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Distribution and some interesting morphological aspects of the South African Podocarpaceae

ELZABÉ SCHOONRAAD & H. P. VAN DER SCHIJFF

SUMMARY

A distribution map of the African *Podocarpus* species is provided and the morphological similarities among African podocarps are discussed briefly. Female cone structure, external and internal leaf morphology, xylotomy and the roots and root nodules of the four South African species are discussed in greater detail. A key based on the xylotomy of the four species is given.

RÉSUMÉ

Les auteurs présentent une carte de distribution des espèces africaines du genre *Podocarpus* et discutent brièvement de leurs affinités morphologiques. Les quatre espèces sud-africaines sont comparées d'une manière plus détaillée en ce qui concerne les cônes femelles, la morphologie externe et interne des feuilles, la xylotomie, les racines et les nodosités radiculaires. Une clef de ces quatre espèces basée sur la xylotomie est donnée.

African Podocarpaceae

The genus *Podocarpus* L'Hérit. ex Pers. consists of trees and shrubs which are confined chiefly to the southern hemisphere. Of the approximately 110 species ten are indigenous to Africa, being mainly restricted to coastal and montane forests (Fig. 1). Of these, four species, *P. falcatus*, *P. elongatus*, *P. henkelii* and *P. latifolius* occur in South Africa.

Of the African species, *P. falcatus*, *P. gracilior*, *P. manii*, *P. usambarensis* and *P. usambarensis* var. *dawei* belong to the section *Afrocarpus*, and *P. elongatus*, *P. ensiculus*, *P. henkelii*, *P. latifolius* and *P. milanianus* to the section *Eupodocarpus*.

There is a fair degree of similarity between *P. henkelii* and *P. ensiculus*, between *P. latifolius* and *P. milanianus*, and among *P. falcatus*, *P. gracilior*, *P. usambarensis* var. *usambarensis* and *P. usambarensis* var. *dawei*. During the study of nearly 3000 herbarium specimens of *Podocarpus* it became clear that *P. henkelii* and *P. ensiculus* are so similar in external leaf and female cone morphology (the two criteria given the most consideration by Melville, 1954, in the creation of the new species *P. ensiculus* from material obtained from Tanzania), that the division of these two taxa into two separate species is not justified. Anatomical studies of the leaves of these two taxa

