THE OCCURRENCE OF ROOT NODULES IN THE GINKGOALES, TAXALES, AND CONIFERALES

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(Plate 1)

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Synopsis

The roots of 57 species of the Ginkgoales, Taxales, and Coniferales were examined for the presence of nodules of the *Podocarpus*-type and for the occurrence of mycorrhizal associations. Of the conifers, those placed in the Araucariaceae, Podocarpaceae, and Sciadopityaceae all bore nodules, whereas species of the Cupressaceae, Pinaceae, and Taxodiaceae did not. No nodules were observed on *Gingko biloba* or *Taxus baccata*.

Vesicular-arbuscular mycorrhizas were of general occurrence amongst the plants examined except for the members of the Pinaceae, which bore the ectotrophic type.

INTRODUCTION

Records of the occurrence of root nodules amongst the Ginkgoales, Taxales and Coniferales have been tabulated by Allen and Allen (1965) and a fuller report of the occurrence of structures variously described as exostoses, mamelons, tubercles, and nodules is given in Table 1. However, apart from the records for *Podocarpus* spp. by numerous authors, for *Dacrydium franklinii*, *Microcachrys tetragona*, *Phyllocladus trichomanoides* and *Saxegothaea conspicua* by Sprat (1912), for *Pherosphaera hookeriana* (*Microstrobus niphophilus*) and *P. fitzgeraldii* (*M. fitzgeraldii*) by Saxton (1930*a*, 1930*b*) and for species of *Agathis*, *Dacrydium*, and *Phyllocladus* by Baylis *et al.* (1963), no evidence has been reported which indicates that the structures described differ in any way from short roots.

TABLE 1

Records of the Presence of Nodules Amongst the Coniferales

Family, Genus and Species	Literature Citations
ARAUCARIACEAE	
Agathis australis	Cockayne, 1921 ; Yeates, 1924 ; Bieleski, 1959 ; Baylis *et al.*, 1963 ; Morrison and English, 1967.
A. robusta	Janse, 1897 (as *Dammara robusta*).
A. vitiensis	Allen and Allen, 1965.
Araucaria spp.	Hooker, 1854.
A. angustifolia	Daugherty, 1963.
A. heterophylla	Janse, 1897 ; Yeates, 1924 (both as *A. excelsa*).
CUPRESSACEAE	
Cupressus sp.	Hooker, 1854.
C. sempervirens	Janse, 1897 (as *C. fastigiata*).
Libocedrus bidwillii	Yeates, 1924.
Sabina chinensis	Janse, 1897 (as *Juniperus chinensis*).
Thuja sp. (*Platycladus ?*)	Hooker, 1854.
PODOCARPACEAE	
Acmopyle pancheri	Sahni (1920).
Dacrydium sp.	Hooker (1854).

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TABLE 1—*Continued*

Records of the Presence of Nodules Amongst the Coniferales—Continued

Family, Genus and Species	Literature Citations
PODOCARPACEAE—*Continued*	
D. bidwillii	Yeates, ex Allen and Allen, 1965.
D. biforme	Yeates, 1924 ; Baylis *et al.*, 1963.
D. colensoi	Yeates, 1924.
D. cupressinum	Yeates, ex Allen and Allen, 1965 ; Baylis *et al.*, 1963.
D. intermedium	Yeates, ex Allen and Allen, 1965 ; Baylis *et al.*, 1963.
D. franklinii	Sprat, 1912.
D. kirkii	Yeates, ex Allen and Allen, 1965.
D. laxifolium	Yeates, ex Allen and Allen, 1965.
Microcachrys tetragona	Sprat, 1912.
Microstrobos fitzgeraldii	Saxton, 1930*a*, 1930*b* (as *Pherosphaera fitzgeraldii*).
M. niphophilus	Saxton, 1930*a*, 1930*b* (as *Pherosphaera hookeriana*).
Phyllocladus sp.	Hooker, 1854.
P. alpinus	Baylis *et al.*, 1963.
P. glaucus	Yeates, ex Allen and Allen, 1965.
P. trichomanoides	Sprat, 1912.
Podocarpus spp.	Hooker, 1854 ; von Tubeuf, 1896, according to Nobbe and Hiltner, 1899 ; Bond, 1959.
P. acutifolius	Yeates, ex Allen and Allen, 1965.
P. blumei	Becking, 1965.
P. dacrydioides	Hooker, 1865 ; Petri, 1903 ; Yeates, 1924 ; Baylis *et al.*, 1963.
P. elatus	Petri, 1903 ; McLuckie, 1923.
P. elongatus	Petri, 1903 ; Sprat, 1912 ; Phillips, 1932 (both as *P. elongatus* and *P. thunbergii* var. *angustifolia*).
P. falcatus	Phillips, 1932.
P. ferrugineus	Yeates, 1924 ; Baylis *et al.*, 1963.
P. gracilior	Parker, 1932.
P. hallii	Yeates, 1924 ; Baylis *et al.*, 1963.
P. henkelii	Phillips, 1932.
P. imbricatus	Janse, 1897 (as *P. cupressinus*).
P. latifolius	Saxton, 1930 (as *P. thunbergii*) ; Phillips, 1932 ; Bond, 1967.
P. macrophyllus	Nobbe and Hiltner, 1899 ; Shibata, 1902 ; Petri, 1903 ; Schaede, 1943 (all as *P. chinensis*) ; Petri, 1903.
P. macrophyllus var. *maki*	Becking, 1965.
P. nagi	von Tubeuf, 1896, according to Nobbe and Hiltner, 1899 ; Shibata, 1902 (both as *P. nageia*) ; Becking, 1965.
P. neriifolius	van Tiegham, 1970, according to Becking, 1965 ; von Tubeuf, 1896, according to Shibata, 1902 ; Egle and Munding, 1951 ; Becking, 1965.
P. nivalis	Yeates, ex Allen and Allen, 1965 ; Bond, 1967.
P. nubigenus	Schaede, 1943.
P. "*prostrata*" (no such name known)	Yeates, ex Allen and Allen, 1965.
P. rospigliosii	Furman, 1964 ; Becking, 1965.
P. salignus	Sprat, 1912 ; Bottomley, 1913 (both as *P. chilina*).
P. spicatus	Yeates, 1924 ; Baylis *et al.*, 1963.
P. spinulosus	McLuckie, 1923.
P. totara	Sprat, 1912 ; Yeates, 1924 ; Baylis *et al.*, 1963.
P. "*variegatus*" (a cultivar ?)	Ferreira dos Santos, 1947, ex Allen and Allen, 1965.
P. wallichianus	Petri, 1903 (as *P. latifolia* Wall.).
Saxegothaea conspicua	Sprat, 1912.
TAXODIACEAE	
Cunninghamia sp.	Hooker, 1854.
Taxodium sp.	Hooker, 1854. According to Hooker, the elder de Candolle had earlier noted exostoses on *T. distichum* (*Theorie Elementaire*, Ed. 2, p. 356).
SCIADOPITYACEAE	
Sciadopitys verticillata	Uemura, 1964.

Allen and Allen (1965) found no nodules on *Ginkgo biloba* and, although they recorded Hiltner (1903) as having reported their occurrence, no evidence of this could be found in his paper. Similarly, it was not found that Yeates (1924) had recorded nodules on *Araucaria cunninghamii*.

Uemura (1964) appears to be the only person to have reported nodules on *Sciadopitys verticillata*, stating that they closely resembled those of *Podocarpus macrophyllus* but were smaller and appeared as " narrow ellipsoides ". He gave no detail of their structure but reported that Noelle (1910) and Laing (1923) had found them to be mycorrhizal. These authors, however, recorded the presence of endotrophic mycorrhizas but made no mention of nodules.

Daugherty (1963) saw beaded roots on the fossil *Araucariorhiza joae* and suggested that the bulb-like expansions at the tips might possibly be incipient nodules. Such an occurrence, however, has not been observed in living conifers and it seems probable that he was observing beaded roots at the commencement of a new growth cycle.

It has now been shown that the nodules of *Podocarpus* spp. develop as normal features of the roots, are not dependent on any microorganisms for their development, and differ markedly from short roots, being fully differentiated structures with no root cap or apical meristem and with an endodermis surrounding and overarching the vascular strand (Khan, 1967). Hence, in view of the uncertainty concerning the nature of many of the structures described as exostoses, mamelons, tubercles, and nodules for other members of the Coniferales and for members of the Ginkgoales and Taxales, the survey reported below was carried out.

Plants were obtained from a variety of sources in New South Wales, their root systems examined for the presence of nodule-like structures, and sections made to observe their anatomy.

Results and Discussion

The results of this survey are set out in Table 2. All species of the Araucariaceae, Podocarpaceae and Sciadopityaceae examined bore nodules analogous to those described for *Podocarpus* spp., bore short roots as well, produced beaded roots as a result of metacutization and subsequent regrowth, and contained a vesicular-arbuscular endophyte in the cortices of both the nodules and young roots.

Table 2

A Record of Nodules, Mycorrhizas and Beaded Rootlets Observed on Species of the Ginkgoales, Taxales and Coniferales

(+ = present, − = absent, V = vesicular-arbuscular, E = ectotrophic)

Order, Family, Genus, Species	Nodules	Beaded Rootlets	Mycorrhiza
Ginkgoales			
Ginkgoaceae			
Gingko biloba L.	−	+	+V
Taxales			
Taxaceae			
Taxus baccata L.	−	+	+V
Coniferales			
Araucariaceae			
Agathis australis Salisbury	+	+	+V
A. dammara (Lambert) L. C. Richard	+	+	+V
A. moorei (Lindley) Masters	+	+	+V
A. robusta (C. Moore) F. M. Bailey	+	+	+V
A. vitiensis (Seeman) Drake	+	+	+V
Araucaria araucana (Molina) K. Koch	+	+	+V
A. cunninghamii Aiton ex D. Don	+	+	+V
A. heterophylla (Salisbury) Franco	+	+	+V
A. columnaris (Forster f.) Hooker	+	+	+V

TABLE 2

A Record of Nodules, Mycorrhizas and Beaded Rootlets Observed on Species of the Ginkgoales, Taxales and Coniferales

(+ = present, − = absent, V = vesicular-arbuscular, E = ectotrophic)

Order, Family, Genus, Species	Nodules	Beaded Rootlets	Mycorrhiza
CUPRESSACEAE			
Austrocedrus chilensis (D. Don) Florin et Boutelje	−	−	−
Callitris muelleri (Parl.) F. Mueller	−	−	+V
C. columellaris F. Mueller	−	−	+V
C. rhomboidea R.Br. ex A. et L. C. Richard	−	−	+V
Chamaecyparis obtusa (Sieb. et Zucc.) Endl.	−	+	+V
Cupressus arizonica Greene	−	+	+V
C. funebris Endl.	−	+	+V
C. glabra Sudworth	−	+	+V
C. sempervirens L.	−	+	+V
C. torulosa D. Don	−	+	+V
Fokienia hodginsii (Dunn) Henry et Thomas	−	+	+V
Juniperus communis L.	−	+	+V
Libocedrus plumosa (D. Don) Sargent	−	+	+V
Platycladus orientalis (L.) Franco	−	−	+V
Thujopsis dolabrata (L.f.) Sieb. et Zucc.	−	−	−
Tetraclinus articulata (Vahl) Masters	−	−	+V
Widdringtonia whytei Rendle	−	−	+V
PINACEAE			
Abies nordmanniana (Steven) Spach	−	+	+E
Cedrus deodara Loudon	−	−	+E
Keteleeria davidiana (Bertrand) Beissner	−	+	+E
Larix kaempferi (Lambert) Carriere	−	+	+E
Picea abies (L.) Karsten	−	+	+E
Pinus radiata D. Don	−	+	+E
P. wallichiana A. B. Jackson	−	+	+E
Pseudotsuga menziesii (Mirbel) Franco	−	−	+E
Tsuga canadensis (L.) Carriere	−	−	+E
PODOCARPACEAE			
Dacrydium franklinii Hooker f.	+	+	+V
Microstrobos fitzgeraldii (F. Mueller) Garden et Johnson	+	+	+V
Phyllocladus hypophyllus Hooker f.	+	+	+V
P. trichomanoides D. Don	+	+	+V
Podocarpus brassii Pilger	+	+	+V
P. compactus Wasscher	+	+	+V
P. elatus R.Br. ex Endl.	+	+	+V
P. falcatus (Thunberg) R.Br.	+	+	+V
P. ladei F. M. Bailey	+	+	+V
P. latifolius (Thunberg) R.Br.	+	+	+V
P. lawrencei Hooker f.	+	+	+V
P. macrophyllus (Thunberg) D. Don	+	+	+V
P. spinulosus (Sm.) R.Br. ex Mirbel	+	+	+V
TAXODIACEAE			
Cryptomeria japonica (L.f.) D. Don	−	+	+V
Cunninghamia lanceolata (Lambert) Hooker	−	+	+V
Glyptostrobus pensilis (Staunton ex D. Don) K. Koch	−	−	+V
Metasequoia glyptostroboides Hu et Cheng	−	−	+V
Sequoia sempervirens (Lamb.) Endl.	−	−	+V
Sequoiadendron giganteum (Lindl.) Bucholz	−	−	+V
Taxodium distichum (L.) L. C. Richard	−	−	+V
T. mucronatum Tenore	−	−	+V
SCIADOPITYACEAE			
Sciadopitys verticillata (Thunberg) Sieb. et Zucc.	+	+	+V

All members of the Podocarpaceae examined bore numerous nodules, of more or less uniform size within a species and usually in two opposite rows, giving the roots a most distinctive appearance (Pl. 1, Fig. *a*). The size of the nodules varied according to the species, the smallest (0·3–0·5 mm. diameter) being those of *Microstrobus fitzgeraldii*, those of *Phyllocladus hypophyllus*, *P. trichomanoides* and *Dacrydium franklinii* being medium sized (0·5–0·9 mm.), and those of *Podocarpus* spp. being the largest (0·8–1·5 mm.). As observed by Sprat (1912) and Baylis *et al.* (1963), the vascular strand in species with small nodules is very rudimentary, but in *Podocarpus* spp. it is sufficiently developed to show a diarch structure. Unfortunately, material of *Microcachrys* and *Acmopyle* was not obtained, as it would be particularly interesting to confirm the occurrence of nodules in these genera. The only record for *Acmopyle* is that for *Acmopyle pancheri* by Sahni (1920). He reported that the roots of this plant bore tubercles but gave no details of their structure, and his only illustration was of a longitudinal section of what he claimed to be a tubercle regenerating and becoming a root. This illustration shows no evidence of the structure peculiar to the nodules of other genera of the Podocarpaceae.

In the Araucariaceae the roots of all species of *Agathis* and *Araucaria* examined bore nodules analogous to those occurring in *Podocarpus*, although they were more elongated and arranged in a much less regular fashion (Pl. 1, Fig. *b*). The root systems of these plants, therefore, presented a much less characteristic appearance than those of members of the Podocarpaceae. Only in *Araucaria araucana* was anything approaching the regular arrangement occurring in *Podocarpus* seen. However, although the nodules in *Agathis* and *Araucaria* were elongated and less regularly arranged, they were structurally analogous to those of *Podocarpus*, being fully differentiated, lacking a root cap and apical meristem and having a vascular strand completely overarched by the endodermis (Pl. 1, Fig. *c*). Like the nodules of members of the Podocarpaceae, they exhibited regeneration from cells of the pericycle, and it seems reasonable to suppose that they occur throughout the Araucariaceae.

The only other plant on which such nodules were found was *Sciadopitys verticillata* (Pl. 1, Fig. *d*), the single representative of the family Sciadopityaceae. Here again the nodules were elongated, variable in size, and arranged irregularly. These nodules, too, exhibited regeneration from the pericycle.

All members of the Pinaceae examined were involved in mycorrhizal associations of the ectotrophic type and had short roots, each with an apical meristem, open-ended endodermis, and root cap. Several of them had developed beaded rootlets as well.

In *Ginkgo biloba*, *Taxus baccata*, and all members of the Cupressaceae and Taxodiaceae examined, the long roots bore short lateral roots only and, with the exception of *Austrocedrus chilensis* and *Thujopsis dolabrata*, contained vesicular-arbuscular endophytes. Many of them were exhibiting beaded rootlets as well, and it may well be that these occur also in those species for which they were not recorded in this survey, just as *A. chilensis* and *T. dolabrata* would be expected to be mycorrhizal under other circumstances.

The root systems of many of these plants, with their short roots and beaded rootlets, bore a striking resemblance to those of members of the Araucariaceae. Thus it is not surprising that authors should have reported the presence of nodules on their root systems and even, as was done by Janse (1897), on angiosperms such as *Acer* spp., which have root systems very similar in appearance.

As a result of the present survey, then, a clear pattern has emerged with regard to the occurrence of nodules and mycorrhizas amongst the Ginkgoales, Taxales and Coniferales. Nodules of the *Podocarpus*-type have been found only in the Araucariaceae, Podocarpaceae and Sciadopityaceae, and vesicular-arbuscular mycorrhizas seem to be of general occurrence in all families except the Pinaceae, the members of which form the ectotrophic type. It must be

emphasized, however, that most of the plants examined were growing in cultivation far from their natural habitats and only a selection of species was examined. Thus there may well be exceptions to the generalization stated above. As far as mycorrhizas are concerned, it may yet be shown that some species can form more than one type. Such an occurrence, for instance, is reported by Filer (1969), who records, amongst other observations, that *Quercus phellos* and *Populus deltoides* have mostly ectotrophic, frequently ectendotrophic, and sometmies endotrophic mycorrhizas.

The taxonomic significance of the occurrence of nodules has been mentioned by Sprat (1912), who discusses the affinities of the Podocarpaceae and Araucariaceae, noting that they have much the same geographical distribution. Both she and Saxton (1930*b*) regard the universal occurrence of nodules to be a factor lending weight to the grouping of genera in the Podocarpaceae.

The occurrence of nodules in *Sciadopitys* is also a factor strengthening the separation of this monotypic genus from the Taxodiaceae and its placement in a family of its own. This Japanese plant occurs within the distribution of *Podocarpus* and, according to Dallimore and Jackson (1966), Greguss places it in the Podocarpaceae on the basis of the similarities in wood structure. In the present study it was also observed that when the short roots became dormant the tips underwent the same type of metacutization as that observed in *Podocarpus*.

It is unfortunate that the word " nodule " should have been applied at all to structures produced laterally on the root systems of conifers and their relatives, since it suggests analogies with the nodules of legumes and plants such as *Casuarina* spp. Had they been given a different name to begin with, it is doubtful whether confusion would ever have arisen in the literature concerning their function and mode of origin. Much work still remains, however, before it can be decided whether or not their function differs in any way from that of other roots with vesicular-arbuscular endophytes.

