Great Basin Naturalist 53(1), pp. 40–47

SOIL MICROSTRUCTURE IN SOILS OF THE COLORADO PLATEAU: THE ROLE OF THE CYANOBACTERIUM *MICROCOLEUS VAGINATUS*

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ABSTRACT.—The role of the cyanobacterium *Microcoleus vaginatus* in cold-desert soil crusts is investigated using scanning electron microscopy. Crusts from sandstone-, limestone-, and gypsum-derived soils are examined. When dry, polysaccharide sheath material from this cyanobacterium can be seen winding through and across all three types of soil surfaces, attaching to and binding soil particles together. When wet, sheaths and living filaments can be seen absorbing water, swelling and covering soil surfaces even more extensively. Addition of negatively charged material, found both as sheath material and attached clay particles, may affect cation exchange capacity of these soils as well. As a result of these observations, we propose that the presence of this cyanobacterium may significantly enhance soil stability, moisture retention, and fertility of cold-desert soils.

Key words: Microcoleus vaginatus, *cyanobacteria, cryptobiotic crusts, cryptogamic crusts, soil, soil microstructure.*

It has long been reported that cyanobacterial soil crusts enhance soil stability (Anderson, Harper, and Holmgren 1982, Anderson, Harper, and Rushforth 1982, Fletcher and Martin 1948, Harper and Marble 1988, Kleiner and Harper 1972, 1977, Loope and Gifford 1972). Anantani and Marathe (1974), Anderson and Rushforth (1976), Campbell (1979), and Shields and Durrell (1964) all suggest that a network of cyanobacterial filaments binds soil particles together, immobilizing them and thus enhancing soil stability against both wind and water erosion. It has also been shown that these crusts enhance moisture and nutrient retention in sandy soils (Brock 1975, Brotherson and Rushforth 1983, Campbell 1979, Harper and Belnap unpublished data, Shields and Durrell 1964).

On the Colorado Plateau, a biogeographical province that includes southwestern and eastern Utah, northern Arizona, western Colorado and northwestern New Mexico, cyanobacterial-lichen soil crusts often provide up to 70% of the living cover (Belnap 1990a). In these areas the cyanobacterium *Microcoleus vaginatus* (Vauch.) Gom. is the major constituent (Anderson and Rushforth 1976, Campbell et al. 1989), often representing up to 95% of the biomass of the soil in interspaces between vascular plants (Belnap personal observation). This is true for all substrates examined in this biogeographical province, including soils derived from sandstone, gypsum, limestone, and shale parent material, although the degree of development of the cyanobacterial-lichen crust may vary among substrates.

Since *Microcoleus* is so prevalent in these soil systems, this study examines the influence of this species on the structure and function of soil crusts on various soil types. In particular, the possible contribution of this organism to stability of arid land soils is examined.

Figs. 1–6 (facing page). *Microcoleus vaginatus* in sandy soils: 1, note the large extracellular sheath surrounding the filaments (bar = 10μm); 2, close-up of *M. vaginatus* filaments (note the cell walls along each filament [bar = 5μm]); 3, external surface of polysaccharide sheath material secreted along exposed filament (note partially exposed filament [bar = 5μm]); 4, dried *M. vaginatus* filaments encapsulated in a polysaccharide material (arrow indicates encapsulated filament [bar = 5μm]); 5, sheaths may be a single cavity (arrrow indicates cavity [bar = 5μm]); 6, sheaths may contain many cavities (arrows indicate multiple cavities [bar = 10μm]).