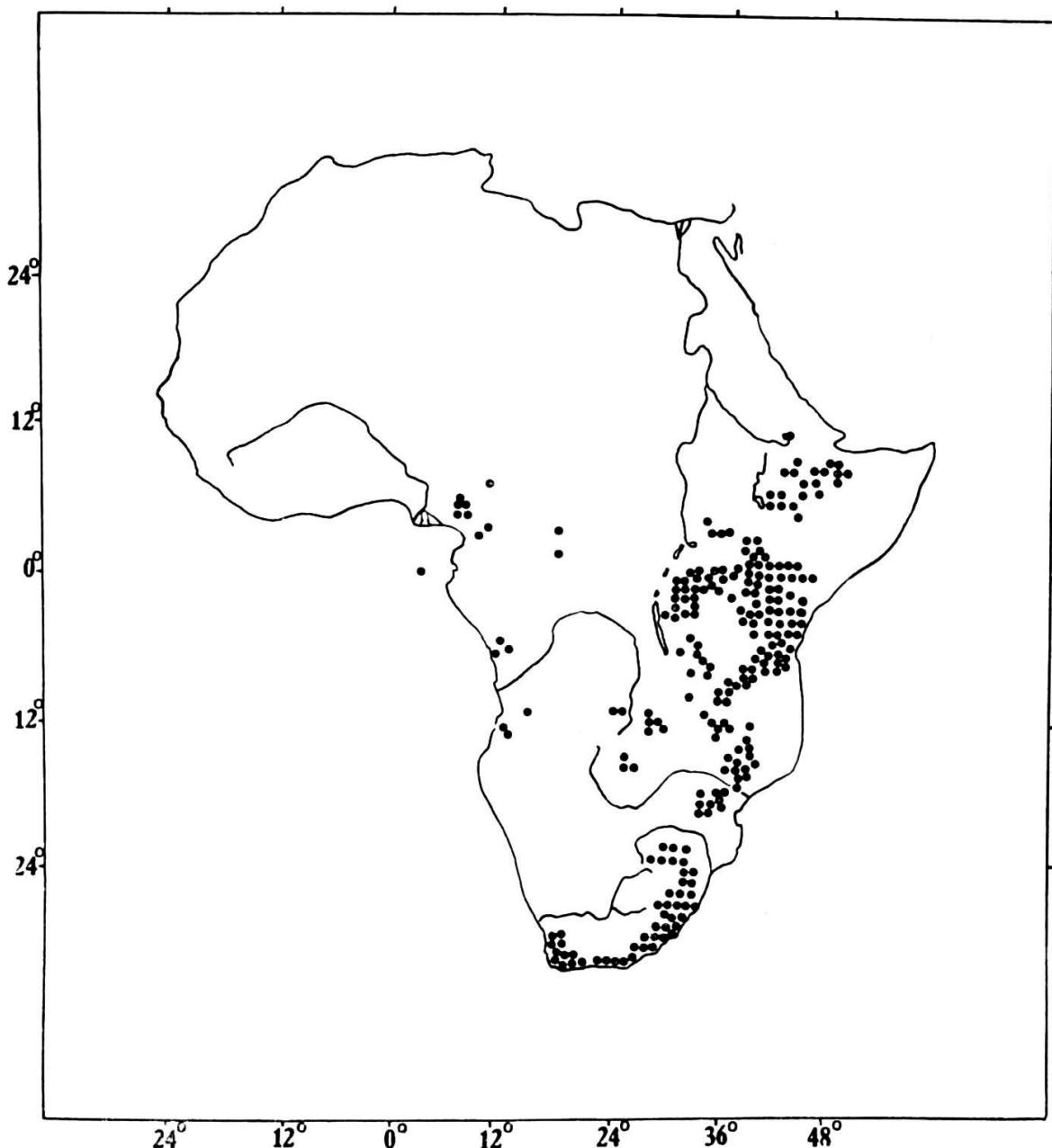


Fig. 1. — Distribution of *Podocarpus* in Africa.

also support this conclusion. External and anatomical studies have therefore led us to believe that *P. henkelii* and *P. ensiculus* represent varieties, ecotypes or ecophenes of the same species, as has also been suggested by Chapman & White in 1970.

A similar similarity exists between *P. falcatus* on the one hand and *P. gracilior*, *P. usambarensis* and *P. usambarensis* var. *dawei* on the other. These four taxa which differ practically only in their geographical distribution, are probably also only varieties of the same species, in this case *P. falcatus*.

In 1969, De Laubenfels created the new genus *Decussocarpus*, incorporating the three sections *Polypodiopsis*, *Afrocarpus* and *Nageia* of the genus *Podocarpus* of

L'Héritier. Accordingly the name of the South African taxon was changed from *P. falcatus* to *Decussocarpus falcatus*. This study, however, indicates that the generic name *Podocarpus* should be retained for the South African taxon. Without going into too much detail, a few discrepancies should be pointed out. Within the section *Afrocarpus* of the genus *Decussocarpus*, De Laubenfels (1969) recognizes the three species, *D. falcatus*, the type species of the section, *D. gracilior*, and *D. manii* which is endemic to the island of St. Thomas. In *D. manii*, he includes three species originally recognized by Buchholz & Gray (1948), viz. *Podocarpus manii*, *P. usambarensis* and *P. dawei*. It is not quite clear why De Laubenfels includes these last three taxa in *D. manii*, while he keeps the taxa *D. falcatus* and *D. gracilior* as two distinct species. Our research has shown that *P. usambarensis* and *P. dawei* have many more characteristics in common with *P. falcatus* and *P. gracilior* than with *P. manii*. According to leaf and female cone morphology *P. manii* ought to be maintained as a separate species, while the other four taxa may be combined under one species.

Although it has become apparent that *P. falcatus* differs in many characteristics from the *Eupodocarpus* species of South Africa, e.g. leaf anatomy, xylotomy, male and female cone morphology and embryology, these characteristics do not, however, justify the creation of a separate genus.

The retention of *P. latifolius* and *P. milanjanus* as two distinct species is probably justified.

South African Podocarpaceae

The aim of this paper is to give a general review of the most salient morphological aspects of the four South African *Podocarpus* species.

In the demarcation of the four species, the external and internal morphology of the leaves, and the external morphology of the female cones are the most significant.

Female cones

The female cones of *P. elongatus*, *P. henkelii* and *P. latifolius* show similarities. The strobilus consists of a peduncle, podocarpium and one or two anatropous ovules, each surrounded by the epimatium. The podocarpium is formed by 2, 3 or 4 fused bracts. When four bracts are present they are decussate with one pair bearing two or one axillary anatropous ovule(s). Between these ovule-bearing bracts are situated the apical meristem of the strobilus as well as the other two bracts. When three bracts are present, the two opposite ones bear the ovule(s) and the third occurs between them on the side of the podocarpium nearest to the vegetative shoot. The laminae of these bracts are reduced so that only very short leaf tips are present. Whereas the podocarpium of the mature cone of *P. elongatus* and *P. latifolius* is always fleshy and bright red or purple in colour, that of *P. henkelii* is smaller, dark green or brown and never fleshy or brightly coloured.

Normally no leaves or bracts occur on the proximal side of the podocarpium in the African *Eupodocarpus* species. Such bracts, however, do occur on the female

strobili of those species belonging to sub-section B of *Eupodocarpus* (Buchholz & Gray, 1948; Pilger, 1926), occurring in Asia, Southern Pacific Ocean Islands, and Australia, e.g. in *P. macrophyllus* (Morvan, 1971).

During this study it was found, however, that proximal bracts do sometimes occur directly beneath the podocarpium of the female cones of *P. latifolius* (Pl. I). Where these bracts do occur, either one or two bract(s) of the lower decussate pair, or a single bract, in cases where the podocarpium consists of three fused and swollen bracts, are free. Free proximal bracts were studied on cones formed during January and February 1974, on two separate trees growing in the same area in Pretoria, 3 kilometres apart. Approximately 25% of the female cones on each of these trees bore free proximal bracts, which dried out and were shed by the time the cones were mature. These bracts resemble the proximal bracts of the cones of *P. macrophyllus* but as this was the first time these bracts were observed in *P. latifolius*, it was impossible to study their ontogeny to determine whether they are homologous with those of *P. macrophyllus*.

