

MICROCODIUM REVISITED: ROOT CALCIFICATION PRODUCTS OF TERRESTRIAL PLANTS ON CARBONATE-RICH SUBSTRATES

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ABSTRACT: *Microcodium* is a problematic calcitic microfeature of many calcrites and calcareous paleosols in the Cretaceous and Tertiary continental and marine successions of the peri-Tethyan realm. The main controversy about the *Microcodium* structures is their origin and possible relation with calcified plant roots. *Microcodium* and rhizogenic (root-formed) microfibrils were studied in calcrite profiles within the Paleocene shallow-marine carbonate succession in southwestern Slovenia. The prominent laminar calcrite horizons contain abundant calcite aggregates, 150 μm to 1 cm in size, with perfectly preserved structural details of plant root tissues. Morphology and structure of these aggregates indicate that they formed through biologically controlled precipitation of calcium carbonate within the root cortical cells. The morphologies intermediate between the typical *Microcodium* aggregates, composed of a single layer of individual, elongate pyramidal or prismatic crystals of calcite (measuring 100–500 μm in length and 20–70 μm in width) and calcified roots with multilayer arrangement of isodiametric cells were observed, and this supports previous rhizogenic interpretations of *Microcodium* structures. Intermediate forms show that the typical *Microcodium* aggregates formed through morphological transformation of the root tissue by growth of the calcite within the cortical cells, which distorted the cell shape. Calcification of roots and the creation of *Microcodium* structures can be explained as an effective nutrient-acquiring mechanism used by certain types of terrestrial plants inhabiting nutrient-poor calcareous substrates. The widespread occurrence of *Microcodium* in almost unaltered shallow-marine limestones indicates that its formation took place during early stages of paleosol development, probably reflecting specific types of vascular plants of a pioneer community that were able to colonize carbonate substrates during the early phases of subaerial exposure.

INTRODUCTION

Plant roots and associated microorganisms in the rhizosphere produce important accumulations of calcium carbonate in near-surface terrestrial settings. Root calcification structures are among the most prominent features in many soils and paleosols and may actually constitute the dominant fabrics in some forms of calcrite (Wright et al. 1995).

Criteria for the recognition of root calcification macrofeatures in the rock record are relatively well established (Klappa 1980a; Esteban and Klappa 1983; Retallack 1988; Wright and Tucker 1991) and are based on well-documented Quaternary examples. However, some biogenic microstructures found commonly in paleosols and at paleo-exposure surfaces lack reliable modern analogs, and consequently, their origin is highly controversial (e.g., Verrecchia et al. 1995, 1996; Frey et al. 1997; Wright et al. 1996; Wright et al. 1997; Wright et al. 1998; Alonso-Zarza et al. 1998).

Microcodium is one such problematic feature, especially in early Paleogene and Miocene continental and marine successions (see, e.g., Klappa 1978; Wright and Tucker 1991, and references therein). *Microcodium* structures consist of cellular aggregates composed of individual crystals of calcite. A root origin for *Microcodium* was proposed by Klappa (1978), who interpreted it as a calcification product of a mycorrhizal (fungal and plant root) association. Support for this rhizogenic interpretation has been presented by Jaillard (1987a, 1992) and Jaillard et al. (1991), who described

intracellularly calcified root cells from present-day soils that closely resemble *Microcodium* structures.

Frey et al. (1997) disagreed with the interpretation of Klappa (1978) because they found the root origin unable to explain laminar forms of *Microcodium*. Furthermore, Frey et al. (1997) have argued that in spite of their obvious morphological similarity, the multilayer cell arrangement in modern calcified roots described by Jaillard and coworkers (e.g., Jaillard 1983, 1987a; Jaillard and Callot 1987; Jaillard et al. 1991) differs significantly from that of the typical ancient *Microcodium* aggregates, which are composed of a single layer of elongate crystals.

This paper documents examples of calcified plant roots and *Microcodium* from subaerial exposure profiles in a succession of Paleocene shallow-marine carbonates in southwestern Slovenia. A crudely laminar horizon in one of the studied profiles contains abundant calcite aggregates which exhibit exquisitely preserved structural details of plant root tissues, and thus provide direct and unambiguous evidence for their rhizogenic origin. Moreover, morphologies intermediate between the typical *Microcodium* aggregates and calcified roots were observed in this laminar horizon and this observation supports previous rhizogenic interpretations of *Microcodium* structures. The aim of this paper is to present the morphological evidence for the root origin of *Microcodium*, as well as to discuss its paleoecological significance and the processes and causative factors for precipitation of calcium carbonate in the root cells of terrestrial plants inhabiting carbonate-rich substrates.

CALCIFICATION PRODUCTS OF PLANT ROOTS AND THE PROBLEM OF MICROCODIUM

Root calcification structures (rhizoliths, rhizocretions, rhizomorphs; see review of terminology by Klappa 1980a) exhibit various degrees of biological activity responsible for their formation. Except for their gross morphology, some forms may show no biologically influenced fabrics (for example, simple root molds left after roots have decayed and subsequently filled with a cement), whereas others are characterized by biologically controlled precipitation of calcium carbonate in, on, or around roots (Klappa 1980a; Jones and Ng 1988; Jones 1994; Wright et al. 1995; Alonso-Zarza 1999). With regard to location, two styles of calcification processes can be distinguished: (1) rhizosphere calcification (extracellular calcification of Wright et al. 1995), i.e., accumulation of calcium carbonate in the area immediately surrounding and influenced by plant roots; and (2) intracellular calcification. The former process is mediated mainly by the root-associated microorganisms in the soil (Jones 1994), but the latter is controlled directly by plants through the precipitation of calcium carbonate within their cortical root cells (Jaillard 1987a, 1992; see below). The term *calcification*, as used throughout this paper, denotes deposition of calcium salts (carbonate) in biological systems.

Intracellular calcification of roots appears to be a common phenomenon in modern soils. Products of intracellular root calcification are widespread in some present-day calcareous soils and may represent up to a quarter of the soil mass (Jaillard 1984, 1992; Jaillard et al. 1991). Active calcification in the living cortical root cells has also been reported in experimental work performed by Jaillard (1987a, 1987b, 1992) and Ross and Delaney (1977). Calcified root cells may constitute significant quantities of secondary carbonate in Quaternary loess, loess paleosols (Becze-Deák et al. 1997 and

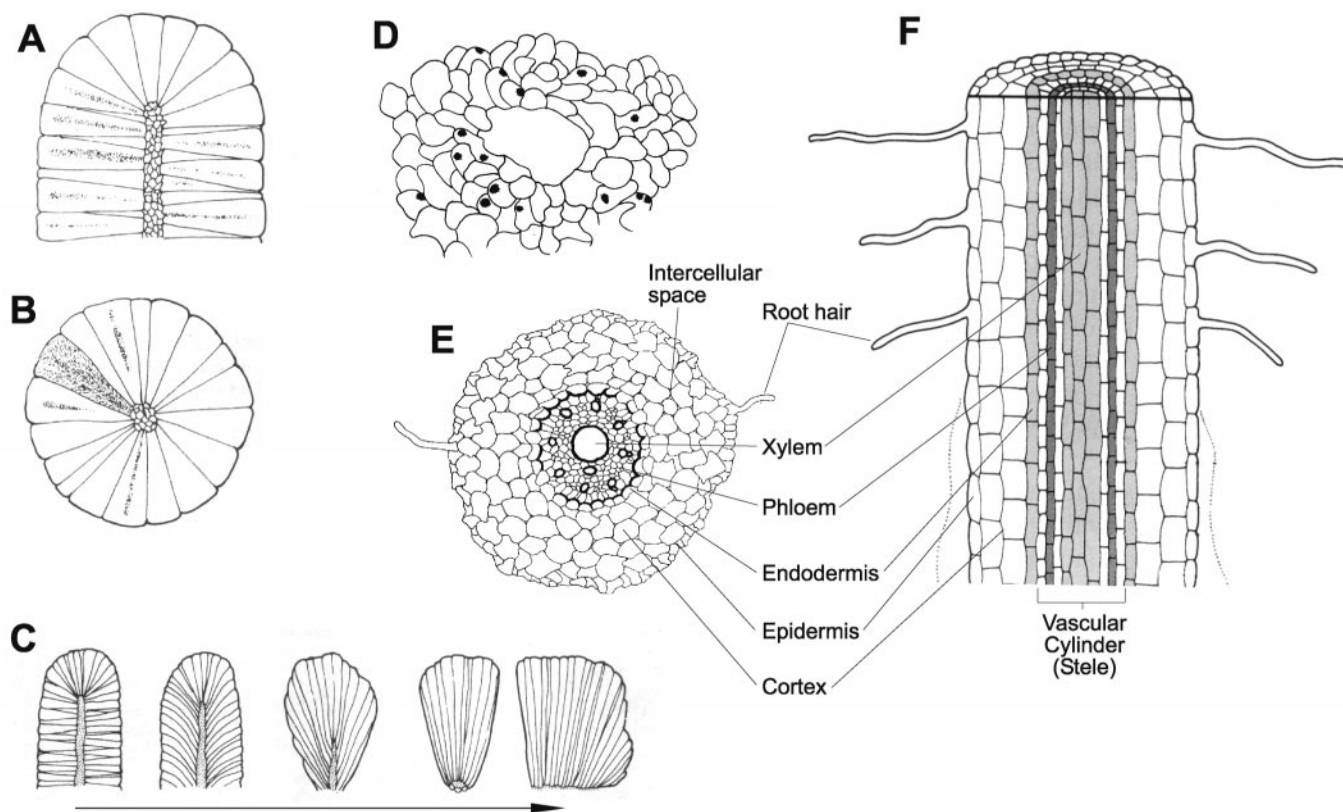


FIG. 1.—Morphotypes of *Microcodium* and the structure of plant roots. Typical *Microcodium* structure is composed of a single layer of elongate calcite prisms forming root-like growths composed of **A**) cylindrical “corn-cob” aggregates, or **B**) spheroidal (rosette) aggregates. **C**) Morphological continuum between “corn-cob” and laminar *Microcodium* morphologies (from Freydet and Plaziat 1982). **D**) Sketch of multilayer cell arrangement in *Microcodium* type 3 of Bodergat (1974) (= *Microcodium* (b) of Esteban 1974; from Bodergat 1974). **E**) Cross section of a root (Fahn 1982) and **F**) diagrammatic longitudinal section of a primary root, showing major structural elements of the root tissue (Tais and Zaiger 1998).

references therein), and chernozems (Khokhlova et al. 2001a; Khokhlova et al. 2001b), whereas pre-Quaternary unambiguous examples of intracellularly calcified plant roots are rare (Goldstein 1988; Alonso-Zarza et al. 1998; Alonso-Zarza 1999; Bowen and Bloch 2002).