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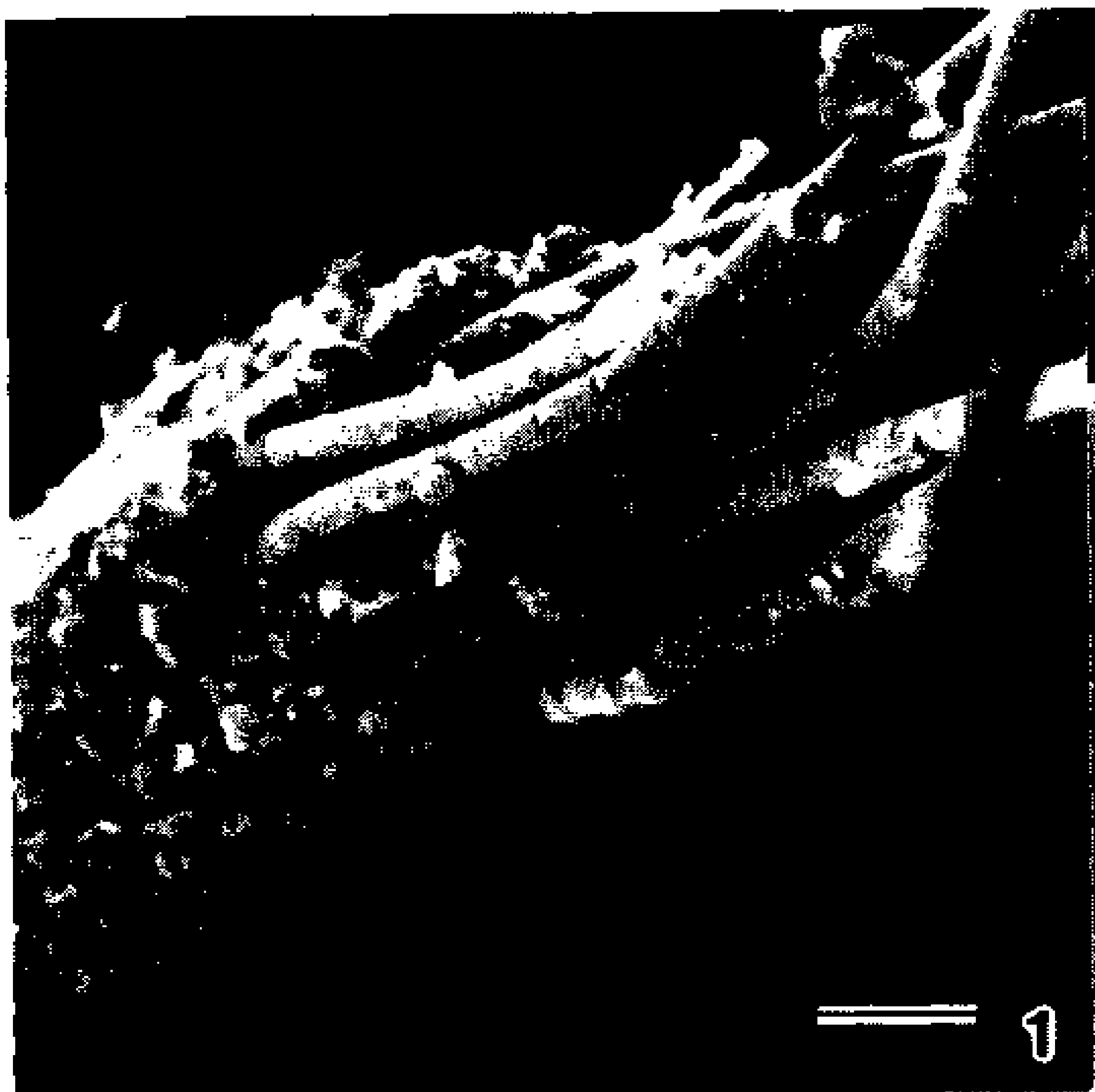
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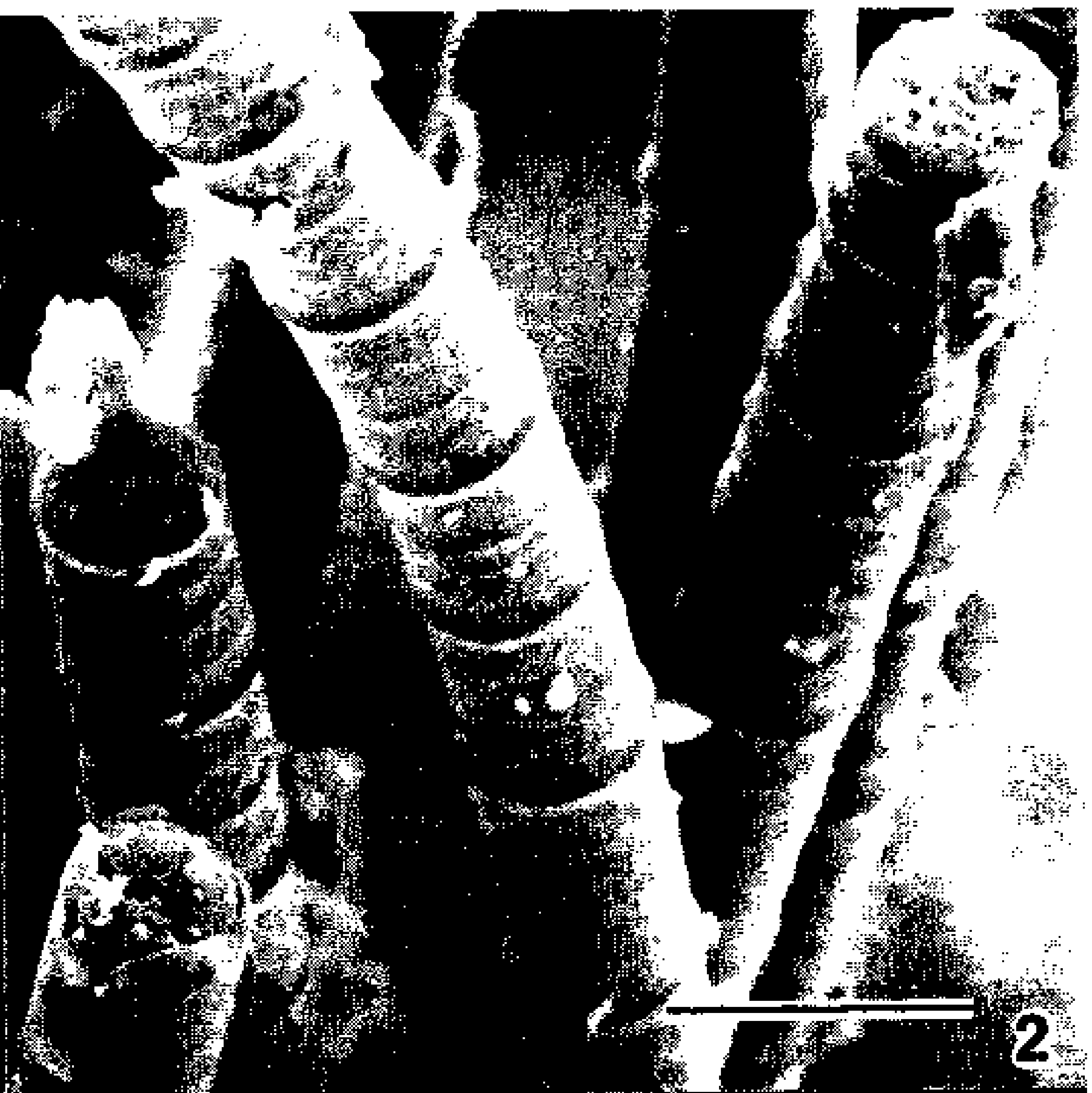