Whereas Pilger (1926) based his subdivision of the section *Eupodocarpus* into two subsections on the presence or absence of free proximal bracts beneath the podocarpium, Buchholz & Gray (1948) based their division of the section into five subsections mainly on geographical distribution. Although this is usually an unsatisfactory criterion, the presence of proximal bracts in the African *Eupodocarpus* species supports the delineation of Buchholz & Gray in preference to that of Pilger (1926).

The female cone of *P. falcatus* is regarded as being more primitive than those of the other three species. The ovules are borne on short vegetative shoots 10-20 mm long which bear 8-14 spirally arranged bracts. The distal single bract is fertile and bears a single, axillary, anatropous ovule. In exceptional cases two bracts, each bearing a single ovule, are present. No podocarpium is formed.

Internal leaf morphology

The leaves of *P. henkelii* and *P. latifolius* are dorsiventral and hypostomatic. This is characteristic for most of the leaves of the section *Eupodocarpus*. According to Orr (1944), the distribution of the stomata in the section *Eupodocarpus* is of no diagnostic value since all species of this section are hypostomatic. The South African *Eupodocarpus* species *P. elongatus*, is exceptional, however, as stomata occur ad- and abaxially. This has proved to be an important diagnostic characteristic. Fewer stomata occur, however, in the adaxial than in the abaxial epidermis. Stomata in the abaxial epidermis are arranged in 15 to 30 parallel rows on both sides of the midrib. In the adaxial epidermis the stomata are arranged singly or in short rows mostly near the leaf margin and petiole.

The leaves of *P. falcatus* are isobilateral and amphistomatic, with approximately the same number of stomata occurring adaxially as abaxially. They are arranged lengthwise in 14 to 20 parallel rows over the entire lamina.

Seen in transverse section, the stomata of the South African *Podocarpus* species are sunken in shallow grooves. The irregularly thickened guard cells with their large nuclei are recessed partly into the substomatal cavity, with the subsidiary cells extending over the guard cells. In *P. latifolius*, *P. elongatus* and *P. falcatus*, the

subsidiary cell lumen extends towards the cuticle thus internally forming a narrow groove (Pl. IIa). This narrow groove has proved to be an important diagnostic characteristic in distinguishing between the leaves of *P. latifolius* and *P. henkelii*, which are anatomically very similar. The only distinct difference between the leaves is the presence of the cuticular groove in subsidiary cells of *P. latifolius* and its absence in those of *P. henkelii* (Pl. IIb).

Florin (1931) described the cuticular groove in the stomata of certain species of *Podocarpus* as "eine innere schlitzartige Furche in der Kutikularschicht", and divided the section *Eupodocarpus* into two groups according to the presence or absence of this groove. According to Florin's classification, *P. elongatus* and *P. latifolius*, which both have fleshy, bright red podocarpia in the mature female cone, would belong to his group I (subsidiary cells with cuticular groove) while *P. henkelii* which has a non-fleshy, unobtrusive podocarpium, would belong to group II (subsidiary cells without cuticular groove). It is interesting to note that *P. falcatus*, which belongs to a different section, *Afrocarpus*, also has a cuticular groove in the subsidiary cells.

In the leaves of all four species, living, thin-walled parenchyma cells lie laterally adjacent to the phloem of the single vascular bundle. These radially elongated parenchyma cells often resemble cambium cells and as seen in transverse section, are arranged in up to three radial rows. Towards the leaf margin side of each parenchyma group are groups of tracheids similar to those observed in *P. macrophyllus* by Griffith (1957). These parenchyma cells and the tracheids are together considered to form transfusion tissue (Pl. IIIa). The secondary walls of the tracheids are spirally, scalariformly or reticulately thickened. Bordered pits may occur in combination with the scalariform and reticulate thickenings. This phenomenon is more common in *P. falcatus* than in the other three species. There is a progressive decrease of transfusion tissue towards the base of the leaf and petiole where it is sometimes absent. Even though the transfusion tracheids in *P. falcatus* are smaller than those of the other three species, the tissue occupies about two thirds of the space from the vascular bundle to the leaf margin, a much wider range than in the other three species.

Between the adaxial palisade and the abaxial spongy parenchyma in *P. elongatus*, *P. henkelii* and *P. latifolius* parenchyma cells and thick-walled elements form the so-called accessory transfusion tissue. The cells of this tissue are elongated at right angles to the vascular bundle. The accessory transfusion tissue in *P. falcatus* is poorly defined. Although parenchyma cells which contain dense cytoplasm, but which are less conspicuously elongated than in the other three species, do occur, elongated tracheids are absent.

The number and position of resin ducts in the leaves are also taxonomically important. In transverse sections of leaves of *P. henkelii* and *P. latifolius* five resin ducts are present, in *P. elongatus* three and in *P. falcatus* only one. In *P. elongatus*, *P. henkelii* and *P. latifolius* one duct, called the lateral duct, is situated in each leaf margin while lateral ducts are absent in *P. falcatus*. In *P. henkelii* and *P. latifolius* three median resin ducts are associated with the vascular bundle (Pl. IIIb), one immediately below the phloem and the other two on either side of the phloem. In *P. elongatus* and *P. falcatus* only one median resin duct below the phloem is present. (A more detailed account of the morphology of the leaves of the South African podocarps will soon be published.)

XYLOTOMY

Podocarps are generally known in South Africa as "Yellowwoods" or "Geelhout", the name being derived from the light yellowishbrown colour of the fine grained wood. *Podocarpus falcatus* and *P. latifolius* are economically two of the most important indigenous timbers of South Africa.