Intracellular calcification of roots has also been considered as a mechanism creating *Microcodium* structures (Klappa 1978; Wright et al. 1995). *Microcodium* does not appear to exist today, although it has been reported from Quaternary carbonate eolianites on Isla Contoy, off the Yucatan Peninsula (Ward 1975; McKee and Ward 1983), the Mediterranean island of Mallorca (Calvet et al. 1975), and from calcrete crusts on San Salvador, Bahamas (Bain and Foos 1993; Foos and Bain 1995). Accumulations of *Microcodium* are abundant in Cretaceous, Paleogene, and Miocene continental and marine carbonate successions, especially in the peri-Mediterranean area. These accumulations can form stratigraphic levels, several meters in thickness, composed almost entirely of *in situ* *Microcodium* aggregates (Freydet and Plaziat 1982; Wright et al. 1995; Rossi and Cañaveras 1999). *Microcodium* can be the dominant component in paleo-calcretes (Esteban 1974; Wright et al. 1995) and is also common in paleosols and paleokarstic horizons, as well as within floodplain and palustrine deposits (Bodergat 1974; Freydet and Plaziat 1982; Wright et al. 1995; Alonso Zarza 2003).

Typical *Microcodium* structures (Bodergat 1974; Freydet and Plaziat 1982; Morin 1993) consist of millimetric aggregates composed of a single layer of individual cell-like crystals of calcite (Figs. 1A, B, C, 2B). These pyramidal or prismatic crystals are polygonal in cross section and are usually strongly elongate, measuring 100–800 μm in length and 20–70 μm in width (Freydet and Plaziat 1982). *Microcodium* aggregates occur in two

basic forms (Bodergat 1974; Freydet and Plaziat 1982): (1) in root-like growths composed of cylindrical (“corn-cob”) aggregates (Fig. 1A) or connected or unconnected spheroids (rosettes; Fig. 1B), both with the polyhedral elements arranged in a radiating pattern around a hollow central channel, and as (2) laminar (lamellar) structures composed of asymmetrical aggregates (Fig. 1C).

Bodergat (1974) and Esteban (1972, 1974) extended the definition of *Microcodium* to include atypical forms (Fig. 1D), called “*Microcodium* type 3” by Bodergat (1974), and “*Microcodium* (b)” by Esteban (1972, 1974), which consist of several layers of isodiametric crystals. The structure of these atypical forms resembles the morphology of modern plant roots (Fig. 1E; Klappa 1978; Jaillard et al. 1991; Alonso-Zarza et al. 1998) but differs considerably from the shape of “cells” and their organization in “classical” *Microcodium* aggregates (Freydet and Plaziat 1982; Freydet et al. 1997). The original rhizogenic interpretation of *Microcodium* (Klappa 1978) was derived from Holocene material which appears to be identical to the calcified roots described by Jaillard (1987a) and Jaillard et al. (1991) (Figs. 3–5; compare with Figs. 2–4 in Klappa 1978). This fundamental morphological difference between the cell architecture in calcified roots and *Microcodium* aggregates (Fig. 1A–E) appears to be the main issue in the controversy about the rhizogenic origin of *Microcodium* (Freydet et al. 1997; Wright et al. 1997). Comparison of the two morphologies is also shown in Figure 2.

Another problematic feature which is commonly seen with all morphotypes is the ability of *Microcodium* to dissolve and intensely corrode carbonate substrates. Freydet and Plaziat (1982) found the corrosive nature of

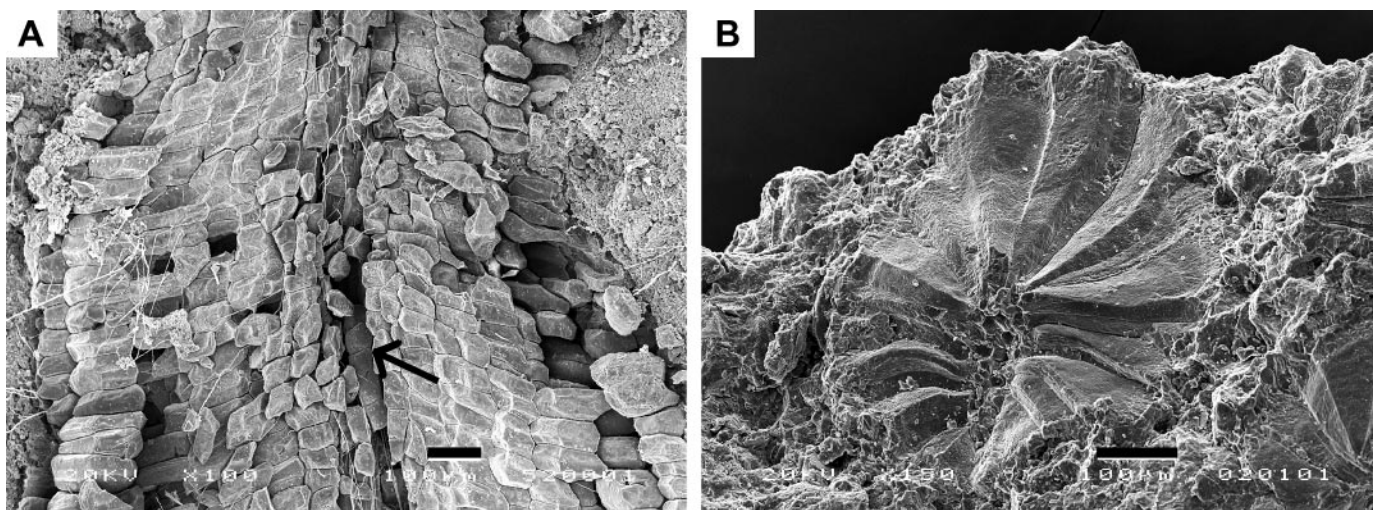


FIG. 2.—Scanning electron microscope photographs, showing a fundamental difference in cell organization between modern calcified roots and ancient *Microcodium*. **A**) Longitudinal section through the calcified root from a Quaternary calccrete at Sella, SE Spain. Note the multilayer architecture of calcified cortical cells. Darker part in the middle of the root (arrow) corresponds to noncalcified vascular cylinder. Scale bar 100 μm . **B**) Broken *Microcodium* aggregate (“rosette”) from the Paleocene fluvial deposits at Fontjoncouse, southern France, composed of a radiating pattern of elongate calcite pyramids. Axial channel is filled with microsparite. Scale bar 100 μm .

Microcodium incompatible with the activity of roots and proposed that *Microcodium* formed through symbiotic association of several microorganisms (probably fungi and bacteria), in which some might attack calcite and others might synthesize it.

In situ aggregates or disaggregated elements have been found in a great variety of facies (Klappa 1978; Freytag and Plaziat 1982; Wright and Tucker 1991; Wright 1994), making paleoecological interpretation of *Microcodium* extremely difficult. To add to the controversy, some spheroidal carbonate microfeatures and forms of diagenetic calcite have been confused with *Microcodium* although they are obviously different in microstructure, morphology, and size (e.g., Chafetz and Butler 1980; Esteban 1982; Chafetz and Butler 1982; Monger et al. 1991; see discussion in Verrecchia et al. 1995 and Rossi and Cañaveras 1999).

GEOLOGICAL SETTING

The material studied in this paper occurs within a succession of upper Paleocene (Thanetian) shallow-marine limestones of the Trstelj Formation, which represent the middle part of the Kras Group (Košir and Otoničar 2001). The Kras Group is a widespread carbonate unit throughout the northeastern Adriatic coastal region, particularly in southwestern Slovenia (Fig. 3A). It corresponds to the terminal megasequence of the Adriatic-Dinaric Carbonate Platform and overlies a major regional unconformity expressed by a paleokarst and bauxite deposits. This megasequence was deposited during major tectonic events in the Late Cretaceous and Early Paleogene when the carbonate platform was subaerially exposed, subsequently reestablished, and finally buried by prograding deep-water clastics (flysch) (Drobne 1977; Cousin 1981; Košir and Otoničar 2001).

A generalized stratigraphic column of the Upper Cretaceous, Paleocene, and Eocene deposits in southwestern Slovenia is shown in Figure 3B (for more detailed stratigraphy and facies characteristics of these formations see Pavlovec 1963; Bignot 1972; Drobne 1977; Jurkovec et al. 1996; and Ogorelec et al. 2001). The lower part of the Kras Group (i.e., The Liburnian Formation of Maastrichtian and early Paleocene age) is characterized by restricted, marginal marine and palustrine carbonates, which show pedogenic modifications, including root-related laminar calccrete horizons and massive accumulations of *Microcodium* (Otoničar and Košir 1998). Prominent subaerial exposure surfaces, including calcretes, occur also in a succession of Upper Paleocene and Lower Eocene bioclastic limestones of the

Trstelj Formation and Alveolina-Nummulites Limestone. The calccrete profiles described herein occur in a succession of miliolid-dominated packstone and grainstone facies, typical of inner-ramp depositional settings (Luterbacher et al. 1991; Davaud and Septfontaine 1995; Košir 1997), which were deposited in a relatively high-energy, barrier-related depositional environment on a foram-dominated carbonate ramp.

MATERIAL AND METHODS

Subaerial exposure profiles were studied in well-exposed outcrops of the Trstelj Formation, situated along forest roads on the northern margin of the Kras Plateau (Figs. 3A, 4). Two calccrete profiles were sampled in detail. Calccrete macrofabric was studied in outcrops and in polished slabs. Calccrete microfabric was analyzed in more than 150 thin sections, using a standard transmitted light microscope. Standard thin-section petrography was supplemented with cathodoluminescence (CL) and UV fluorescence petrography. Nine selected thin sections were polished and examined under cathodoluminescence on CITL cold cathode luminoscope (model CL8200 Mk4) at the Karst Research Institute ZRC SAZU, Postojna, Slovenia, operating at approximately 15 kV beam energy and 400 mA beam current. Three polished thin sections were studied in reflected light under Opton-Axiophot (Zeiss) microscope, linked to a fluorescence-inducing blue light source. The chemical composition of four uncoated polished thin sections was obtained from electron microprobe analyses performed at the National Building and Civil Engineering Institute, Ljubljana, using an energy dispersive spectrometer (EDS), linked to a JEOL 5500 LV low-vacuum SEM. Elemental spectra were acquired at 20 kV and pressure of approximately 12 Pa. Scanning electron observation of broken surfaces and polished and etched slabs was carried on a JEOL JSM 330A microscope at the Institute of Paleontology ZRC SAZU, Ljubljana.