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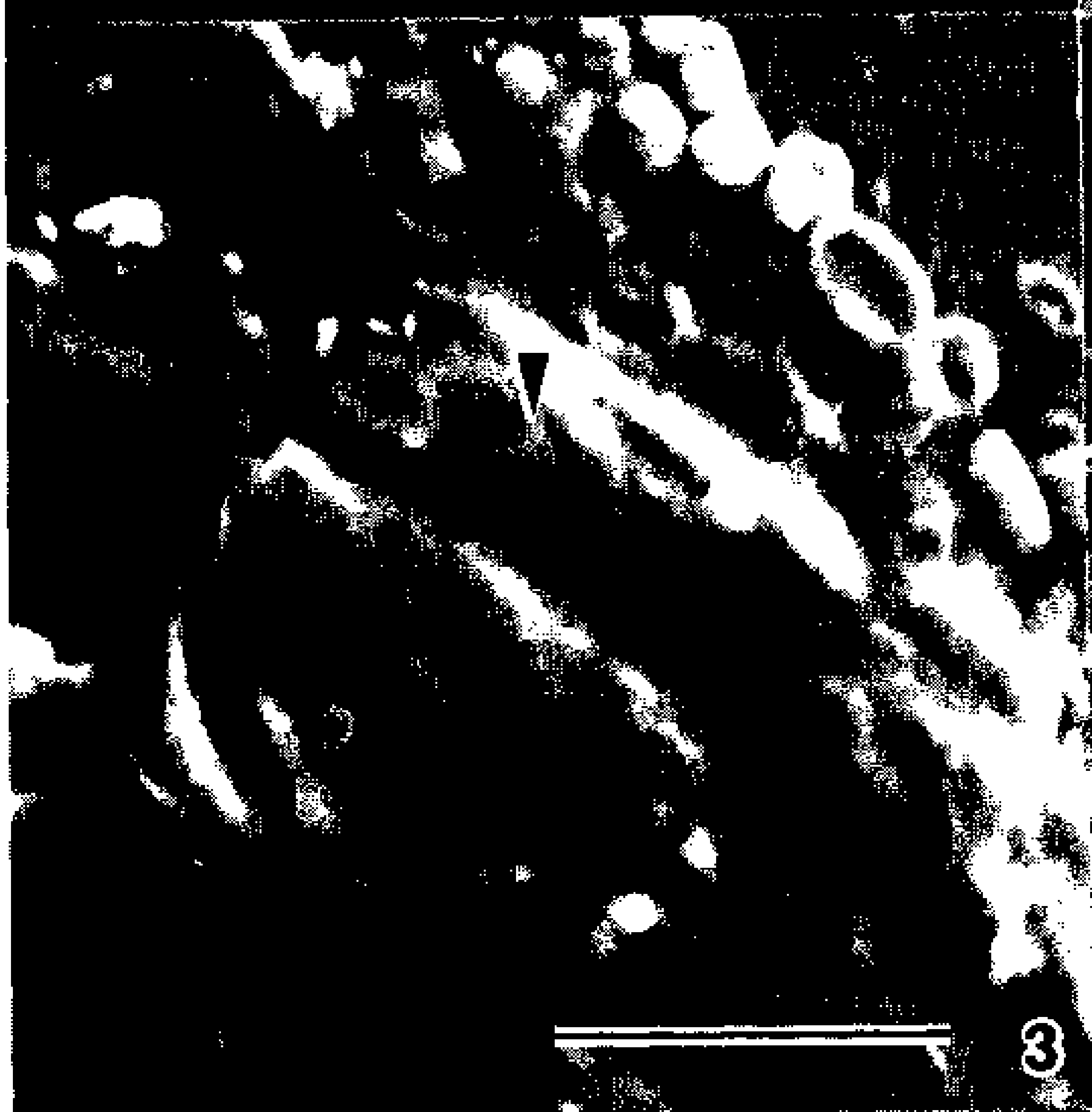
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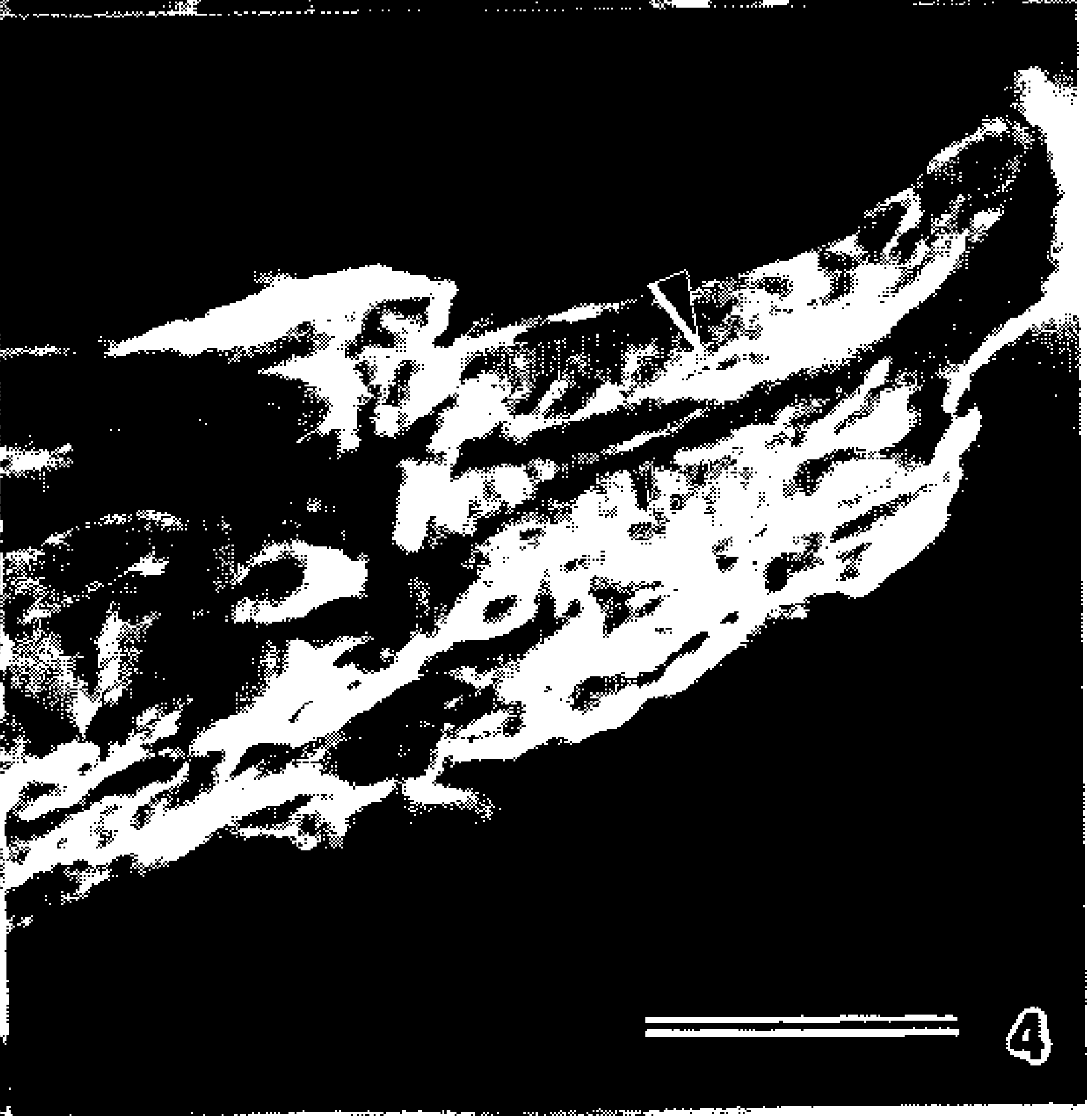
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