A detailed account of the xylotomy of the South African podocarps was published by Schoonraad (1973). Only the salient points will be summarized here.

Resin ducts, ray tracheids and spirally thickened elements are absent from the South African podocarp wood. In this respect the wood is similar to that of other podocarp species (Patel, 1967; Phillips, 1941; Kaeiser, 1950, 1954; Jane 1956; Patton, 1927).

In transverse section growth rings are generally indistinct, but are more conspicuous in the wood of lateral branches than in the main stem. Axial parenchyma occurs in broken tangential bands, mostly in short rows of 2 or 4 cells.

The presence or absence of simple pits in the horizontal walls of the ray parenchyma is diagnostically important, being present in the wood of *P. latifolius*, *P. henkelii* and *P. elongatus*, but absent in the wood of *P. falcatus*. The pits are also distinguishable in radial section.

In tangential section the vascular rays are homogeneous and uniseriate or sometimes biseriate for the height of one or two cells. The height of the rays varies from 1 to 31 cells being generally taller in *P. falcatus* and *P. henkelii* than in *P. elongatus* and *P. latifolius*. Rays occurring in the wood of lateral branches are generally shorter than in the wood of the main stem.

In all four species the rays are bordered on the upper and lower sides by triangular, thin-walled cells approximately a quarter of the size of the other ray cells (Pl. IVa) as seen in tangential and radial sections. Schultze-Motel (1966) observed these cells which he called "Randzellen" or border cells, in fossil material and found them to be diagnostically important in the palaeoxylotomy. Apart from the "marginal ray parenchyma" mentioned by Greguss (1955, 1957) for *P. polystachus*, and as far as is known, this is the first time that border cells have been described for species of the section *Eupodocarpus*. Both Kaeiser (1954) and Patel (1967) described the wood of podocarp species belonging to this section, but did not mention the presence of border cells.

The arrangement of the podocarpoid pits in the radial walls of the tracheids are abietoid. The pits occur in one row, sometimes forming two rows for short distances, particularly in *P. elongatus* and *P. latifolius*. Where two rows of pits occur, the pits lie next to each other at the same height, thus forming twin pits or "Zwillings-tüpfel" (see also Eckhold, 1921). Cross field pits in the ray parenchyma are taxodioid or cupressoid, usually one pit per cross field. More than one pit per cross field occurs in those cells forming the upper or lower border of the vascular rays.

There is a marked difference between the wood structure of the main stem and that of a lateral branch within a single species, e.g. rays in a lateral branch are generally shorter vertically than in the main stem; simple pits in the horizontal walls of the rays are more conspicuous in the wood of the lateral branch than the main stem;

and bars of Sanio are more conspicuous in the radial walls of tracheids in the main stem than in a lateral branch.

The following is a key to the South African podocarps based on their xylotomy:

1. Simple pits in the horizontal walls of the vascular rays absent *P. falcatus* 2.
- Simple pits in the horizontal walls of the vascular rays present
2. Vascular rays, as seen in tangential view, from 1-15 (30) and on an average 5 cells tall. *P. henkelii*
- Vascular rays from 1-10 (20) and on an average 3 cells tall 3.
3. Axial parenchyma with resin (resin cells) abundant; pits in tangential walls of axial parenchyma abundant; growth ring field 4 *P. elongatus*
- Resin cells scarce, pits in tangential walls of axial parenchyma scarce or absent, growth ring field 5 *P. latifolius*

ROOTS

The roots of the podocarps show a number of interesting anatomical features.

Unlike the leaves and stem, the roots have no typical resin ducts, although lacunae similar to those described by Werker (1970) in *Pinus halepensis* Mill. occur in the pericycle (Pl. V). Some of these lacunae resemble resin ducts in that they are lined by one layer of cells which are epithelium-like but which have no nuclei. The lacunae usually occur adjacent to the phloem groups towards the outside. They probably arise schizogenously although signs of cell dissolution were also observed.

In transverse sections of the cortex layer immediately adjacent to the endodermis, spool-shaped thickenings occur on the radial and some tangential walls (Pl. V). These thickenings stain light red with safranine and resemble Caspary bands. Von Guttenberg (1961) calls this cell layer the "Phi-scheide", a term he adopted from Strasburger. His drawings of the roots of *Sequoia sempervirens*, *Taxus baccata*, *Cupressus sempervirens* and *Araucaria araucana* show structures in the cell layer immediately outside the endodermis which correspond to those in the South African podocarps.

After careful study it became apparent that these thickenings are not Caspary bands, but the first signs of reticulate thickenings or trabeculae that occur in this cell layer as well as in the rest of the cortex in older roots. The trabeculae, therefore, develop centrifugally and are more abundant in the vicinity of the endodermis than nearer the epidermis.

ROOT NODULES

The formation of podocarp root nodules has been previously attributed to bacterial infection by Bottomley (1912), Spratt (1912), McLuckie (1923) and Phillips (1932) and to infection by non-septate fungus hyphae by Nobbe & Hiltner (1899), Saxton (1930) and Coertze (1966). Bayliss & al. (1963), Kahn (1967) and Furman (1970) found that root nodules could develop in the absence of fungi. Endophytic fungi of the vesicular-arbuscular type, and most probably of the genus *Endogone*, occur in the nodules of the South African podocarps.

It is generally accepted that root nodules are metamorphic lateral roots, whether they are caused by an infection of some kind or not. In the very early stages of development it is impossible to distinguish between a lateral root and a root nodule primordium. Both arise in the pericycle opposite the protoxylem groups of the diarch stele. There are, however, interesting anatomical differences between young lateral roots and root nodules, once the developing organ has broken through the endodermis of the parent root.

In the apical meristem of the lateral root different growth areas can be delineated, whereas the primordium of the root nodule consists of homogeneous meristematic cells. The lateral root endodermis differentiates in the normal way, originating in the stelar tissue of the parent root and open on the distal side. The root nodule endodermis differentiates as an unbroken domeshaped layer to enclose the vascular cylinder (Pl. IVb). A calyptra is formed in the lateral root but not in the root nodule.

It might be argued that the root nodule and the lateral root are not necessarily homologous. However, as both organs originate endogenously from the pericycle of the parent root and as both adult organs consist of the same tissue types, viz. epidermis with root hairs, cortex and stele, the root nodule must be regarded as a metamorphic lateral root. The arrested growth of these metamorphic roots occurs independently of bacterial or fungal infection.

NITROGEN-FIXATION

Bergerson & Costin (1964) and Becking (1965, 1967) found that ^{15}N -fixation took place in the root nodules of *P. lawrencii* and *P. rospigiosii* respectively.

In this study one-year-old seedlings of *P. latifolius* were tested for ^{15}N -fixation at the Margaretha Mes Institute for Plant Physiology and Biochemistry of the University of Pretoria.

Nodulated roots were washed and exposed in the dark to a mixture of 20% oxygen and 80% nitrogen containing 54 atom % ^{15}N , for 72 hours at 27°C. The treated roots contained a 0.0201 atom % excess of ^{15}N relative to the normal value. Nodulated roots were also tested for nitrogen fixation using the acetylene reduction method. The material was exposed in the dark to a mixture of one volume of acetylene to three volumes of air for six hours. Slow but significant acetylene reduction occurred (Table 1). Since all *Podocarpus* roots develop nodules, no non-nodulated roots were available for control tests. It is therefore not possible to say to what extent micro-organisms in the rhizosphere are responsible for these results.

In presence of acetylene	In absence of acetylene	Acetylene reduction
A 7	B 0.2	A-B 6.8

Table 1. — *Podocarpus* root nodules. Ethylene production per gram fresh material per hour.

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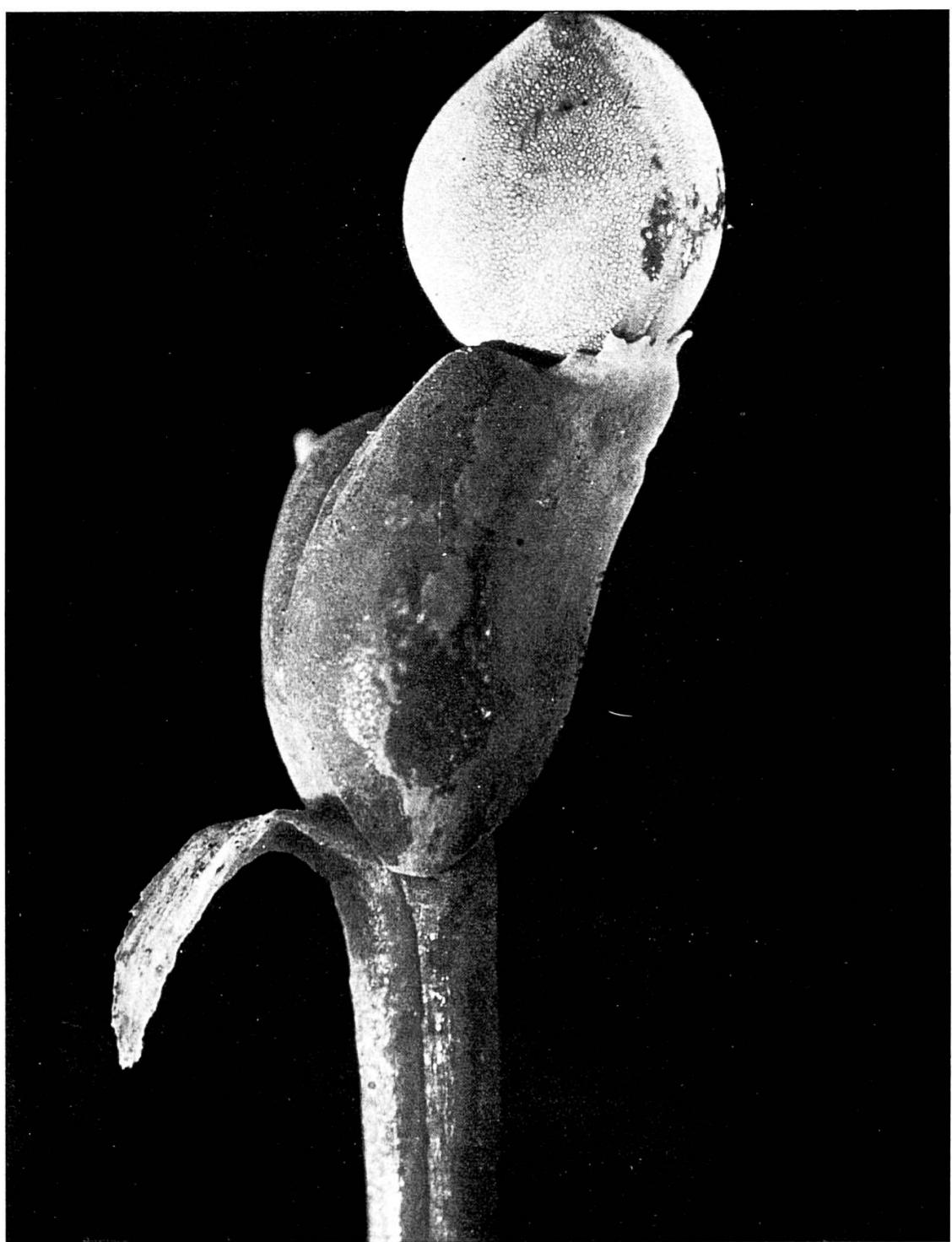
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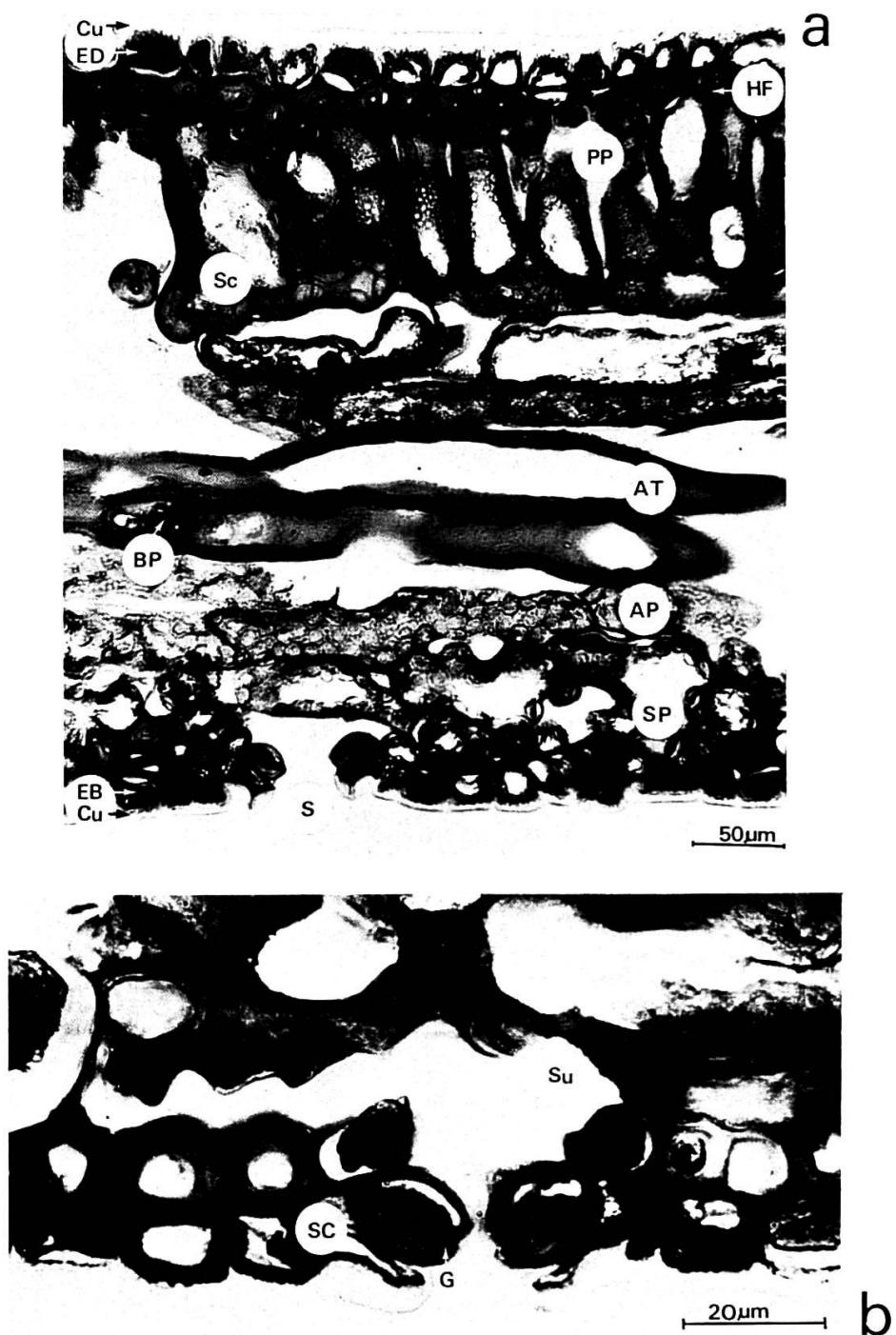
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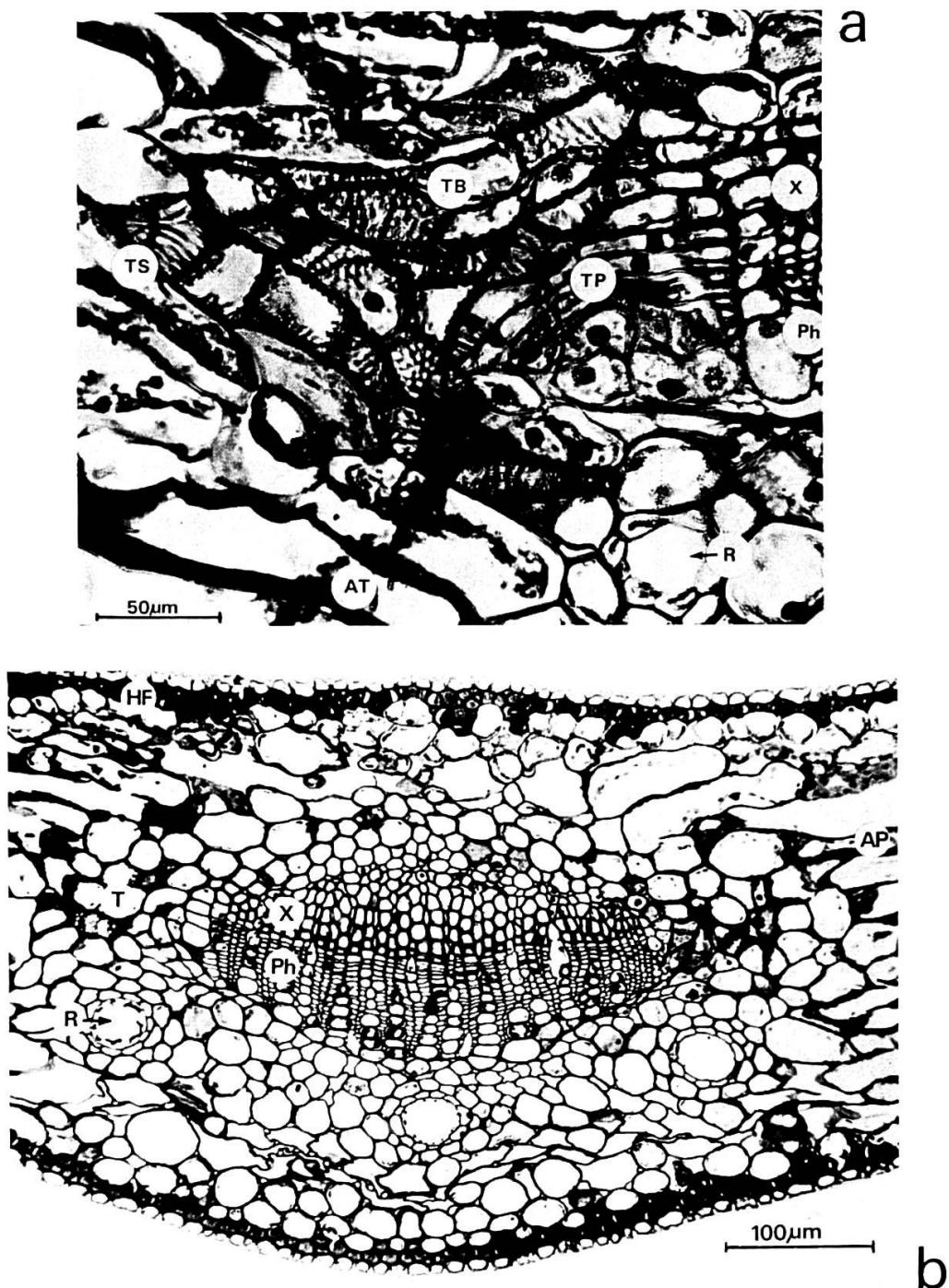
Female cone of *P. latifolius* showing free bract on proximal side of the podocarpium.



a, leaf of *P. latifolius* in transverse section, showing structure of the transfusion tissue.
 AT: accessory transfusion tissue tracheid; Ph: phloem; R: resin duct; TB: transfusion tissue tracheid with bordered pits; TP: parenchymatous transfusion tissue; TS: transfusion tissue tracheid with spiral thickenings; X: xylem.

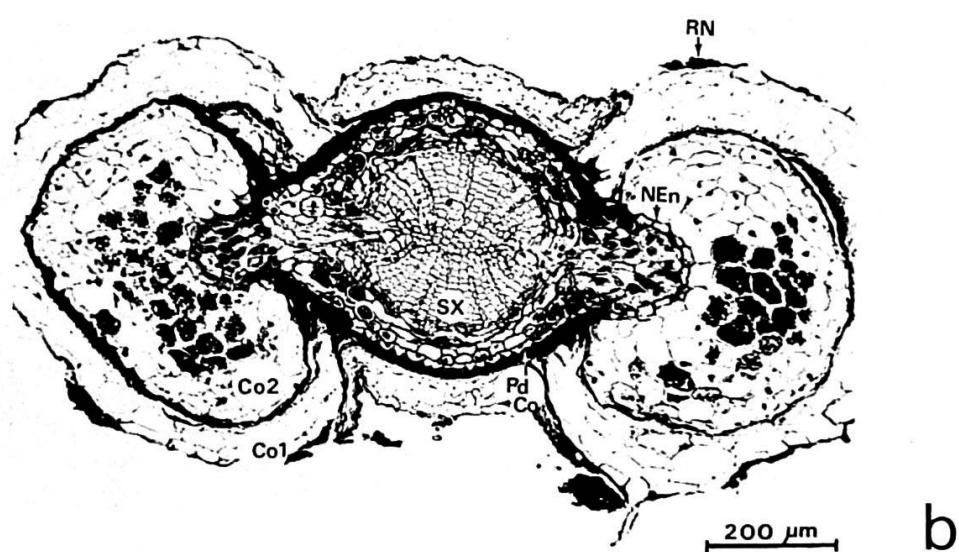
b, transverse section of the leaf vascular bundle of *P. latifolius* showing the distribution of the three median resin ducts.

