RELATIONSHIPS BETWEEN STRUCTURE AND ADVENTITIOUS ROOTING

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A comparison of the anatomical structure of stems with their capacity to form adventitious roots has shown that a relationship exists between anatomy and rooting capacity in a wide range of species (1, 2, 4, 5, 6, 7, 8). In considering structure as it may affect rooting, it is important to have a clear, visual image of the location of the tissues that are chiefly concerned. They occur near to the outside of stems and include cork, cortex, and phloem. A sclerenchymatous sheath derived from the primary phloem is, for example, often present in plants that are difficult to root from cuttings (Fig. 1-*above*) and it may provide a physiological barrier to the initiation of roots, or a mechanical barrier to their emergence (1, 4). In contrast, only scattered groups of fibres (Fig. 1— *below*) are present in this zone in many free-rooting plants. In stems from shy— and free-rooting clones of pome fruits viewed at a higher magnification one can discern both individual fibre elements and parenchymatous cells composing the intervening zones of living tissue (Figs. 2 and 3). At a still higher degree of magnification, details of cell contents and of wall structure become visible as in Figures 4 and 5 depicting sections of growing stem tips. Groups of axially-orientated fibres are present in both clones. In the shy-rooting clone (Fig. 4), cells of the zone intervening between fibres have elongated periclinally and are in process of being transformed into thick-walled sclereids lacking living contents, while in the free-rooting clone (Fig. 5) thin-walled cells in a similar location show signs of recent division and they contain cytoplasm and organelles of which the nuclei are clearly visible.

In many free-rooting plants including those illustrated in Figures 1—*below*, 3, and 5, adventitious roots are not initiated in the living zones between fibre groups but they arise in the secondary phloem usually in association with a ray (Fig. 6). Such a ray would have contact at its distal end with living cells by means of cytoplasmic strands passing through the walls and it would not abut, as do most of the rays of shy-rooting plants, on fibres, sclereids, or other elements, without living protoplasts (Fig. 2).

Although a sclerenchymatous sheath blocking the distal ends of the rays is not the only anatomical feature apparently related to rooting capacity, it is the one most frequently recorded in shy-rooting varieties of hardy fruit plants grown at East Malling Research Station, and in samples of exceedingly shy-rooting plants received from many parts of the world. Such sheaths have, for example, been observed in the black wattle, *Acacia mearnsii* De Wild; an ornamental tree, *Brownea* x

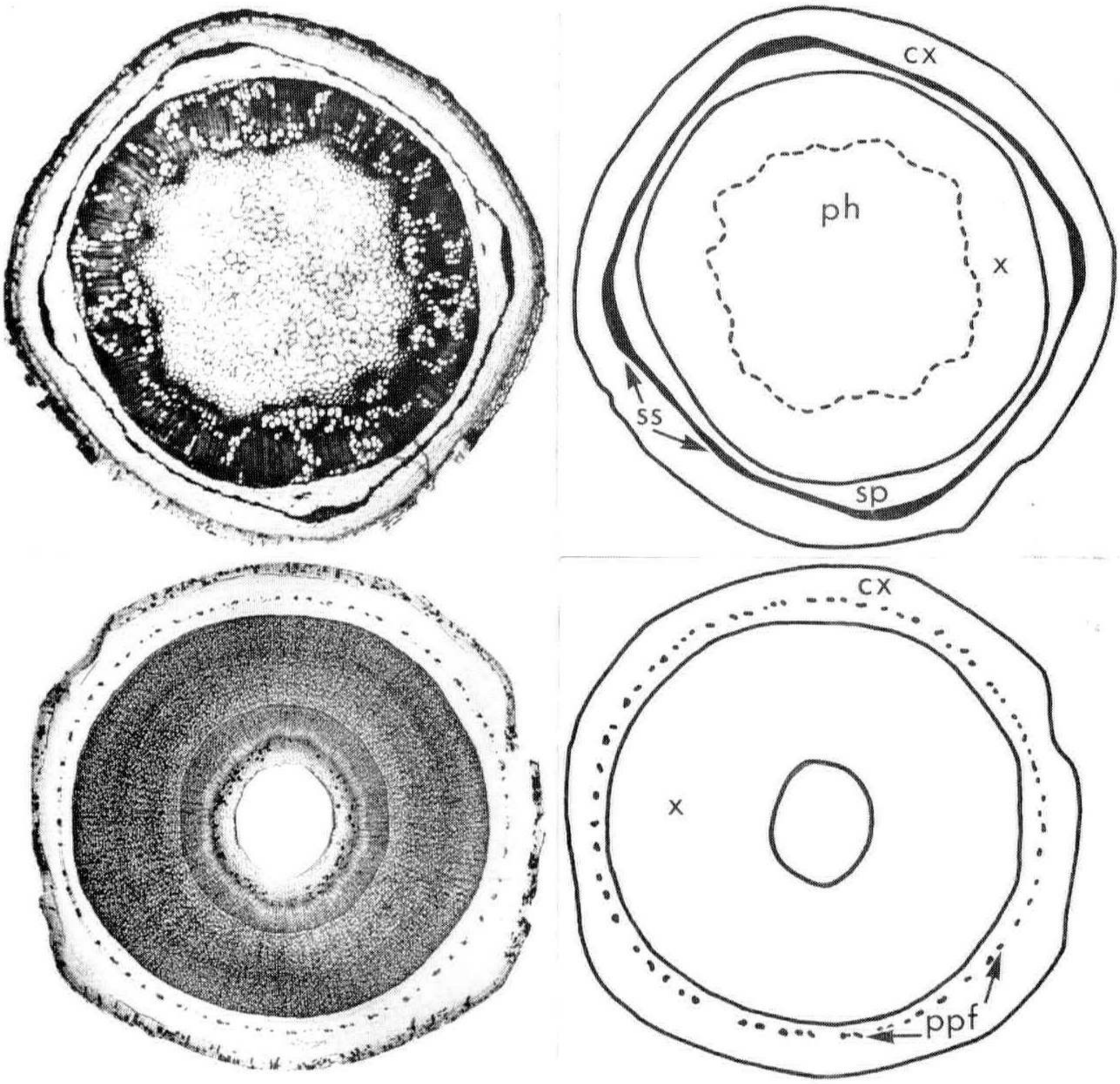

Figure 1. Transections of dormant, one-year-old stems of *Chimonanthus praecox* L. (*above*) and *Forsythia* x *intermedia*. (*below*).
cx, cortex; ph, pith; ppf, primary phloem fibre groups; sp, secondary phloem; ss, sclerenchymatous sheath of fibres and sclereids; x, xylem.

Crawfordii; cinnamon, *Cinnamomum zeylanicum* Blume; heaths, *Erica* spp.; beech, *Fagus sylvatica* L.; para rubber, *Hevea brasiliensis* (Willd.) Muell.-Arg.; an ornamental shrub, *Mahonia japonica* var. *bealei* Bean; oaks, *Quercus* spp.; and a sub-tropical legume, *Pueraria thunbergiana* (Sieb. & Zucc.) Benth. (= *P. hirsuta* Schneid.).

The pattern of development of sclerenchymatous sheaths varies among species and, in some instances, among genotypes within a species besides being subject to variations related to environmental conditions. The onset of tissue senescence in the primary phloem may be rapid, as in *Brownea* x *Crawfordii*, with the result that a fibrous sheath of elements without living contents occurs quite near to the stem tip. Such plants are usually exceedingly difficult to root even from soft, young shoots propagated under mist. In other species, such as *Acacia mearnsii*, lignification of the walls of cells derived

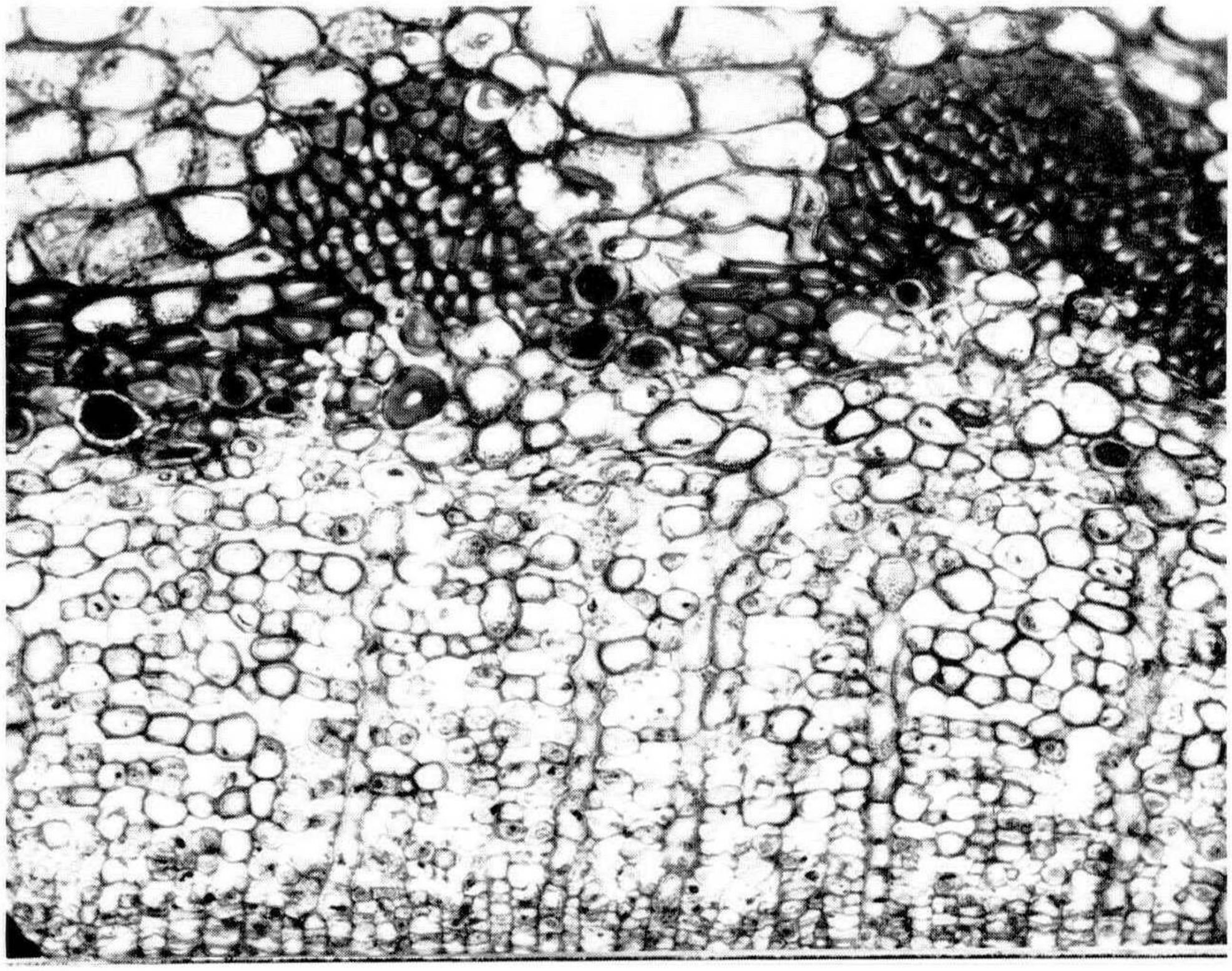

Figure 2. Transection of dormant one-year-old stem of Conference pear. r, rays; sp, secondary phloem; ss, sclerenchymatous sheath.

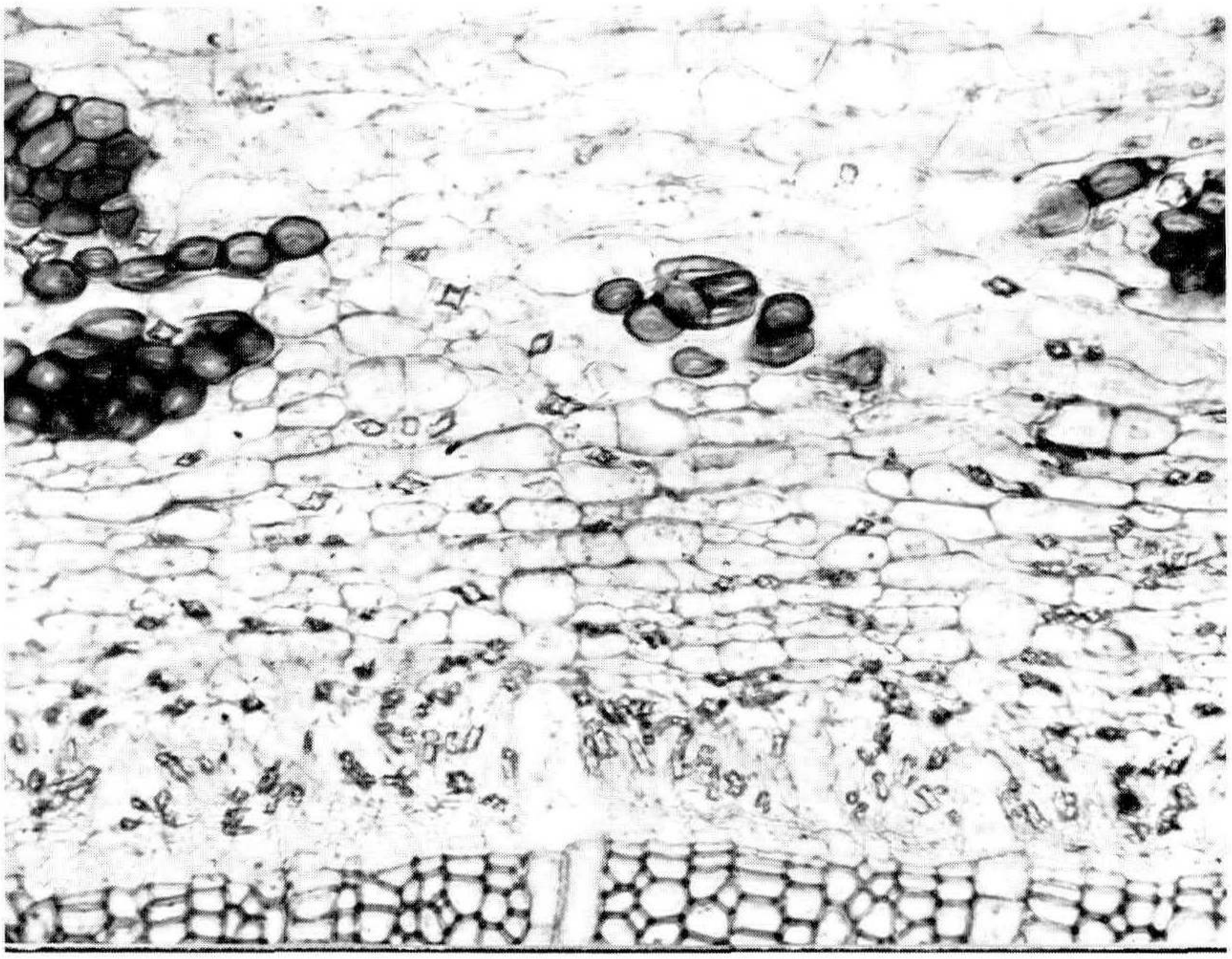

Figure 3. Transection of dormant one-year-old stem of Malling V apple rootstock.
pa, parenchyma; ppf, primary phloem fibre groups; r, rays; sp, secondary phloem.

from the primary phloem may take place some considerable time before these cells lose their living cytoplasmic contents. Specimens in this stage of development have been rooted under mist although the species is normally considered to be shy-rooting from cuttings. Sheaths may even be sloughed off soon after their formation, as in *Erica* where a phellogen is laid down on the inner side of a discontinuous sheath of fibres (Fig. 7). Subsequently a thick layer of cork is formed from the phellogen and it covers the distal ends of the rays with non-living cells in much the same way that a sclerenchymatous sheath of fibres and sclereids does in other shy-rooting plants. Thus, it may be significant that nurserymen usually propagate heaths from very young stem tips in which no cork has yet been formed.

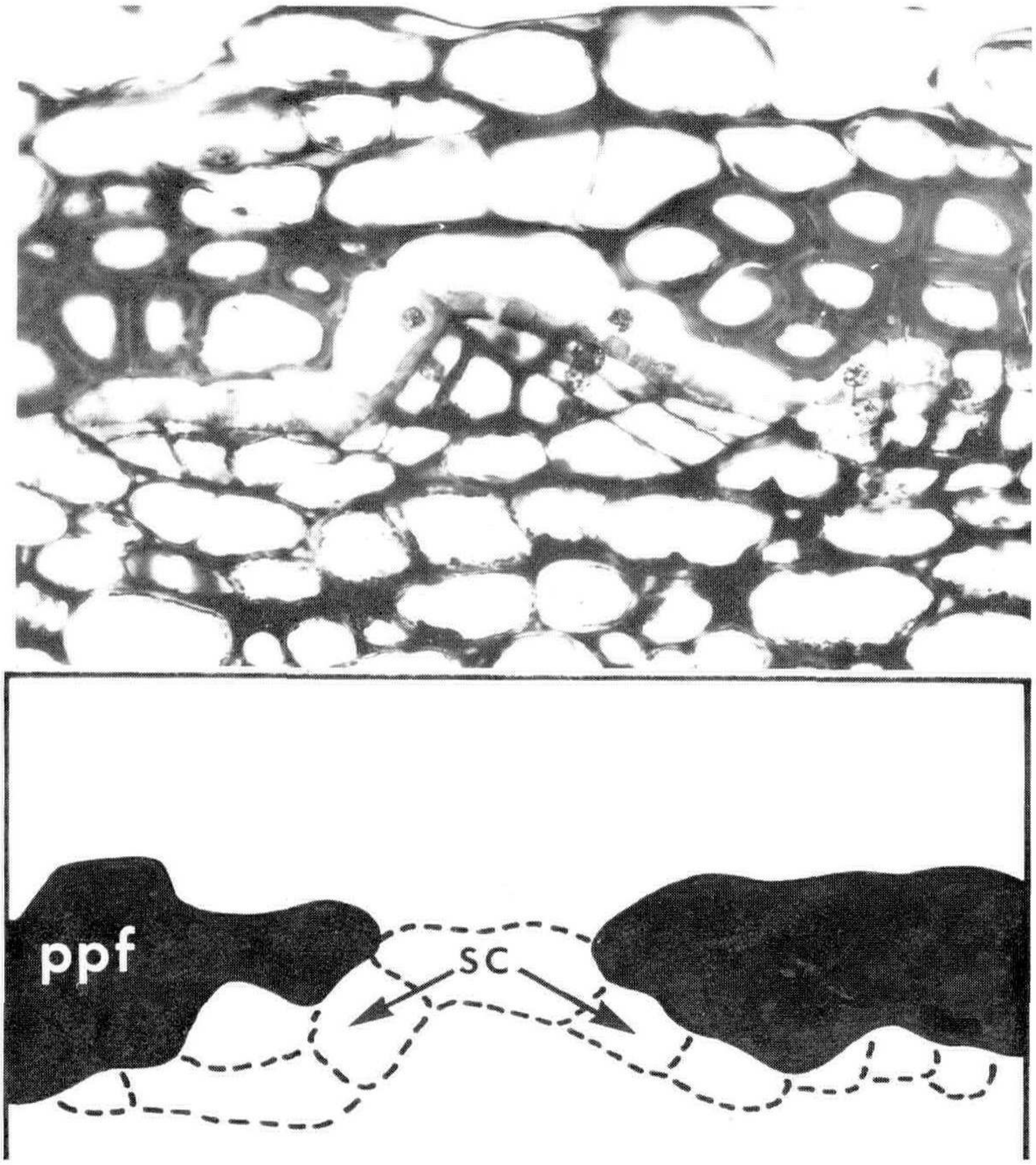

Figure 4. Transection of growing shoot tip of a shy-rooting clone of *Camellia sinensis* L.
ppf, primary phloem fibres; sc, sclereids differentiating from senescent cells of the primary phloem.

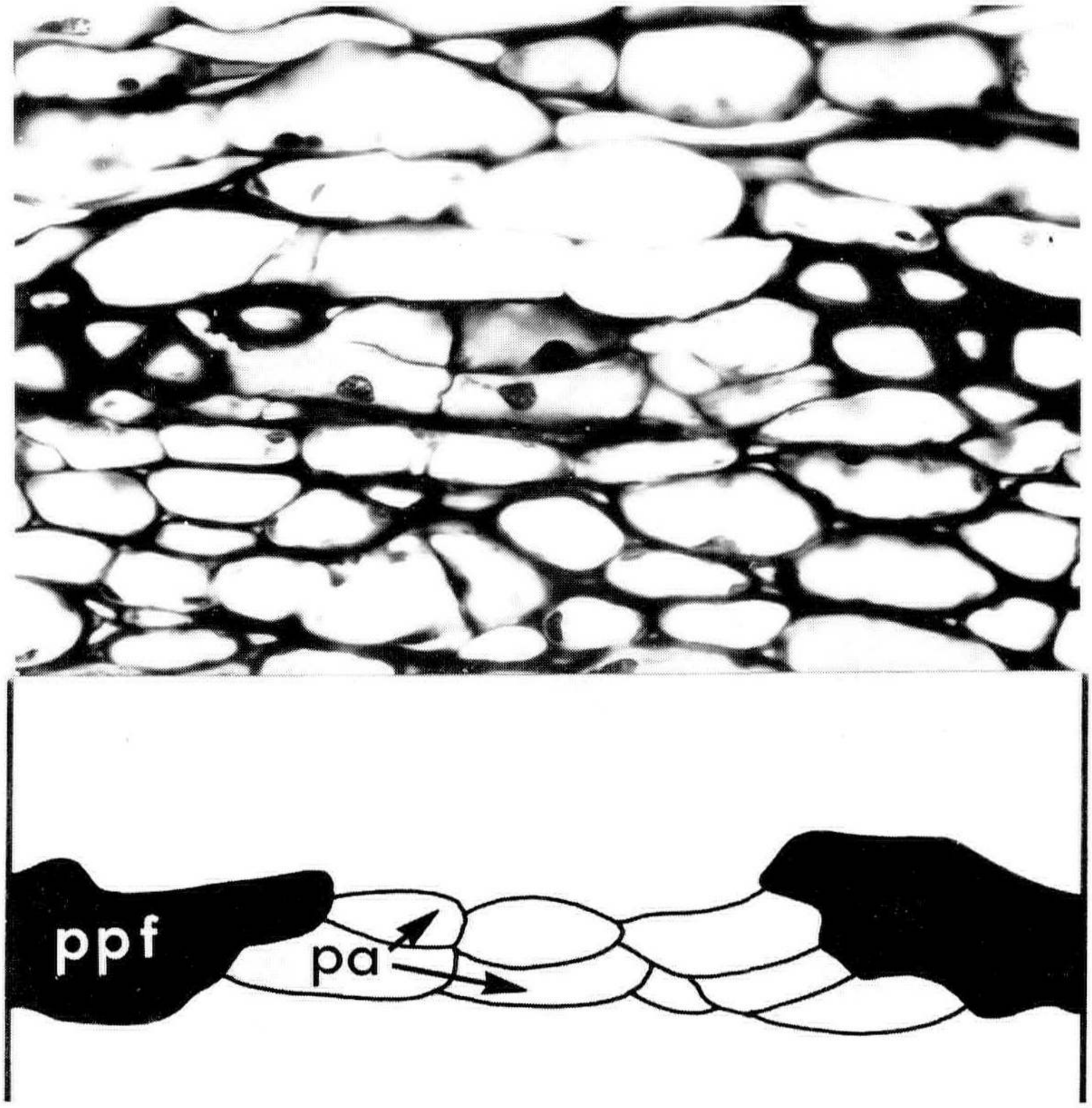

Figure 5. Transection of growing shoot tip of a free-rooting clone of *Camellia sinensis* L.
pa, parenchymatous cells in active division; ppf, primary phloem fibres.

In certain plants, as for example *Pittosporum*, secretory canals rather than fibres and sclereids develop in the primary phloem as it becomes senescent. The disruption of cells during the formation of the canals results in the breaking of many of the cytoplasmic connections with cells of the secondary phloem and cortex and, in this way, the canals may have a somewhat similar effect to that of a sheath of fibres and sclereids. In addition, cells at the distal ends of the rays may be bathed in the secretion released from the canals when the cutting is severed from the source plant.

Where anatomical features apparently inimical to adventitious rooting are likely to develop during the ageing of primary tissues, there are various courses of action that may be taken in order to obtain suitable material for propagation. Shoots from plants — or parts of plants — in the juvenile phase of growth may, for example, provide a source of free-rooting material. Differences in morphology observed between

juvenile and adult shoots from ten-year-old seedling apple trees at East Malling Research Station were found to be associated with differences in anatomical structure (4). At the base, these trees produced shoots with a pose, leaf shape, and cell structure typical of the juvenile, free-rooting condition, while growths from the topmost branches, which were bearing fruit, resembled those of adult apple trees in outward form and in tissue structure. Where one is dealing with clones rather than seedlings, advantage may be taken of the fact that not all parts of plants age — in the physiological sense — at the same speed. Primary tissues derived from apical meristems may retain certain juvenile characters, including that of free-rooting, long after secondary tissues formed from lateral meristems, such as the vascular cambium, have lost these properties. In shy-rooting plants one may, therefore, be able to root shoots arising from sphaeroblasts — small nodules sometimes formed in the primary phloem, or cortex (3). Shoots of this type, grown from sphaeroblasts formed in the apple rootstock Crab C, rooted more readily (6) and possessed fewer primary phloem fibres than normal shoots (4).

Reference has been made on several occasions to the *inherent* rooting capacity of stems — that is their capacity to form roots under conditions approximating those occurring naturally. Some exceedingly shy-rooting plants — even some of the most unrootable among them, such as *Asparagus officinalis* L. — have been induced to produce roots when grown *in vitro* un-

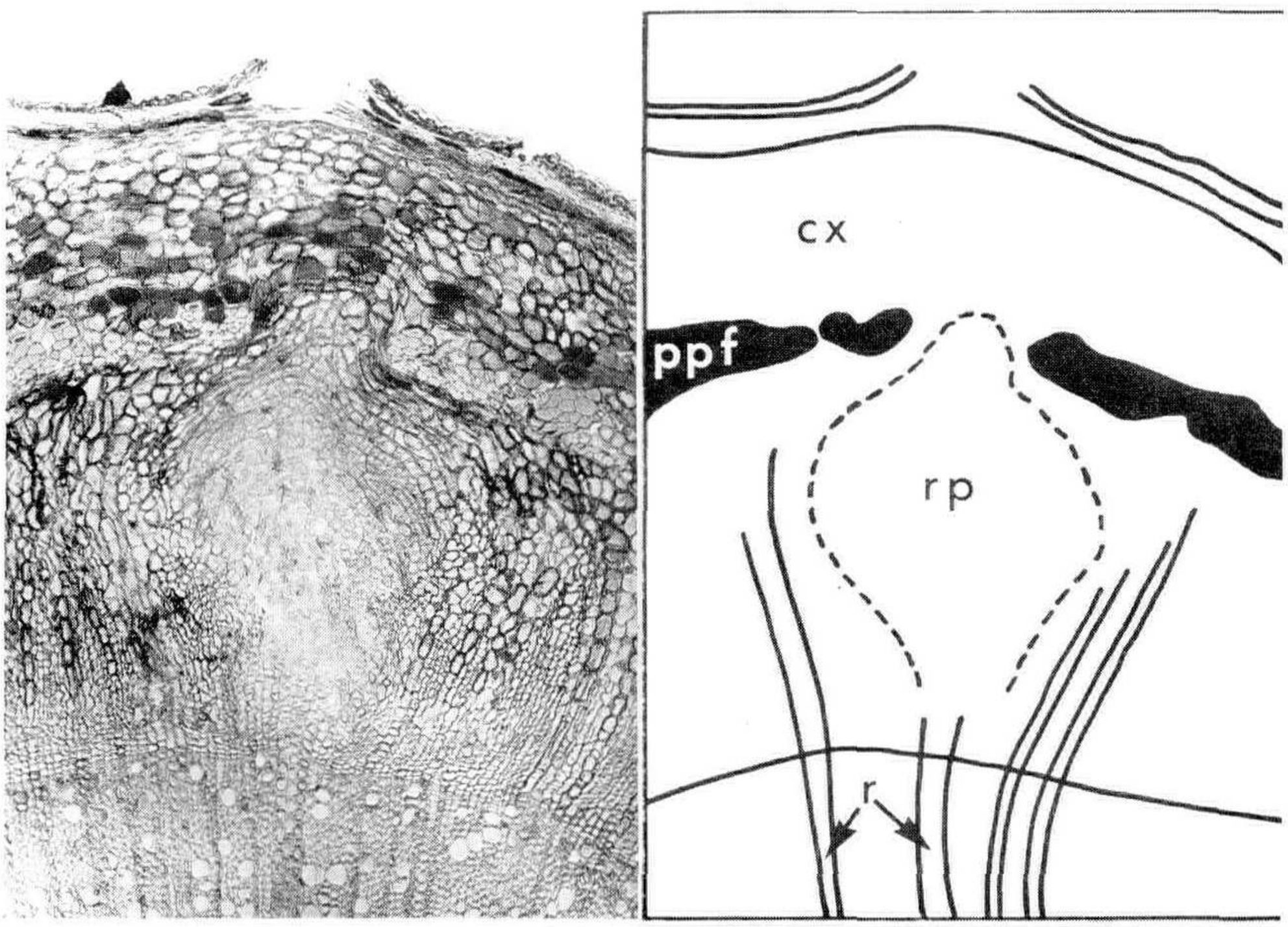

Figure 6. Transection of a dormant stem of Brompton plum rootstock. cx, cortex; ppf, primary phloem fibres; r, rays; rp, root primordium.

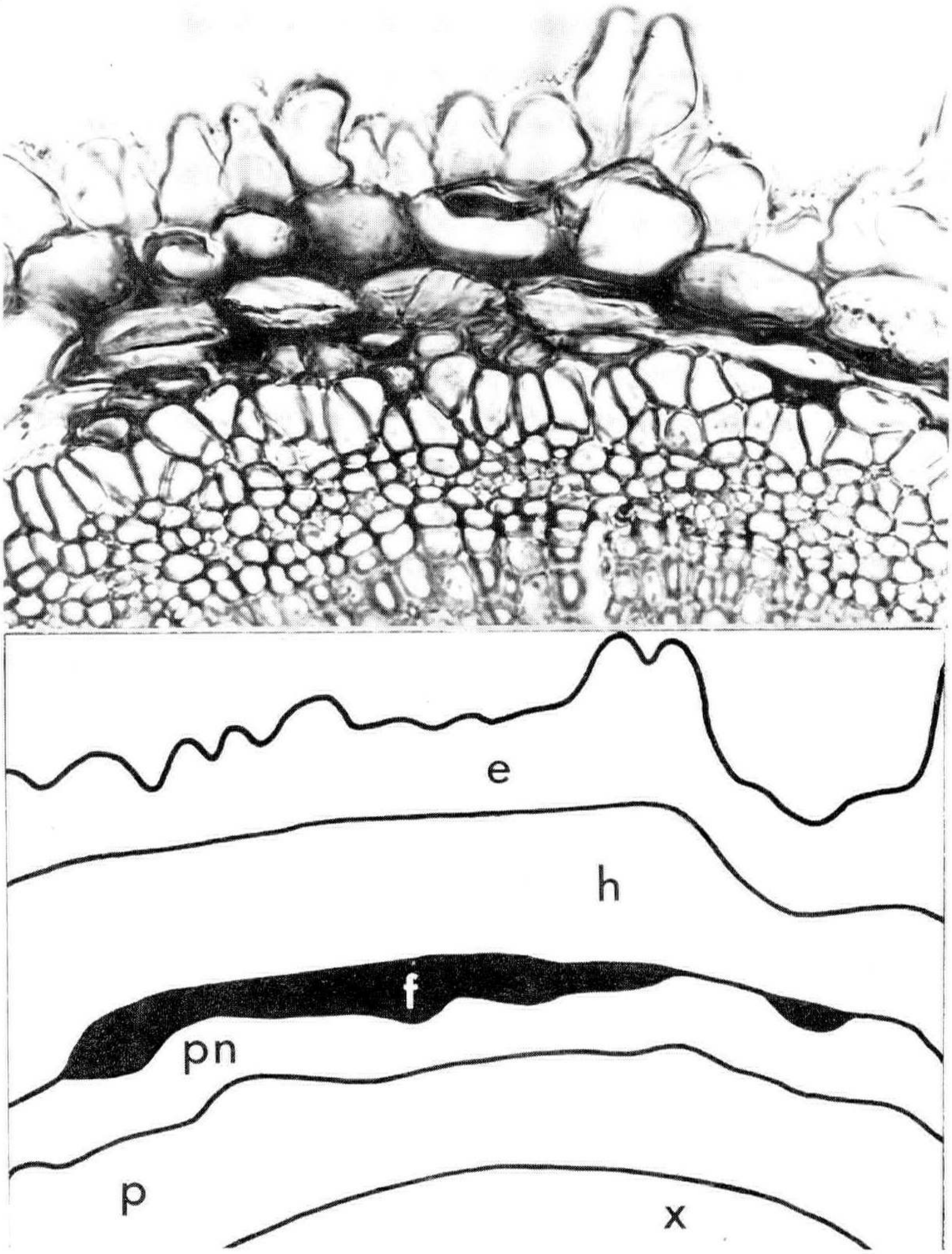

Figure 7. Transection of young shoot tip of *Erica arborea* L. var. *alpina* Bean. e, epidermis; f, fibres; h, hypodermis; p, phloem; pn, phellogen; x, xylem.

der aseptic conditions, and supplied with a nutrient medium and a growth factor supplement (5, 7, 8). Asparagus is, of course, a monocotyledon lacking a vascular cambium. The central ground tissue in which the vascular bundles are embedded, is surrounded by a massive sheath of fibres as shown in Figure 8. If a plant with such a tough peripheral structure can be rooted then, perhaps, there may be few plants that will not respond to techniques now being developed in the course of the present remarkable advances in the propagator's art.

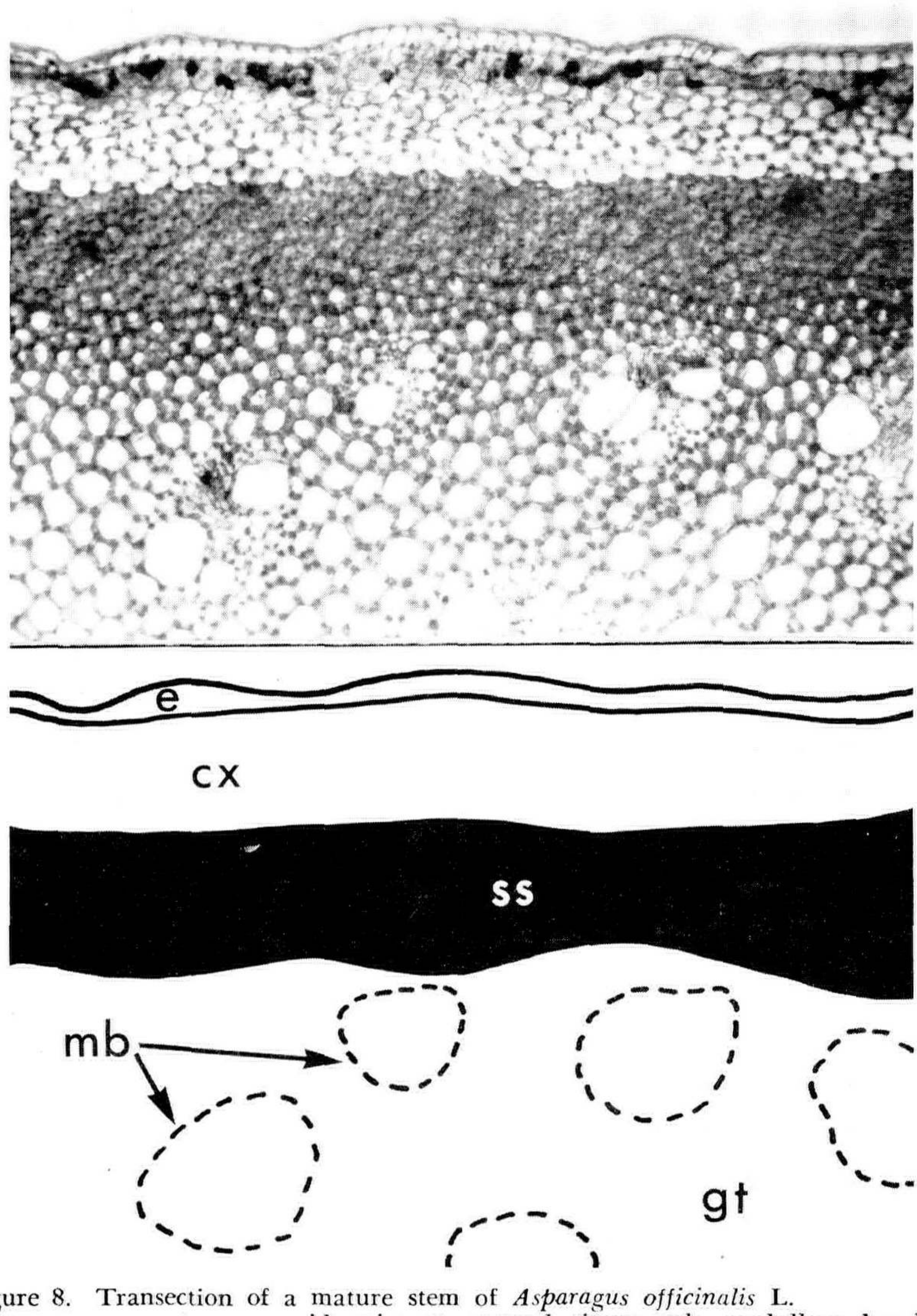

Figure 8. Transection of a mature stem of *Asparagus officinalis* L.
cx, cortex; e, epidermis; gt, ground tissue; mb, medullary bundles; ss, sclerenchymatous sheath.

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