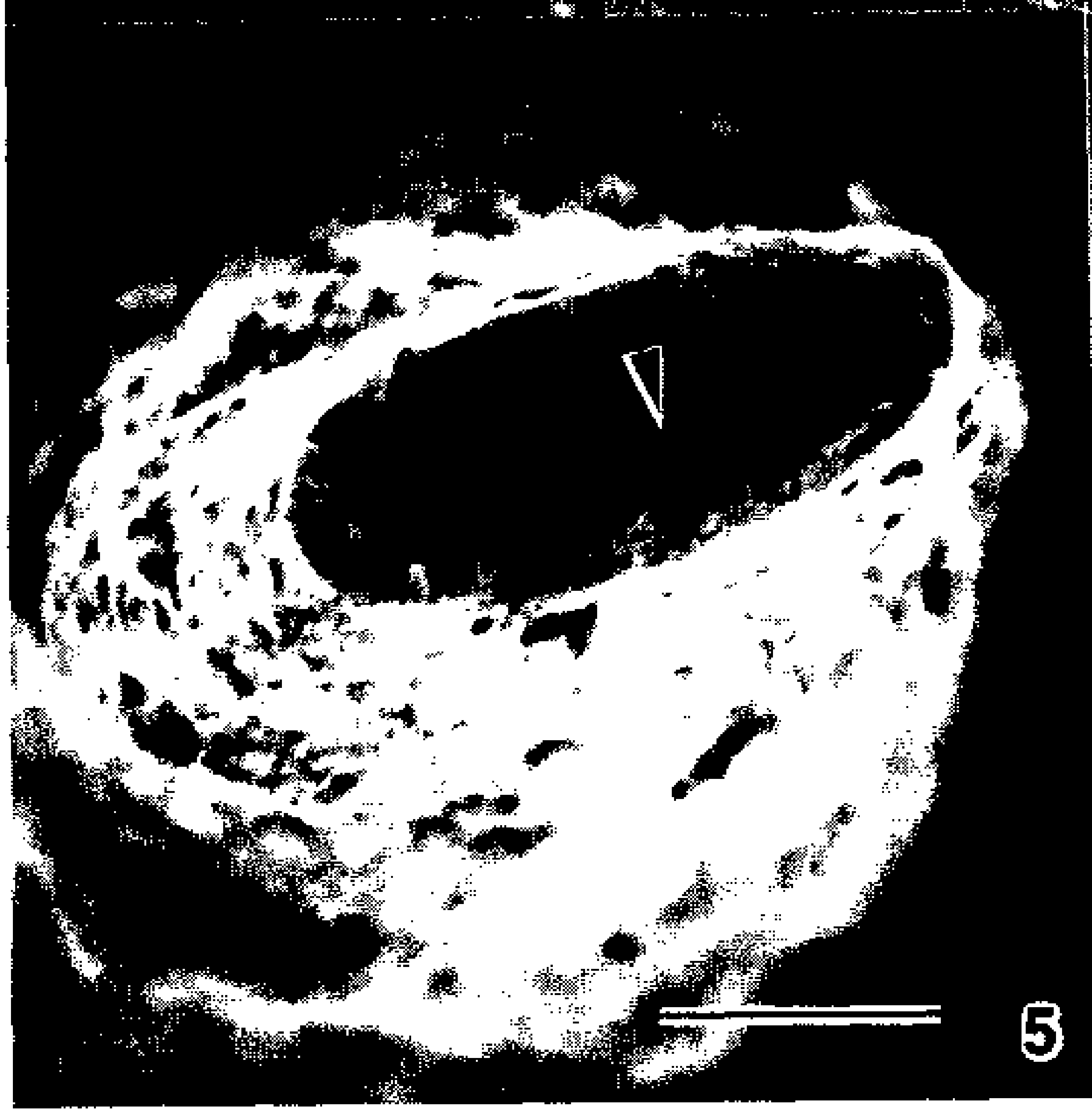
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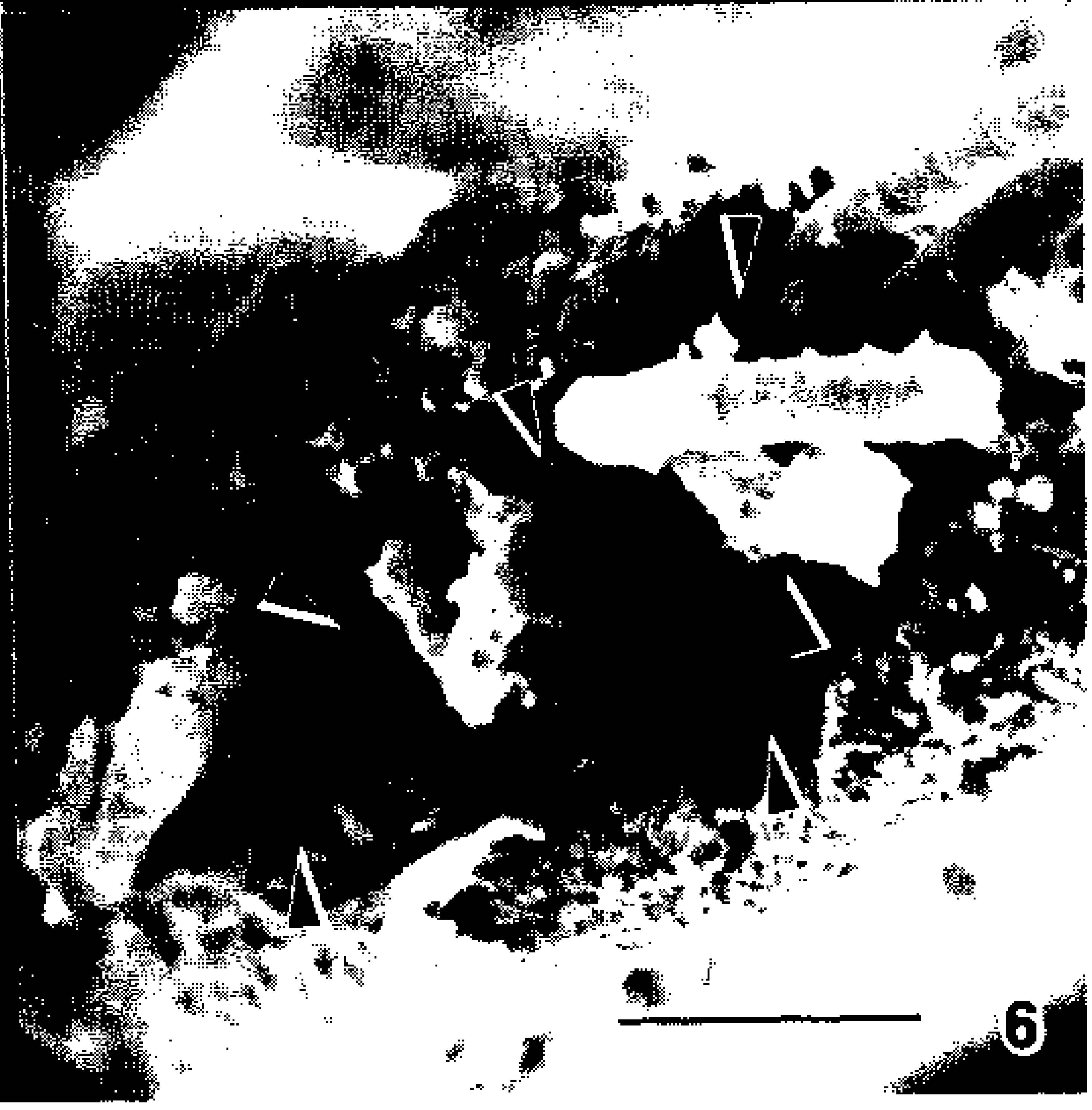
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