CALCRETE PROFILES

Most subaerial exposure surfaces from the studied succession of the Trstelj Formation are characterized by root-influenced fabric but differ in form and stage of development. The following profiles provide two examples of well developed calcretes with distinctive laminar horizons, composed almost entirely of root-calcification structures.

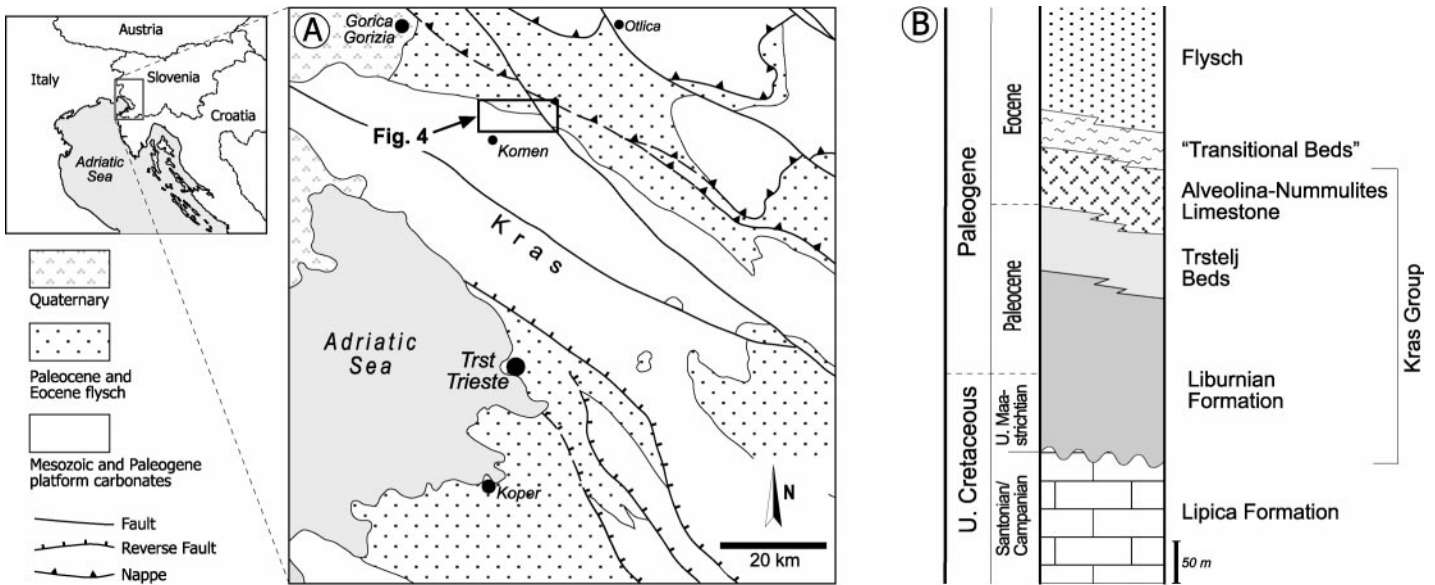


FIG. 3.—A) Geographical position and simplified geological map of SW Slovenia showing major structural elements (modified from Placer 1981). B) Generalized stratigraphic column of upper Cretaceous–Eocene succession in the Kras (Karst) region, SW Slovenia, showing major lithostratigraphic units.

Trstelj Calcrete

The Trstelj calcrete was studied in several small outcrops along a forest road, NW of Trstelj Hill (Fig. 4). The calcrete caps the Trstelj Formation and corresponds to the boundary with the overlying Alveolina-Nummulites Limestone. The calcrete is developed on gray bioclastic grainstones and packstones, which are composed mostly of miliolid and small rotaliid forams, echinoderm fragments, and peloids. Thickness of the calcrete ranges from 10 to 30 cm. A schematic section of the calcrete profile, composed of three layers, is shown in Figure 5A. The lower unit is represented by distinctive dark mottles which occur in a layer, 10–15 cm thick, of grainstones and packstones below the massive calcrete horizon. Thin sections of the mottled limestone exhibit distinctive dark micritic coatings on the bioclasts and abundant alveolar septal structure in the intergranular spaces. The mottled horizon gradually passes upwards into the beige to dark gray colored massive/brecciated horizon. Thin sections of the massive horizon show dense microfabric of intensively micritized bioclasts, micrite cements, and pores with alveolar septal structure. Brecciation is mostly restricted to the upper part of the horizon but can also constitute almost the entire horizon. Highly irregular to subrounded clasts in the brecciated part differ in color but exhibit microfabric characteristics similar to the matrix and the non-brecciated, massive part. Composite clasts (Fig. 6A) indicate that the horizon formed through multiple phases of brecciation and subsequent ce-

mentation by micrite. Root traces within the brecciated horizon indicate that the brecciation probably resulted from penetrative growth of roots (Klappa 1980b). Root-induced brecciation is further evidenced by root tubules, observed in cracks which penetrate into clasts.

The brecciated horizon is capped by a discontinuous, laminar horizon up to 4 cm thick (Fig. 6A). The laminar fabric also fills cavities several centimeters deep in the brecciated horizon. The lamination pattern results from the alternation of millimetric gray peloidal layers and dark brown to black layers, composed of intertwined tubules with micritic walls (Fig. 7A). Some micritic tubules exhibit indistinctive cellular structure, composed of thin arcuate septa (alveolar septal structure), which rarely show the well-preserved structure of root tissues (Fig. 7B). In parts of the laminar horizon, distinctive layers containing abundant isolated polygonal or slightly elongate calcite elements (Fig. 7C) occur within the peloidal and tubular laminae. These calcite elements are rarely joined in small radial aggregates forming incomplete *Microcodium* rosettes (Fig. 7C) or are arranged in seriate structures that resemble laminar (lamellar) *Microcodium* colonies (Freyet and Plaziat 1982). The calcrete profile is directly overlain by bioclastic grainstone, composed of alveolinids and coral fragments and, in the basal part, with a transgressive lag of centimeter-size clasts of calcrete.

The Trstelj calcrete profile exhibits characteristic structure of well developed calcretes (Wright and Tucker 1991). The tubular microfabric of

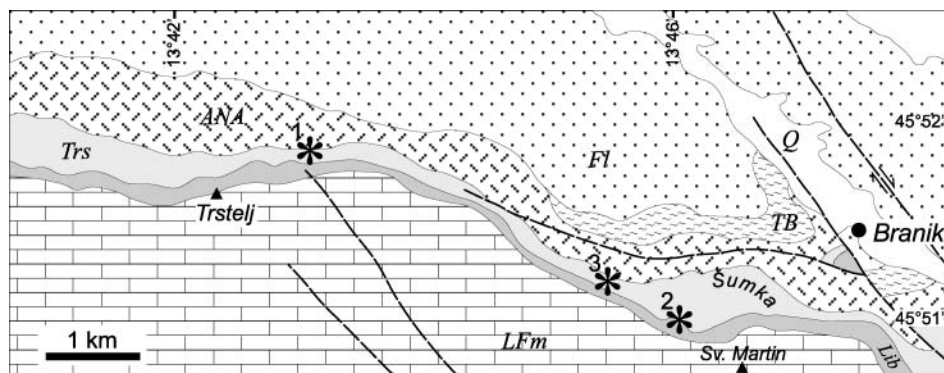


FIG. 4.—Geological map of the studied area (modified from Buser 1968). Position of the area is indicated on the map in Figure 3A. Asterisks indicate position of Trstelj calcrete (1), Sv. Martin calcrete profile (2) and the Šumka section (3). Key to stratigraphic units: LFm, Lipica Formation; Lib, Liburnian Formation; Trs, Trstelj Formation; ANA, Alveolina-Nummulites Limestone; TB, Transitional Beds (*Globigerina* Marl); Fl, Flysch. For the stratigraphic range of the lithostratigraphic units see Figure 3B.

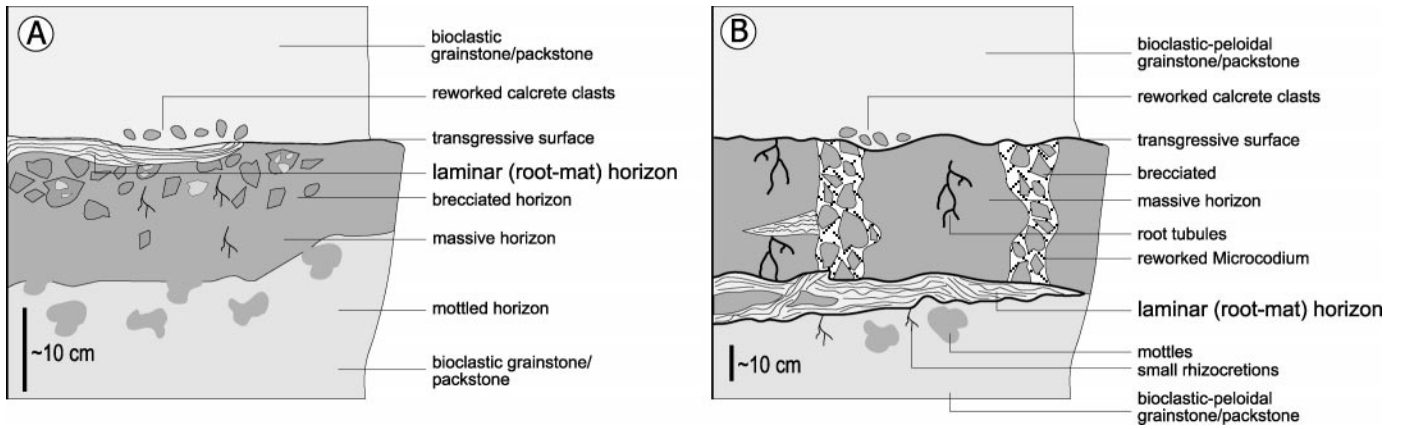


FIG. 5.—Schematic diagram showing stratigraphy and major macrofeatures of the studied calcrete profiles. A) Trstelj calcrete profile. B) Sv. Martin profile.