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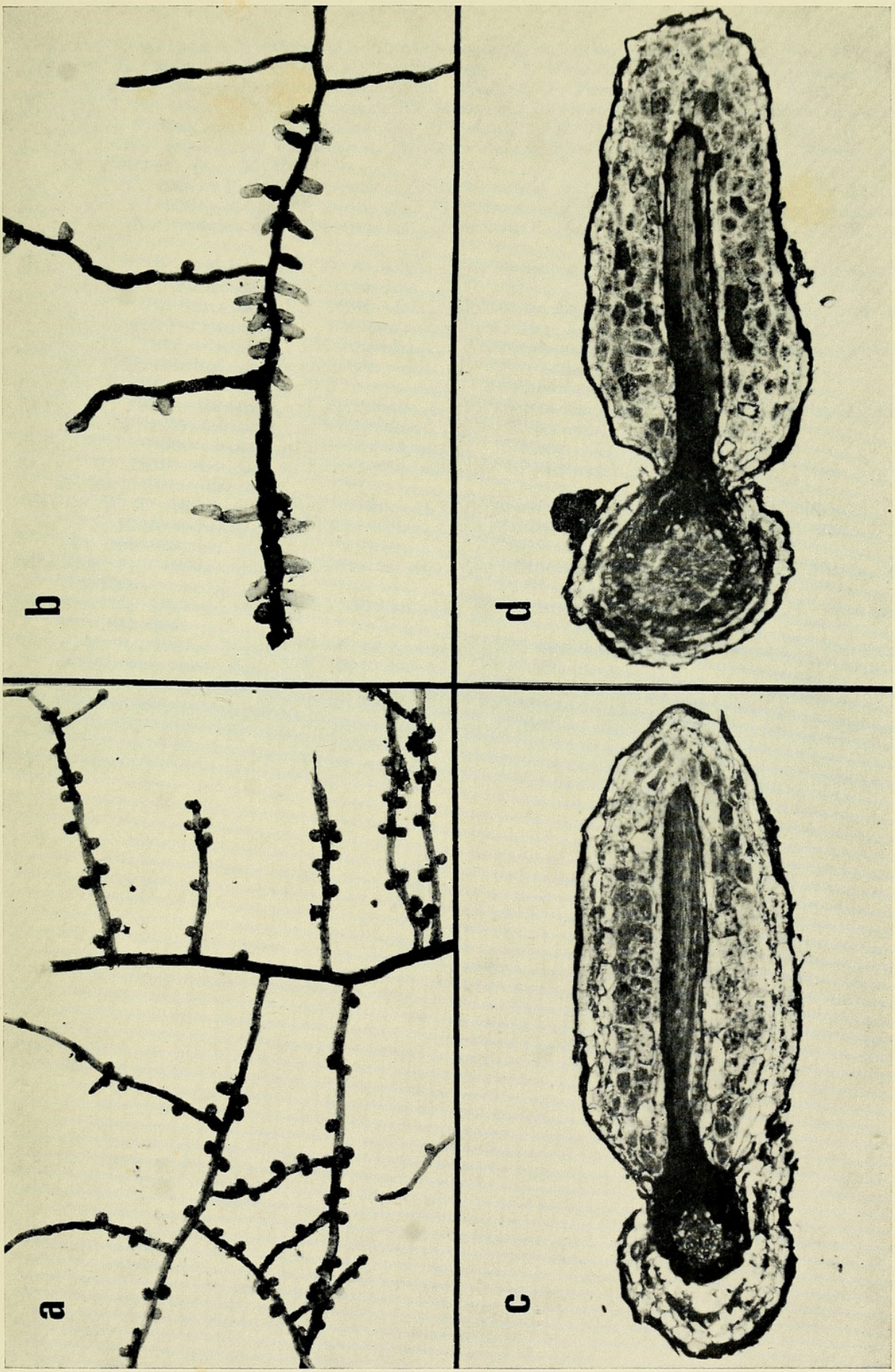

Plate 1

(*a*) Root of *Podocarpus spinulosus* showing nodules. ×1½.
(*b*) Root of *Araucaria cunninghamii* showing nodules and beaded rootlets. ×1½.
(*c*) Longitudinal section of nodule of *A. cunninghamii*, showing endodermis enclosing the vascular system and absence of root cap and apical meristem. ×24.
(*d*) Longitudinal section of nodule of *Sciadopitys verticillata*. ×24.

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