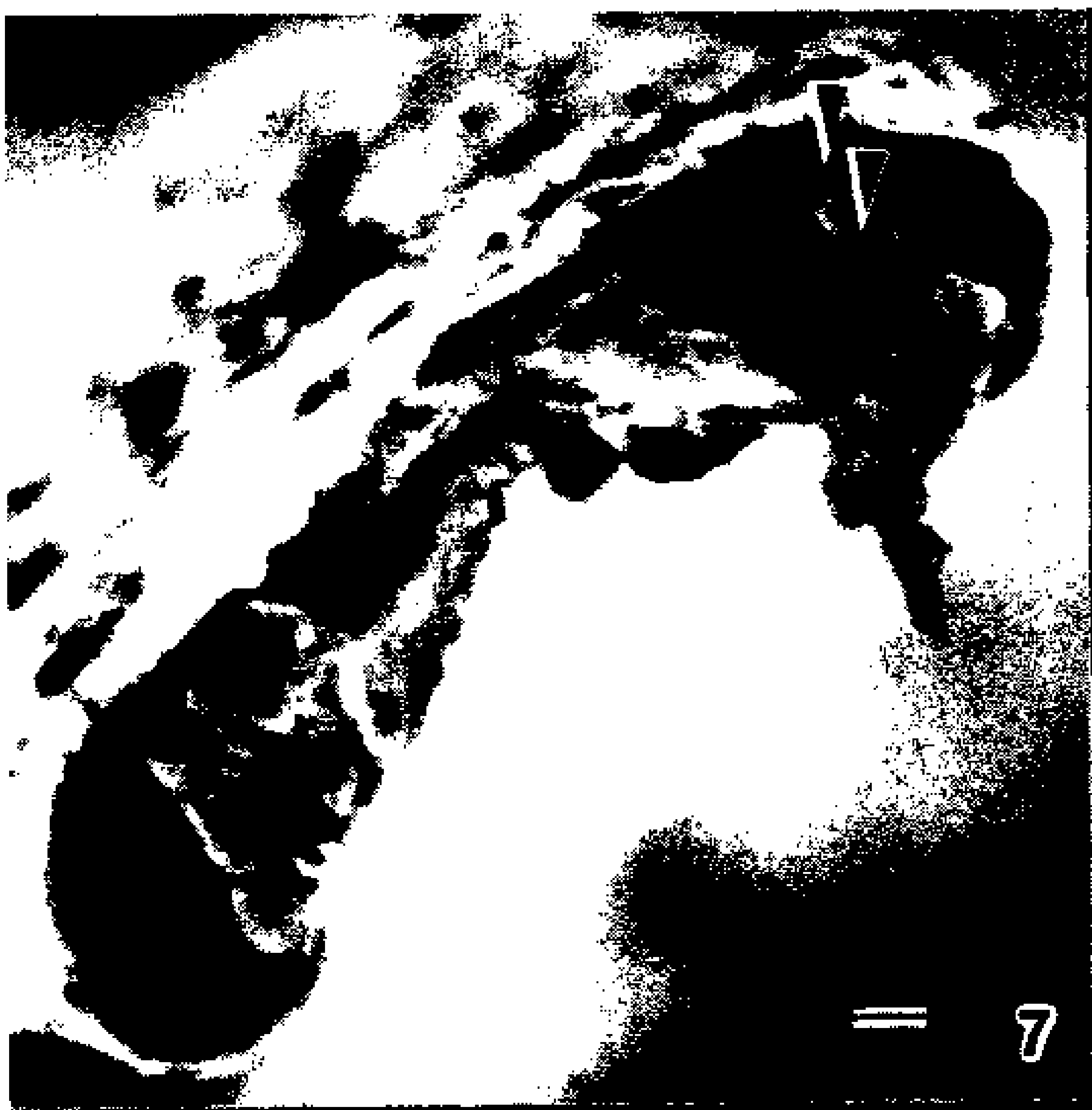
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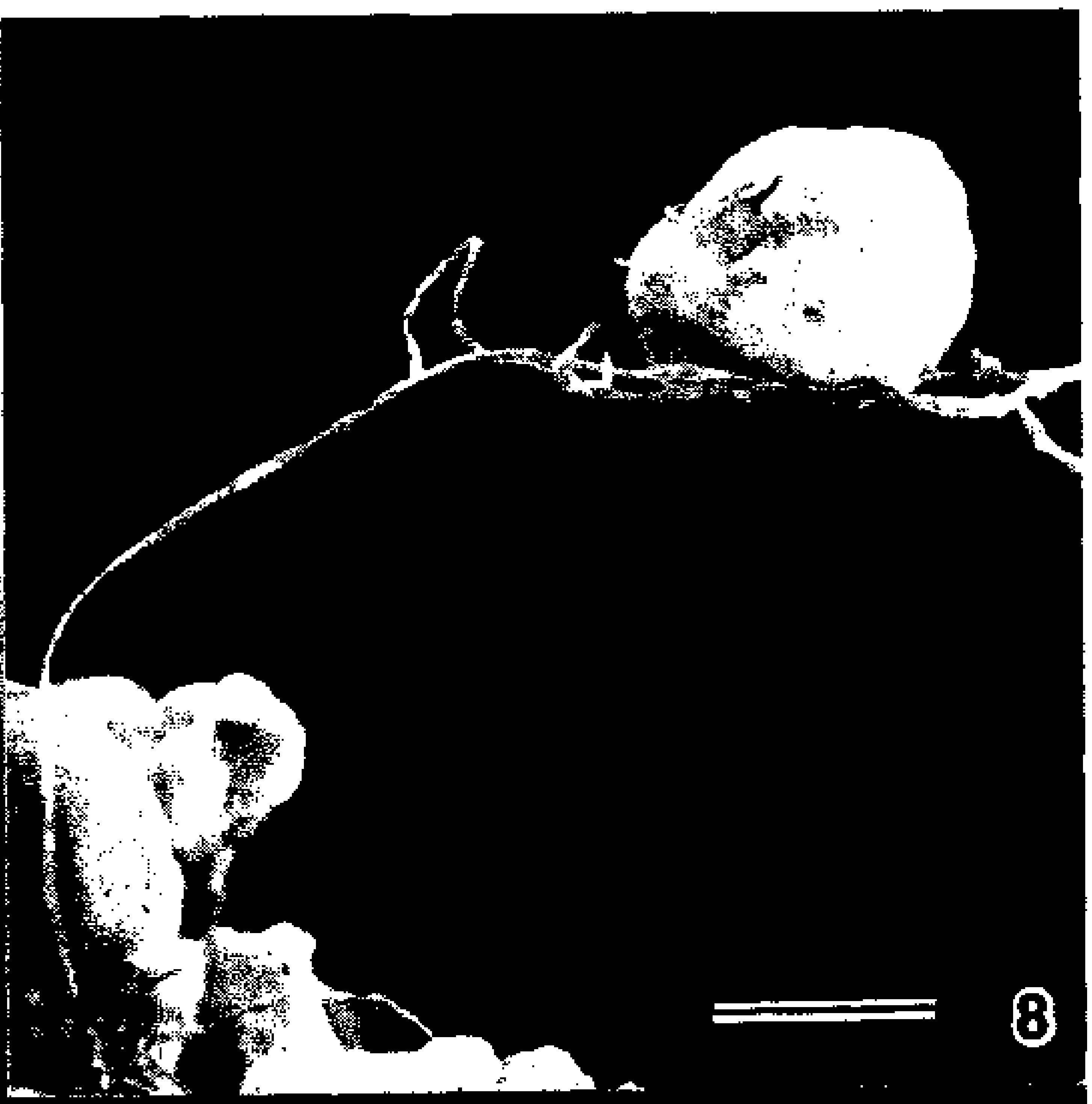
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MATERIALS AND METHODS