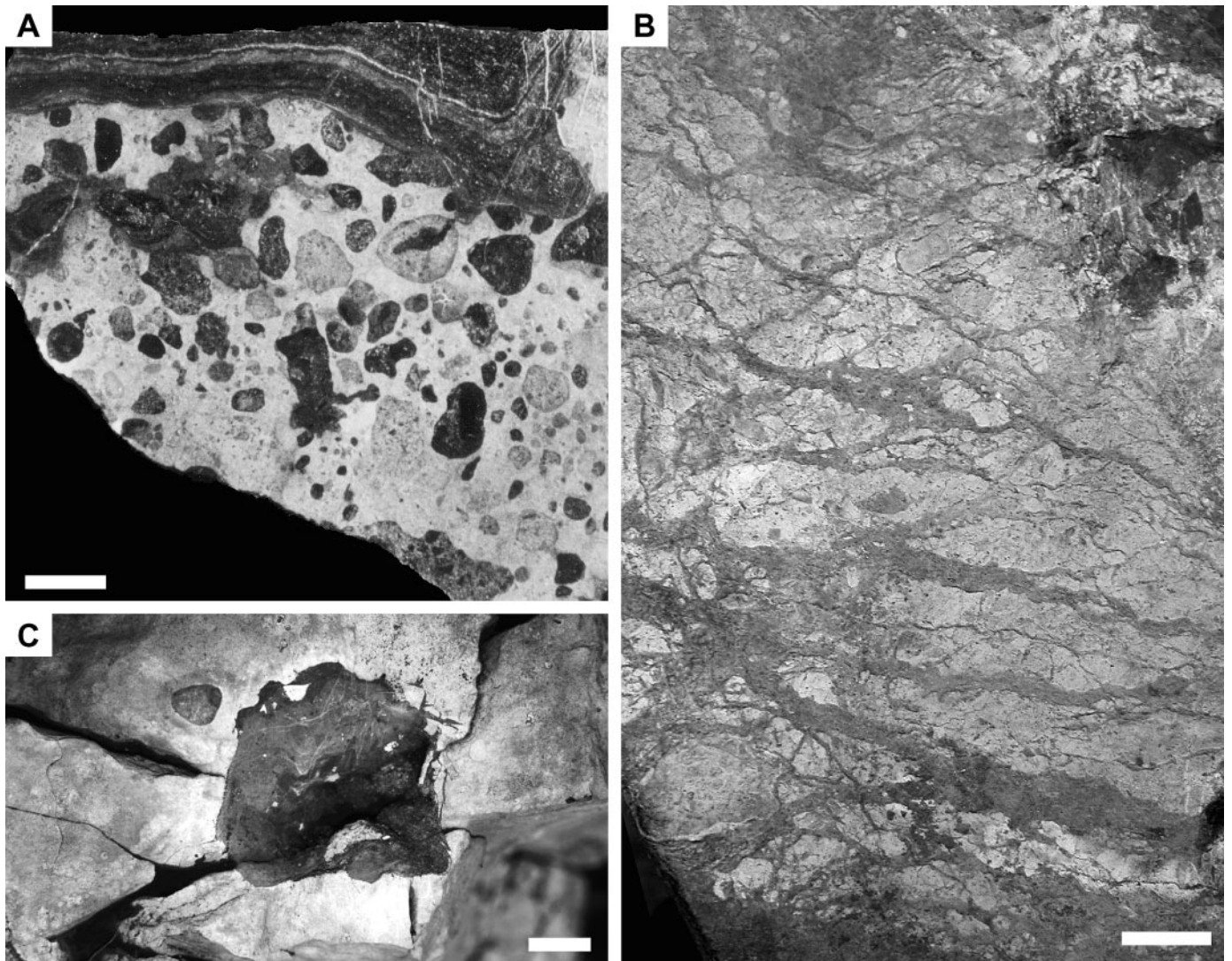


FIG. 6.—A) Polished slab of the upper part of the Trstelj calcrete. Distinctive laminar horizon overlying the brecciated horizon. Scale bars in all figures 1 mm. B) Weathered surface of the crudely laminar horizon of the Sv. Martin calcrete, showing anastomosing pattern of subhorizontal to subvertical laminae, composed mostly of calcified roots (see photomicrograph in Fig. 7D). C) Subcircular void (dark) on the upper bedding surface of the massive horizon of the Sv. Martin calcrete, representing a mold of a large subvertical root that penetrates through the massive carbonate. The cavity is filled by dark micrite containing abundant disaggregated *Microcodium* elements and small calcrete clasts.

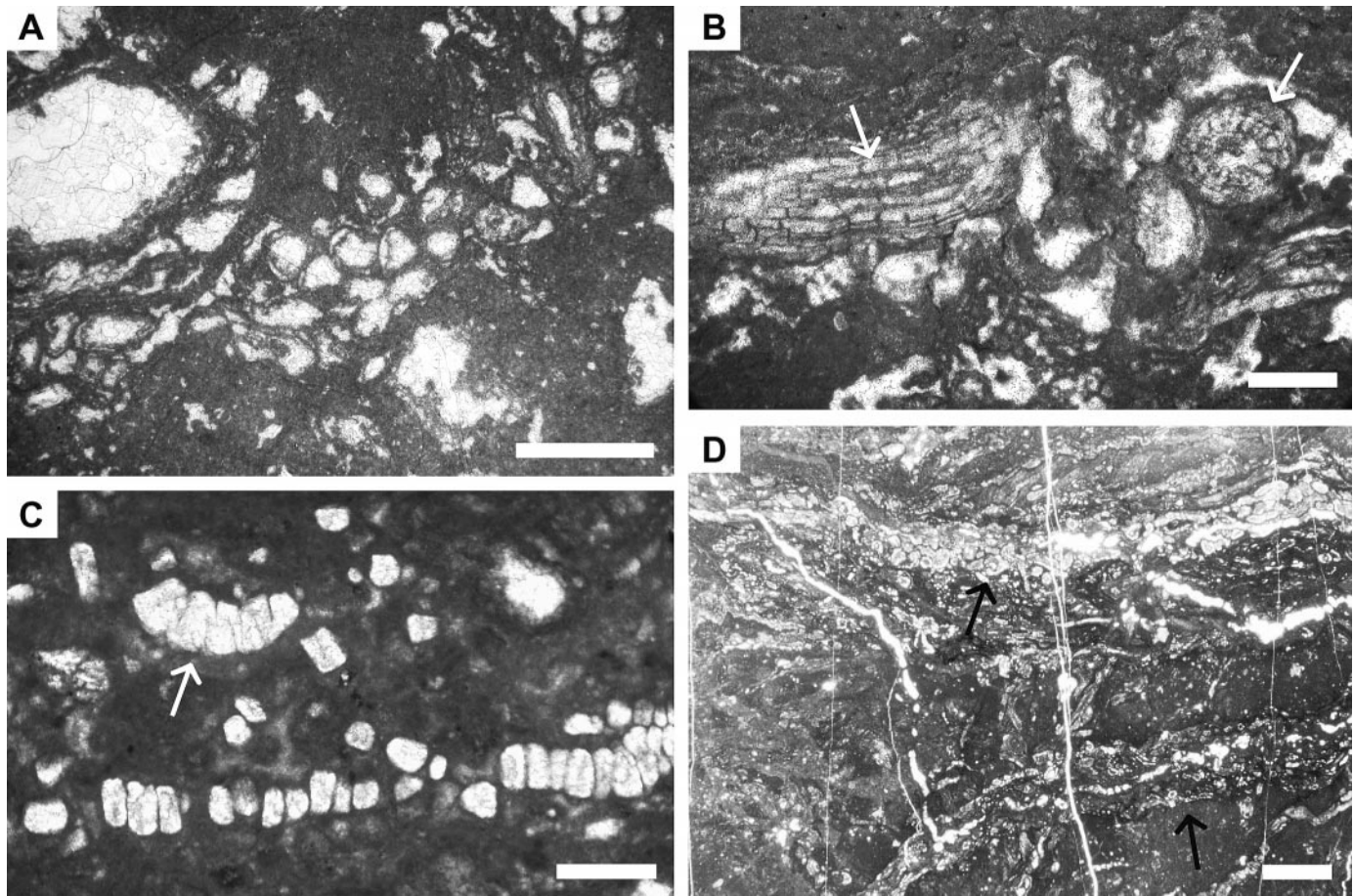


FIG. 7.—**A**) Photomicrograph of the laminar horizon of the Trstelj calcrete (see Fig. 6A). Porous laminar microfabric is composed of spar-filled tubules within dark, microlaminar matrix. Plane-polarized light, scale bar 3 mm. **B**) Calcified micritic tubules with preserved root structure (arrows) in the Trstelj laminar crust. Plane-polarized light, scale bar 200 μm . **C**) Layer of isolated calcified root cells within the peloidal-laminar horizon of the Trstelj calcrete and an incomplete *Microcodium* aggregate (arrow). Plane-polarized light, scale bar 0.5 mm. **D**) Photomicrograph of the laminar horizon of the Sv. Martin calcrete showing abundant intracellularly calcified roots (mainly in cross sections; arrows) in intertwined, irregular root laminae in a subhorizontal root mat. Thin section in plane-polarized light. Scale bar 4 mm.

the laminar layer, capping the massive and brecciated horizon, is typical of root-mat calcretes (Wright et al. 1988). The micromorphology of the laminar crust is dominated by features that can be interpreted as products of calcification in the rhizosphere (Wright et al. 1995). The unique feature is the occurrence of *Microcodium* aggregates within the laminar calcrete fabric (see below).

