THE STUDY ON AERIAL ROOT OF *FICUS MICROCARPA* L. f.

(1) The structure of root cap[1]

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Abstract: Numerous thin, adventitious aerial roots develop on the stems of *Ficus microcarpa* L. f.. They bear root caps, but lack root hairs. In this paper, the tips of aerial roots of *Ficus microcarpa* were investigated by means of light microscopy, scanning electron microscopy and transmission electron microscopy. In the median longitudinal section, the meristem of aerial root shows an open type of construction. The cap columella consists of 8-15 layers of living parenchyma cells derived from the calyptrogen. The peripherial cells of the root cap are collapsed and sloughed off. The cells of calyptrogen have a large nucleus with a pronounced nucleolus and many small vacuoles. The plastids are proplastids. When the cells of the cap leave the initial zone, the alteration in the ultrastructure of plastids including the build-up and the breakdown of starch grains, mitochondria and endoplasmic reticulum can be recognized. The columella cells (statocytes) of aerial root cap in *Ficus microcarpa* show no strict ultrastructural polarity.

INTRODUCTION

Aerial roots are quite common in tropical plants. They arise from an aerial organ and become exposed to air. Therefore, without the disturbance of substratum many kinds of biological adaptations and morphogenetic response of the aerial roots can be studied in situ (Gill and Tomlinson, 1978).

Ficus is a pantropical genus of about 800 species (Liu & Liao, 1976). They are often with free-hanging aerial roots which arise from the stems or the existing roots with well-developed secondary tissues. Natural grafts between aerial roots have been recorded in *Ficus globosa* (Rao, 1966). Zimmermann *et al.* (1968) have studied *Ficus benjamina* with particular attention to the formation of tension wood in aerial roots. The initiation and the development of adventitious root in leaf bud cuttings of *Ficus pumila* have been researched by Davies *et al.* (1982).

Caps are found on the roots of all plants and are normally interpreted as the site of perception of gravity (Volkmann and Sievers, 1979). The statocytes in root caps of the primary roots of *Lepidium* are characterized by a clear ultrastructural polarity (Sievers and Volkmann, 1972). In *Zea mays* the statocytes in the primary root contain both amyloplasts and a well developed endoplasmic reticulum (Juniper and French, 1970). However, no account of the ultrastructure of the root tip in *Ficus* is available. It is, therefore, interesting to study the struture of root cap of aerial root in order to understand its role in the tropic tendency of the aerial root.

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MATERIALS AND METHODS

The tips of aerial roots of *Ficus microcarpa* L. f. were collected during July-October, 1988–1990 from the campus of National Taiwan University.

For light microscopy, the sample was fixed in formalin-acetic acid alcohol, dehydrated in a tertiary butyl alcohol series, embedded in paraffin, sectioned on a rotary microtome (at 10 μm), and stained with modified Delafield's hematoxylin (Chiang, 1975). Micrographs were taken with a Nikon Optiphot microscope.

The materials for SEM were fixed in 2.5% glutaraldehyde followed by 1% OsO_4, dehydrated in an ethanol-acetone series, dried with a Hitachi Critical Point Dryer (HCP-1), coated with IB-2 ion coater (Dawes, 1979), and examined with the Hitachi S-550 SEM.

For TEM, the material was fixed in glutaraldehyde and OsO_4, followed by dehydration in a acetone series and embedded in Spurr's resin (Spurr, 1969). Section were stained with methanolic uranyl acetate and lead citrate, and viewed with a Hitachi H-600 TEM at 75 kV or Joel JEM-1200 EX 2 at 80 kV. Some 1 μm thick sections were stained with 1% toluidine blue, and viewed on a Nikon Optiphot microscope.

RESULTS AND DISCUSSION

Morphology of aerial roots

Like in many other *Ficus* species, numerous thin, adventitious aerial roots develop on the stems of *F. microcarpa* (Fig. 1A-F). They are brown, hard and brittle, and lack root hairs (Fig. 2A-B). However, in *F. globosa* some epidermal cells of the aerial root give rise to unicellular root hairs (Rao, 1966), and their growth and fusion result in the contact between aerial roots and then the formation of root grafts.

In *F. microcarpa* the tips of aerial roots are cream-coloured, 1–2 mm in diameter (Fig. 2A). They bear root caps, which are 1–2 mm in length, and can be detached from the root tip (Fig. 2A, E-G). Normally the root tips die at the end of the growing season, and in the next spring or early summer the lateral roots are formed (Fig. 2B). In *F. benghalensis* the branched aerial roots are formed mainly in growing season without injury (Kapil and Rustagi, 1966). It was suggested that this is a response to resumption of growth after a period of dormancy. The aerial roots of *Vitis* remain unbranched until they strike a substratum or are injured (Turner, 1934).

Anatomy of root tips

In the median longitudinal section the tip of aerial root of *F. microcarpa* shows an open type of construction (Fig. 3A-C). It is not so easy to see exactly where the cap is delimited from the root proper. Although there is no separate protoderm, the epidermis develops in one layer. The columella, the central region of the root cap, consists of 8–15 layers of living parenchyma cells derived from the calyptrogen (Fig. 3B-C). As new cells are produced, cells on the periphery of the root cap are collapsed and sloughed off (Fig. 3B, G). Latex cells are scattered in the tissues of cortex, stele, and root cap (Fig. 3A).