Cyanobacterial soil crusts were collected from three different substrate types on the Colorado Plateau in early fall. Crusts from sandstone- and gypsum-derived soils were collected from Arches National Park in southeastern Utah near Moab. Crusts from limestone-derived soils were collected from Bryce Canyon National Park in southwestern Utah near Panguitch. All crusts were transported to the lab, where they were prepared for observation using scanning electron microscopy (SEM). Two types of preparation were used: samples were either directly gold-coated and examined with a JEOL 840A scanning electron microscope or were prepared by freeze-substitution (Ichikawa et al. 1989), gold-coated, and then examined with SEM.

The presence of chlorophyll *a* was used to estimate the depth and distribution of living cyanobacteria and green algae in the crusts found on the sandy and gypsiferous soils from Arches National Park. Two-centimeter-deep cores of the crust were cut in 2-mm segments, beginning at the soil surface. Chlorophyll *a* was extracted from samples with dimethyl sulfoxide (DMSO). The DMSO extraction samples were centrifuged and spectrally analyzed on a diode array spectrophotometer (Belnap 1990b) at 665 nm to obtain relative values for the amount of chlorophyll *a* present.

RESULTS AND DISCUSSION

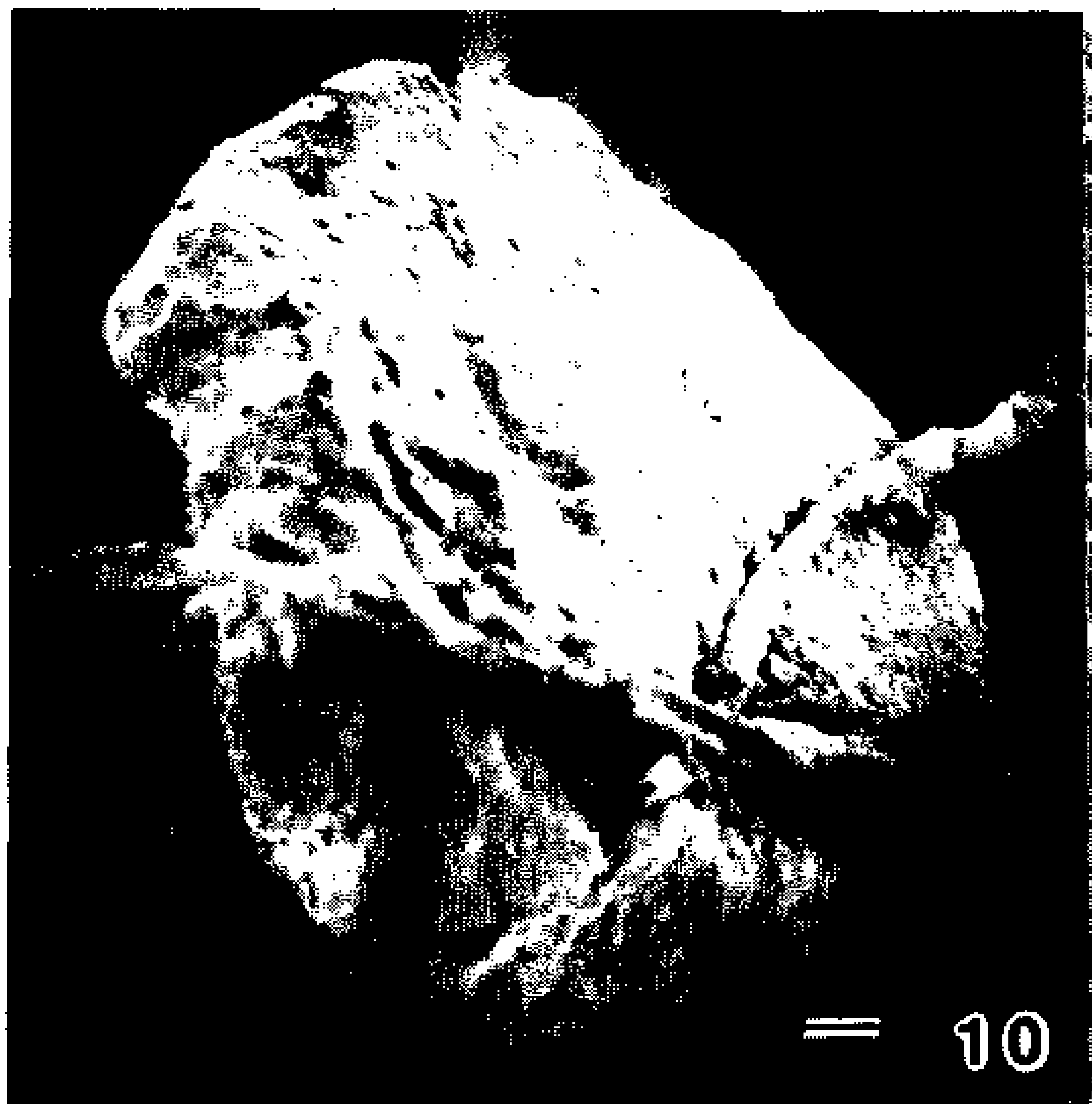
Microcoleus vaginatus and *M. vaginatus*-dominated crusts from sandstone-derived soils are shown in Figures 1–13. A large and distinct polysaccharide sheath surrounds groups of living filaments of *M. vaginatus* (Fig. 1). Close examination shows cellular divisions in the cyanobacterial filaments (Fig. 2). When wet, the polysaccharide sheaths swell and the filaments within are mechanically extruded from the sheath and through or across the soil surface. As the surface dries, the filaments retract somewhat into the sheath. Exposed portions of the filaments then secrete additional polysaccharide material (Fig. 3). When dry, the cyanobacterial filaments are completely encased in the polysaccharide sheaths (Fig. 4). The interior of the sheath of *M. vaginatus* may contain from one (Fig. 5) to many cavities (Fig. 6). The sheath itself can be formed by more than one secretion event (Fig. 7)

The strength of this sheath material can be seen in Figure 8, where a single strand of sheath material holds a sand grain aloft above the supporting surface. The binding effect of these cyanobacterial sheaths on sandy soil surfaces is illustrated in Figure 9. Sheaths of *M. vaginatus* wind among the sand particles, connecting individual grains, much like fibers in fiberglass. Although the sheath material is dry, it can be seen still firmly adhering to the soil particles. Secure and extensive connections to the sand grains by the sheath material are shown in Figures 10 and 11. Multiple sheaths can often be seen attached to the same sand grain, as shown in Figure 10. In Figure 11 the intimate association between sand grain and polysaccharide material can be seen.

When wet, the polysaccharide sheath material swells and covers the soil surface even more extensively than when dry. Sheath material can absorb up to eight times its weight in water almost instantaneously; thus, it absorbs precipitation quickly and increases the water-holding capacity of sandy soils (Brock 1975, Cameron and Blank 1966, Campbell 1979, 1989). Sheaths and filaments become swollen and round, forming a net over the surface of the sand (Fig. 12). Even when swollen, however, there is still space for rainwater and vascular plant roots to penetrate into the soil between sheaths.

The presence of cyanobacterial soil crusts has been demonstrated to increase the availability of many nutrients in sandy soils. Levels of N, P, K, Fe, Ca, and Mg were higher in the annual grass *Festuca octoflora* growing on crusted soils than in plants growing on comparable non-crusted soils (Belnap and Harper unpublished). Essential nutrient concentrations were also shown to be higher in the tissue of the biennial plant *Lepidium montanum* growing on soils covered by cyanobacterial-rich crusts than on paired plots where the surface 1.0 cm of crust had been stripped from around the plants three

