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ABSTRACT

THE RHIZOME ANATOMY OF THE FERN GENERA NOTHOLAENA AND PELLAEA WITH A REVIEW OF STELAR CONCEPTS AND ONTOGENETIC DEVELOPMENT

By

Joseph Howard McCulloch III

The "Cheilantheid" ferns, considered to be the genera Cheilanthes, Notholaena and Pellaea plus other smaller genera, are an assemblage of closely related species. A literature review of work done on the three main genera is included and illustrates the complexity of the group. The rhizome anatomy of selected species of Notholaena and Pellaea were examined to detail the stelar condition, tissue organization and composition, and to try and determine if the stele type could serve as a diagnostic character in identification of the three genera. A review of the literature of rhizome descriptions of various fern genera and, in particular, Pellaea and Notholaena revealed two things: first, that there was very little anatomical information available concerning these two genera; second, that there were many discrepancies in the descriptions of stelar types. There were a variety of interpretations and opinions as to stelar conditions as they exist in the ferns. The solenostele is the dominant stele type in Pellaea and Notholaena, with the transitional stele type occurring frequently and the dictyostele occurring in Pellaea only. An examination of the xylem (by maceration and longitudinal sections) of some Notholaena and Pellaea species

confirmed the fact that the metaxylem is composed of scalariform tracheids. Although it is impossible to determine, in cross section, protoxylem from metaxylem, the former's presence is attested to by the occurrence of helical tracheids. An examination of the ontogenetic development of the rhizome stele in Pellaea viridis confirms the concept that the vascular cylinder is protostelic at first. The stelar condition of Pellaea and Notholaena probably cannot be used as a diagnostic character to separate the two genera until many more taxa are examined.

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By

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INTRODUCTION

The purpose of this research is to examine and report upon the anatomy of the rhizome in selected species of Notholaena and Pellaea. We shall compare our findings with what has been previously reported in these genera by others. Especially we shall correlate our findings with what is known of the rhizome structure of members of the genus Cheilanthes with the hope that the rhizome anatomy of members of the three genera listed above will be of diagnostic value in separating the genera from each other.

The genera Cheilanthes, Notholaena and Pellaea represent a complex assemblage of organisms containing approximately 325 species (Pichi-Sermolli, in Jermy, 1973). The species belonging to the genera Cheilanthes, Notholaena and Pellaea or any combination or segregates of these genera are commonly referred to as the "Cheilanthoid ferns" (Hevly, 1963).

Pichi-Sermolli (in Jermy, 1973) considers the family Sinopteridaceae a member of the order Pteridales, of the class Filicidae and the division Filicopsida. The family Sinopteridaceae contains fourteen genera; Sinopteris C. Chr. and Ching, Aleuritopteris Fée, Cheilanthes Swartz, Myriopteris Fée, Adiantopsis Fée, Aspidotis Nuttall, Notholaena R. Brown, Mildella Trevisan, Neurosoria Mett., Choristosoria Mett., Pellaea Link, Cheiloplecton Fée, Ormopteris J. Smith and Doryopteris J. Smith (Knobloch, Tai and Adangapuram, 1975). Within the order

Pteridales the following families are included by Pichi-Sermolli (in Jermy, 1973): Pteridaceae, Negripteridaceae, Sinopteridaceae, Cryptogrammaceae, Parkeriaceae, Gymnogrammaceae, Adiantaceae and the Vittariaceae.

Bala Krishann Nayar (1970) considered the following classification scheme for the Cheilanthoid ferns: Class Filicopsida, subclass Filicidae, order Schizaeales and family Cheilanthaceae (the Cheilanthoid genera; Pellaea, Cryptogramma, Hemionitis, Bommeria, Trachypteris and Gymnopteris).

Rolla Tryon (1956) placed the three genera (Cheilanthes, Notholaena and Pellaea) in the tribe Cheilantheae of the family Polypodiaceae. Tryon lists fifty-nine species of Notholaena in the western hemisphere, grading into Cheilanthes in the characteristics of eighteen species and into Pellaea in the characteristics of sixteen species at the other extreme.

Copeland (1947) placed Cheilanthes, Notholaena and Pellaea in the family Pteridaceae and treated Notholaena as being an artificial assemblage of plants belonging mostly in the genera Cheilanthes and Pellaea.

Christensen (1938) included the genera Adiantopsis Fée, Sinopteris C. Chr. and Ching, Doryopteris J. Sm. and Saffordia Maxon in the Pteridaceae.

Index Filicum (Christensen, 1906) and as described by Posthumus (1924) cited the following genera in the family Polypodiaceae: Cheilanthes Swartz, Cryptogramma R. Brown, Doryopteris J. Sm., Hypolepis Bernhardt, Llavea Lagasca, Notholaena Brown, Pellaea Link and Plagiogyria Mettenius.

The number of classification systems for the Cheilanthoid ferns and ferns in general derive in part from the ". . . different aptitude of pteridologists to split or to lump, but it depends also on some peculiarities of the pteridophytes, particularly their antiquity and their genetic plasticity" (Pichi-Sermolli, in Jermy, 1973).

Not only have there been many problems associated with locating the Cheilanthoid genera within a particular family, but there have been and still are serious taxonomic questions as to the species composition of each genus. The following descriptions of the Cheilanthoid genera illustrate the tedious taxonomic problems and uncertainties relating to generic and species affinities that researchers have had to cope with, and some of the still unanswered problems that remain to be delineated.

Tryon (1956) published "The American Species of Notholaena," a compilation of Mr. Weatherby's notes, maps and charts, plus taxonomic interpretations. This treatment included fifty-nine species, seven of which were divided into seventeen varieties. Within the United States 19 species were listed, Mexico has 34, Central America 7, Greater Antilles 8 and South America 20, including 9 species and 4 varieties in Peru. Not all of these are endemic to the countries listed and some species are found in more than one area.

In his monograph of the genus Notholaena, R. Tryon (1956) pointed out some problems. Notholaena grades suspiciously into Cheilanthes on the one hand (via N. peruviana Desv., N. brachypus (Kze.) J. Sm., and a few others) and into Pellaea on the other hand (N. Palmeri Baker, N. pallens Weath., N. pilifera Tryon, N. chilensis (Fée and Remy) Sturm, N. peninsularis Maxon and Weath., N. Jonesii (Maxon, N. Lumholtzii Maxon and Weath., N. limitanea Maxon, N. dealbata (Pursh) Kze., N. Fendleri

Kze., N. delicatula Maxon and Weath., N. incana Presl, N. nivea (Poir.) Desv., N. parvifolia Tryon and N. formosa (Liebm.) Tryon).

Notholaena peruviana and N. brachypus are similar to Cheilanthes in having a slightly to moderately developed marginal indusium and the others are similar to Pellaea in rhizome scales and their imparipinnate lamina. Notholaena parvifolia and N. formosa were previously placed in the genus Pellaea (Tryon, 1956).

Characteristically, Notholaena possesses a flat, unmodified margin, but sometimes it is revolute and sometimes it is modified into a marginal indusium. Notholaena species that possess wax can be distinguished from Pellaea by that character and from Cheilanthes by an unmodified margin.

From the time of Linnaeus to Desvaux's Prodrôme (1827) six of the entities mentioned in Alice Tryon's (1957) monograph on the genus Pellaea section Pellaea were included in the genus Pteris, which was one of the major and larger fern genera of the earlier botanical works.

Link (1841) proposed the genus Pellaea from collections at the Berlin Gardens and Smith (1841) applied the name Platyloma to the same group of plants from the collections at the Kew Gardens. Smith's name which was published in August of 1841 seems to have preceeded that of Link. Tryon (1957) mentioned that in the British Museum's copy of Link's work, it was issued between September 3 and 10, 1841.

Copeland (1947) in the Genera Filicum recognized the genus Pellaea as a natural one although he remarked that the affinities of the group did not entirely support his view.

A committee on nomenclature for Pteridophytes reported a unanimous vote to conserve Pellaea and the International Code adopted by the

8th Congress at Paris, 1954, included Pellaea among the genera to be conserved (Tryon, 1957).

Tryon (1957) stated some problems that existed in typifying the Cheilantheid group of ferns. She considered the section Pellaea to be a restricted but natural group that was based on vegetative morphology such as nearly glabrous, imparipinnate blade and free venation, and on the continuous marginal indusium and terminal sori on discrete vein ends.

Tryon and Britton (1958) considered Pellaea to belong to the tribe Cheilantheae of the family Polypodiaceae; while Nayar (1963a) presented us with a glimpse of how confused the state of the art was concerning the genus Cheilanthes.

Cheilanthes is included by many pteridologists (Christensen, 1938; Copeland, 1947 and Diel, 1902) in the pteroid phylum, but often regarded as representing a line of evolution separate from that of Pteris and related ferns. Bower (1926-28) has separated Cheilanthes and its allies from the Pteroids, designating them a "Gymnogrammoid fern" and suggesting for them an origin from the primitive Superfiliciales: the Cheilantheid ferns are regarded as showing much similarity to the Schizaeaceae. Copeland (1947) and more recently Pichi-Sermolli (1957, 1960) support the possible Schizaeoid ancestry of Cheilanthes. According to Copeland, Hemionites and Pityrogramma are derived from the Cheilantheid ferns, Onychium is a close relative and Actiniopteris (a genus regarded as a Pteroid derivative by most other pteridologists) is a variant of the group. On the other hand, Christensen (1938), Ching (1940) and Alston (1956) regard the majority of the Gymnogrammoid ferns, including Cheilanthes, as related to the Pteroid phylum. According to Ching, the Sinopteridaceae (which includes Cheilanthes and Onychium) are Pteroid derivatives and these in turn have given origin to the Gymnogrammeaceae (the Central Group of Gymnogrammoideae of Bower) and Adiantum, Holttum (1947, 1949 and 1954) associates the Gymnogrammoid ferns with the Vittarioids in the family Adiantaceae, phylogenetically separate from the Pteroids, and regards them as derived from the Osmundaceae-Schizaeaceae group. The association of the Vittarioid ferns and Adiantum with the Gymnogrammoideae is supported by Pichi-Sermolli, as according

to him "the Gymnogrammoid, Cheilanthoid, Adiantoid and Vittarioid ferns may be held to represent phyletic lines which branched off early from a common stock (Pichi-Sermolli, 1957), viz. ferns like the present Schizaeaceae."