In the transverse sections the young aerial roots, from the differentiation zone to the root apex, show the root cap covering single layered epidermis, broad cortex and stele (Fig. 3D-G). There are 4-5 xylem bundles with exarch protoxylem, which alternate with groups of phloem (Fig. 3D). The pith is distinct and has disintegrated leading to the formation of a cavity.

Ultrastructure of root cap

The cells of calyptrogen in the aerial roots of *F. microcarpa* have a large nucleus with pronounced nucleolus (Fig. 4A-B). There are many small vacuoles and the cytoplasm is filled with organelles. The plastids are present as simple proplastids (Fig. 7A-B). They contain few thylakoids and several dense osmiophilic plastoglobuli. Many mitochondria are observed in the cap initials. The dumb-bell shape of some mitochondria (Fig. 4A-B) and proplastids may indicate that they are about to divide (Gill and Tomlinson, 1978). In *Zea mays* the plastids double their number by division, and the mitochondrin continue to be formed throughout the life of a cap cell (Juniper and Clowes, 1965). The profiles of endoplasmic reticulum (ER) are scattered at random in the cytoplasm. The plasmodesma are found in all cell walls of the initials (Fig. 4A-B).

When the cells of the cap leave the initial zone, changes in the structure of the cytoplasmic organelles can be recognized. In the younger columella cell the proplastids develop into amyloplasts (Figs. 4C-D, 7C-D). They are in round or oval form, and with several small starch grains and few plastoglobuli. The amyloplasts continue to grow till they reach about 2–3 μm in diameter (Figs. 5A-B, 7D). In the cells at the peripheral region of the cap the starch grains in the amyloplasts are then broken down (Figs. 6A-B, 8A-B). They may be converted into lipids. The build-up and the break-down of starch grains may be concerned with the balance between the enzymic activities (Huber, *et al.*, 1973). Like in *Medicago*, the alteration of the amount of starch in the amyloplast may be correlated with the presence of the plastoglobuli. But in *Zea mays* there are no this correlation (Juniper and Clowes, 1965).

As the cells pass down the cap from the initial zone, the cristae of the mitochondria become more developed and are found to have a somewhat swollen appearance (Figs. 6C-D, 8A-B). In all cells of the cap endoplasmic reticulum is covered by groups of polysomes (Figs. 4A-D, 5A-D). In the initial cells the profiles of endoplasmic reticulum are scattered at random in the cytoplasm (Fig. 4A-B). As the cap cells mature, the total amount of endoplasmic reticulum increases. The profils some endoplasmic reticulum lie parallel to the plasmalemma (Fig. 7C). Sometimes they may be found thrown into loops and whorls. There are microtubules around the cell (Figs. 5C-D, 6D). But an distal endoplasmic reticulum complex, as in the central cap cells (statocytes) of primary root in *Lepidium* (Sievers and Volkmann, 1972), is seldom to be observed. In the root statocytes of *Lepidium*, microtubules have been shown to function in stabilizing the distal endoplasmic reticulum complex in coordination with cross-bridging structures (Hensel, 1984).

Latex cells are observed throughout the root cap (Figs. 4C-D, 6A-D) as reported in other *Ficus* spp. (Kapil and Rustagi, 1966). The latex occur in small vacuoles. In the more mature laticifers, latex are released into a large central vacuole (Figs. 4C, 6A-B).