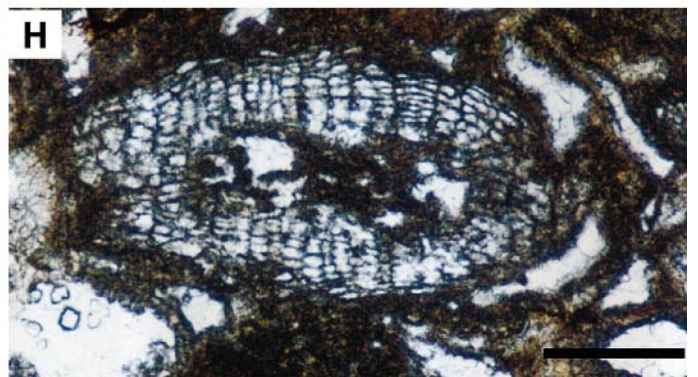
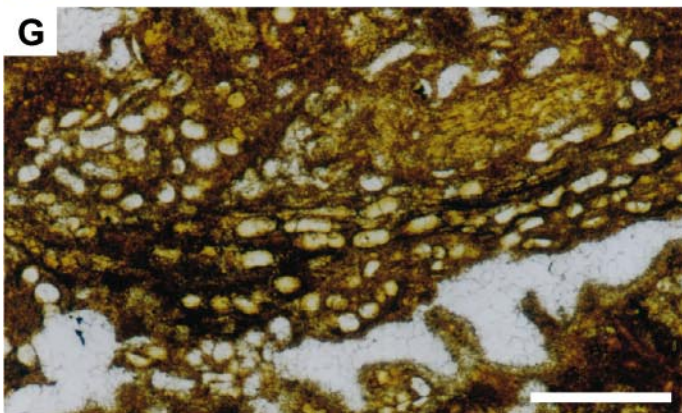
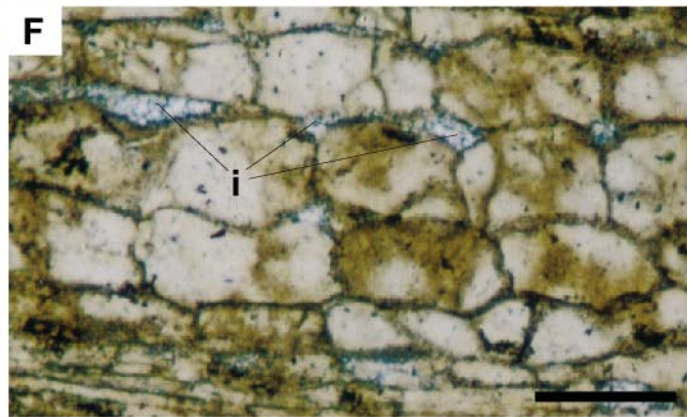
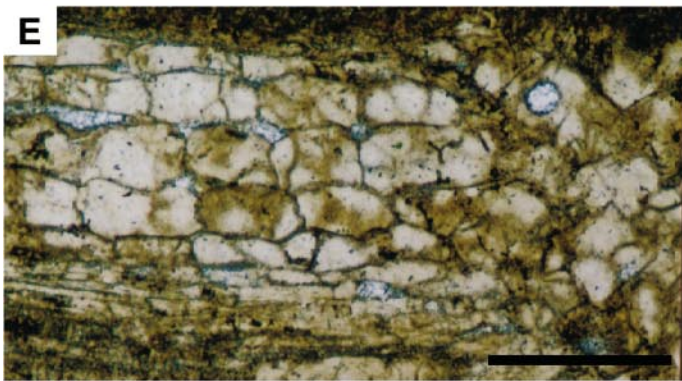
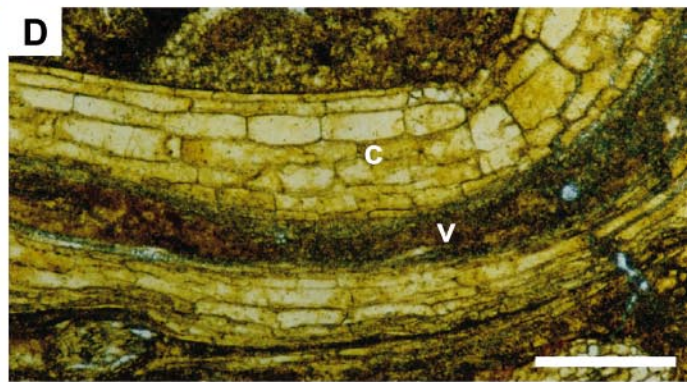
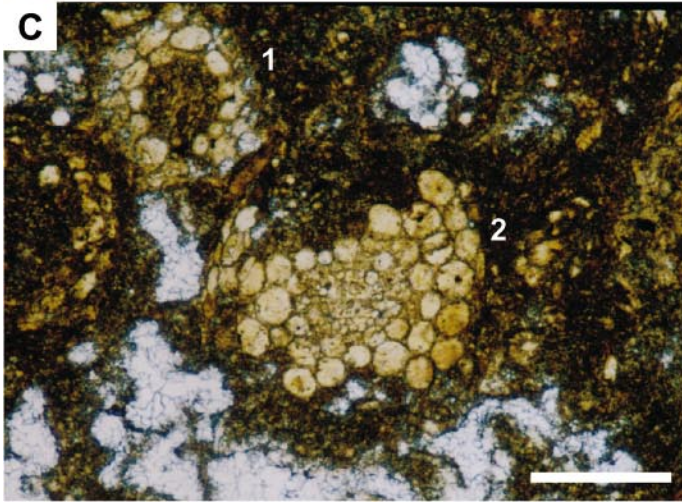
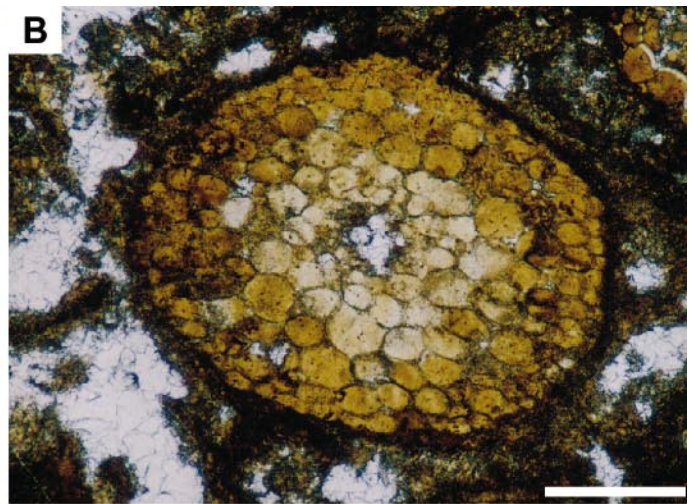
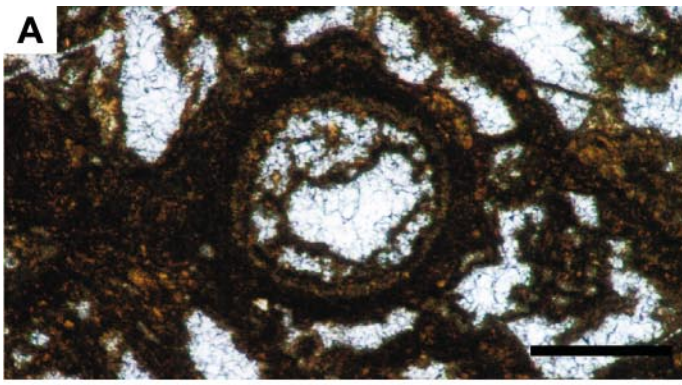
Sv. Martin Calcrete

The second studied calcrete profile is exposed in a section along a forest road-cut below Sv. Martin Hill, about 2.5 km SW of Branik Village (Fig.

4). The calcrete appears as a bed, 60–80 cm thick, of dark brown limestone within gray bioclastic (skeletal) grainstones and packstones, which are composed mainly of miliolid and small rotaliid forams, dasycladacean algae, coral fragments, and peloids. Two distinctive calcrete horizons can be recognized in the profile (Fig. 5B): (1) the lower, crudely laminar horizon (Fig. 6B) which is overlain by (2) massive and partly brecciated horizon.

The crudely laminar horizon is 5–25 cm thick. Its lateral extent cannot be determined because of the small extent of the outcrop, but it appears to pinch out laterally. The crudely laminar fabric consists of intertwined and anastomosing millimeter-thick subhorizontal to subvertical sheets and stringers. The laminar horizon is dark, almost black, and the laminae can

FIG. 8.—Photomicrographs of calcified roots from the Sv. Martin calcrete, all in plane-polarized light. **A**) Cross section of a root tubule, formed through precipitation of dark micrite around a root. The tubular void which marks the position of a decayed root is filled with sparry calcite cement and shows no evidence of intracellular calcification. Note prominent alveolar septal structure in and around the root tubule. Scale bar 200 μm . **B**) Completely intracellularly calcified root in cross section. Almost the entire volume of this root is composed of calcified cortical cells. Small central part of the root, corresponding to the vascular cylinder, is filled by sparry calcite cement. The root is coated by a layer of dark micrite. Scale bar 200 μm . **C**) Two incompletely calcified roots in cross section. Central part of (1) is filled by micrite. Indistinctive cellular microstructure can be seen in the central cylinder of the other root (2), probably representing calcified xylem vessels. Scale bar 200 μm . **D**) Longitudinal section of a root, showing longitudinally elongate calcified cortical cells (c), and noncalcified central cylinder (v); compare with schematic root section in Figure 1F. Scale bar 200 μm . **E**) Longitudinal section of a calcified root cortex. Scale bar 200 μm . **F**) Detail of part E showing intercellular spaces in the cortex (i), filled by sparite calcite cement. Scale bar 100 μm . **G**) Individual calcified root cells, representing several roots in longitudinal section with incompletely calcified root cortex. Scale bar 500 μm . **H**) Permineralized root in cross section. Although the cellular structure is well preserved, this root differs essentially from the calcified roots in parts B–G in that it exhibits no evidence of active, plant-controlled intracellular calcification but only impregnation of lignified cellular tissue by sparite cement. Scale bar 200 μm .



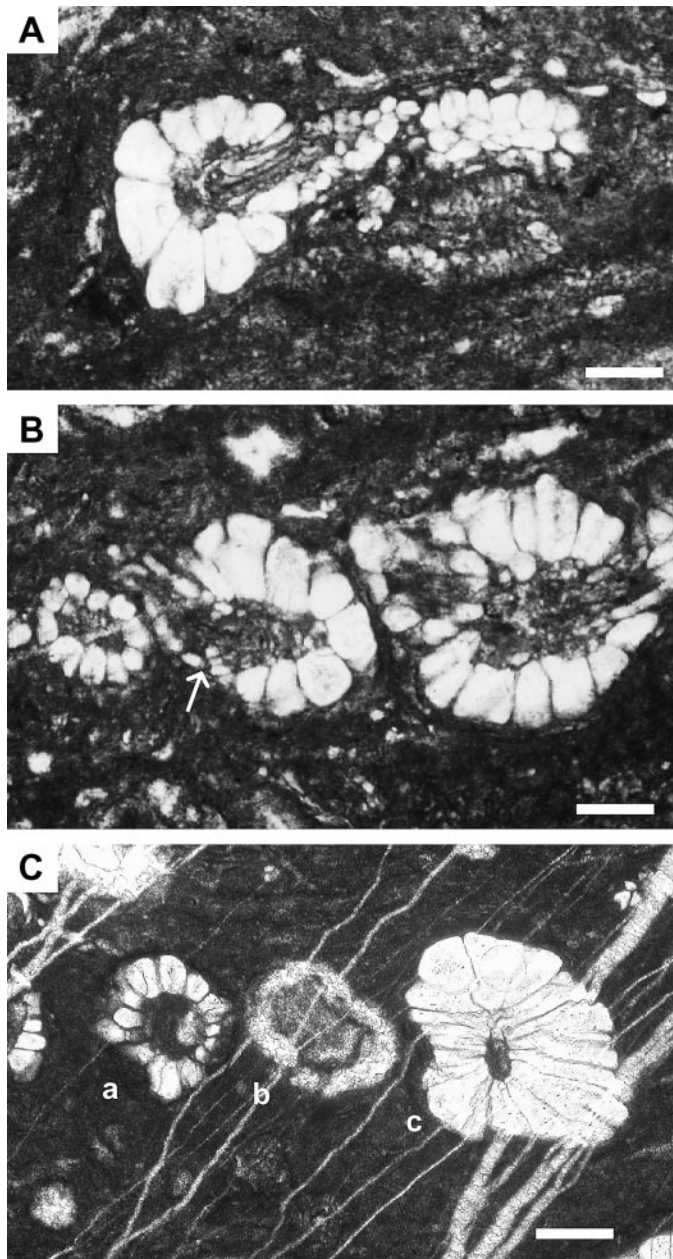


FIG. 9.—Photomicrographs of modified roots, all in plane-polarized light. Scale bar in all figures 100 μm . **A, B**) Calcified root structures composed of elongate prismatic cells, creating typical *Microcodium* structure. Relicts of a multilayer root structure can be seen in some sections (arrow). **C**) Cross sections of three roots, exhibiting different degree of calcification and cell elongation; (a) is composed of a single layer of isodiametric to slightly elongated cells; (b) noncalcified root tubule; (c) typical *Microcodium* (“rosette”) structure.

be seen only on strongly weathered rock surfaces (Fig. 6B). Thin sections exhibit dense networks of millimeter- and submillimeter-size tubiform cylinders with dark micritic (laminar) walls (Fig. 7D). These tubular structures are filled with a drusy cement and are commonly associated with the alveolar septal structure which occurs within and between the tubules (Figs. 8A). However, the most characteristic and abundant microfeatures of the laminar horizon are: 1) calcitic cylinders which display exceptionally well-preserved details of root cellular structure (Fig. 8B–F); 2) typical *Microcodium* aggregates (Fig. 9); and 3) intermediate forms between the former two features (Fig. 10).

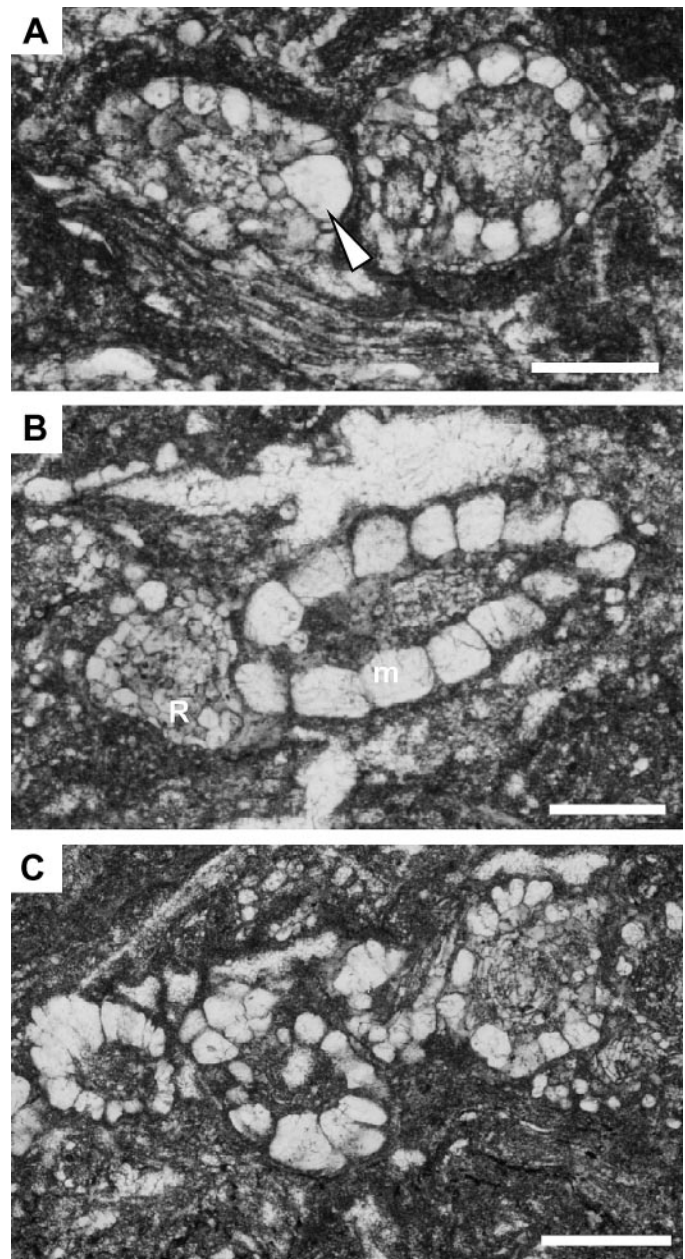


FIG. 10.—Photomicrographs of modified roots from the Sv. Martin calccrete, all in plane-polarized light. Sections of calcified roots show different degrees of cell elongation and increase in size. **A**) Single enlarged cell in the outer cortical layer (arrow). Scale bar 100 μm . **B**) Strongly enlarged quadrangular cells (m) and smaller, normal-sized cells (R). Scale bar 100 μm . **C**) Several cross sections of calcified roots with enlarged and elongated cortical cells. Scale bar 150 μm .

The massive horizon consists of a dark brown limestone which shows no distinctive macrostructures in the outcrop. Thin sections show that it is composed of a dense and partly microbrecciated micrite. The micrite includes rare, almost completely micritized, but still recognizable bioclasts, mostly miliolid and rotaliid forams, fragmented gastropod shells, and scattered, disaggregated *Microcodium* prisms. The massive horizon is cut by irregular subvertical fissures, several centimeters to decimeters wide, filled by brecciated limestone (Fig. 5B), and more regular cylindrical voids (Fig. 6C). The later most probably represent infilled molds of large subvertical roots. The brecciated parts are composed of centimeter-size angular to subangular clasts of massive micrite, and a complex matrix of *Microcodium*

fragments, micritic coatings, internal sediments, drusy sparite cement, and subordinate clayey material.

Most of the macrofeatures and microfeatures observed in the Sv. Martin calcrete profile can be interpreted as due to the activity of plants. Well-preserved calcified roots provide obvious and unambiguous evidence for the rhizogenic origin of the laminar horizon. Its occurrence below the massive calcrete horizon suggests that it represents a penetrative calcified root mat, whereas the brecciation of the massive horizon was most probably caused by the penetrative growth of roots (cf. Klappa 1980b). Similar calcrete profiles that have been interpreted as a result of constructive and destructive processes in the rhizosphere have been described from the Quaternary soils of the Turks and Caicos islands (Rossinsky and Wanless 1992; Rossinsky et al. 1992).

RHIZOGENIC MICROFABRIC

Intracellularly Calcified Roots

Calcified roots from the laminar horizon of the Sv. Martin calcrete exhibit high variability in size, shape, and structure (Fig. 8). The diameter of roots, as seen in cross sections, varies from 150 μm to more than 1 mm. The length of calcified roots ranges from several millimeters to more than 1 cm. The maximum observed length of a longitudinal root section was more than 2 cm. The shape of the roots can be straight or curved, rarely showing branching and development of lateral roots. In plane-polarized light, the calcified root cells are most commonly light pale brown or yellow in color owing to dark inclusions in the calcite. Under crossed polars, the calcite in the root cells typically shows monocrystalline structure with uniform or sweeping extinction, or an aggregate pattern, composed of several calcite crystals.

Many of the calcified roots in thin sections exhibit perfectly preserved original cellular structure of the root cortex (Fig. 8B–F). The arrangement of cortical cells in individual roots is highly variable. The cortex can be composed of two to more than ten layers of cells. As seen in many longitudinal and cross sections, all the cells of the cortex are completely calcified (Fig. 8B, D, E, F), whereas some root sections are calcified incompletely (Fig. 8B) or only show few individual calcified cortical cells (Fig. 8G) without any other distinguishable elements of the root structure.

Except the cortex, other parts of the root exhibit almost no evidence of calcification. The central part of the root, corresponding to the vascular cylinder (stele; see Fig. 1E, F), is not calcified. This area is usually subsequently filled by dark brown micrite (Fig. 8C, D) or sparry calcite cement (Fig. 8B). In some cases, indistinctive cellular structures can be seen in the central cylinder; these may represent relicts of xylem vessels (Fig. 8C). Thin outermost cells, observable only in few sections of roots (Fig. 8D), probably represent calcified epidermis (cf. Fig. 1E, F). Significantly, calcified roots from the Sv. Martin calcrete exhibit no evidence of secondary growth (development of root tissues resulting from secondary thickening), indicating that the calcification was limited to the young parts of the fine roots.

Microcodium, Calcified Roots, and Intermediate Morphologies

The typical architectural elements of *Microcodium* structures, as defined above (Fig. 1A, B, C), are elongate polyhedrons (pyramids or prisms) of calcite. Calcified cortical root cells described and illustrated in the previous section (Fig. 8B–G) are generally isodiametric in shape in transverse cross sections but can be distinctly elongate in longitudinal sections (Fig. 8D, G; compare with Fig. 1F). However, many examples of calcified roots from the crudely laminar horizon of the Sv. Martin calcrete exhibit strong *radial* elongation of outer cortical cells, thus creating features which appear to be identical to “classical” *Microcodium* aggregates. Actually, a complete range of intermediate morphologies can be observed (Figs. 9, 10).

Some of the root cross sections exhibit only slightly increased size of individual cells in the outer layer of the cortex (Fig. 10A, B) but still

display recognizable root cellular structure. Other examples show significantly enlarged single cortical cells which have isodiametric or polygonal morphology in cross section. The root in Figure 10B exhibits a completely modified single cortical layer consisting of strongly enlarged cells of quadrangular shape.

Outer cortical cells in some root sections show only an accentuated elongate shape (Fig. 10C). Many examples, however, consist of strongly radially elongate pyramidal (Fig. 9A, B) or prismatic cells (Fig. 9C) characteristic of *Microcodium*. Relicts of the root structure can be seen in some of these sections (Fig. 9A, B), whereas most of the sections exhibit no evidence of multilayer cellular structure (Fig. 9C) as seen in nonmodified roots. Aggregates composed of elongate polyhedral cells can be radially symmetrical, forming “rosette” structures with a noncalcified axial canal (Fig. 10B, C), or of strongly asymmetrical shapes, exhibiting subparallel orientation of cells typical of laminar forms of *Microcodium* (Freytet and Plaziat 1982).

Petrographically, the modified cells and prisms do not differ significantly from nonmodified calcified root cells except that they can be clearer and of lighter color, and contain fewer dark inclusions in the calcite. Strongly elongate polyhedral cells from the Sv. Martin calcrete (Fig. 9) have the typical microstructure of *Microcodium* (Klappa 1978; Freydet and Plaziat 1982). The monocrystalline pyramids or prisms frequently exhibit a distinctive central part, composed of more limpid or fine-grained calcite (Fig. 9A, B). Rare longitudinal sections through the internal part of the pyramids show indistinctive filamentous structure similar to filaments (striae) documented by Lucas and Montenat (1967), Freydet and Plaziat (1982), and Morin (1993).

Different phases of calcite precipitation are most clearly seen in plane-polarized light. Both isodiametric calcified root cells and elongate morphologies are composed of light brown or yellowish calcite with a cloudy appearance which differs significantly from clear white spar mosaics that fill individual pores and vascular cylinders and surround individual calcified roots (Fig. 8A, B). Under cathodoluminescence both the cell-filling calcite and clear spar are either nonluminescent or exhibit hardly distinguishable variations of dull red luminescence. Under UV fluorescence calcified cells and *Microcodium* prisms rarely show very weak brown fluorescence. Weak yellow fluorescence was observed in thin layers surrounding the roots, which are dark brown in transmitted light and probably correspond to the remnants of organic matter of the root epidermis.

Electron microprobe (EDS) microanalyses revealed that all calcite generations consist of low-Mg calcite with 0.2–0.8 mol % Mg. No significant variation was observed between different forms of calcite except minor amounts of sulfur (less than 0.3 wt % SO_3) which have been detected in several calcified root cells and *Microcodium* prisms. The presence of sulfur indicates that dark inclusions in calcite of the calcified roots consist of sulfur-rich organic matter.

DISCUSSION

Calcification and Morphological Modification of Cortical Root Cells: Development of Microcodium

Abundant calcite aggregates in the crudely laminar horizon of the Sv. Martin calcrete (Fig. 8) and calcified tubules in the Trstelj laminar crust (Fig. 7) exhibit perfectly preserved structural details of plant root tissues. In both cases, the root textures provide direct proof for the rhizogenic origin of these laminar horizons. Importantly, the exceptional preservation of root structural details in the Sv. Martin laminar horizon is not just a consequence of favorable physicochemical conditions in the soil, leading to permineralization of plant tissues (Fig. 8H; Scott 1992; Martin 1999; Retallack 1997, 2001) but results from biologically controlled precipitation of calcite in living cortical cells of plant roots.

Active calcification (biomineralization) in living roots is indicated by

selective (incomplete) calcification seen in some sections, in which only some of the cortical cells are calcified (Fig. 8C, G). This is particularly true of noncalcified *intercellular* spaces in the root cortex (Fig. 8F) that are filled by clear sparite, identical to sparite cements in larger pores and between the individual calcified roots.

The most important features of the Sv. Martin laminar calcrite are morphologies intermediate between the typical *Microcodium* aggregates and intracellularly calcified roots. These forms provide unambiguous evidence for the root origin of *Microcodium* and thus support previous rhizogenic interpretations (Klappa 1978; Morin 1993; Wright et al. 1995; Alonso-Zarza et al. 1998). However, most of the previous studies which considered *Microcodium* as a product of calcification of plant roots are based on atypical material, which either closely resembles the structure of plant roots (Alonso-Zarza et al. 1998) or is identical to the recent calcified roots (Klappa 1978) but does not exhibit the single-layered structure of strongly elongate cells, which are the main characteristics of *Microcodium*.

The morphological continuum of calcification structures described herein provides a missing link between modern calcified roots (e.g., Jaillard et al. 1991) and atypical forms of *Microcodium* (Bodergat 1974; Esteban 1972, 1974; Klappa 1978; Goldstein 1988; Alonso-Zarza et al. 1998) on one side, and the typical ancient *Microcodium* structures on the other. The intermediate forms show that the typical *Microcodium* aggregates formed through the morphological transformation of the root cortical cells. These transitional forms actually show calcified roots in different stages of *Microcodium* development. Characteristically, the process of morphological modification starts with the increase in size of the cells in the outermost cortical layer, producing large cells of relatively isodiametric shape (Fig. 10C). With the continuation of growth in radial direction, the cortical cells develop elongate pyramidal (polyhedral) shape. The polygonal arrangement of elements, similar to honeycomb structures, appears to be a consequence of a densely packed structure formed through the increased radial growth of cells. This kind of morphology, size, and arrangement of root cells has not been observed in modern plants, but there is a large body of evidence for the morphological transformation of the root structure and production of special forms of roots due to the adaptation of plants to specific ecological conditions (e.g., Fahn 1982; Vartanian 1996). Although the shape and structure of *Microcodium* may reflect distortion of the normal root cells prior to calcification, it is more likely that it developed by growth of the calcite within the cells, which distorted the cell shape, creating strongly elongate polyhedral forms. Similar but less pronounced radial distortion (elongation) of the cortical cells has also been documented in modern calcified roots (Jaillard 1987a).

Physiology of Root Calcification

Calcification of roots presumably enhances production of protons (McConnaughey and Whelan 1997) through exchange of Ca^{2+} and 2H^+ using plant-respired CO_2 (Fig. 11). Considerable proton effluxes from roots, often encountered in the rhizosphere, represent one of the modes of rhizosphere acidification as a profitable strategy for acquiring mineral nutrients. Rhizosphere acidification strategies are particularly evident in plants that grow preferentially on carbonate-rich alkaline soils of high acid-neutralizing capacity (Marschner 1995; Hinsinger 1998).

Significantly, modern calcified roots and virtually all occurrences of *Microcodium* are typically, although not exclusively (e.g., Alonso-Zarza et al. 1998), associated with nutrient-poor calcareous soils and carbonate substrates (Jaillard 1987a; Jaillard et al. 1991; Freydet and Plaziat 1982; Wright 1994; Wright et al. 1995). Calcification within the vacuoles of root cortical cells, coupled with extrusion of protons (Fig. 11B), thus most probably represents an effective mechanism for nutrient acquisition (Jaillard and Hinsinger 1993; McConnaughey and Whelan 1997; McConnaughey 1998; Hinsinger 1998). Proton (acid) secretion in itself enables plants to mobilize sparingly soluble nutrients in the rhizosphere and to cope with constraints

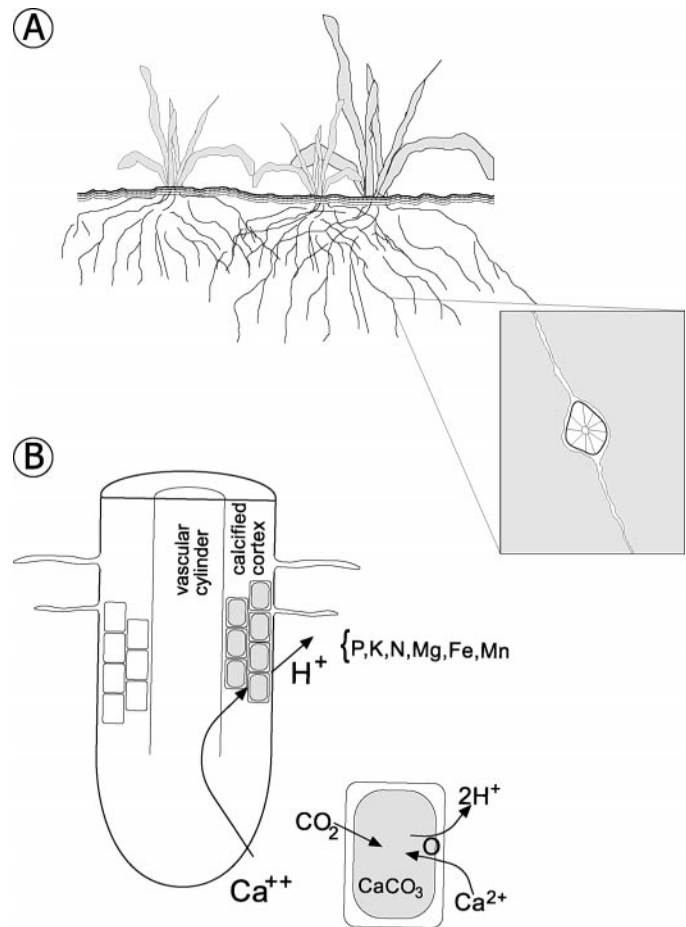


FIG. 11.—A) Roots penetrate into fissures and dissolve carbonate substrate through acid secretion into the rhizosphere and simultaneous calcification of root cells, creating *Microcodium* structures. B) Diagrammatic longitudinal section of the apical region of a root. Calcification within the vacuoles of root cortical cells act as a proton generator, allowing the plant to acidify the rhizosphere and thus acquire mineral nutrients from the soil. Production of protons is enhanced through exchange of Ca^{2+} and 2H^+ using plant-respired CO_2 (from McConnaughey and Whelan 1997).

on mineral nutrition, such as low iron and zinc availability (Marschner 1995). Carbonate precipitation in the vacuoles of cortical cells may additionally increase production of protons, which are potentially useful for nutrient assimilation (McConnaughey and Whelan 1997). Simultaneously, accumulation of CaCO_3 in the root tissue might reflect protection of the plant from excessive calcium and bicarbonate concentrations in the soil solutions (Marschner 1995).

This nutrient-acquiring mechanism can explain both the motivations for carbonate precipitation in living root cells of terrestrial plants and the ability of *Microcodium* to dissolve and corrode carbonate substrate (Fig. 12A, B). The latter effect has actually been observed in modern calcified plant roots as well. In concert with rhizosphere acidification, calcified roots in calcareous soils are often surrounded by a decalcified rhizocylinder of aluminosilicate clayey matrix (Jaillard 1985, 1992; Jaillard and Callot 1987; Jaillard and Hinsinger 1993). Subsequent disintegration of the calcified roots can create distinctive channels on the surface of corroded hard carbonate substrate (Fig. 12C), analogous to corrosive features typical of *Microcodium* (e.g., Freydet and Plaziat 1982; Morin 1993).