Figs. 7–9 (facing page). *Microcoleus vaginatus* in sandy soils: 7, sheaths may be created by more than one secretion event (arrow indicates two discrete layers of polysaccharides [bar = 1μm]); 8, sheath material possesses a great deal of strength (note single sheath holding a sand grain aloft [bar = 100μm]); 9, sheath material binds sand grains together (note the sheaths are wound around and among the sand grains [bar = 100μm]).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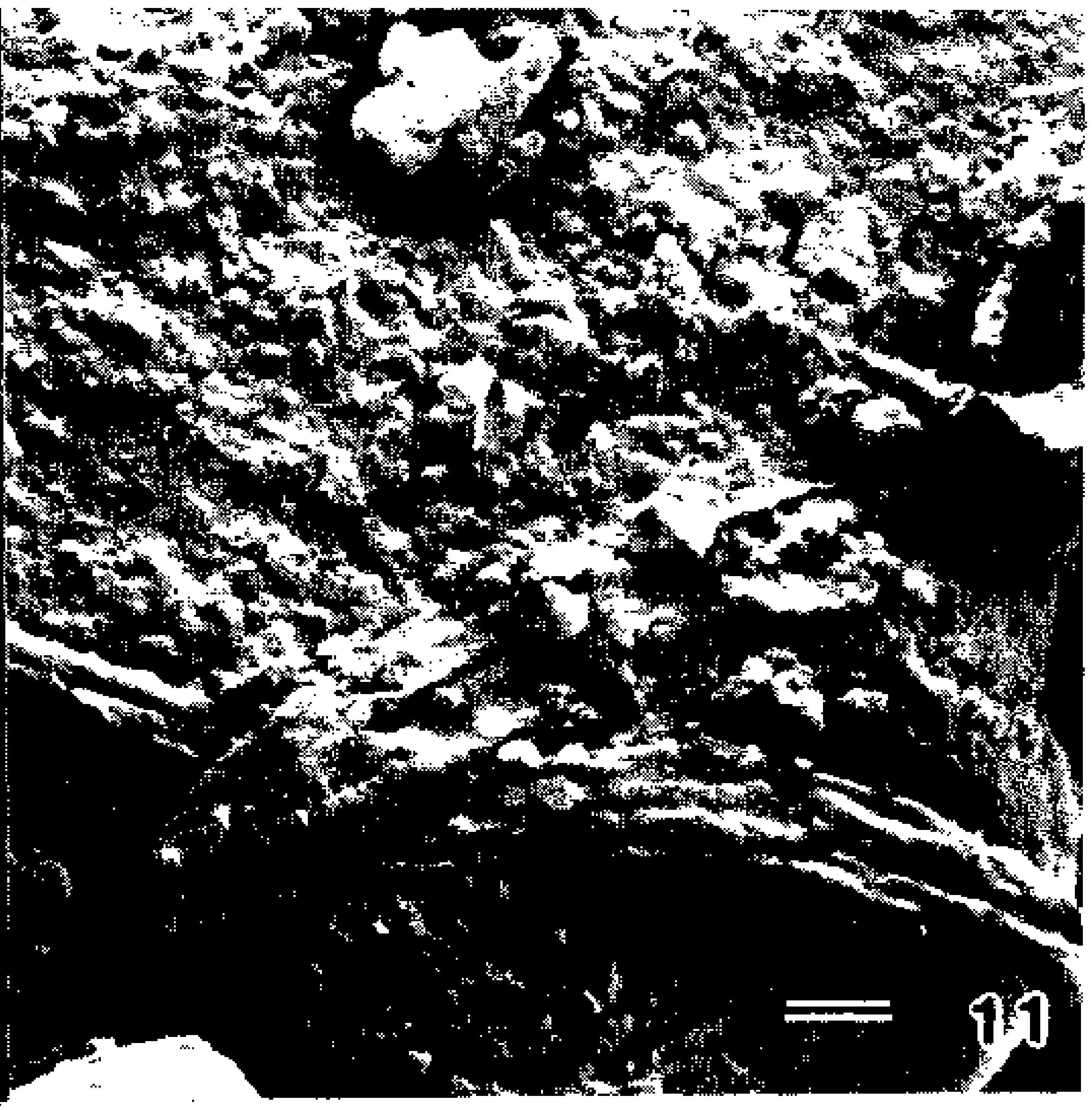
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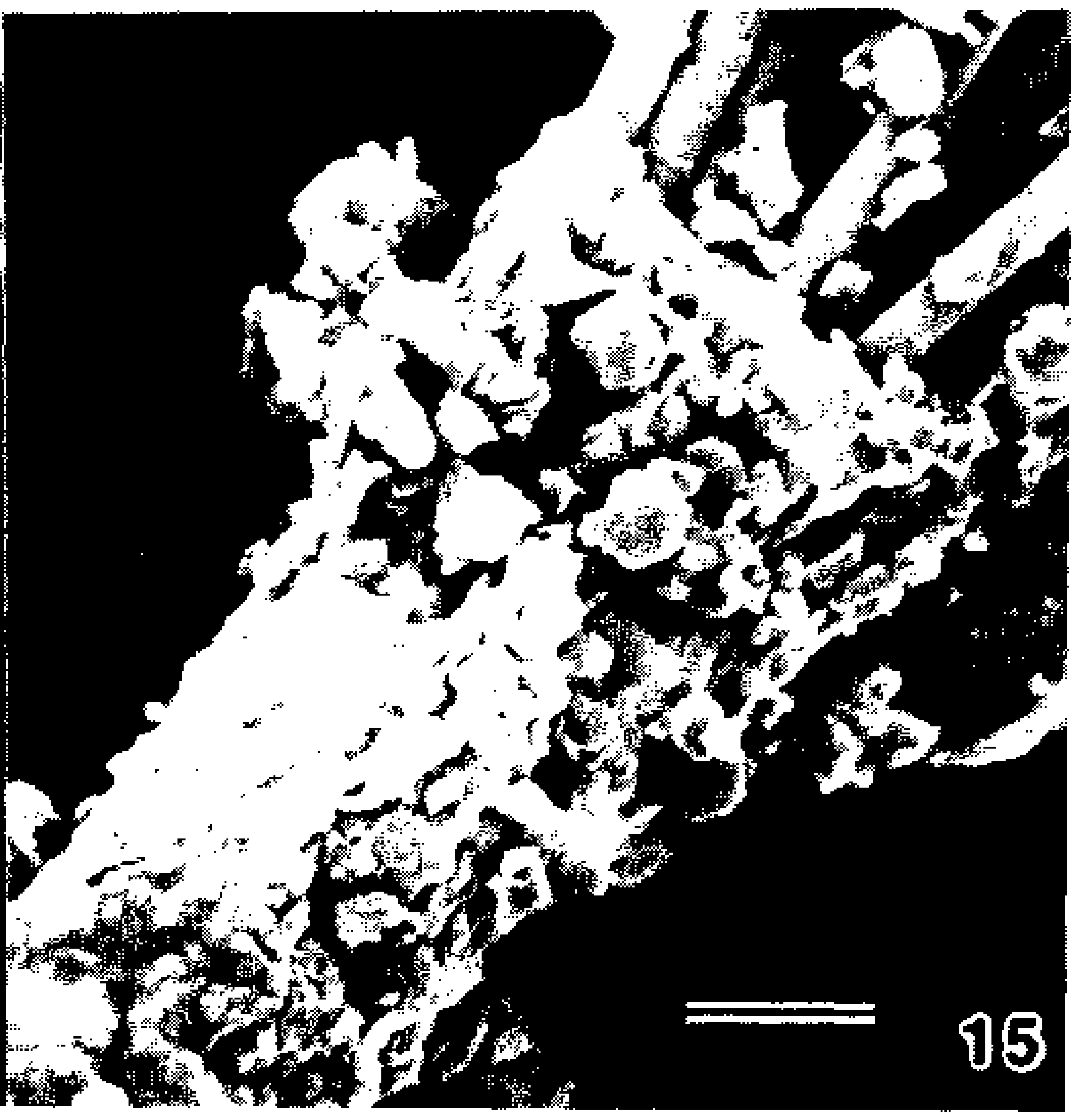
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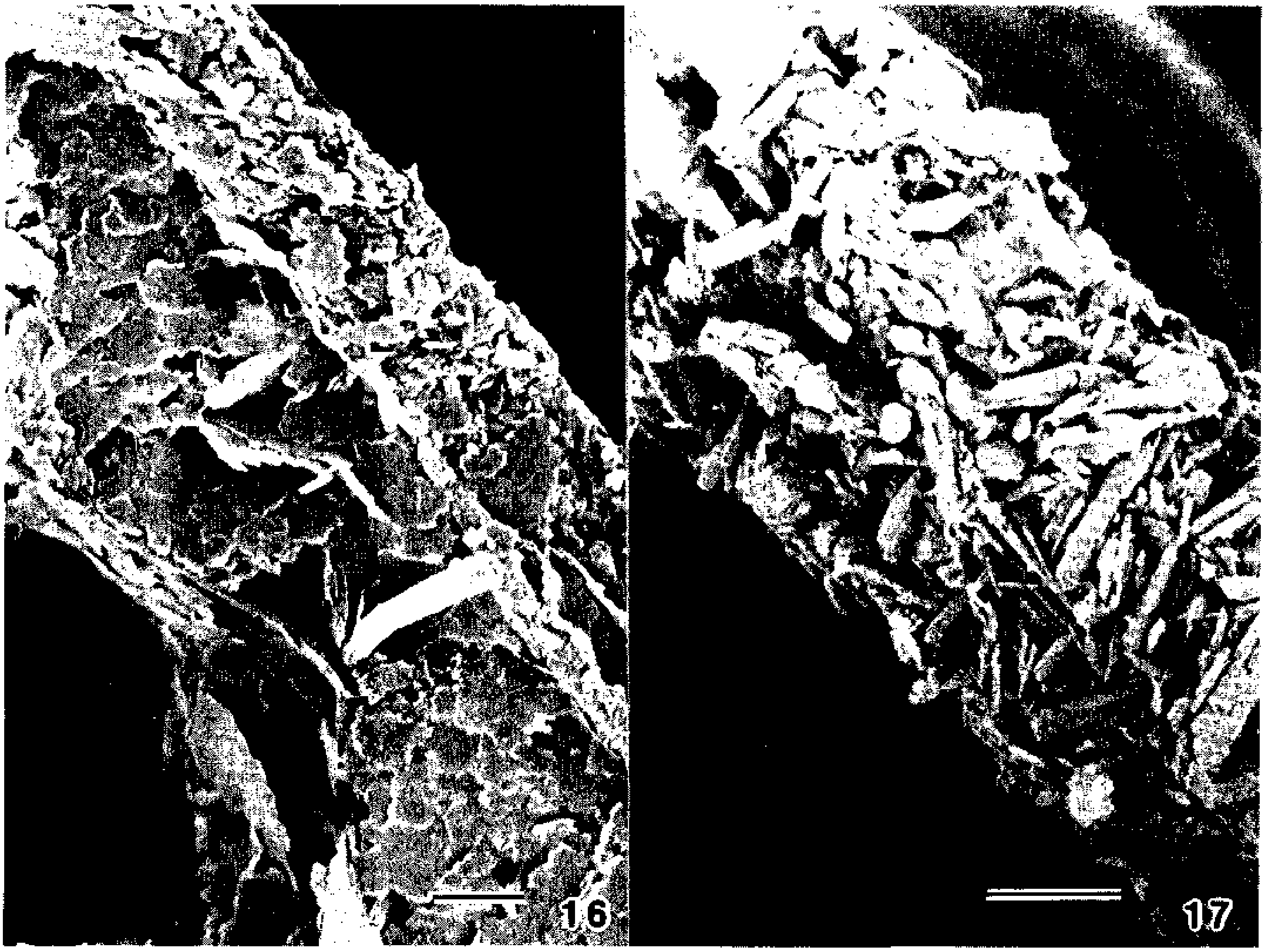

Figs. 16–17. *Microcoleus vaginatus* in gypsiferous soils: 16, sheaths in gypsiferous soils can be made of both organic and inorganic material (bar = 10μm); 17, sheaths in gypsiferous soils are often coated with gypsum crystals (note the gypsum crystals on the sheath surface [bar = 5μm]).

months prior to tissue nutrient analyses (Harper and Marble unpublished). One possible mechanism by which the cyanobacteria alters mineral availability in supporting soils is suggested in Figure 13: clay particles can be seen bound to, and incorporated into, the polysaccharide sheath material. Consequently, positively charged macronutrients bound to these negatively charged clay particles and to the negatively charged sheath material would be held in the upper soil horizons and in a form readily available to vascular plants, instead of being leached away by percolation water or bound in a chemically unavailable form.

Chlorophyll *a* distribution in the soil shows that cyanobacterial cells are probably concentrated in the top 4 mm of sandy soils, but some chlorophyll *a* is found as deep as 1 cm. Measurements of the bumpy surface topography of undisturbed crusts show that few bumps are greater than 8 mm across. Analysis shows that cyanobacterial filaments ramify throughout such surface irregularities. The volume of cyanobacterial filaments per unit soil surface coverage is thus increased greatly in areas where microtopography of the soil surface is very complex.

Figs. 10–15 (facing page). *Microcoleus vaginatus*: 10, 11, sheaths adhere firmly to sand grain surfaces (note the intimate connection between the sheath and grain surfaces [bars = 10μm]); 12, when wet, sheaths and filaments swell, covering the soil surface (note the mass of entangled sheaths covering the sand grains [bars = 100μm]); 13, clay particles (arrows) may be incorporated into sheath material (bar = 10μm); 14, in fine-textured soils such as this limestone-derived substrate, many small particles adhere to the sheath material (bar = 10μm); 15, sheath surface texture in fine-textured soils is much smoother than that in coarse-grained soils (note smooth material at the base of the sheath, which appears similar to the surrounding inorganic material [bar = 10μm]).

Trampling negatively affects the cohesion and coverage of cyanobacterial crusts, since the filaments are brittle when dry and easily crushed (Campbell et al. 1989, Harper and Marble 1988, Kleiner 1982). Visual examination of undisturbed soil crusts on sandy soils of the Colorado Plateau shows cyanobacterial sheath material occuring as deep as 10 cm below the surface of the soil. Heavily trampled areas support only a thin veneer of cyanobacterial sheaths (Belnap unpublished data). Since no chlorophyll *a* is found below 1 cm, sheath material below that depth must represent remnants of cyanobacterial crusts once found near or at the soil surface and later buried by sediments. Though no longer associated with living filaments, such sheath material is still capable of binding soil particles together and still increases nutrient and moisture retention of associated soil. However, any damage to such abandoned sheath material is non-repairable, since living cyanobacteria are apparently no longer present at these depths to regenerate filament and sheath materials. As a consequence, trampling may not only reduce soil stability, but soil fertility and soil moisture retention as well.

In finer-textured soils the sheaths of *M. vaginatus* assume a different appearance. In such soils fine particles adhere to the outside of most sheaths, as can be seen in sheaths from a limestone-derived soil (Fig. 14). Also, the sheath surface appears much smoother in these limestone-derived soils (Fig. 15) and is much harder to the touch. It may be that water-soluble matter in these soils goes into solution when the soil is thoroughly wetted by rain. Such periods would also coincide with the time of maximum activity for the cyanobacteria. Under such conditions, secretion of polysaccharide material could be expected to mix with the soil particles and materials in solution and, upon drying, form sheaths that are part organic and part inorganic.

An even more graphic illustration of cyanobacterial sheaths that are both organic and inorganic is presented by the sheaths of *M. vaginatus* in gypsiferous soils (Figs. 16, 17). Gypsum, being more soluble in water than carbonate salts of calcium, appears to dissolve when soils are wet and recrystallize on the surface of the polysaccharide sheath material of the cyanobacterium to produce sheaths such as those seen in Figure 16. In Figure 17 the same sheath is locally covered with gypsum crystals that totally obscure the polysaccharide material. This ability to mix with solubilized soil materials may render sheaths less vulnerable to physical breakage.

In combination these SEM micrographs demonstrate that cyanobacterial soil crusts strongly alter the microstructure of soils in cold-desert ecosystems. The interwoven filaments of *M. vaginatus* and other filamentous cyanobacteria undoubtedly enhance soil surface stability in such environments. When undisturbed for long periods, cyanobacterial sheaths may be found at depths as great as 10 cm below the surface of sandy soil. Thus, as aeolian and waterborne materials are trapped in the polysaccharide sheaths of *M. vaginatus* and other cyanobacteria growing on the surface of desert soils, these sheaths are gradually buried, but their ameliorating influences on water-holding capacity, cation exchange capacity, and soil stability may extend far below the depth to which light can penetrate.

ACKNOWLEDGMENTS

This study was funded by a grant from the U.S. Army Corps of Engineers to the Intermountain Research Station, United States Forest Service, and by the National Park Service, WASO-Air Quality Division. We offer special thanks to Retsik Belnap, Kimball Harper, Bob Greenberg, Bill Hess, and the Electron Optics Lab, Brigham Young University.

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