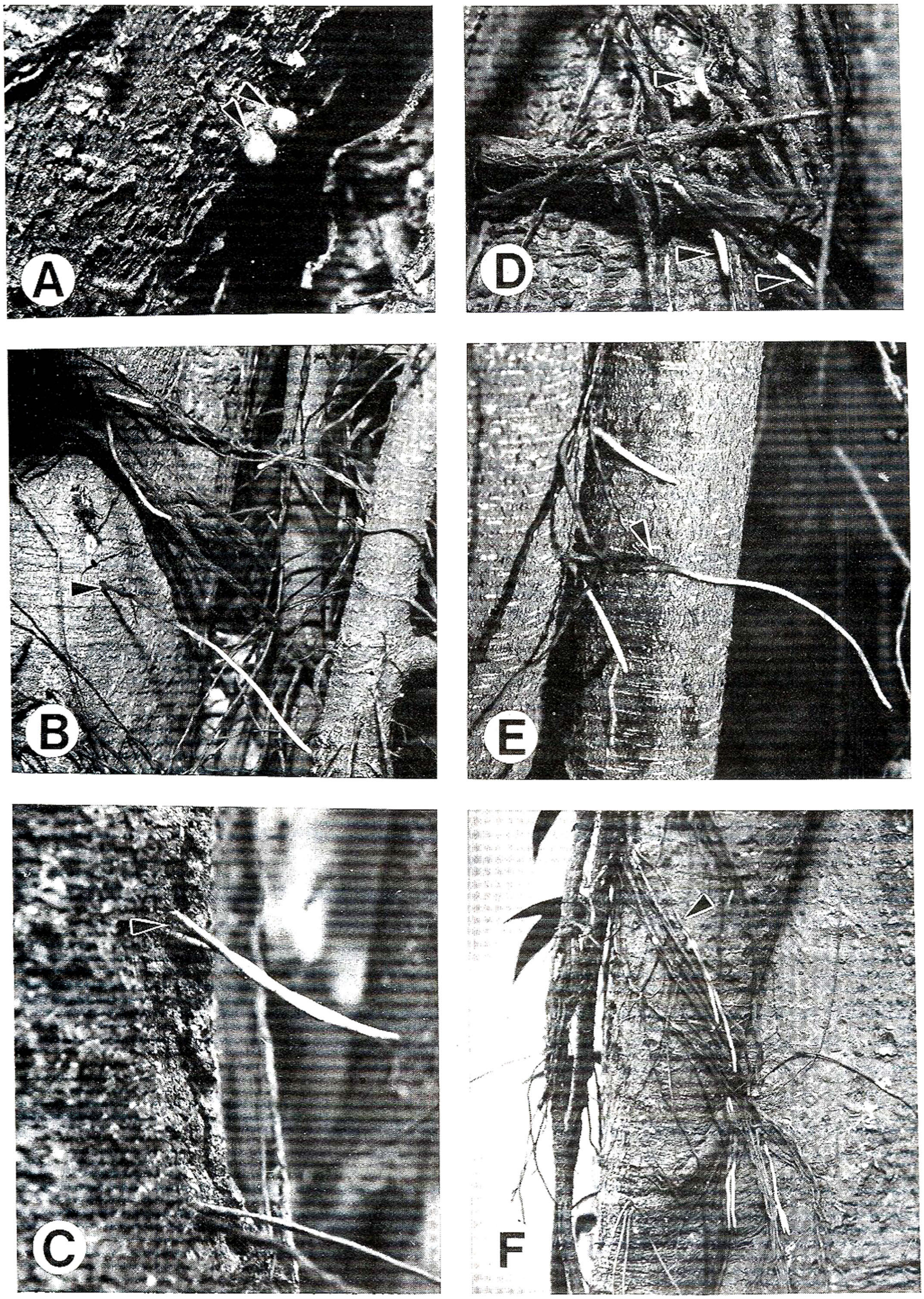

Fig. 1. (A-F) Aerial roots emergent singly or doubly from the shoot (▶)

Key to labeling (For Figs. 2-8)

A: amyloplast	M: mitochondrium	PD: plasmodesma
C: calyptrogen	MT: microtubule	S: starch grain
D: dictyosome	N: nucleus	V: vacuole
ER: endoplasmic reticulum	P: proplastid	W: cell wall

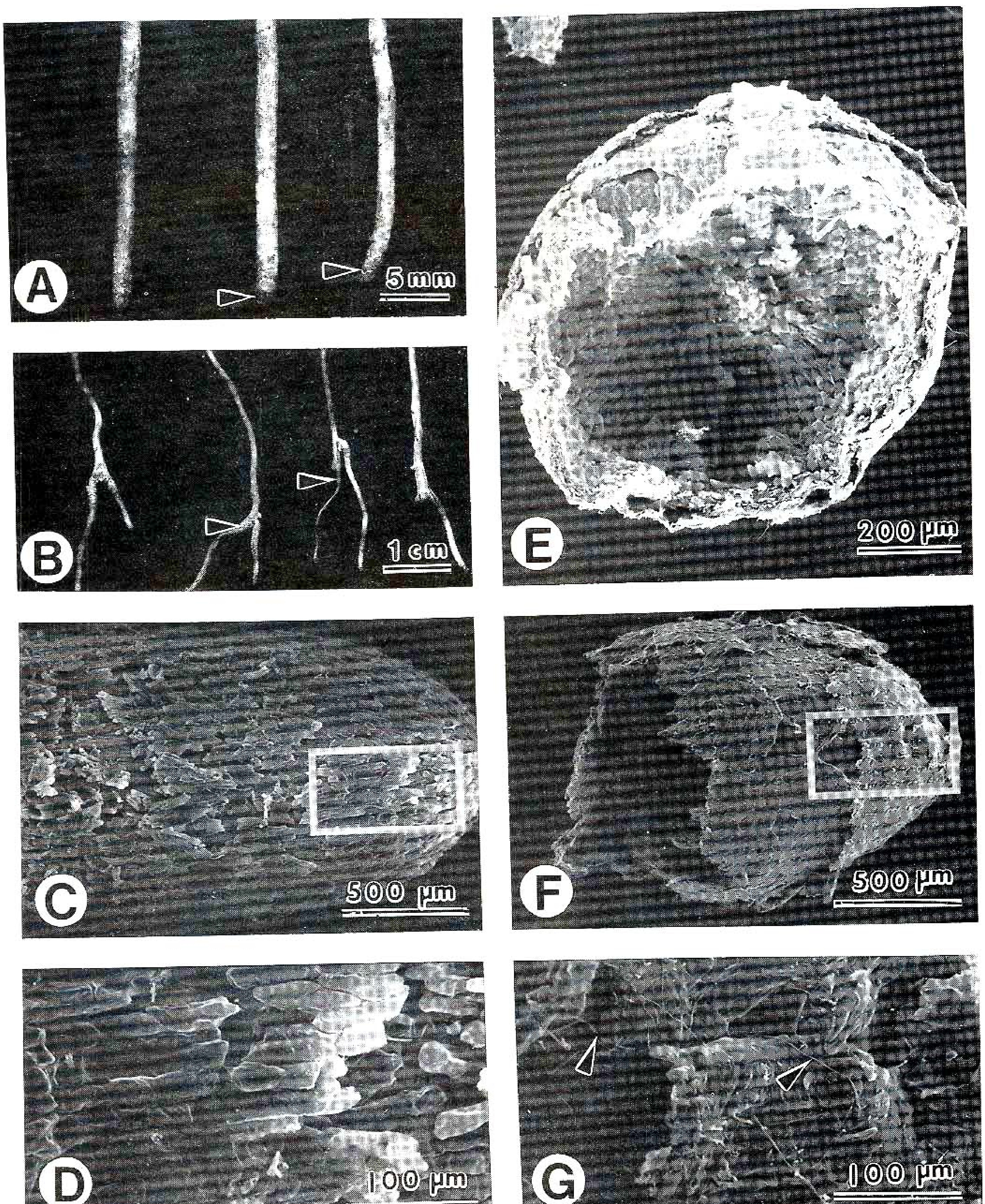

Fig. 2. (A) The tips of aerial root. Note the root cap (▶); (B) The branched aerial roots; (C)-(G) SEM photographs of aerial root tip; (C), (D) Root tip without cap; (E), (G) Detached root cap. There are fungal hyphae on the outside of the root cap (▶).

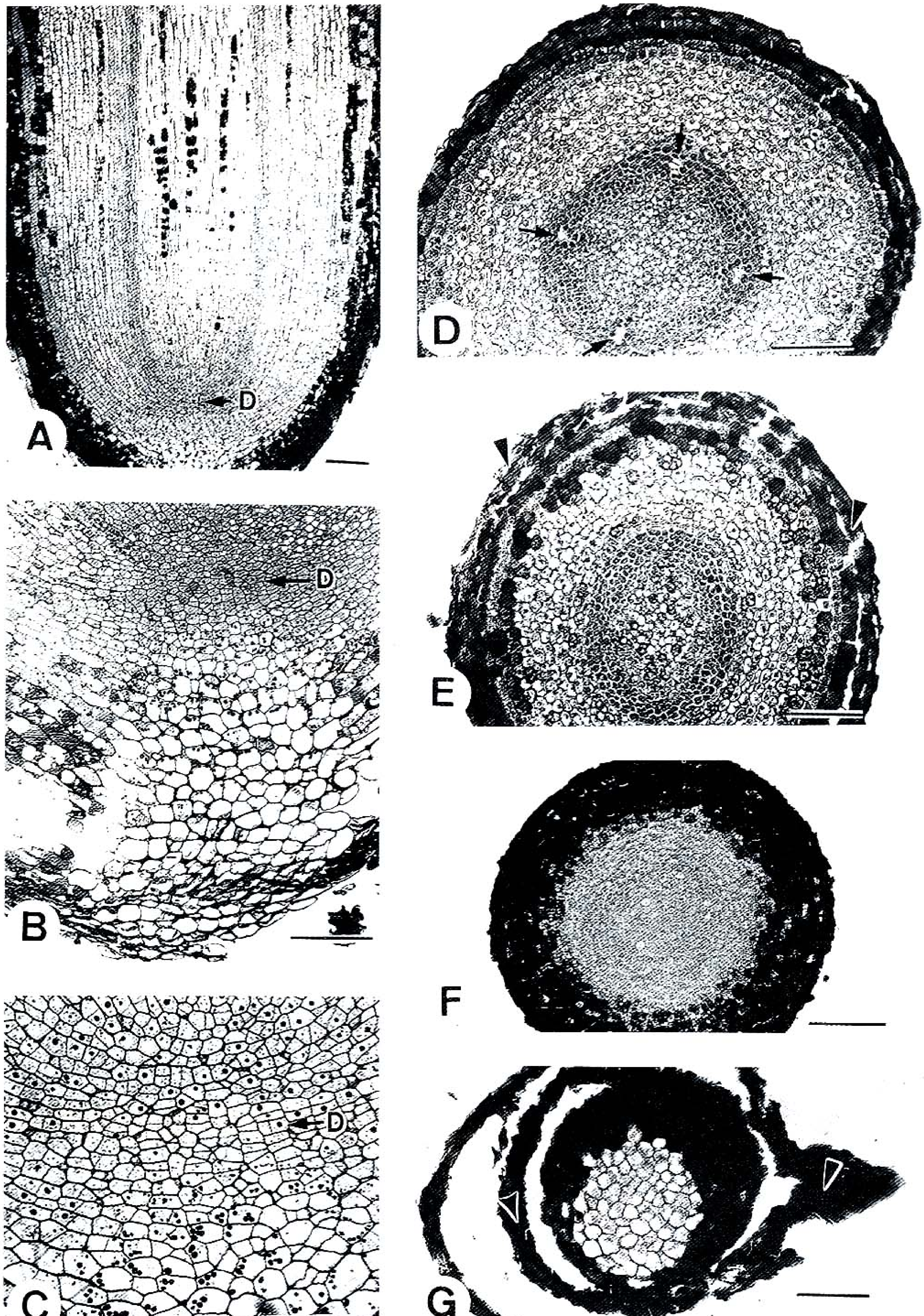

Fig. 3. Anatomy of the tips of aerial roots. All bars represent 100 μm. (A)-(C) Median longitudinal sections of apex of aerial root; (D)-(G) Transverse sections of aerial root in the region from the differentiation zone (D) to the apex (G). Note the protoxylem (D) ($\rightarrow$) and the collapsed peripherial cells (E, G) (▶).

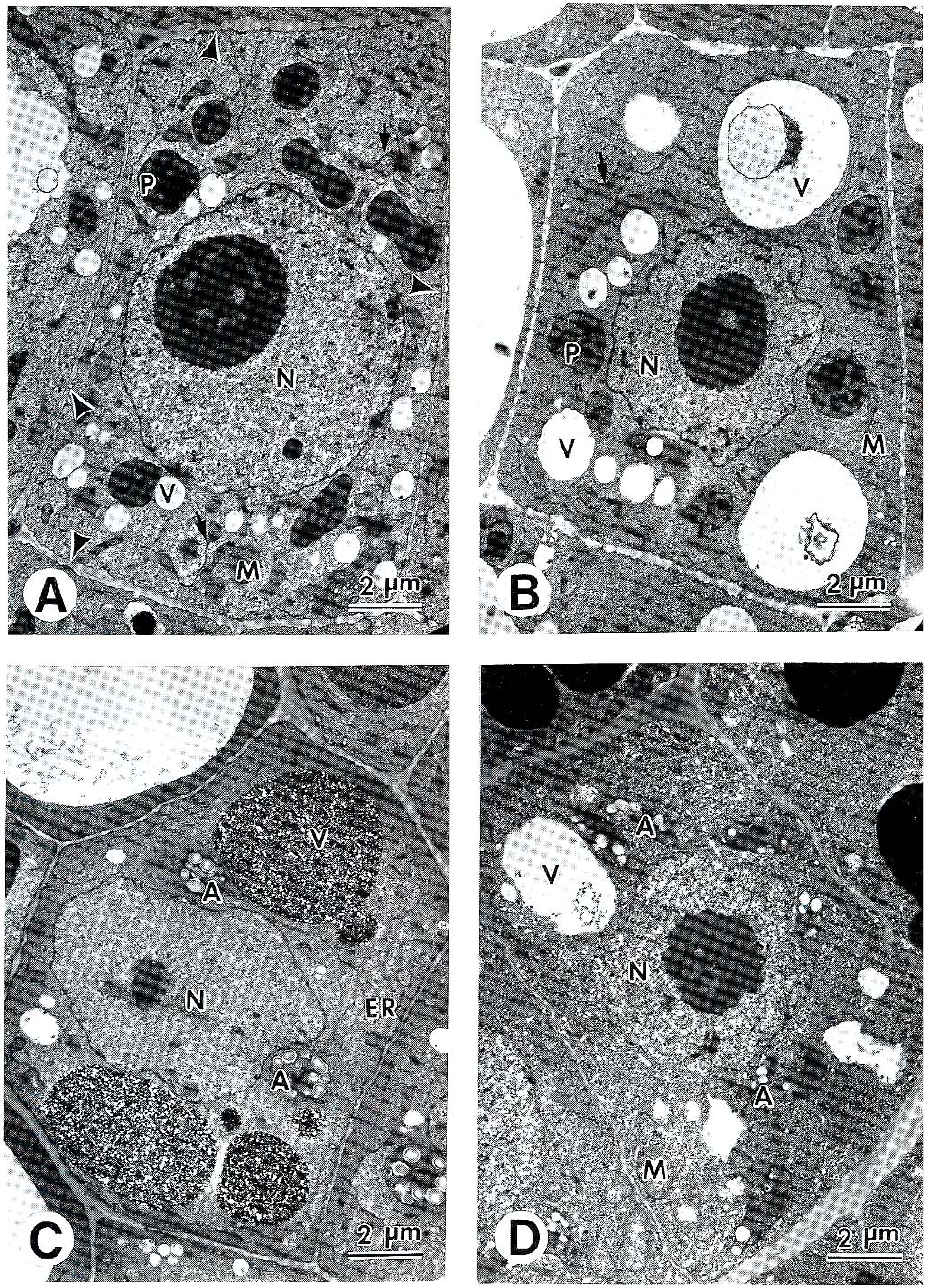

Fig. 4. (A)-(B) Cells in calyptrogen. The Nucleus is large and with pronounced nucleolus. The plastids are proplastids and the all vacuoles are small. The walls are transversed by numerous plasmodesmata (▶). Note the dumb-cell shape of mitochondria (→), and proplastids; (C)-(D) Cells distal to the calyptrogen. Amyloplasts contain a few starch grains.