Calcification in the root cells of modern plants appears to be a rapid process. Jaillard (1987a) showed in *in vitro* experiments under controlled conditions that living roots of oilseed rape were able to precipitate calcite

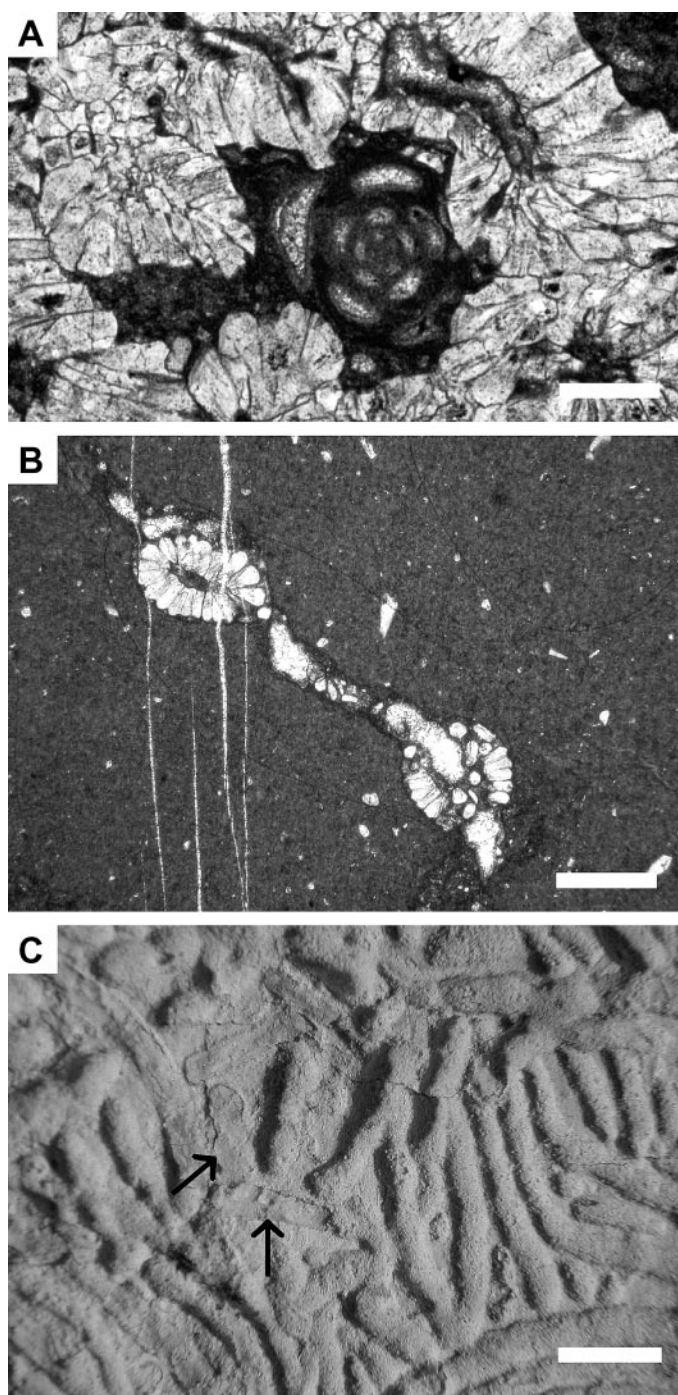


FIG. 12.—A) *Microcodium* corroding miliolid foram in a relatively unaltered bio-clastic packstone. Thin section in plane-polarized light. Scale bar 0.5 mm. B) Typical *Microcodium* corrosion fissure in the massive calcrete of the Sv. Martin profile. Thin section in plane-polarized light, scale bar 1 mm. C) Surface of a clast of marly limestone from the Quaternary calcrete at Sella, SE Spain, showing distinctive corrosive channels left after disintegration of calcified roots. Remnants of calcified roots are still preserved in some channels (arrows). Scale bar 3 mm.

in the cortical cells within only a few hours, and that fully calcified cells were developed in a few days. Presumably, *Microcodium* structures also formed relatively rapidly under favorable conditions.

Most higher plant species facilitate the acquisition of mineral nutrients by the association of mycorrhizal fungi with the root system (Marschner 1995;

Wilcox 1996). Klappa (1978) interpreted *Microcodium* as a calcification product of a mycorrhizal association. Indication of mycorrhizal symbiotic association has also been noted by Alonso-Zarza (1999), who recognized the common occurrence of fungal filaments in the external parts of calcified roots in Miocene laminar calcrites from central Spain. However, Jaillard (1987a, 1992) and Jaillard et al. (1991) found no evidence of mycorrhizae in calcified cells from present-day calcareous soils but only traces of post-mortem taphonomic alteration of calcite crystals by endolithic microorganisms. Likewise, there is no clear evidence of mycorrhizae in *Microcodium* structures. Calcification products of fungi (e.g., needle-fiber calcite forming alveolar septal structure; Wright 1986; Verrecchia and Verrecchia 1994; Verrecchia 2000) are one of the most prominent biogenic constituents of calcrites and are often associated with *Microcodium* and calcified roots, but there is no direct proof for the role of fungi in precipitation of calcium carbonate within the root cells and formation of *Microcodium*.

Environmental Significance of Calcified Roots and *Microcodium*

Recent calcified roots almost invariably occur in calcareous soils in semi-arid regions with a pronounced seasonal moisture regime (Jaillard et al. 1991). Similarly, *Microcodium* is most abundant in calcic paleosols and calcrites that have been interpreted as a product of seasonal semiarid climate (Wright 1994; Wright et al. 1998). In general, calcite precipitates in extracellularly calcified roots (rhizcretions) are formed through evapotranspiration and calcification mediated by root-associated microorganisms in the rhizosphere during relatively dry periods with a net moisture deficit (Jones and Ng 1988; Wright 1994). In contrast, calcified root cells and *Microcodium*, as supposed products of a nutrient-acquiring mechanism, most probably formed through increased metabolic activity of plant roots during times when the soil was adequately moist and, correspondingly, when the soil environmental conditions became favorable for growth and proliferation of fine roots (e.g., North and Nobel 2000).

Paleoenvironmental distribution of *Microcodium* is characterized by two important attributes. First, as noted above, occurrence of *Microcodium* is almost invariably associated with carbonate rocks and calcareous soils. Second, most of the accumulations of *Microcodium* occur within continental depositional settings that are affected by pedogenesis and/or calcrete formation within palustrine, fluvial, and, rarely, karstic settings (Freytet and Plaziat 1982; Wright and Tucker 1991; Wright 1994; Alonso-Zarza 2003). The presence of disaggregated *Microcodium* in shallow marine deposits may result from erosion of a subaerial exposure surface during transgression and subsequent incorporation of eroded material into the overlying marine sediments, whereas *in situ* occurrence of *Microcodium* aggregates in shallow marine facies always indicates subaerial exposure and pedogenic modification of the sediment.

Examples of the *Microcodium* occurrences in almost unaltered shallow-marine limestones (Fig. 12A; Košir 1998) indicates that its formation took place during early stages of calcrete development. Similar association of *Microcodium* with early stages of soil development in the Upper Cretaceous peritidal carbonates has been noted by Martin-Chivelet and Gimenez (1992). However, aggregates of *Microcodium* can be reworked and included in more developed calcrites. Furthermore, because of the constructive-destructive nature of many rhizogenic calcrites, *Microcodium* colonies can often be seen corroding indurated horizons from earlier stages of soil development (Fig. 12B).

Accumulations of *Microcodium* probably reflect a specific type of vascular plants of a pioneer community (i.e., initial stage of a primary plant succession; Barbour et al. 1999) which were able to colonize carbonate substrates during early phases of subaerial exposure. Calvet et al. (1991) suggested that *Microcodium* represents the product of garrigue (scrub) vegetation, whereas Wright et al. (1995) mentioned that it was likely associated with riparian vegetation. Jaillard (1984, 1992), Becze-Deák et al. (1997), and Alonso-Zarza (1999) noted a possible relationship of modern and fossil

calcified roots with Graminae. However, there is no conclusive evidence for the relationship of *Microcodium* and even modern calcified roots with any specific group of plants. It is likely that the root calcification is and was used by plant species of different, and probably not even closely related, taxonomic groups.

Similarly, *Microcodium* may reflect a specific vegetation type and possibly mycorrhizal or non-mycorrhizal symbiotic association that appeared by the Mesozoic. The fossil record of *Microcodium* is unusual, with its peak occurrence in the early Paleogene (especially the Paleocene and early Eocene), and later in the Miocene (Wright and Tucker 1991; see also review of geographical and stratigraphical distribution in Klappa 1978). Smit (1979) and Bignot (1994, 1995) stated that *Microcodium* did not appear before the early Paleocene, arguing that its appearance in Cretaceous rocks resulted from a deep penetration of *Microcodium* into the older rocks from the overlying Tertiary formations. However, there are numerous unambiguous and well-documented reports on *Microcodium* from the Upper Cretaceous carbonate successions of the peri-Tethyan region (Martin-Chivelet and Gimenez 1992; Gušić and Jelaska 1990; Landrein et al. 2001; amongst others), whereas most of the older records are not reliable and/or are based on material that neither resembles typical *Microcodium* aggregates (e.g., Goldstein 1988; Immenhauser et al. 2000) nor exhibits the structure of non-modified calcified roots.

SUMMARY

The crudely laminar calcrete horizon from the succession of Paleocene shallow-marine carbonates of the Trstelj Formation contains calcite aggregates which exhibit perfectly preserved structural details of plant root tissues. Morphology and structure of these aggregates indicate that they formed through biologically controlled precipitation of calcium carbonate within the root cortical cells. Furthermore, morphologies intermediate between the typical *Microcodium* aggregates and intracellularly calcified roots provide unambiguous evidence for the root origin of *Microcodium* and thus support previous rhizogenic interpretations. These transitional forms show that *Microcodium* aggregates formed as a consequence of morphological transformation of root cortical cells due to growth of the calcite within the cells, which distorted the cell shape in the radial direction. The morphological continuum of observed calcification structures provides a missing link between the cellular structure of fine roots in modern plants, typically composed of several layers of isodiametric cells, and the architecture of classical *Microcodium*, which is characterized by a single layer of elongate pyramidal or prismatic crystals of calcite.

Calcification of cortical cells and creation of *Microcodium* structures can be explained as an effective mechanism used for nutrient absorption by certain type(s) of vascular plants. Formation of *Microcodium* and intracellular calcification of roots in general most probably represent a special adaptational strategy of plants that enhance mobilization of elements on nutrient-poor calcareous substrates through proton secretion into the rhizosphere. This mechanism explains both the motivations for carbonate precipitation in living root cells of terrestrial plants and the ability of *Microcodium* to corrode carbonate substrate.

The widespread occurrence of *Microcodium* in almost unaltered shallow-marine limestones indicates that its formation took place during early stages of calcrete development. Accumulations of *Microcodium* probably reflect specific types of vascular plants of a pioneer community which had the capacity to colonize carbonate substrates during early phases of subaerial exposure.

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