AP: parenchymatous accessory transfusion tissue; HF: hypodermal fibres; Ph: phloem; R: resin duct; T: transfusion tissue; X: xylem.

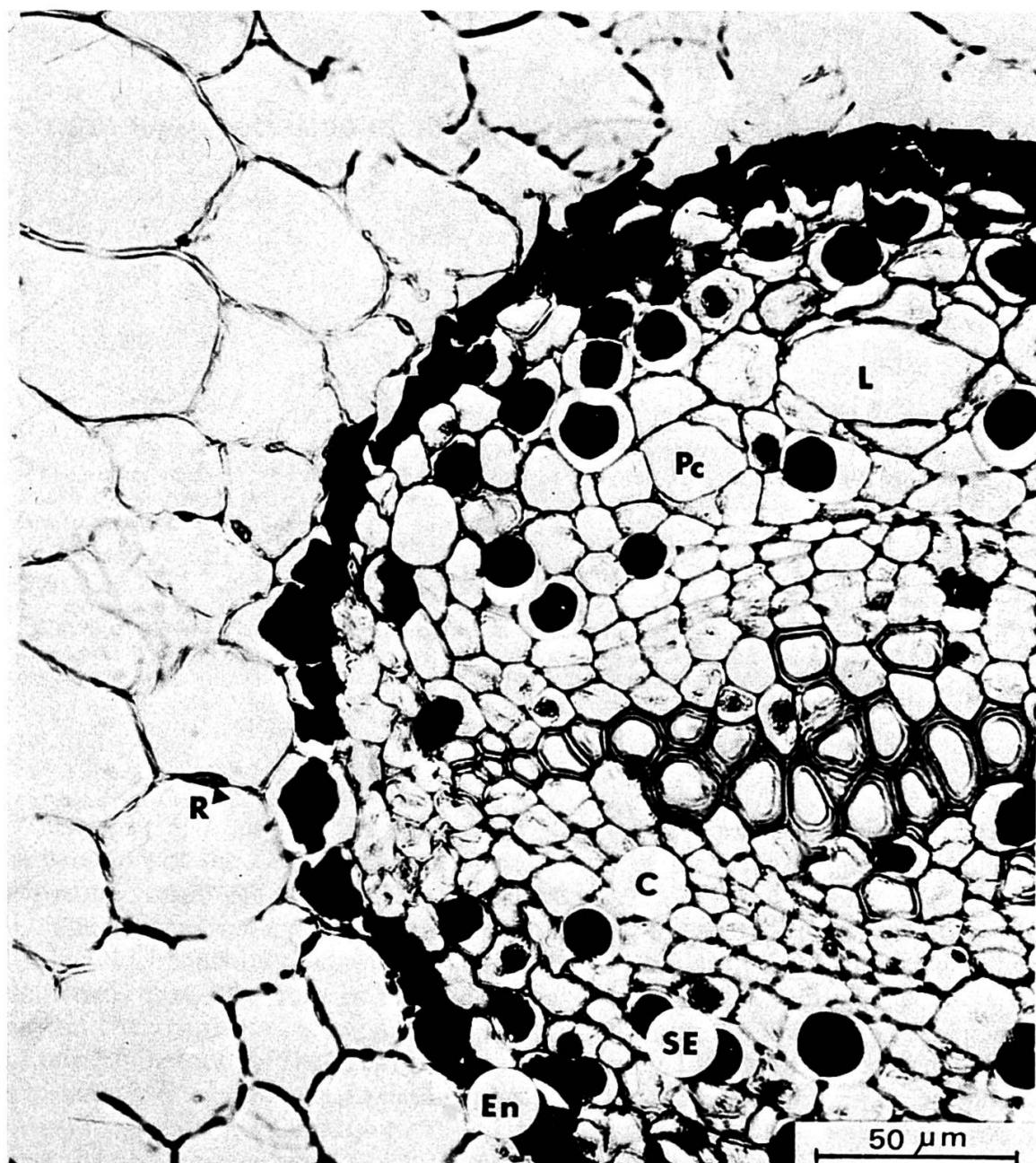


a, leaf of *P. latifolius* in transverse section.
 AP: parenchymatous accessory transfusion tissue; AT: accessory transfusion tissue tracheid;
 BP: bordered pit; Cu: Cuticle; EB: abaxial epidermis; ED: adaxial epidermis; HF: hypodermal
 fibre; PP: palisade parenchyma; S: stoma with subsidiary cells with cuticular grooves; Sc:
 sclereid; SP: spongy parenchyma.

b, leaf of *P. henkelii* in transverse section showing stomatal structure.
 G: guard cell; SC: subsidiary cell without cuticular groove; Su: substomatal cavity.



a, tangential section of the wood of *P. latifolius* showing the structure of border cells (BC).
b, transverse section of a nodulated root of *P. latifolius*. *Co*: root cortex; *Co1*: cortex of nodule formed initially; *Co2*: cortex of nodule formed subsequently; *NEn*: nodule endodermis differentiating as an unbroken dome-shaped layer enclosing the vascular cylinder; *Pd*: periderm; *RN*: root nodule; *SX*: secondary xylem.



Transverse section of a young root of *P. latifolius*.

C: cambium; *En*: endodermis; *L*: lacuna; *Pc*: pericycle; *R*: early reticulate thickening; *SE*: secretion cells.