The next page represents the taxonomic scheme of Pichi-Sermolli (in Jermy, 1973).

Knobloch and Volz (1964) expressed concern regarding the separation of the three genera as there are few if any naturally occurring, exclusive characteristics that can be used to differentiate the representatives of Cheilanthus, Notholaena and Pellaea.

Knobloch (personal correspondence, April 14, 1975) stated, ". . . until more definite studies are made, the only distinctions I know of is that Cheilanthus and Notholaena are hairy, scaly or both on the leaves with the leaf margins scarcely enrolled in Notholaena and fully enrolled in Cheilanthus. Pellaea has enrolled leaf margins but the plant's leaves are generally free of scales or hairs, the adoption of such a definition would, of course, necessitate moving a number of species about, out of one genus and into another genus."

Based on these introductory remarks, Rolla Tryon (1956) has stated the problem most accurately.

It is not likely that an adequate classification of the genera of the Cheilantheae; Cheilanthus, Notholaena, Pellaea, Doryopteris and related smaller genera, can be achieved without a previous knowledge of the species concerned . . . It seems that the basic problem will be to determine lines of evolution so that the meaning of characters is sufficiently clear, which characters are of generic value, which are convergent and which are only of specific expression . . . The uncertainty of the definition of Notholaena is not all of the difficulty, for if Cheilanthus and Pellaea were well defined, the task might be more certain, but the problems in those genera are in their own way, as perplexing as those in Notholaena.

Having briefly reviewed the classification schemes employed in treatments of the "Cheilanthoid ferns," it is appropriate now to mention previous researches in morphological, ecological, physiological, distributional, genetical and cytological and evolutionary areas, limiting our review to what is known in Cheilanthes, Notholaena and Pellaea.

TABLE 1. Classification of the Filicopsida.

Filicopsida	Filicidae	Irishopteridales	Arachnoxyllaceae Irishopteridaceae
		Zygopteridales	Clepsidropsidaceae Zygopteridaceae
		Botryopteridales	Botryopteridaceae Tubicaulidaceae
		Anachoropteridales	Anachoropteridaceae
		Stauropteridales	Stauropteridaceae
		Ophioglossales	Ophioglossaceae
		Marattiidae	Marattiales
			Psaroniaceae Angiopteridaceae Marattiaceae Danaeaceae Kaulfussiaceae
		Osmundidae	Osmundales
			Osmundaceae Sphenopteridaceae Klukaceae Tempskyaaceae Acrostichopteridaceae Schizaeaceae
		Schizaeales	
	Pteridales		Pteridaceae Regipteridaceae Siropteridaceae Cryptogrammeaceae Parkeriaceae Gymnogrammeaceae Adiantaceae Vittariaceae
		Dicksoniales	Dicksoniaceae Dennstaedtiaceae Lindsaeaceae
		Davalliales	Davalliaceae Oleandraceae
		Hymenophyllales	Hymenophyllaceae
		Loxsomales	Loxsomaceae
		Gleicheniales	Oligopodriaceae Gleicheniaceae
		Cystheales	Lophosoriaceae Cystheaceae
		Aspidiales	Thelypteridaceae Asplenaceae Atypaceae Aspidaceae Lomariopsidaceae
		Blechnales	Blechnaceae
		Hatoniales	Hatonaceae
	Marsileidae	Polypodiales	Dipteridaceae Cheimolauriaceae Polypodiaceae Grammitidaceae
		Platygyriales	Platygyriaceae
		Hymenophyllales	Hymenophyllaceae
		Marsileidae	Marsileales
			Marsiliaceae
		Salvinidae	Salviniales
			Salvinaceae Azollaceae

LITERATURE REVIEW

A. MORPHOLOGICAL

Maxon (1918) contributed a key for some of the lip ferns (Cheilanthes) of the southwestern parts of the United States. Specifically he was concerned with: Cheilanthes myriophylla, C. Wootonii, C. Covillei, C. villosa, C. Fendleri, C. Clevelandii and C. intertexta. Of particular note and interest was that the habit of the rhizome was used as the first key character.

Rolla Tryon (1938) expressed an interest in the forking of ferns and collected over three hundred specimens that represented some twenty-eight species. One of the species collected was Pellaea atropurpurea var. cristata Trelease, which was described as a plant that would exhibit forked fronds in successive years. Forking is primarily a problem for the cytologist and geneticist, stated Tryon, but gross observations can shed some light on the phenomenon.

Wagner (1952b) established a system for treating the dichotomy of the major vascular axes of leaves in living ferns, stating that they exist in four distinguishable forms (excluding the Gleicheniaceae). Each type is named for the feature of the leaf which accounts for its organization. Pellaea atropurpurea, P. rotundifolia and P. viridis are mentioned as three of the representatives considered in the midribless blade type. This is the commonest type found and can be characterized

as having regular or symmetrical dichotomy of the major veins, no midrib present and with mature fronds like the juveniles.

Abeywickrama (1956) noted the occurrence of gemmae on Cheilanthes thwaitesii and that the gemmae would germinate soon after separating from the parent plant if they landed in a suitable environment (moist soil).

General morphological characteristics of the rhizome, paleae, leaves (rachis, stipe and pinnae), sporangia, indusium, spores, prothallus and early juvenile leaves of the genus Cheilanthes are presented by Nayar (1962a). In addition to the general characteristics of the genus, the following taxa are treated morphologically: C. albomarginata, C. bullosa, C. chrysophylla, C. dalhousiae, C. farinosa, C. mysurensis, C. pteridioides, C. rufa, C. tenuifolia and C. thwaitesii. A key based on morphological characteristics of the taxa is provided to identify the species. The problematical nature of the genus is also pointed out.

Nayar (1963a) described ten species of Cheilanthes. He concluded that the vascular cylinder was dictyostelic, and considering the rest of morphological information, further concludes that there was a close affinity of Cheilanthes with Hemionites and Doryopteris, and that the Schizaeoid ferns seem like more probable ancestors of Cheilanthes than the Pteroid or other groups of ferns.

Knobloch (1965) analyzed some species of Cheilanthes as to their type of vernation. It was found that 11 species exhibited circinate vernation and 18 species exhibited non-circinate vernation. Knobloch concluded that the type of vernation possessed by each taxa was a fixed genetic response and not changeable by environmental factors.

Pellaea andromaedifolia (Kaulf.) Fee was first morphologically described in 1824 and since then various forms of this Californian species have received systematic recognition (Pray, 1968).

Knobloch (1966b) presented a preliminary review of the spore number and apogamy in the genus Cheilanthes. A review of the species that had been reported as apogamous was presented along with the spore number for 14 additional species. Knobloch (1969) described the spore patterns of 32 taxa of Cheilanthes. It was noted that all taxa had radially symmetrical spores and that seventeen taxa showed some degree of spore abortion.

Hitt and Knobloch (1967) point out the complexity of past morphologic and taxonomic considerations of the Cheilanthes eatonii, C. castanea and C. tomentosa complex. In an attempt to clarify this complex, spore, gametophyte and various aspects of sporophyte morphology (rhizome, rhizome scales, frond size, hairs and scales and sporangia) were considered. Previously Knobloch (1966b, 1967) reported C. eatonii and C. castanea as $2n = 87$ and C. tomentosa as $2n = 90$. This indicates that these species are triploids (Cheilanthes $n = 29$ and 30). From this study it appears that C. eatonii and C. castanea are more closely related to one another than they are to C. tomentosa.

B. ECOLOGICAL

Most of the species of Cheilanthoid ferns grow in rocky habitats, for example, on ledges, crevices of cliffs, on talus slopes, at the base of large rocks or in rocky ground.

They are especially abundant in areas where such habitats are common and there is a dry period during part of the year. Species are

fewer or entirely absent in regions where it is dry most of the year and in regions with cold or constantly wet climates (Tryon and Tryon, in Jermy, 1973).

Many species of the Cheilanthoid ferns have morphological characteristics which are evidently adaptive to seasonally dry habitats. Hevly (1963) concerned himself specifically with this subject. Some of the adaptations that are found within the group include the following: complex leaves with many small ultimate segments, or a compact lamina architecture, a densely scaly, pubescent or ceraceous lamina indument, very coriaceous blades, and an abscission zone in the stipe. Parallel evolution has undoubtedly been frequent. Convergent evolution, as used by Hevly (1959, 1963), means similarity among unrelated taxa.

Cheilanthus, Notholaena and Pellaea are related taxa, and the author would prefer the use of the term "parallel evolution." Pellaea andromaedifolia (Kaulf.) Fée and Notholaena parvifolia Tryon, each with numerous, small coriaceous leaf segments; Cheilanthus scariosa (Sw.) Presl and Saffordia induta Maxon, each with densely scaly lamina (Tryon and Tryon, in Jermy, 1973).

Wherry (1920), while contributing ecologic information concerning soil reactions of certain rock ferns, did mention Cheilanthus lanosa and C. tomentosa plus Pellaea atropurpurea and P. glabella. Wherry concluded that both species of Pellaea were to be considered calcareous soil plants with a moderate tolerance for acid reactions. For Cheilanthus he concluded that the data was inadequate for evaluation.

Hayes (1924) mentioned a number of different culture methods for Pellaea atropurpurea that were used for an examination of the sex organs on the prothallia. She suggested that her findings (failure to produce

archegonia) indicated a possible adaptation to a xerophytic habit. She also described the development of the sporophytes on the gametophyte and noted that the sori were produced in one year. Subsequent work by many workers has shown that P. atropurpurea and many other ferns fail to develop archegonial cells on the prothallus; this is an indication of the apogamous condition. Large oil vacuoles were found in the prothallus and sporophyte, with the younger leaves having more oil than the mature leaves. The presence of bi-nucleate cells in a continuous layer around the notch of the gametophyte tissue surrounding the growing sporophyte was noted with the supposed function of increasing the nuclear surface as an aid in metabolic processes (Hayes, 1924). Chromosome counts of both gametophytes and sporophytes were obtained with some difficulty, both counts were recorded as +40. It has been subsequently determined that the gametophytic and sporophytic number in P. atropurpurea is the same, namely 87.

Thomas Pray (1968) and others familiar with the species have recognized its plasticity in response to the environment. The variety rubens D. C. Eaton and the variety gracilis Summers ex Farlow are examples of environmentally induced variants. Pray recognized, however, that the variety pubescens D. C. Eaton was decidedly distinct. The variety pubescens appears to be strictly a coastal ecotype occurring from San Luis Obispo, California, south to Cedros Island off the coast. The distinctions are based on evidence of the vein pattern in fresh material of the variety pubescens, lack of the vein pattern in andromaedifolia, bipinnate leaves in variety pubescens and tri-pinnate leaves in the typical variety and leaves of only 35 cm. in length in the typical form. Based on the above and other criteria, Pray stated that the evidence was

sufficient to recognize the systematic position of the variety pubescens. In Pray's (1968) opinion the varieties are comparable to good subspecies in other groups.

C. PHYSIOLOGY

Tryon (1957) pointed out the remarkable tolerance to desiccation that the spores and gametophytes of Pellaea have. As an example of this, the research conducted by Pickett and Manuel (1925) was cited. Pickett and Manuel (1925) carried out desiccation experiments with P. atropurpurea and P. glabella in which some plants were air-dried for nine and some for 18½ months. When watering was resumed some of the plants became green and continued to grow. Five years later Pickett (1931) examined the same cultures and 5 percent showed whole or partial recovery when satisfactory growth conditions were restored.

With the appearance of more chemo-taxonomic studies present in the literature and with the increase in acceptability and significance of the data, it is a wonder that the article by Mathews (1945) concerning the toxicity of Notholaena sinuata and N. sinuata var. cochisensis had not been more widely accepted and cited in the literature, especially as it related to the taxonomy of the sinuous cloak-fern complex. Mathews' data on feeding the ferns to sheep and goats is conclusive. The results were as follows: those animals fed a total of 4.5 to 8.4 pounds of N. sinuata (Lag. ex Sw.) Kaulf. for 6 to 9 days showed no ill effects. The animals fed from 1.8 to 6 pounds of N. sinuata var. cochisensis (Goodding) Weath. for 2 to 3 days (feeding was stopped as toxic effects were noticed) showed marked toxic effects.

"In view of the fact that the two plants occur in the same soil formation, that one is toxic and the other is not and that the two plants can be readily differentiated, the present classification is certainly inadequate. The gulf between these two plants should provide sufficient reason for classifying var. cochisensis as a species rather than a variety" (Mathews, 1945). The physiology of the two taxa is clearly different as the plants utilize the same nutrients in different manners.

A good deal of physiological and biochemical work on ferns is now underway in various laboratories throughout the world, but the Cheilan-thoid ferns have not been extensively involved so far in this area.

D. GENETICS, CYTOLOGY AND EVOLUTION

Tryon and Britton (1958) contributed a paper on cytotaxonomic studies in the fern genus Pellaea. This paper dealt with apogamy in Pellaea and listed a number of species and their meiotic chromosome numbers.

Knobloch and Britton (1963) established the somatic chromosome number of Pellaea Wrightiana as 87 and stated that the probable parents of this triploid hybrid (or backcross) were Pellaea longimucronata 2X and Pellaea ternifolia 4X. A comparison of characteristics and ranges was presented indicating areas of overlap in both morphology and range between supposed parents and the hybrid.

Recognition of Pellaea longimucronata in the eastern Mohave desert, California, was noted by Shreve and Wiggins (1964) and Pray (1967). Earlier collections of this species are in herbaria from the Providence Mountains, California (Dunkle 4251, AHFA) and the New York Mountains, California (Ferris and Bacigalupi, 8076, RSA). These reports were not

cited by either A. Tryon (1957) or Munz (1959). Pray (1967) reflects on the fact that the eastern Mohave region also includes the eastern limits of Pellaea mucronata (D. C. Eaton) D. C. Eaton and that many intermediates exist between P. longimucronata and P. mucronata in that region which are most likely hybrids.

Wagner (1965) described the hybrid origin of P. Wrightiana and noted its variability and most obvious affinities with P. ternifolia and P. longimucronata. P. Wrightiana is intermediate in characteristics between P. longimucronata and P. ternifolia; Wagner (1965) stated that the hybrid P. Wrightiana should be reinstated as a species as had been done by Hooker.

Cytological and taxonomic studies were carried out by Manton, Roy and Jarrett (1966) on living material of two African cytotypes, Cheilanthes farinosa (Forsk.) Kaulf. and of one, as yet unnamed sexual diploid of the same genus from northern India. It was found that the Indian diploid would hybridize with one of the African cytotypes. The authors recommend further exploration of living material from both continents before any decisions were made concerning the number of taxa worthy of binomial treatment that are present in either flora.

The chromosome numbers of five species of Cheilanthes were analyzed by Knobloch (1966a). Previous to this date only 16 of 180 (Copeland, 1947) species of Cheilanthes had been counted. Knobloch's study added 4 new counts and confirmed a fifth species. Cheilanthes Wrightii was counted as a diploid of 58. Cheilanthes tomentosa, at meiotic metaphase had 90 units, indicating that the plant is a triploid hybrid. Cheilanthes (Aspidotis) californica was established as having a haploid number of 30, and C. (Aspidotis) carlotta-halliae was given a number of

30 bivalents and 30 univalents, suggesting that it was a backcross of C. carlotta-halliae with one of its parents. Cheilanthes carlotta-halliae has been previously described as a hybrid of C. siliquosa and C. californica by Wagner and Gilbert (1957).

A review of spore number and apogamy, as it was known to exist within the genus Cheilanthes, was published by Knobloch (1966b). Twenty-four species were listed with their spore numbers and some twenty species were mentioned as being apogamous.

The results of Knobloch (1967) on the chromosome numbers of Cheilanthes, Notholaena, Llavea and Polypodium added pertinent data to the literature concerning those genera.

The cytology of all known representatives of the genus Cheilanthes described at the rank of subspecies and above from Europe and the Canary Islands was done by Vida, Page, Walker and Reichstein (1970). In all, ten taxa were examined.

Knobloch, Tai and Adangappuram (1975) added considerable more information on chromosome counts in the Sinopteridaceae. Confirmatory, corrective and one new count of the chromosome condition of Cheilanthes and Aspidotis were included in the paper. It should be mentioned that Knobloch et al. (1975), found Pichi-Sermolli's classification system (in Jermy, 1973) useful. Knobloch et al. (1975), also mentioned that there is not enough chromosomal or morphological data to evaluate the evolutionary relationships in Cheilanthes.

The sinuous cloak-fern complex (Notholaena sinuata) has long been a subject of intensive study because of its polymorphy. Until recently little was known of this complex other than gross morphological characters and those have not been well understood (Hevly, 1965). Anatomical

data was practically non-existent until Rolla Tryon (1956) noted the presence of two vascular bundles in the stipes of the sinuous cloak ferns. Considerable taxonomic confusion has existed concerning the status of the N. sinuata complex and the names applied to them (Tryon, 1956). Weatherby (1943) largely resolved the issue by delimiting three major taxa within the complex: sinuata, cochisensis and integerrima. Another taxon of the N. sinuata complex is N. sinuata var. pruinosa (Fée) Fourn. N. sinuata v. pruinosa was not recognized by Weatherby (1943) but he suggested that it might be recognized as a distinct variety of N. sinuata. Rolla Tryon (1956) did not recognize N. sinuata var. pruinosa as distinct but rather synonymized it with N. sinuata var. sinuata. Based on the anatomy and morphology of prothallia, pH tolerances, temperature tolerances for spore germination, light intensities for growth, phosphate requirements, spore size, size of pinnae, stomatal number, xylem trace of the stipe, palisade layer of pinnae, indument of rhizome, indument of the pinnae, scales, spores per sporangium and range, Hevly (1965) identified the following species: N. cochisensis, N. X integerrima and N. sinuata. Notholaena sinuata was divided into two subspecies, each composed of two varieties (subsp. sinuata, vars. sinuata, robusta and subsp. madriensis, vars. madriensis, pruinosa).

Knobloch et al. (1973), based on cytological evidence, states that all the taxa studied by him and treated as varieties in the sinuous cloak fern complex should be elevated to specific rank. This differs from Hevly's opinion stated above. Notholaena pruinosa Fee (chromosome number $2n = 87$) is again elevated to species rank because it does not seem logical that a presumed hybrid (N. pruinosa) could be a variety of another presumed hybrid (N. sinuata var. sinuata, chromosome number

2n = 87). Notholaena integerrima Hook. (chromosome number 2n = 87) is presumably a hybrid although usually listed as a variety of N. sinuata, but Knobloch discarded precedent for the same reasons as stated above for this taxa also.

Apogamy as it occurred in Notholaena (Nothochlaena) distans R. Br. was first reported by Berggren in 1888, while Goebel (1905) was the first to report the existence of apogamy in the genus Pellaea, working with Pellaea nivea (Poir) Prantl (now called Notholaena nivea (Poir) Desv. var. nivea). Helena Woronin (1908) observed apogamy in Pellaea flavens (Sw.) C. Chr. (Notholaena nivea flava), P. tenera (Gill.) Prantl, Notholaena (Nothochlaena) sinuata (Lag. ex Sw.) Kaulf., and Notholaena (Nothochlaena) eckloniana Kunze, and Steil (1911) recorded a preliminary note on the apogamous development of Pellaea atropurpurea Link.

Tryon (1968) attempted to understand the evolutionary role of the apogamous mechanism in Pellaea, against a background of rapidly increasing information on the frequency of the apogamous phenomenon in the Pteridophyta. Ferns that exhibit the apogamous habit were considered to be of hybrid origin (Manton, 1950, 1961; Walker, 1966). Apogamy in Pellaea is known to exist in six of the 15 species in the section Pellaea (Tryon, 1968). She reported on three species of the "light-stiped" group which represent a separate evolutionary line in the section. Pellaea ovata, P. intermedia and P. andromaedifolia were reported to be apogamous. The three species reported, however, were unique in the occurrence of both sexual diploids and apogamous triploids which have similar morphologies in each species. In each of the species reported by Tryon she stated that each sexual diploid form has

probably served as a parent in the cross that produced a morphologically similar triploid. Tryon (1968) further stated a number of possibilities as to the other parent. Comparisons were also made of epidermal cell size, stomatal guard cell numbers, geographic distribution and spore size of the sexual diploids and apogamous triploids. All three species are triploids and are similar to the classic example of apogamy as reported by Manton (1950) for Pellaea atropurpurea and also reported by Tryon and Britton (1958) for P. sagittata.

E. DISTRIBUTIONAL NOTES

Alice Tryon (1957) published a major work entitled "A Revision of the Fern Genus Pellaea section Pellaea." The entities included in this review numbered 15 species and 5 varieties. A note concerning speciation processes was mentioned whereby apomixis, polyploidy and hybridization had influenced speciation in P. glabella, P. sagittata and P. ovata. The series related to P. ternifolia appeared to Tryon to have evolved through gradual quantitative differentiation and through isolation of the resulting populations.

The southwestern United States and adjacent Mexico were mentioned as the most probable centers of dispersal for Cheilanthes, Notholaena and Pellaea based on the fact that all the species described except P. Breweri and P. glabella either converged on the above area or seemed to be derivatives of those species that did.

Tryon and Britton (1958) note that the "diploids Pellaea Breweri and P. glabella var. occidentalis are closely allied morphologically and in several characters the two resemble some species of Cheilanthes which occur within the same general geographical range."

Hevly (1965) contributed distributional information concerning the Notholaena sinuata complex, while geographical data was contributed by Wagner et al. (1965) concerning Pellaea glabella var. glabella.

In 1967 Pray contributed some additional material as it related to the distribution of American Cheilanthoid ferns. New collection sites were added for various species and an attempt was made to bring the distributional records up to date.

Pray (1968), in his paper on Pellaea andromaedifolia, contributed distributional notes and ecologic relationships for Pellaea andromaedifolia and its valid varieties, plus P. mucronata, P. longimucronata and P. intermedia.

Tryon and Tryon (in Jermy, 1973) discussed the geography, spores and evolutionary relationships in the Cheilanthoid ferns while synthesizing past research information as it related to evolutionary relationships within the group. The concentration of the Cheilanthoid fern species has been shown to occur in six major geographic areas (Mexico, Andean, Australian, Brazilian, African and Sino-Himalayan) where 282 of the 325 species occur. Nearly one-third (104 species) of the Cheilanthoid ferns grow in the Mexican region. The authors have also pointed out the distinctiveness of each region and have shown that three-quarters or more of the species in one region do not grow in another, with the exception of the Andean region which does share several species with the Mexican and Brazilian regions. The American Cheilanthoid species are almost completely different from the species of the Old World with only Cheilanthes farinosa (Forsk.) Kaulf. and Doryopteris concolor (Langsd. and Frisch) Kuhn. having amphiatlantic ranges.

Nearly all well-defined species groups have their species wholly concentrated in a single region, or a few may extend into other regions. Examples in Notholaena (Tryon, 1956) are the Notholaena geraniifolia Weath. group (including N. venusta Brade, N. eriophora Fee, and N. goyazensis Taub.) Brazilian except for the occurrence of N. eriophora in the northern Andean region and the Notholaena squamosa (Hook. and Grev.) Lowe group (including N. peruviana Desv., N. arequipensis Maxon and N. lonchophylla Tryon) wholly Andean. The Cheilanthes argentea (Gmel.) Kze. group (including, among others, C. duclouxii (Christ) C. Chr. and C. niphobola C. Chr.) Is Sino-Himalayan, except for C. argentea which occurs north eastward on the mainland and to Japan. Speciation in these groups may have been relatively recent; however, they do provide evidence of the major geographic regions as centers of evolution (Tryon and Tryon, in Jermy, 1973).

Wiggins (1973) added geographical and descriptive data on three rare Cheilanthoid ferns (Cheilanthes viscida Davenp., C. peninsularis Maxon and Notholaena peninsularis Maxon and Weatherby) from Baja California, Mexico.

F. ANATOMICAL, OTHER THAN RHIZOME

White (1963) stated that Notholaena sinuata had root tracheary elements which appeared to be vessel members, but because true perforations in the end plates had not been experimentally demonstrated, White referred to them as "presumptive vessel members." Because of the presence of vessel members in Pteridium aquilinum and possibly Woodsia ilvensis, both of which occur in dry habitats, White thought it reasonable that the character might be associated with the xerophytic habit. He also checked species typical of dry areas, including representatives of the genera Cheilanthes and Pellaea. Unfortunately he does not name the species examined, other than N. sinuata. Because of the presence of apparent vessel members in Notholaena sinuata and Woodsia ilvensis, and the taxonomic position of these species, White stated that,

". . . it is possible that the sporadic occurrence of this cell type is still to be found within other species, genera and even families of ferns." He also stated that due to the infrequent occurrence, in a survey of over 200 species, it is not probable that vessel members will ever be found as commonplace structures.

Knobloch and Volz (1964) contributed more detailed studies on the leaf blade anatomy of thirty-five species of Cheilanthes. The xerophytic or near xerophytic habit was again pointed out and certain adaptations to it. It was also reiterated that a great deal more descriptive research of the Cheilanthes genus was needed before a proper perspective on species and species relationships could be attained.

Knobloch and Volz (1968) once again added considerable anatomical information concerning the genus Cheilanthes with their paper on the anatomy of the stipes and rachises. Thirty-two species were described and compared with each other and to the species in the published literature. A statement to the effect that ". . . we found it surprising that there were so many different patterns in the stipe and rachis, going way beyond what had previously been reported. It would seem that the multitude of axis conditions makes it impossible at this time to characterize the genus by the anatomy of its aerial axis alone."

Payne and Patterson (1973) published an interesting paper on the presence of hypodermal layers in fern leaves. Within the family Cheilanthaceae the following species were investigated: Adiantopsis radiata, Anogramma leptophylla, Anopteris hexagona, Bommeria hispida, Cheilanthes alabamensis, C. gracillima, Coniogramme japonica, Cryptogramma acrostichoides, Llavea cordifolia and Pellaea glabella. From these, only Coniogramme japonica was found to have a hypodermis.

The authors stated that the presence or absence of the hypodermal layer may be useful for assessment of relative speciation and of evolutionary relationships.

G. RHIZOME ANATOMY

Jeffrey (1902) mentioned that he had examined the rhizomes of plants from a number of Polypodiaceous species, including some in the genus Pellaea. However, the species he utilized were not mentioned. Jeffrey stated that the young central cylinder of the rhizome was throughout a concentric fibro-vascular tube with foliar lacunae.

Gwynne-Vaughan (1903) stated that a true solenostele was not of very general occurrence, although it was found in several different genera, including Pellaea. He also mentioned that a transitional type of stele, related to the solenostele could be found in Pellaea, Notholaena and Cheilanthes. Pellaea atropurpurea and P. falcata were described as having creeping, more or less dorsiventral rhizomes that were typical solenosteles. Notholaena Marantae and Pellaea rotundifolia were said to specifically possess a transitional type of stele. Cheilanthes lendigera and C. microphylla were described as having an aberrant form of solenostely. The rhizome of Pellaea cordata was described as being dorsiventral with the leaves inserted in several rows.

Tansley (1907) in describing dorsiventral types of dictyosteles and the slight difference between them and dorsiventral solenosteles, mentioned the genera Notholaena and Pellaea. N. Marantae and P. rotundifolia were illustrated and mentioned as in Gwynne-Vaughan (1903). Cheilanthes lendigera and C. microphylla were mentioned as being "closer" to a solenostele, and it is interpreted that these species were described in Gwynne-Vaughan's context of being "transitional."

Tansley (1908) used Notholaena sinuata (Nothochlaena sinuata) to illustrate the "Ontogenetic evolution of dictyostely through solenostely from the Lindsaya-type (amphiphloic protostely) by the development of ground tissue pockets which are from the first in connection to form a pith . . . within the internal phloem, and the subsequent overlapping of successive leaf gaps." Tansley inferred that in the mature condition, Notholaena sinuata was a dictyostele.

Marsh (1914) contributed the first major paper concerning the rhizome anatomy of Cheilanthes and Pellaea. "The stelar anatomy of Cheilanthes and Pellaea is of interest in that each genus contains both solenostelic and dictyostelic forms, together with others that are intermediate between these types." Cheilanthes Fendleri was described (Marsh, 1914) as having leaf gaps that were long, but failed to overlap, hence it was a solenostele. Cheilanthes gracillima and Cheilanthes Feei (as lanuginosa) were interpreted as being transitional in nature because portions of their rhizomes included areas where two leaf gaps overlap, while the greater portion of the rhizome was a solenostele.

Cheilanthes persica was described (Marsh, 1914) as a true dictyostele, Pellaea falcata, a simple solenostele, while once more, P. rotundifolia and P. andromaedifolia were described as transitional. Marsh also started to shed some light on the anatomical problems of the rhizomes which will be encountered when she stated, "The Pellaea andromaedifolia which I examined may perhaps have been older material than that used by Gwynne-Vaughan, for though it showed a dorsiventral dictyostele, its structure was more complicated than that which he describes." Mention was made of a close correlation between stelar structure and the amount and arrangement of the wood within the stele.

Marsh (1914) also mentioned that the total number of "sieve tubes" was very small and that there was no observable differentiation into proto-phloem and metaphloem.

Posthumus (1924) while discussing principles of stelar morphology and reviewing the work of previous investigators mentioned Cheilanthes, Notholaena and Pellaea. In his review of stelar anatomy he lists: Cheilanthes microphylla (dorsiventral solenostele), C. Feei (as C. lanuginosa, dorsiventral dictyostele), C. gracillima (dictyostele transitional to solenostele), C. lendigera (dorsiventral solenostele), C. persica (radial dictyostele), C. Fendleri (dorsiventral solenostele), Notholaena aurea (as ferruginea, dorsiventral dictyostele), N. Marantae (dorsiventral dictyostele), N. sinuata (solenostele), N. trichomanoides (dorsiventral solenostele), Pellaea falcata (dorsiventral solenostele), P. rotundifolia (dorsiventral dictyostele), P. andromaedifolia (dorsiventral dictyostele), P. atropurpurea (dorsiventral dictyostele), and P. cordata (dorsiventral dictyostele). Mention was also made in many instances as to the growth habit, i.e., erect, creeping with long internodes, etc. Posthumus also mentioned the type of leaf trace that was present in many species.

In 1924, May Williams contributed a rather extensive paper on Cheilanthes tenuifolia. The rhizome of this taxon was described as being a dictyostele according to Gwynne-Vaughan's definition.

Of particular significance in the interpretation of rhizome structure is the work of Hevly (1963). "The Cheilanthoid ferns, when grown in greenhouses or transplanted to cooler, more moist regions such as the Puget Sound area of Washington State, retain their typical growth habit and associated anatomical and morphological alterations.

Variation in degree of structural change is not particularly noticeable, indicating that in Cheilanthoid ferns these modifications are genetically fixed" (Hevly, 1963). Xerophytic modifications are apparent including: impregnation of the cell walls of the epidermis, cortex and stele with suberin and lignin, and various epidermal appendages that are found on the rhizomes and the fronds.

Nayar (1963a) contributed morphological descriptions of ten species of Cheilanthes including the rhizome, leaves, sporangia, spores, prothallia and juvenile sporophytes. All the rhizomes of the investigated taxa were considered to be dictyostelic (Nayar, 1963a).

Ogura (1973) noted that many authors point out two factors involved in the formation of a dictyostele: (1) the dictyostele could be formed as a result of the elongation of leaf gaps; and (2) from the shortening of the internodes, so that the stem with closely arranged leaves would usually show a dictyostele, whereas those plants with long internodes would show a solenostele. In species such as Adiantum pedatum and Cibotium barometz, a portion of the rhizome that has long internodes is solenostelic, while another portion of the same rhizome with short internodes is dictyostelic. Notholaena and Pellaea rhizomes were specifically mentioned as representatives illustrating such an intermediate type of solenostele and dictyostele.

McCulloch, Volz and Knobloch (1974) reported on the rhizome anatomy of twenty-six taxa in the genus Cheilanthes. A review of some of the pertinent literature as it related to steles and the genus was discussed along with an anatomical analysis of the species. Twenty species were described as solenosteles while six were described as transitional steles.

H. REVIEW OF STELAR DEFINITION

Protostely is a primitive condition, as it is found in all primitive vascular plant stems (except the mature stems in the Equisetales), in juvenile plants of the Filicales, in some fossil ferns and in the adult form of some species of the Filicales (Jeffrey, 1902; Thompson, 1920). Any departure from the simple protostele is commonly regarded as a derived condition (Foster and Gifford, 1959).

Wardlaw (1945) stated that, "The shoot stele, whether it was protostelic, solenostelic or dictyostelic, consisted initially of an uninterrupted solid or hollow subconical mass of tissue and that during the subsequent differentiation of the tissues of the leaf shoot system, distinct changes took place and internal structural features of considerable complexity could be produced."

The term protostely, as such, can be found in the literature by several definitions and in many variations.

Worsdell (1902) described a protostele as being a central mass of wood (xylem), surrounded by a zone of bast (phloem), ". . . this in turn having been derived from the primitive conductive tissues of the sporophyte stem of some bryophytic ancestor."

Gwynne-Vaughan (1903) described a protostele in Lygodium to be the continuing of the central xylem mass not being interrupted by the subsidence of the external tissues, either cortical or vascular, at the departure of the leaf trace. He stated that this has not yet been found in the Polypodiaceae.

Schoute (in Verdoorn, 1938) described a protostele as a monostele with a peripheral phloem and a central mass of xylem.

Foster and Gifford (1959) stated that a protostele was a solid cylinder of xylem in the stem surrounded by phloem.

The protostele as described by Esau (1965) was a solid column of vascular tissue enclosing no pith.

Ogura (1972) described the protostele as a ectophloic concentric vascular bundle, enclosed by an endodermal layer. He defined fourteen types of protosteles: a) primitive protostele; a small protostele that consists of a few tracheids and phloem elements (the primitive protostele of Ogura is the same as the haplostele as described by Fahn, 1967, 1974); b) typical protostele; the circular concentric stele is enclosed by an endodermis and can be distinguished from (a) by its larger size; c) stellate protostele; the xylem is stellate in cross section and on the tip of each arm can be found exarch protoxylem; d) Asteroxylon type; xylem is stellate, but the form and number of the xylem arms are irregular and part of the arm can separate or fuse with each other; e) Arachnoxylon type; this is similar to (d), the only difference is in the existence of a parenchyma island near the external end of each xylem arm; f) protostele with mixed pith; this type has parenchyma cells mixed among the tracheids, this was called a mixed pith by Brebner (1902); g) medullated protostele; this is similar to (f) except that in the center of the xylem there is a mass of parenchyma; h) Lindsaea type, originally the Lindsaya type of Tansley and Lulham (1902); this is an amphiphloic form in which there is a phloem mass within the xylem; i) radial type; a radial vascular bundle enclosed by an endodermis layer; j) dorsiventral type; cross section of the stele would be flattened, elliptical or band-shaped; k) Lycopodium type; a modified radial protostele where the xylem is not truly radial but more or less

irregularly radial or band-shaped, being sometimes arranged in parallel bands in cross section; l) Osmunda type; the xylem ring is interrupted radially by parenchyma in many parts, but the phloem and endodermal layers are situated continuously on the external side of the phloem; m) Hymenophyllaceae type; the typical protostele becomes through dorsiventrality and reduction, dorsiventral and further subcollateral then collateral and lastly, extremely reduced; n) reduced protostele; the xylem and phloem are so extremely reduced that the stele consists of a few tracheids and sieve tubes.

Fahn (1967, 1974) considered a protostele to be a solid cylinder of xylem surrounded by phloem. He described three types of protosteles: a) haplostele; the xylem appears to be more or less circular in cross section (primitive protostele of Ogura, 1972); b) actinostele; the xylem is stellate in cross section; and c) plectostele; the xylem is split into longitudinal plates, some of which are joined and others separated.

It appears that one can be either a "lumper" or a "splitter" when it comes to describing the protostele condition and as we shall see subsequently, other stelar conditions as well. The question of whether to lump or split, then is not confined necessarily to the field of taxonomy, but is also a problem in anatomy. This raises numerous questions when documentation of anatomical information is needed, particularly at the species level.

The following taxa have been recorded as having a particular type of protostele:

PRIMITIVE PROTOSTELE (Ogura, 1972) or HAPLOSTELE (Fahn, 1967, 1974):

Gosslingia (Gwynne-Vaughan, 1903), Hornea (Gwynne-Vaughan, 1903),

Horneophyton (Ogura, 1972), Rhynia major (Gwynne-Vaughan, 1903), Rhynia

(Gwynne-Vaughan, 1903; Ogura, 1972; Fahn, 1967, 1974), Rhyneaceae (Schoute, 1938) and Selaginella (Fahn, 1974).

TYPICAL PROTOSTELE (Ogura, 1972) or HAPLOSTELE (Fahn, 1967, 1974):
Azolla (Bower, 1923; Bierhorst, 1971), Botryopteris (Ogura, 1972),
Botryopteris cylindrica (Bower, 1923), Cheiropleuria (Posthumus, 1924;
 Bower, 1928; Ogura, 1972), Hymenophyllaceae, Lygodium, Gleichenia,
Botryopteris (Worsdell, 1902), Cheiropleuria bicuspis (Posthumus, 1936),
Cochlidium seminudum (Posthumus, 1936), Gleicheniaceae (Ogura, 1972),
Gleichenia flabellata, G. linearis (Bower, 1923), Gleichenia melano-
blasta (Alston, 1958), Hecistopteris pumila (Bower, 1923), Lepidodendron
esnotense, L. pettycurense, L. saalfeldense (Ogura, 1972), Macroglena
meifolia (Ogura, 1972), Monogramme (Bower, 1923), Psilotum (Schoute,
 1938), Salvinia (Bierhorst, 1971), Selaginella selaginoides (Fahn, 1967;
 Ogura, 1972), Selenodesmium (Ogura, 1972), Tmesipteris (Schoute, 1938),
Tubicaulis (Ogura, 1972), Vandenboschia scandens (Ogura, 1972).

PROTOSTELE WITH MIXED PITH: Ankyropteris (Bower, 1923), Cheiropleuria
 (Bower, 1928), Diaplolabis (Ogura, 1972), Gleichenia (Bower, 1923),
Lepidodendron intermedium, L. Selaginoides (Ogura, 1972), Lygodium
 (Bower, 1923), Mecodium demissum (Ogura, 1972), Metaclepsydropsis
 (Ogura, 1972), Thamnopteris Kidstoni (Ogura, 1972) and Vandenboschia
radicans (Ogura, 1972).

MEDULLATED (Ogura, 1972) or ECTOPHLOIC SIPHONOSTELE WITHOUT LEAF GAPS
 (Sporne, 1962): Ankyropteris (Ogura, 1972), Asterochlaena (Ogura, 1972),
Bothrodendron maybe (Ogura, 1972), Lepidodendron aculeatum, L. har-
courtii, L. obovatum (Ogura, 1972), Lepidophloios fuliginosus (Ogura,
 1972), Osmundites dunlopi (Ogura, 1972), Platyzoma microphyllum (Ogura,
 1972), Schizaea spinosa (Ogura, 1972), Sigillaria (Ogura, 1972).

STELLATE (Ogura, 1972) or ACTINOSTELE (Fahn, 1967, 1974): Psilophyton (Fahn, 1967, 1974; Ogura, 1972), Sphenophyllum (Ogura, 1972).

ASTEROXYLON: Asteroxylon (Ogura, 1972; Schoute, 1938), Mesoneuron (Ogura, 1972), Schizopodium (Ogura, 1972), Stenokoleos (Ogura, 1972).

ARACHNOXYLON: Arachnoxyton (Ogura, 1972), Asteropteris (Ogura, 1972), Iridopteris (Ogura, 1972), Reimannia (Ogura, 1972).

DORSIVENTRAL: Hymenophyllaceae (Ogura, 1972), Mecodium scabrum (Ogura, 1972), Selaginella species (Schoute, 1938), Selaginella involiens, S. Karsteniana, S. serpens (Ogura, 1972) and Trichomanes reniforme (Ogura, 1972).

HYMENOPHYLLACEAE TYPE: Crepidomanes (Ogura, 1950), Crepidopteris (Ogura, 1972), Didymoglossum giesenhagenii, D. hymenoides, D. labiatum (Ogura, 1972), Gonocormus (Ogura, 1950), Hymenophyllum (Ogura, 1950), Hymenophyllum barbata (Ogura, 1972), Lecanium membranaceum (Ogura, 1972), Mecodium (Ogura, 1950), Meringium Bakeri blandum (Ogura, 1950), Pleuromanens (Ogura, 1950), Scledodesmium (Ogura, 1950) and Vandenboschia (Ogura, 1950, 1972).

LINDSAEA: Davallia hymenophylloides, D. Parkeri, D. repens, D. tenuifolia (Gwynne-Vaughan, 1903), Lindsaea (Bower, 1928; Ogura, 1972), Lindsaea clavata, L. trapeziformis (Bower, 1928), L. Blumeana, L. cuneata, L. cultrata, L. composita, L. guianensis, L. hymenophylloides, L. lancea, L. linearis, L. microphylla, L. orbiculata, L. Parkerii, L. reniformis, L. repens, L. rigida (Posthumus, 1936), Schizoloma ensifolium (Posthumus, 1936), Stenoloma chusanum, S. clavatum, S. retusum (Posthumus, 1936), Tapaenidium (Posthumus, 1924; Bower, 1928), Tapeinidium Brooksii, T. moluccanum and T. pinnatum (Posthumus, 1936).
RADIAL: Lycopodium (in some young species, Ogura, 1972).

LYCOPODIUM: Lycopodium (Schoute, 1938; Ogura, 1972).

OSMUNDA (Ogura, 1972) or ECTOPHLOIC SIPHONOSTELE (Foster and Gifford, 1959): Osmunda (Bower, 1923; Foster and Gifford, 1959; Ogura, 1972).

REDUCED: Azolla (Bierhorst, 1971), Isoetaceae (Ogura, 1972) and Salviniaceae (Bierhorst, 1972; Ogura, 1972).

The development of the solenostele and/or dictyostele from a primitive protostele is well documented in the literature. A fuller explanation of this will be made under the heading "Ontogeny of the Stele."

"In short, it (the concept) has been described by many authors that the solenostele is derived from the protostele through the formation of pith, internal phloem and internal endodermis" (Ogura, 1963).

If we consider that the solenostele is derived from a protostele, then the origin of the pith and other internal tissues must be accounted for. There are two theories as to the origin of the pith, i.e. the "extrastelar" and "intrastelar." According to Jeffrey (1897, 1902, 1910) medulation could be derived by the invagination of the cortical tissue into the pith; more simply stated the pith would be homologous with the cortex.

According to the "intrastelar" theory, however, the pith could have originated within the stele itself and, therefore, the pith and cortex would not be homologous.

The "intrastelar" theory has been supported (since Tansley and Chick, 1900) by many authors, including Farmer and Hill (1902), Tansley and Lulham (1905), Charles (1911), Lang (1913-15), Gwynne-Vaughan (1914) and Thompson (1920). Thompson (1920) found that the pith did arise in situ by the differentiation of procambial cells as reported in

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Schizaea malaccana, S. dichotoma, Gleichenia pectinata, Loxosoma Cunninghamii, Achrosticum aureum and Lindsaya adiantifolia.

As stated before, in most primitive vascular plants the stele of the youngest portion is a primitive protostele (Jeffrey, 1902; Thompson, 1920, Ogura, 1972). If we trace the stele from the youngest part basally, the stele widens in a conical fashion and the parenchyma mass appears within the xylem (Ogura, 1972). This is the first step in pith formation and it should be noted that there is no direct connection with the cortex and that there is no gap at the node (Ogura, 1972). It is in older tissue that the pith and cortex connect with each other through the leaf gap (Ogura, 1972). During ontogenetical development, the parenchyma of the cortex appears to "enter" the xylem from the leaf gap downwards as if it were a "pocket" (Boodle, 1903; Ogura, 1972). The pocket can be seen in the phloem as well as the endodermis and has been observed by Boodle (1903) and Thompson (1920) in the Gleicheniaceae or Schizaeaceae (Ogura, 1972).

"The pocket formation seems to be favorable for the extrastelar hypothesis, but the appearance of the internal tissues can be in a more or less lower part of the pocket, and the connection of the external and internal tissues seems to be rather secondary. Moreover, in the young part of Acrostichum aureum and Schizaea dichotoma, the internal endodermis is enclosed within the pith in a spindle or 'endodermal island'" (Thompson, 1920).

"This phenomenon may be also favorable for the intrastelar hypothesis" (Ogura, 1972).

More support for the intrastelar origin of the pith can be found in the existence of the mixed pith and medullated pith, as found in the

Osmundaceae, Ophioglossaceae, Coenopteridales and Lepidodendron (Ogura, 1972). The existence of medullation in Lepidodendron is very clear, as there are no leaf gaps, the medullated protostele could have been derived from the typical protostele going through the stage of mixed pith (Ogura, 1972). Cells with tracheidal thickening among the pith have also been reported in Schizaea (Tansley and Chick, 1900), Osmunda (Gwynne-Vaughan, 1914), Todea (Seward and Ford, 1903), Osumndites (Kidston and Gwynne-Vaughan, 1910), Ophioglossaceae (Bower, 1911; Lang, 1912, 1913-15; Vasisht, 1927; Nozu, 1956), Ankyropteris (Scott, 1912), Asterochlaena (Stenzel, 1889) and Asterochlaenopsis (Sahni, 1930; Ogura, 1972).

The term siphonostele seems to be the most widely accepted term for a stele with pith. We will subsequently find out, however, that there are different terms being applied to the same or very similar stelar conditions. A review of the concept of a siphonostele by various authors follows.

Schoute (1938) defined a siphonostele as a medullated protostele with an internal endodermis.

Foster and Gifford (1959) stated that a siphonostele was a stele with pith.

Esau (1965) said that a siphonostele had a pith, and Fahn (1967, 1974) explained that a siphonostele was a condition where there was a cylinder of pith within the xylem.

Ogura (1972) on the other hand does not use the term siphonostele but seems to equate the term solenostele with it. He defined a solenostele as one with a cylindrical stele with a central pith, which can connect at the leaf gap with the cortex. The vascular bundle consists of the xylem and external and internal phloem that are enclosed by the

external and internal endodermal layers (Ogura, 1972). There are not more than two leaf gaps in a cross section (Ogura, 1972).

Gwynne-Vaughan (1903) does not use the term siphonostele.

Further confusion sets in when an analysis of the sub-categories of the siphonostele concept are delineated.

Schoute (1938) described three types of siphonosteles: a) amphiphloic siphonostele; a siphonostele with a second phloem ring on the inside of the xylem; b) solenostele; a siphonostele perforated by scattered leaf gaps; c) dictyostele; a solenostele with more leaf or other gaps, so as to show more than one interruption in any one transverse section.

Foster and Gifford (1959) describe two sub-categories of siphonosteles with one sub-category having two types: a) ectophloic siphonostele; having an external cylinder of phloem only; b) amphiphloic siphonostele; having internal and external cylinders of phloem (also endodermis), type 1) solenostele, without overlapping leaf gaps and 2) dictyostele, an amphiphloic tube of vascular tissue in which parenchymatous leaf gaps overlap.

Esau (1965) differentiated three sub-categories of a siphonostele: a) ectophloic siphonostele; the phloem occurs only on the outer side of the xylem cylinder; b) amphiphloic siphonostele or solenostele; phloem differentiates on the inner side of the xylem as well as the outer side, in its simplest form this type has no leaf gaps; c) dictyostele; large leaf gaps that overlap to the extent that the vascular system appears dissected into a net-like structure with each segment constituting a concentric vascular bundle.

Fahn (1967, 1974) differentiates five sub-categories of siphonosteles, with one sub-category having two types: a) ectophloic siphonostele; the phloem surrounds the xylem externally; b) amphiphloic siphonostele; where the phloem surrounds the xylem both externally and internally and where the endodermis appears both outside, bordering the cortex, and inside the vascular tissue on the border of the pith, 1) solenostele, an amphiphloic siphonostele in which the successive leaf gaps are considerably distant, one from another, 2) dictyostele, an amphiphloic siphonostele with overlapping gaps, i.e. that in which the lower part of one gap is parallel with the upper part of another gap. In this condition the vascular bundles are inter-connected to form a cylindrical network and each bundle is of a concentric structure consisting of a central strand of xylem surrounded by phloem. Individually the bundles are termed meristeles, from an anatomical view these are amphi-cribal bundles; c) eustele; collateral bundles, developed from the ectophloic siphonostele; d) polycyclic stele; two or more concentric cylinders of vascular tissue are present; e) polystelic; stems and roots containing more than one stele.

The earliest reference to a solenostelic type of structure was made in 1838 by Robert Brown who noted the presence of a complete ring of "vasa scalariformia" in Polypodium Horsfieldii R. Br. (Dipteris conjugata, Reinw.).

It seems appropriate to introduce Gwynne-Vaughan's (1903) idea of the solenostele and dictyostele at this point. Gwynne-Vaughan formulated his concept in this fashion: a solenostele held an intermediate position between a simple protostelic type and a more complicated form, the dictyostele. The dictyostele, a term first proposed by Brebner

(1902), was the tubular network of vascular tissue that arose by the occurrence and overlapping of gaps (leaf?) in a solenostele.

Ogura (1972) has four sub-categories of solenosteles: a) typical solenostele; an amphiphloic cylinder enclosed by both endodermal layers with the stele radially constructed; b) dorsiventral solenostele; similar to the former, but is different in its dorsiventral structure, having leaf gaps situated mainly on the dorsal side of the stem; c) ectophloic solenostele; the absence of the internal phloem (and endodermis); d) Equisetum type; a ring of collateral bundles accompanied by a peculiar endodermis layer.

The following taxa have been recorded as having some type of solenostele:

TYPICAL SOLENOSTELE: Acrostichum (Bower, 1923), Adenophorus sarmentosus (Wilson and Rickson, 1961), Adiantum pedatum, A. hispidulum (Bower, 1928), Adiantum (Fahn, 1967), Anemia (Bower, 1928; Ogura, 1972), Anemiorrhiza (Bower, 1923), Anogramma subdigitatum (Posthumus, 1924, 1936), Amphidesmium blechnoides (as Metaxya rostrata, Bower, 1928; Stevensen, 1974), Antrophytum plantagineum (Bower, 1928), Arthropteris (Bower, 1928; Tindale, 1961), Asplenopsis decipiens (Posthumus, 1936), Cheilanthes aemula, C. angustifolia, C. Brandegii, C. castanea, C. Cooperae, C. Covillei, C. Eatonii, C. Fendleri (probably misidentified, Bower, 1928), C. gracillima, C. horridula, C. intertexta, C. lendigera, C. Lindhelmeri, C. mexicana, C. myriophylla, C. notholaenoides, C. Pringlei, C. tomentosa, C. Wootonii, C. Wrightii (McCulloch et al., 1974), Christensenia aesculifolia (Kaulfussia aesculifolia, Kuhn, 1889; Stevensen, 1974), Craspedodictyum quinatum (Posthumus, 1924, 1936), Davallia hirsuta, D. marginalis, C. speluncae, D. strigosa, D. platyphylla (Gwynne-Vaughan,

1903), Davallia (Prosaptia) contigua, D. dubia (Bower, 1928),
Dennstaedtia rubiginosa (as Dicksonia rubiginosa, Gwynne-Vaughan, 1903;
 Stevensen, 1974), Dennstaedtia punctilobula (Morton and Neidorf, 1956),
Dennstaedtia sp. (Bower, 1928), Dicksonia apiifolia, D. cicutaria, D.
scabra, D. punctiloba, D. davallioides (Gwynne-Vaughan, 1903), Dicranop-
teris pectinata (Ogura, 1972), Diellia falcata (Bower, 1928), Diplora
longifolia, D. schizocarpa, D. d'Urvillei (Posthumus, 1924, 1936),
Dipteris conjugata (Stevensen, 1974), D. novo-guineensis, D. Wallichii
 (Posthumus, 1936), Dipteris (Ogura, 1972), Doryopteris ludens
 (Posthumus, 1924, 1936), Egenolfia appendiculata (Posthumus, 1924, 1936),
Elaphoglossum latifolium (Bower, 1928), Gleichenia pectinata (Bower,
 1923), Histiopteris incisa (Bower, 1928), Hymenophyllopsis (Ogura, 1972),
Hypolepis tenuifolia, H. millefolium, H. distans, H. repens (Gwynne-
 Vaughan, 1903; Bower, 1928), Jamesonia imbricata (Gwynne-Vaughan, 1903;
 Posthumus, 1936), J. scalaris (Posthumus, 1936), Leptolepia (Posthumus,
 1924; Bower, 1928), Leucostegia immersa, L. pallida (Posthumus, 1924,
 1936), Lindsaya (Gwynne-Vaughan, 1903), Llavea cordifolia (Posthumus,
 1924, 1936), Lonchitis aurita, L. hirsuta (Bower, 1928), Lophosoria
 (Bower, 1923; Ogura, 1972), Loxsoma (Gwynne-Vaughan, 1903; Bower, 1923),
Marsilea (Fahn, 1974), Matonia (Bower, 1923), Metaxya (Bower, 1923;
 Lucansky, 1974), Microlepia haflanensis (Nayar and Kaur, 1964a), M.
marginata, M. pilosella, M. Wilfordii (Ogura, 1972), Microlepia
 (Posthumus, 1924; Bower, 1928), Neocheiropteris palmatopedata (Posthumus,
 1936), Notholaena sinuata (Posthumus, 1924), Odontosoria retusa, O.
aculeata (Posthumus, 1924; Bower, 1928), Paesia podophylla, P. viscosa,
P. scaberula (Bower, 1928), Pellaea atropurpurea, P. falcata (Gwynne-
 Vaughan, 1903; Bower, 1928), Pityrogramma (Nayar, 1964), Polypodium

punctatum (Gwynne-Vaughan, 1903), Polypodium sp. (Posthumus, 1936), Pteris grandifolia (Bower, 1928; Posthumus, 1936), P. elata, P. incisa, P. ludens, P. scaberula (Gwynne-Vaughan, 1903), Pteridium aquilinum (Bower, 1923, 1928), Saccoloma elegans (Stevensen, 1974), Stenochlaena tenuifolia (Stevensen, 1974), Stromatopteris (Bower, 1928), Syngramma alismaefolia (Posthumus, 1924, 1936), S. alsinifolia, S. borneensis (Bower, 1928), S. cartilagidens (Posthumus, 1924, 1936), Taenites blechnoides (Bower, 1928), Trismeria trifoliata (Posthumus, 1924; Bower, 1928) and Vittaria (Bower, 1928).

DORSIVENTRAL SOLENOSTELE: Adiantum macrophyllum, A. monochlamys, A. patens, A. pedatum, A. petiolatum, A. Farleyense, A. Trapeziforme (Posthumus, 1924, 1936), Bolbitis (Nayar and Kaur, 1964b), Cheilanthes Fendleri, C. lendigera, C. microphylla (Posthumus, 1936), Christiopteris tricuspis (Posthumus, 1936), Davallia aculeata, D. hirsuta, D. hirta, D. marginalis, D. platyphylla, D. strigosa (Gwynne-Vaughan, 1903; Ogura 1972), Dennstaedtia adiantoides, D. consanguinea, D. cornuta, D. davallioides, D. dissecta, D. ordinata, D. punctilobula, D. rubigniosa, D. rufescens, D. scabra (Posthumus, 1924, 1936), D. cicutaria (Stevensen, 1974), Dicksonia adiantoides (Gwynne-Vaughan, 1903), D. apiifolia, D. cicutaria, D. scabra, D. punctiloba, D. davallioides (Gwynne-Vaughan, 1903; Ogura, 1972), Egenolfia (Nayar and Kaur, 1964b), Jamesonia imbricata (Gwynne-Vaughan, 1903; Ogura, 1972), Histiopteris (Ogura, 1972), H. incisa (Posthumus, 1936), Hypolepis distans, H. millefolium, H. repens, H. punctata, H. tenuifolia (Gwynne-Vaughan, 1903; Posthumus, 1924, 1936; Ogura, 1972), Lindsaya retusa (Gwynne-Vaughan, 1903; Posthumus, 1936), Loxoma sp. (Ogura, 1972), Marsilea sp. (Ogura, 1972), Microlepia sp. (Ogura, 1972), M. hirta, M. marginata, M. pilosella, M.

platyphylla, M. speluncae, M. strigosa, M. trichosticha, M. Wilfordii (Posthumus, 1936), Notholaena Marantae (Tansley, 1907), Odontosoria aculeata (Ogura, 1972), Pellaea atropurpurea (Gwynne-Vaughan, 1903; Ogura, 1972), P. falcata (Gwynne-Vaughan, 1903; Tansley, 1907; Ogura, 1972), P. rotundifolia (Posthumus, 1936), Polypodium punctatum (Gwynne-Vaughan, 1903; Ogura, 1972), Pteris elata, P. incisa, P. ludens, P. scaberula (Gwynne-Vaughan, 1903; Ogura, 1972), Saccoloma (Posthumus, 1924) and Tapeinidium pinnatum (Ogura, 1972).

ECTOPHLOIC SOLENOSTELE: Antrophyum sp. (Ogura, 1972), Elaphoglossum sp. (Ogura, 1972), Helminthostachys zeylanica (Ogura, 1972), Ophioglossaceae (Nozu, 1956) and Vittaria (Ogura, 1972).

TRANSITIONAL (Between a solenostele and dictyostele): Adiantum Kaulfussii (Gwynne-Vaughan, 1903), A. macrophyllum (Posthumus, 1924, 1936), A. monochlamys (Ogura, 1921; Posthumus, 1924, 1936), A. pedatum (Ogura, 1921), A. peruvianum (Posthumus, 1924, 1936), A. petiolatum (Posthumus, 1924, 1936), A. trapeziforme (Gwynne-Vaughan, 1903; Ogura, 1972), Alsophila Engelii, Antrophyllum reticulatum (Gwynne-Vaughan, 1903), Coenopteris scandens (Posthumus, 1936), Cheilanthes Feei (McCulloch et al., 1974), C. gracillima (Posthumus, 1924), C. Kaulfussii, C. lanosa, C. Parryi, C. viscida (McCulloch et al., 1974), Cheilanthes sp. (Gwynne-Vaughan, 1903; Marsh, 1914), Davallia (Bower, 1928), Diplora longifolia, D. schizocarpa, D. d'Urvillei (Posthumus, 1936), Gymnogramme vestita (Gwynne-Vaughan, 1903), Lophosoria (Lucansky, 1974), Notholaena sp. (Ogura, 1972), N. ferruginea (aurea), N. Marantae, N. trichomanoides (Gwynne-Vaughan, 1903), Pellaea sp. (Ogura, 1972), P. andromaedifolia, P. rotundifolia (Gwynne-Vaughan, 1903), Plagiogyria (Bower, 1923), Pteris arguta, P. biaurita, P. cretica, P. dentata, P. flabellata,

P. heterophylla, P. longifolia, P. pellucida, P. umbrosa, P. Swartziana, P. tremula (Bower, 1928), Quercifilix zeylandica (Posthumus, 1924, 1936) and Vittaria stipitata (Gwynne-Vaughan, 1903; Posthumus, 1936).

RADIAL SOLENOSTELE: Acrostichum aureum, Ithycaulon (Saccoloma) domingense, I. inaequale, Lonchitis aurita, L. hirsuta, Pteris arguta, P. biaurita, P. cretica, P. dentata, P. gigantea, P. Kunzeana, P. longifolia, P. orizabae, P. pellucida, P. podophylla, P. tremula, P. umbrosa and Saccoloma elegans (Posthumus, 1936).

DICTYOXYLIC SOLENOSTELE: Cheilanthes lundigeri (Ogura, 1972), C. microphylla (Gwynne-Vaughan, 1903; Posthumus, 1924, 1936; Ogura, 1972), Llavea cordifolia (Bower, 1928) and Vittaria stipitata (Ogura, 1972).

PERFORATED SOLENOSTELE: Christiopteris tricuspidata (Posthumus, 1936), Neocheiropteris palmatopedata (Posthumus, 1936), Stromatopteris sp. (Bower, 1928).

Thus the solenostelic condition as reported in the literature seems to exist in great variety and profusion. The problems mentioned concerning protosteles recur again, with an obvious need either for clarification of and further explanation of stelar conditions in taxa or a more simplified method of stelar description; I would propose the latter.

Gwynne-Vaughan (1903) noticed that there were many transitional types related to the solenostele, and that the true solenostele was not of general occurrence. He provided a generalized description of the habit of the rhizome in which he stated that the ferns with a solenostelic vascular system had a creeping, more or less dorsiventral rhizome with leaves arranged in two rows on the upper surface. The gaps formed by leaf trace departures never overlap.

Stevensen (1974) noted that Mettenius (1857) observed parenchymatous gaps that were unrelated to either the leaf or branch traces in the solenosteles of Saccoloma elegans Kaulf. and Stenochlaena tenuifolia (Desv.) Moore.

Kuhn (1889) observed the same phenomenon in the solenostele of Christensenia aesculifolia (Blume) Maxon (as Kaulfussia aesculifolia Blume), by Brebner (1902), Tansley and Lulham (1904) and Ogura (1938) in the dictyostele of Danaea simplicifolia Rudge and by Ford (1902) in the dictyostele of Ceratopteris thalictroides.

Gwynne-Vaughan (1903) also mentioned, and was aware of the fact that gaps sometimes occur in the vascular cylinder that are not related in any way to the insertion of leaves. It will be recalled that Schoute (1938) described a dictyostele as a solenostele with more than one leaf or other gaps so as to show more than one interruption in any transverse section.

Tryon (1960) in Stevensen (1974) pointed out that Gwynne-Vaughan's taxa may have been erroneously identified and because he did not file voucher specimens it is impossible to verify the genera and species he investigated. Regardless of the proper identification of the taxa, Gwynne-Vaughan's observations are pertinent (Stevensen, 1974). Gwynne-Vaughan described the gaps that were unrelated to the appendage trace as "lacunae" and considered a solenostele with lacunae as a type of dictyostele that had evolved without overlapping leaf gaps (Stevensen, 1974). He concluded that this type of stele could be considered a type of solenostele.

Tansley (1907) applied the term "perforation" to the type of gap described above and used the designation of "perforated steles" for steles having that type of gap (Stevensen, 1974).

Stevensen's (1974) work, based on examination of past stelar reconstructions and diagrams of those who have noted "lacunae" or "perforations," has found it impossible to ascertain whether or not the perforations are related to root traces.

The conclusive, important point made by Stevensen (1974) is that it may very well be that some dictyostelic forms are not true dictyosteles, but appear dictyostelic because stelar root gaps are present in very close proximity to the leaf traces and their corresponding leaf gaps.

Brebner (1902) adopted the term dictyostele for the tubular network of vascular tissue that arises by the occurrence and overlapping of gaps in a solenostele (Gwynne-Vaughan, 1903).

The term dialystelic was used by Worsdell (1902) to describe the splitting up of the tubular solenostele into a number of secondary solid steles or concentric strands. Worsdell stated that the dialystelic condition was due to the crowded arrangement of the leaves on the stem, so that frequent gaps in the original solenostele became inevitable.

Gwynne-Vaughan (1903) described two factors that could bring about the overlap of leaf gaps: first, if each leaf gap remained open long enough after the departure of the leaf trace; secondly, the same result would be obtained if the leaves were crowded sufficiently close together, even if the leaf gaps were to close rapidly.

Tansley (1907) reiterated Gwynne-Vaughan (1903) by stating that ". . . as soon as two successive leaf gaps have overlapped, either by crowding of the leaf insertions, or by the prolongation forward of each leaf gap till it passes the base of the next trace, the stele technically ceases to be a solenostele by Gwynne-Vaughan's definition and

becomes a simple dictyostele, defined as an amphiphloic cylinder in which at least some transverse sections show two or more leaf gaps."

Schoute (1938) described a dictyostele as a solenostele with one or more leaf gaps or other gaps, so as to show more than one interruption on any transverse section.

Foster and Gifford (1959) described a dictyostele as an amphiphloic siphonostele in which parenchymatous leaf gaps overlap.

Esau (1965) described a dictyostele as a type of siphonostele in which the leaf gaps were large and overlap to the extent that they give the vascular system a dissected, or net-like appearance.

Fahn (1967, 1974) considered a dictyostele to be a type of amphiphloic siphonostele with overlapping gaps.

Ogura's (1972) concept of a dictyostele is one of a cylindrical stele which is interrupted by numerous leaf gaps so that the stele cylinder is separated in a cross section into more than two parts, each part being a meristele. Ogura (1972) lists ten different types of dictyosteles: a) transitional between a solenostele and dictyostele, the solenostele and dictyostele may be found in different levels of an organism; b) dictyoxyllic solenostele, this type is a special case of the transitional variety and is represented by a solenostelic form whose xylem ring is interrupted in some parts, that is dictyoxyllic; c) typical dictyostele, the arrangement of leaf gaps is radial, the number and form of meristeles in a cross section is not constant; d) dorsiventral dictyostele, having the leaf gaps situated mainly on the dorsal side; e) perforated dictyostele, in addition to leaf gaps, perforated gaps are found, but neither can be distinguished in the cross section; f) Davallia type, a type of perforated dictyostele, in which two meristeles at the

median dorsal and ventral parts are larger than the other meristeles; g) Oleandra type, a type of perforated dictyostele in which the meristeles are arranged alternately; h) ectophloic dictyostele, where the internal phloem is absent; i) Kalymma type, in cross section some radially elongated concentric meristeles are arranged in a circle, but the gaps between them are not the leaf gaps; j) Ophioglossaceae type, a solenostele or dictyostele, but the internal phloem is absent with the central pith being very large consisting of parenchyma and the internal endodermis is also absent, but present sometimes in some species.

The following are pertinent dictyostelic conditions and representative taxa as reported in the literature:

TYPICAL DICTYOSTELE: Acrophorus (Nayar and Kazui, 1962; Nayar and Kaur, 1966), A. stipellatus (Bower, 1928), Acrostichum aureum (Bower, 1928), Actinopteris (Nayar, 1962b), Adiantum assamicum (Nayar, 1964), A. capillus veneris, A. petiolatum, A. trapieziforme (Bower, 1928) Alsophila excelsa (Gwynne-Vaughan, 1903; Lucansky, 1974), Ampleopteris prolifera (Chandra and Nayar, 1968), Anemia (Boodle, 1901; Posthumus, 1936), Anetium citrifolium (Bower, 1928), Antrophyum brasilianum, A. lanceolatum, A. lineatum, A. plantagineum, A. reticulatum, A. semicordatum (Posthumus, 1936), Asplenium cardiophyllum (Posthumus, 1936), A. nidus (Posthumus, 1936; Tansley, 1907; Ogura, 1972), A. marginatum (Bower, 1928), A. dalhousiae, A. varians, A. trichomanes, A. exiguum, A. ensiforme, A. planicaule, A. laciniatum, A. subinterrifolia, A. tenuifolium, A. normale, A. cheilosorum, A. unilaterale (Bir, 1957), A. incisum (Ogura, 1921), Athyrium (Bower, 1928; Ogura, 1972), A. nipponicum, A. yokoscence (Ogura, 1921), Belvisia (Tindale, 1961), Blechnum (Lomaria) tabulare (Bower, 1928; Ogura, 1972), Brainea insignis (Bower,

1928), Caenopteris (Posthumus, 1936), Calymmodon cucullatus (Posthumus, 1936), Ceratopteris thalictroides (Ford, 1902; Stevensen, 1974), Cheilanthes gracillima (Bower, 1928), Cibotium sp. (Posthumus, 1936), C. Menziesii (Ogura, 1930), Cnemidaria sp. (Lucansky, 1974), Coniogramme fraxinea (Ogura, 1921), Cyathea Brunonis (Gwynne-Vaughan, 1903), Cyathocaulis Yabei (Ogura, 1941), Cryptogramme crispa (Bower, 1928), Cystopteris (Bower, 1928), Danaea simplicifolia (Brebner, 1902; Stevensen, 1974), Diacalpe (Nayar and Kaur, 1966), D. aspidioides (Bower, 1928), