makes predictions about the systematic position of extant swamp-dwelling species that can be tested by cladistic analyses of taxa that contain species restricted to swamps and bogs. (The criticism that some extant swamp plants contain highly derived vegetative or floral structures is no criticism at all. What one needs to know is the phylogenetic relationships of the plants in question to their non-swamp relatives, and some assessment of the likelihood that such species will survive the demise of the swamps in which they are found today.) The model suggests that swamps may be in some sense evolutionary museums rather than cradles, and that of all species, those found in swamps (or other extreme areas such as high alpine felsenmeers) may be the least likely to give rise to new groups that will become ecologically widespread and evolutionarily important in subsequent floras.

The significance for the present discussion is clear. Silicified and other permineralized peats may provide unparalleled details of anatomical structure, but care must be exercised in the application of this information to problems of phylogenetic reconstruction. It is not *a priori* obvious that the architecture of silicified swamp dominants will differ greatly from that of related floodplain plants from the same or an earlier period, but neither is it clear that swamp species are necessarily good morphological models for all members of ecologically widespread higher taxa. Complication is, of course, introduced by the fact that some elements in permineralized peats did not grow in a swampy environment but were transported to sites where organic matter accumulated. Allochthonous remains in permineralized peats may be unusually valuable in palaeobotany because they combine the exceptional anatomical preservation conferred by burial in a permineralized peat with ecological representation of the evolutionary cradles outside of the swamps.

Conclusions

In this paper, I have not dwelt on the marvels of tissue and cell preservation found in early diagenetic cherts. Many papers have documented the exceptionally good preservation of silicified plant and microbial remains. What I hope to have shown is that in both the Proterozoic and Phanerozoic fossil records, silicified microbial mats and peats constitute a double-edged sword. Our knowledge of ancient photoautotrophs would be immeasurably impoverished without the detailed cellular and anatomical information provided by such assemblages. On the other hand, the environments in which microfossil silicification or peat permineralization have occurred most often comprise a limited subset of the environments available to contemporary organisms. The limited nature and unusual physical characteristics of these environments must be borne in mind when their constituent fossil assemblages are used in evolutionary interpretations of the plant, protist, and moneran fossil records.

This paper is dedicated to the memory of Elso S. Barghoorn, a cherished friend and teacher who taught me that it was not only interesting to think about a wide range of subjects, but sometimes necessary, as well. I thank Warren Allmon, Paul Anderson, Fakhri Bazzaz, H. D. Holland, and Raymond Siever for helpful discussions, and Ruth Stockey and Jean Galtier for kindly providing specimens of silicified peats from British Columbia and France, respectively. The assistance of Elizabeth Burkhardt in preparing the illustrations is gratefully acknowledged. The research through which the ideas in this paper were developed was supported by grants from the National Science Foundation.

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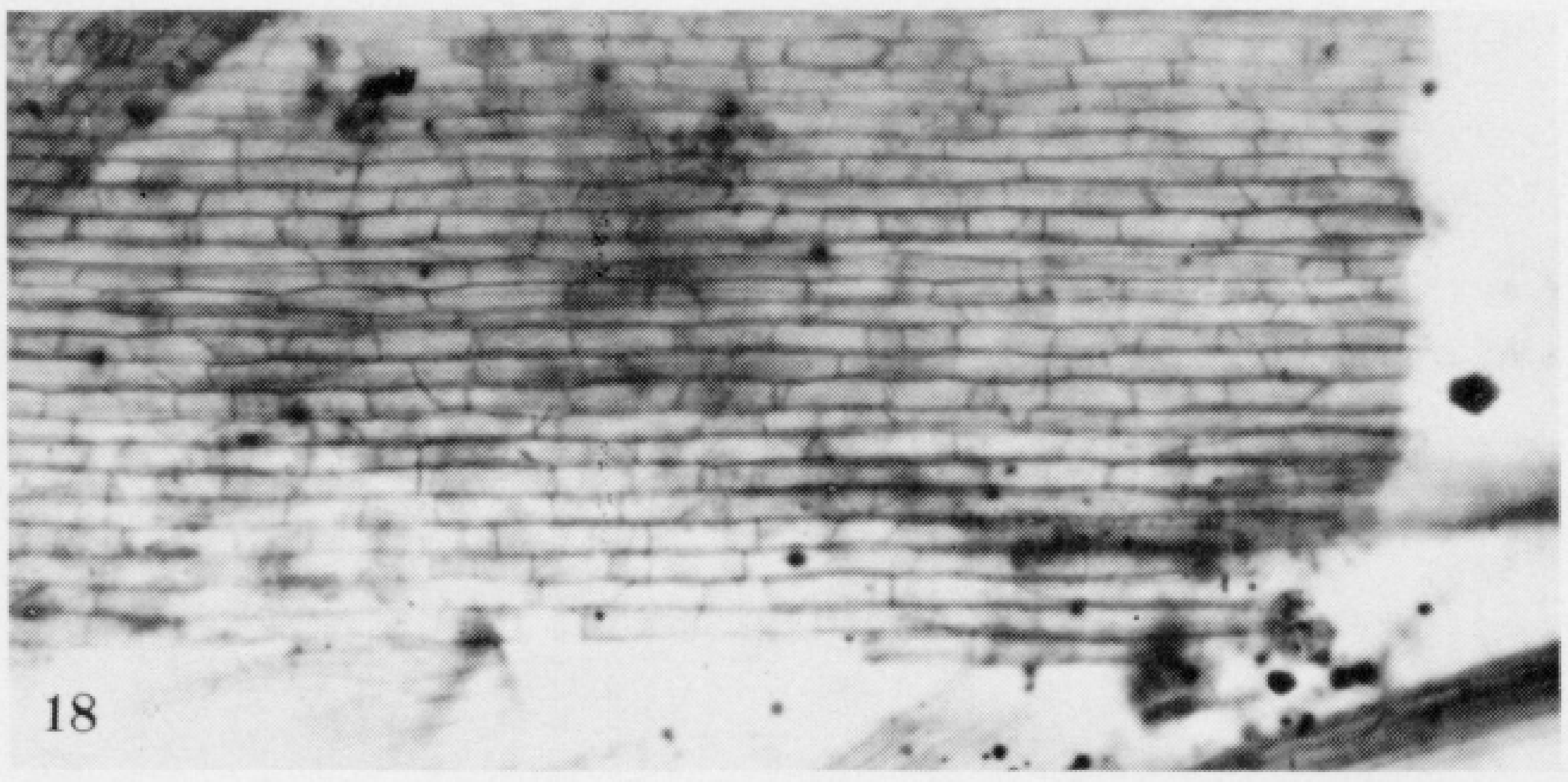
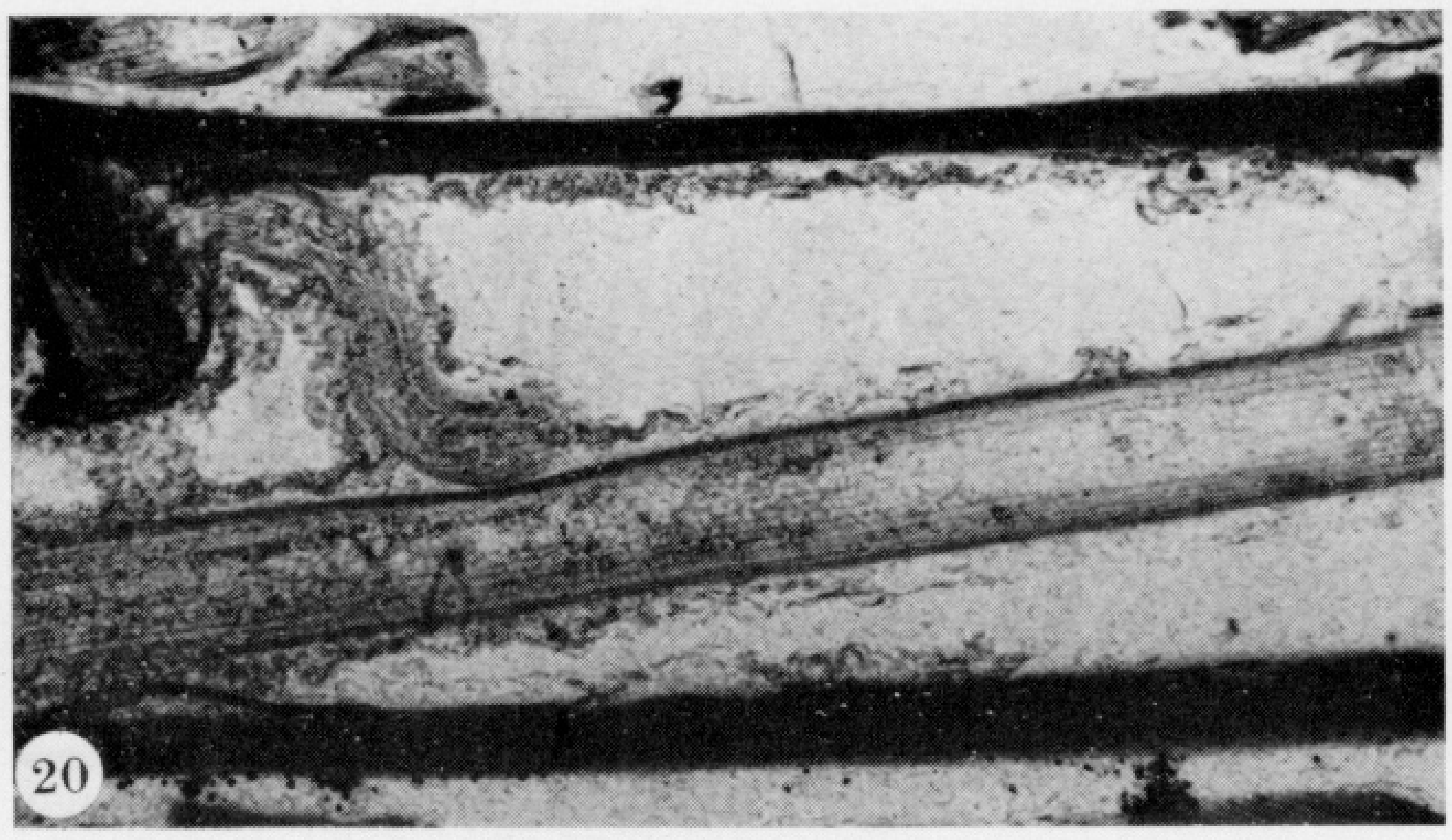
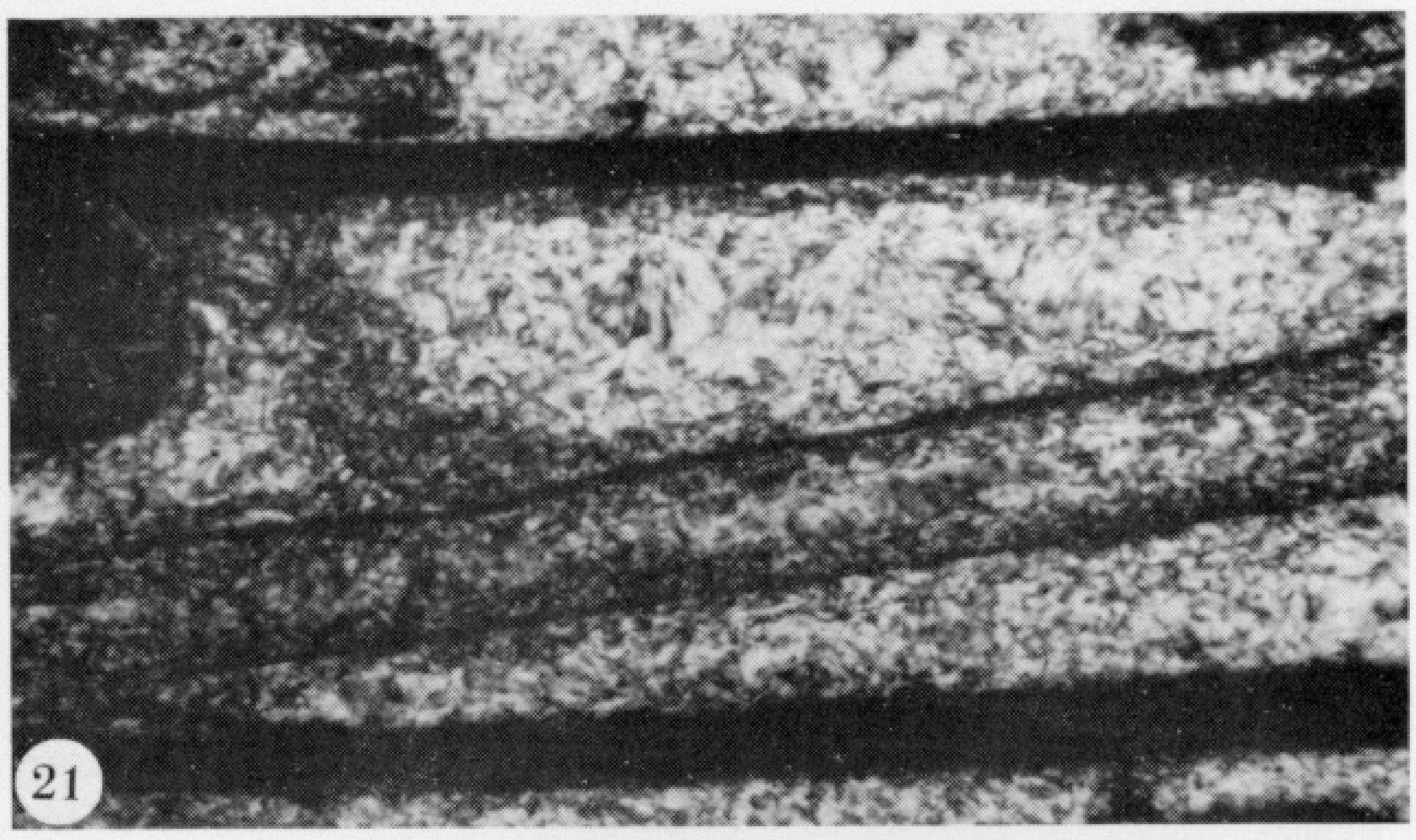
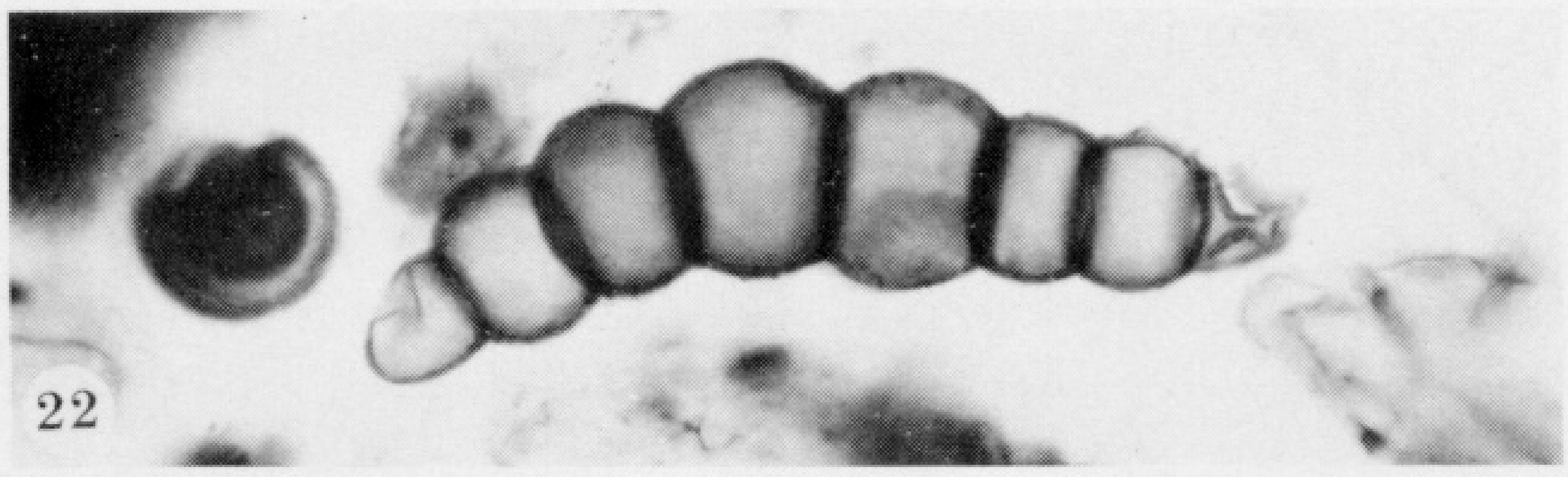
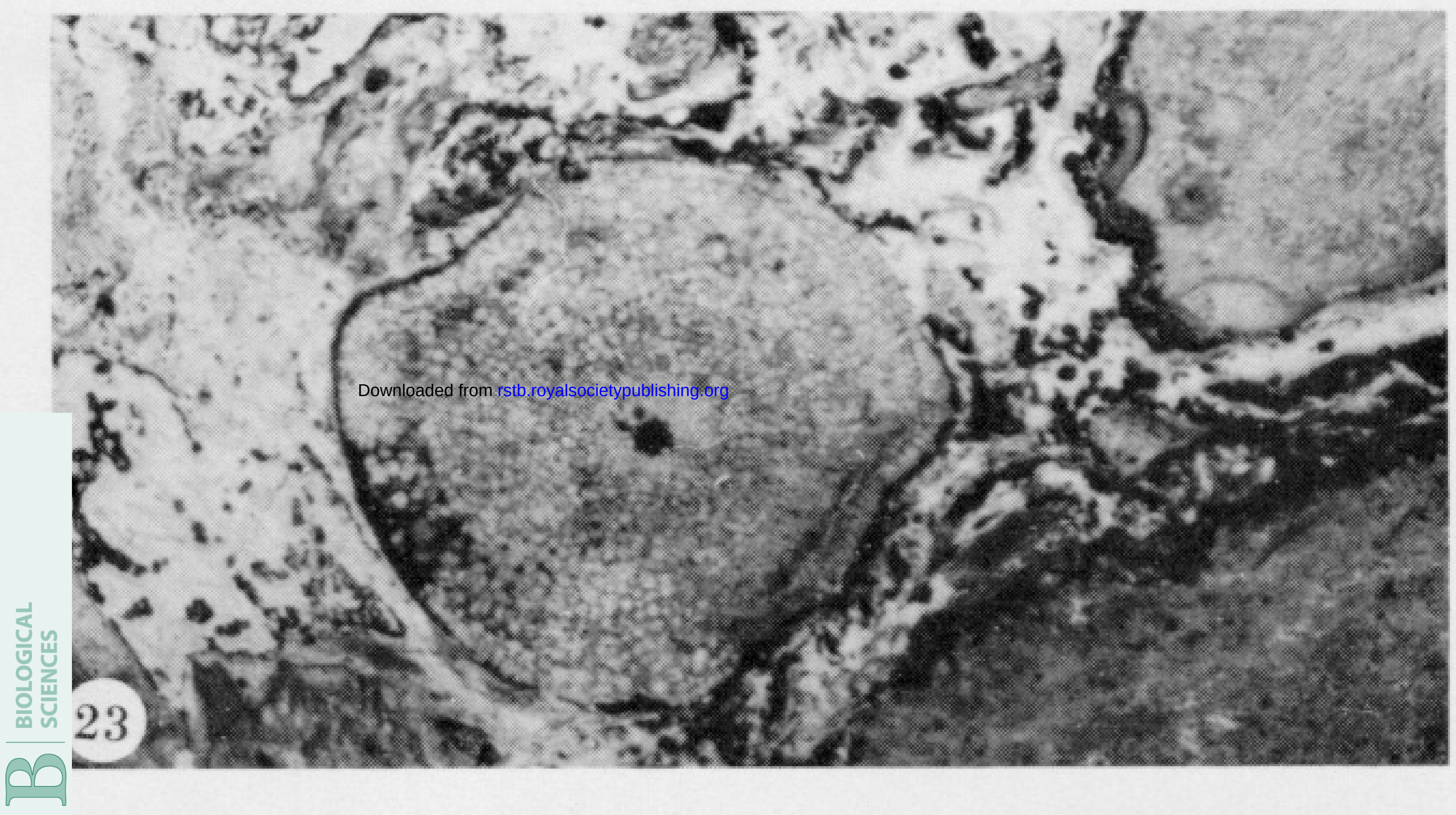
Figures 1–17. For description see opposite.

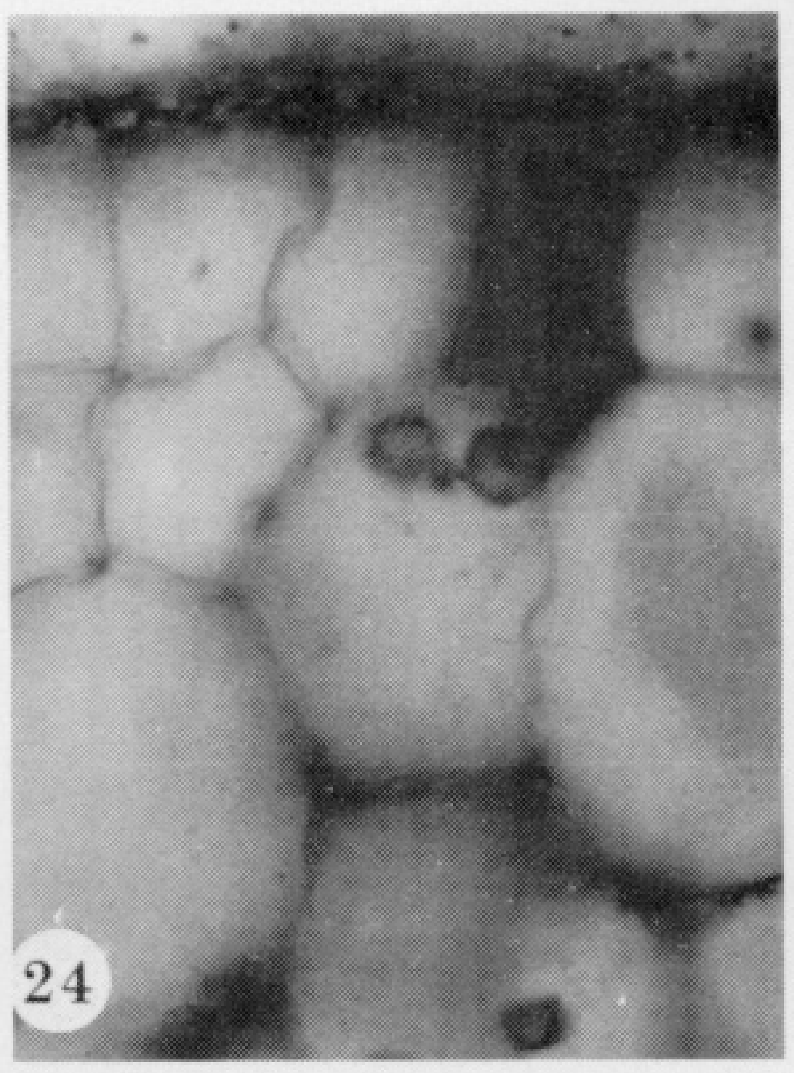


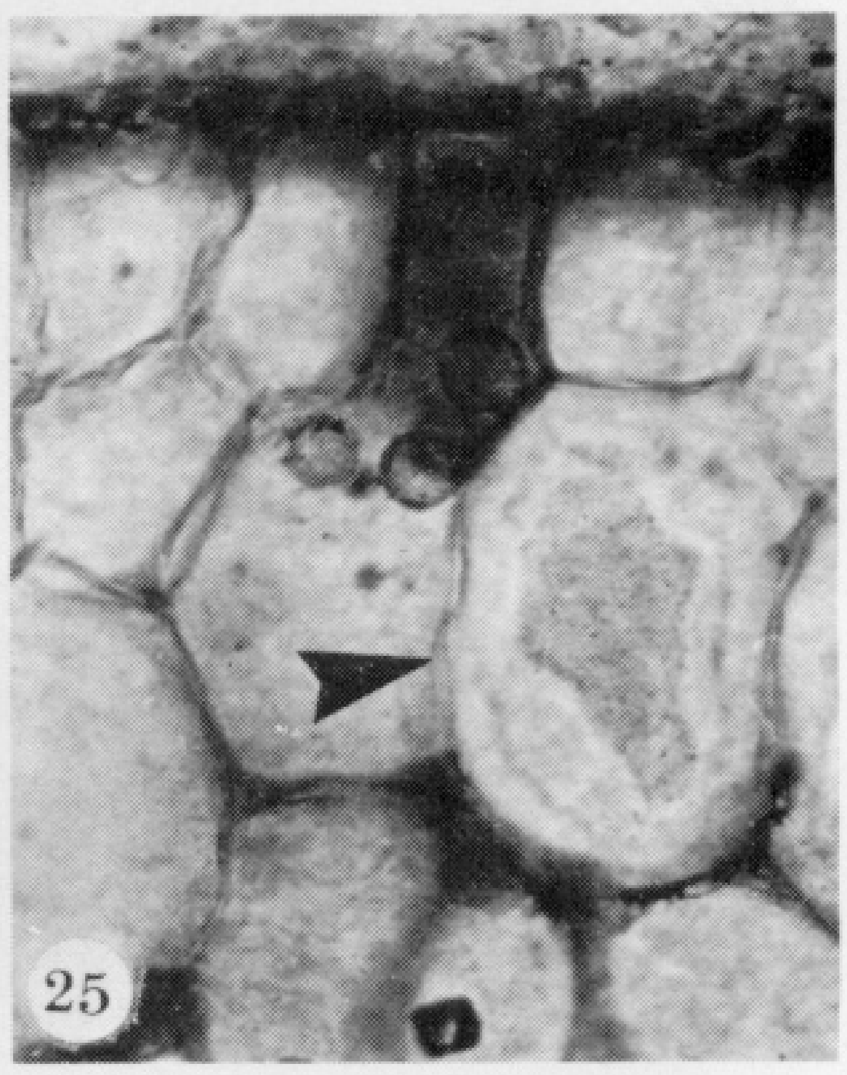


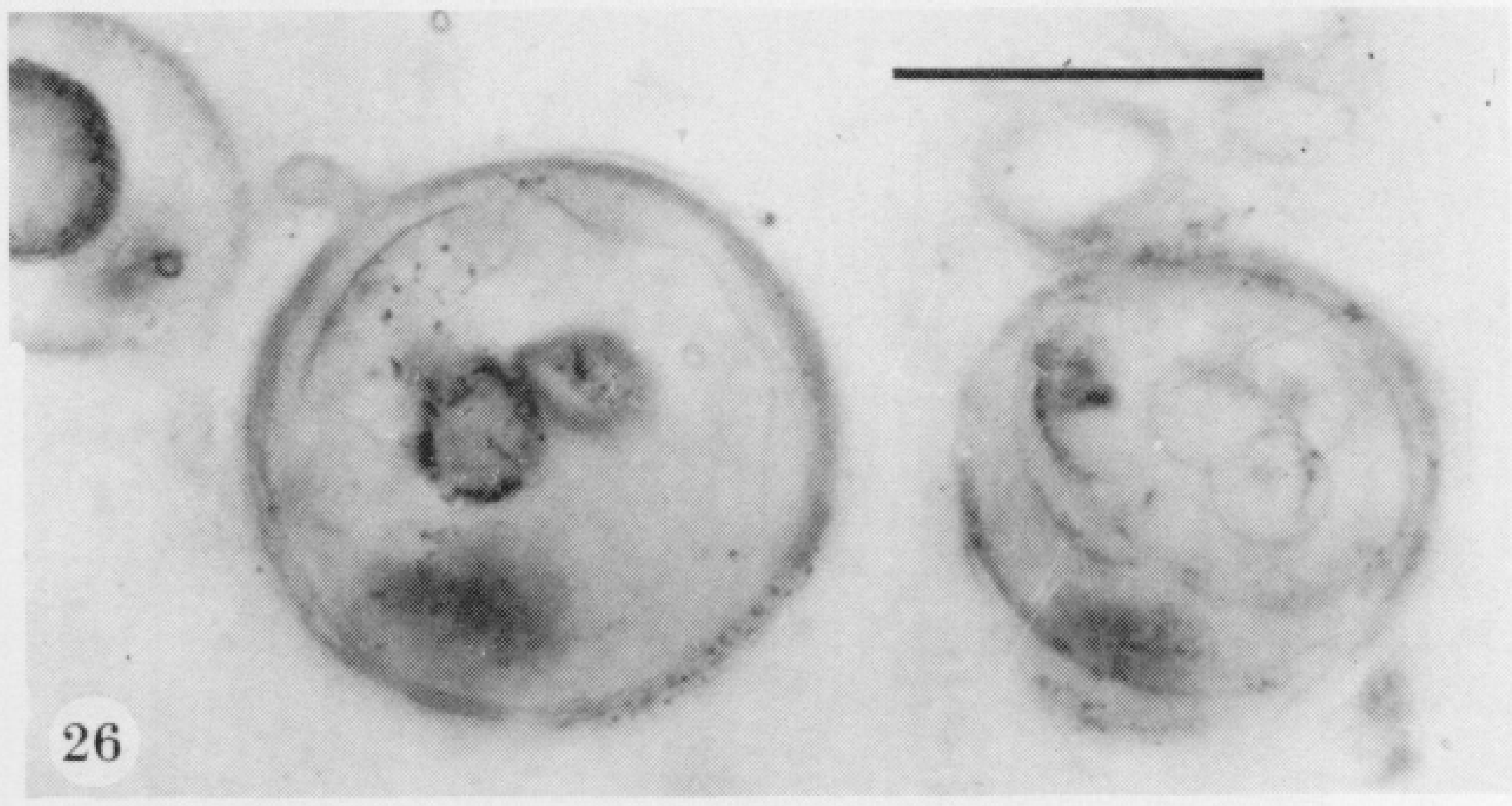


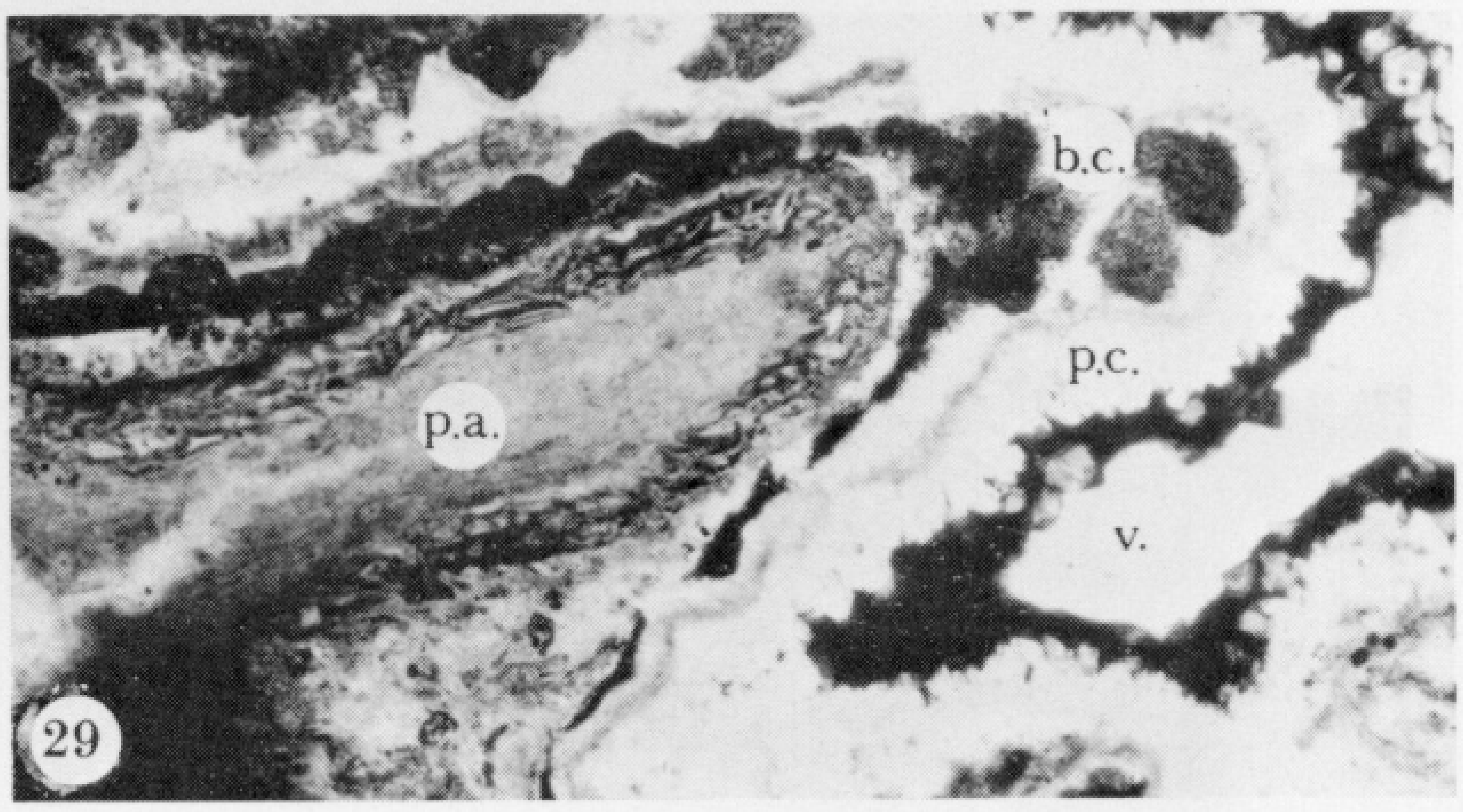












FIGURES 18–29. For description see opposite.