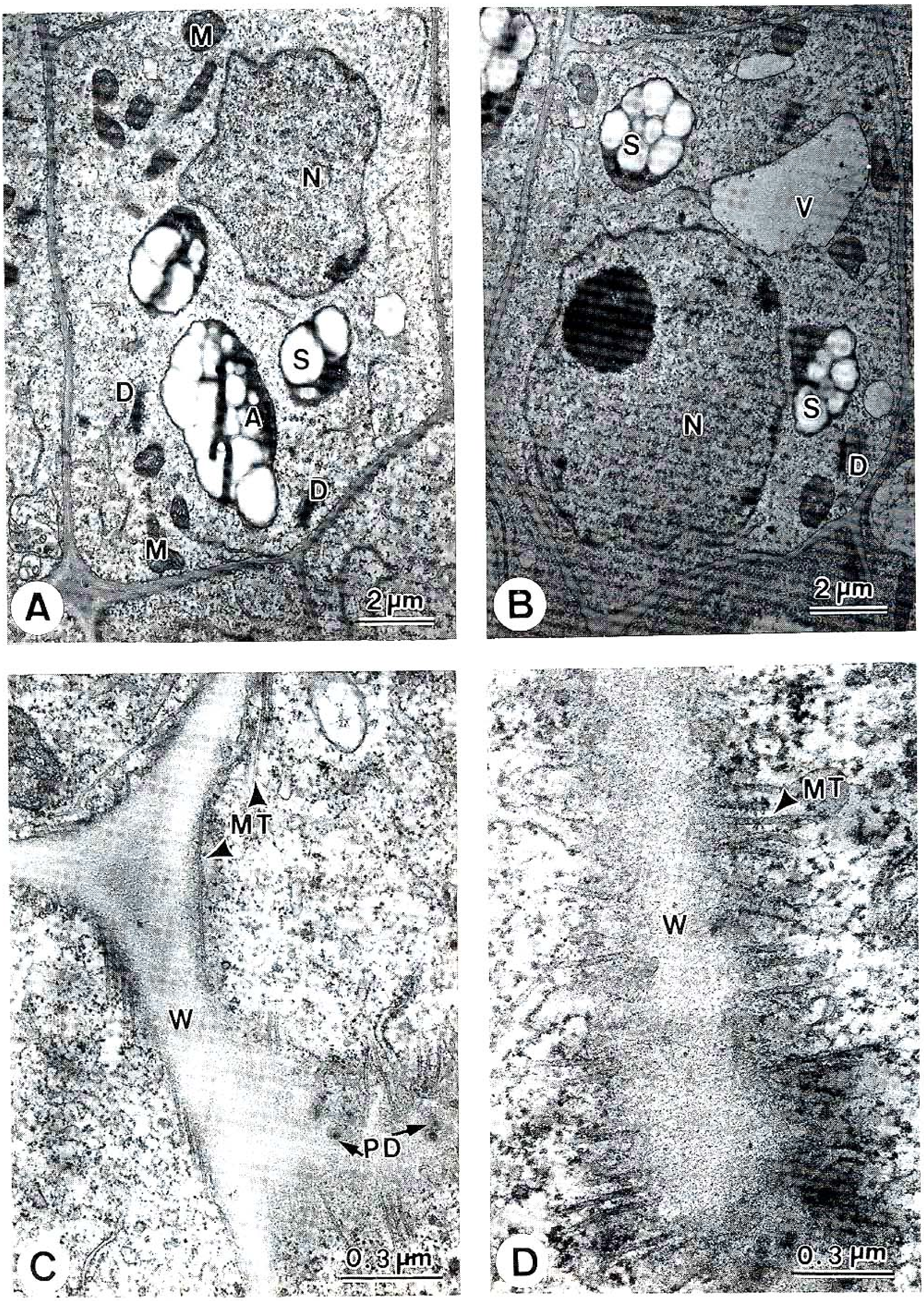

Fig. 5. (A)-(B) The columella cell of root cap. The amyloplasts contain aggregate starch grains; (C)-(D) Portions of the columella cell. There are microtubules around the cell.

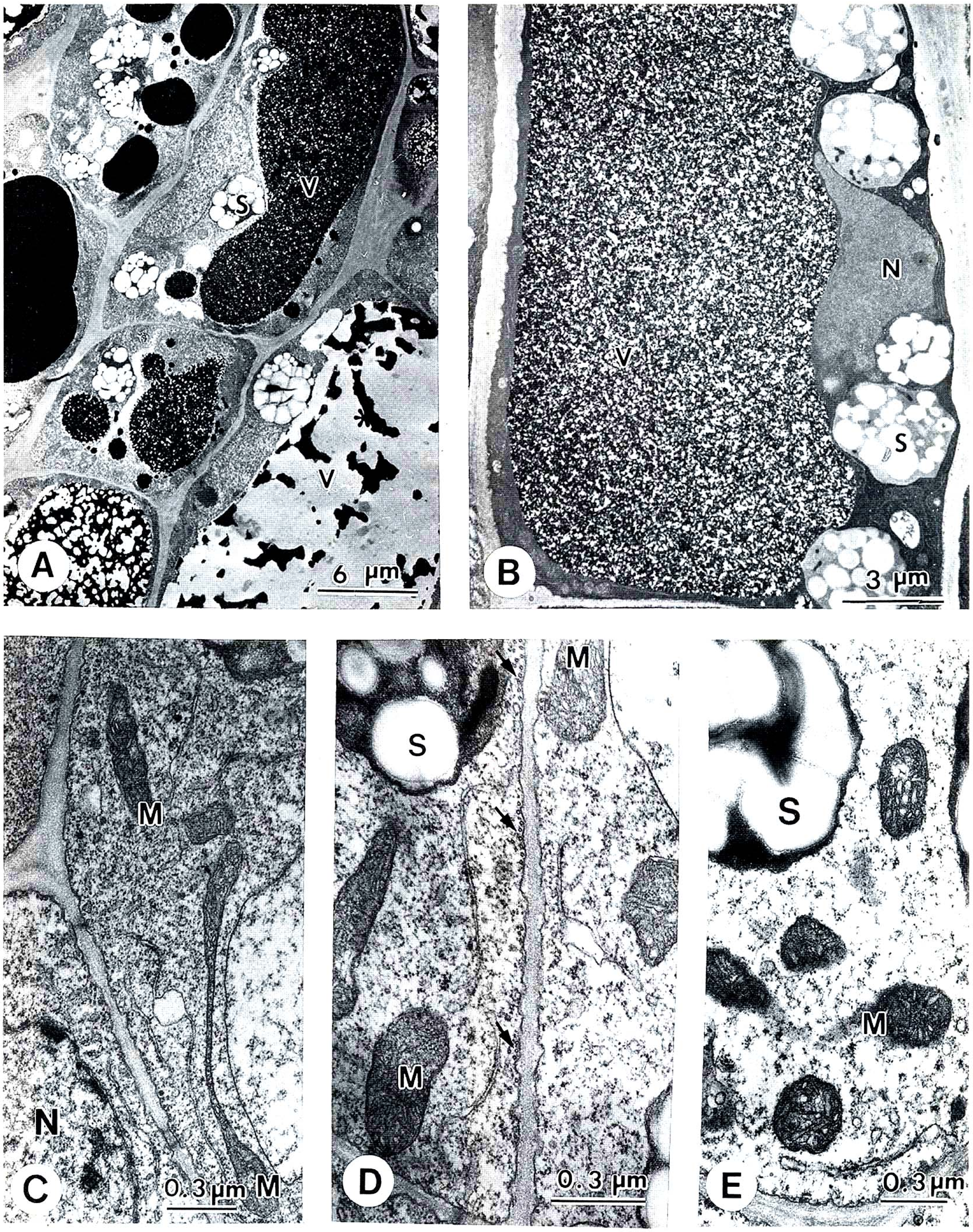

Fig. 6. (A)-(B) Root cap cells at the peripheral region show the vacuolation of the cytoplasm and deposits (∗) in the vacuoles showing osmiophilic; (C)-(E) Mitochondrium development in cap cells, note the microtubules around the cell (→).

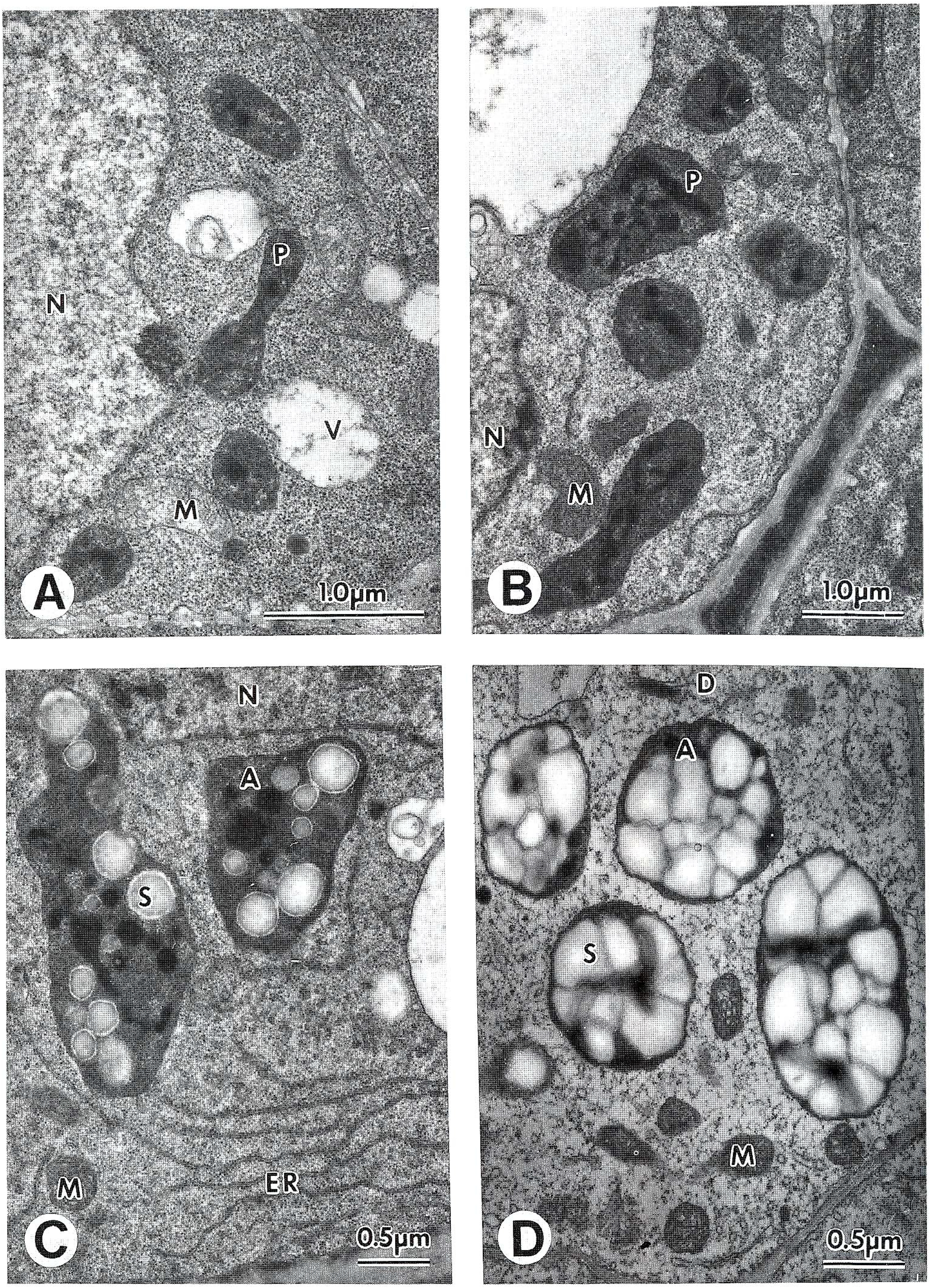

Fig. 7. Plastid development in cap cells. (A)-(B) Proplastids in an cap initial cell; (C) Plastids contain a few starch grains in a cell distal to the calyptrogen; (D) Plastids are filled with many starch grains in a cap columella cell.

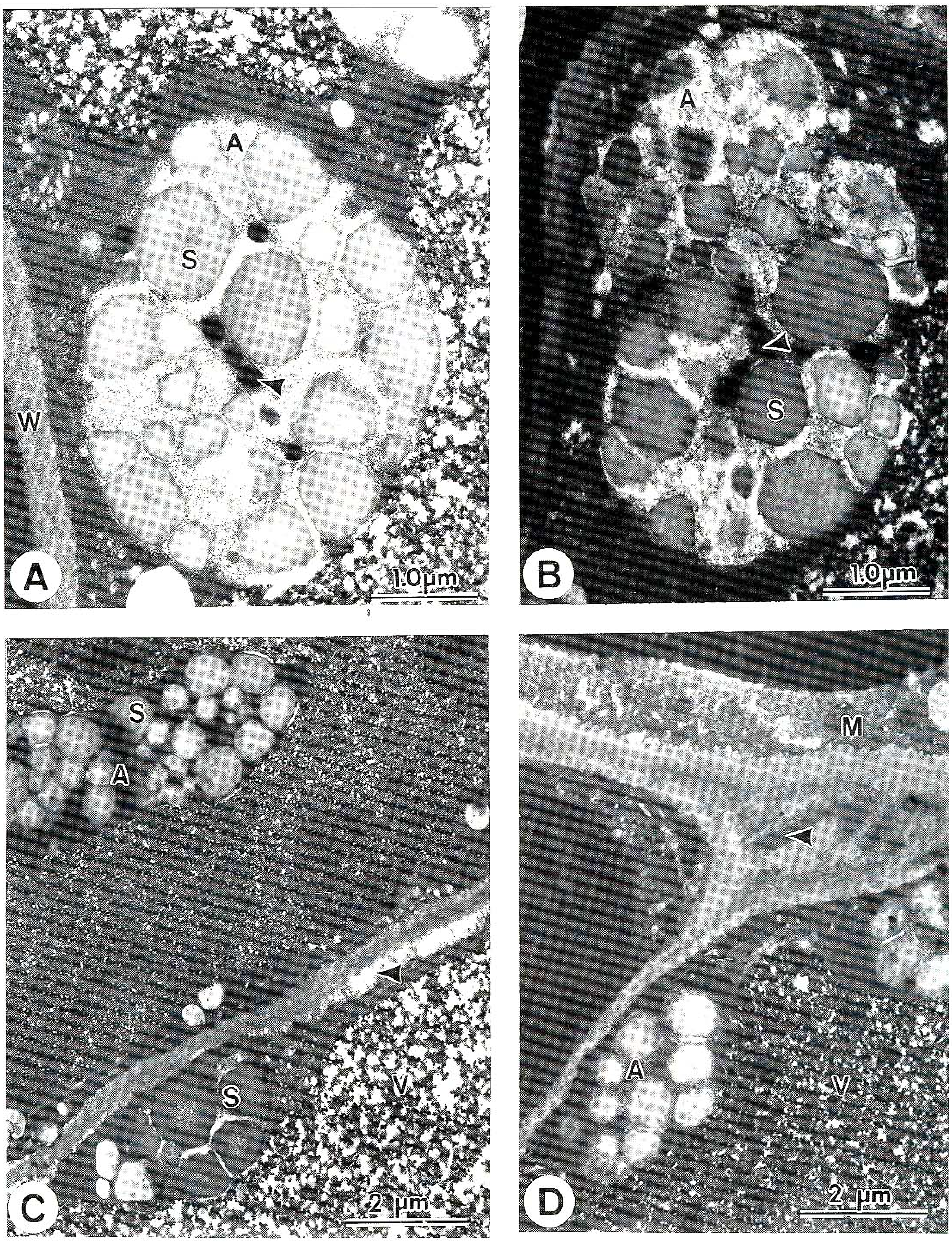

Fig. 8. Peripherial root cap cells. (A)-(B) Some starch grains in plastids are dissolved, and osmiophilic globules are present; (C)-(D) Amorphous mucilaginous substances are filled in the intercellular space (▶), and latex are observed in the vacuoles.

In the primary root of *Lepidium*, which tends typically positive gravitropism, the statocytes are characterized by a distinct polar arrangement of cell organelles. It is expressed by a proximally positioned nucleus and a distal endoplasmic reticulum complex with amyloplasts sedimented thereon (Sievers and Volkmann, 1972). But in the central cap cells of the aerial root of *Ficus microcarpa*, the nucleus and amyloplasts are not preferentially located adjacent to any cell wall or cell organelle, i. e. it shows no strict ultrastructural polarity. The aerial roots of *Ficus* are suggested to be weakly positively geotropic and negatively photot ropic (Gill and Tomlinson, 1978). They develop mostly perpendicularly to the stem and then hang downward by their own weight.

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榕 樹 氣 根 之 研 究

(1) 根 帽 的 構 造

黃 玲 瓏

摘 要

榕樹 (*Ficus microcarpa* L. f.) 莖上發育出許多細長的氣根，此氣根具有根帽，但缺乏根毛。若由中央縱切面觀察，榕樹氣根尖端屬於開放型的分生組織構造。根帽中軸是 8～15 層分裂自根帽源的活薄壁細胞，而位於根帽周圍之細胞則會瓦解、脫落。根帽源之細胞具有一帶明顯核仁之大的細胞核及許多小液胞，其顆粒體爲原顆粒體。在根帽細胞之分化過程中，可確認顆粒體（包括澱粉粒之形成與瓦解）、粒線體及內質網等胞器微細構造之變化。榕樹氣根的根帽中軸細胞之胞器的分佈不具極性。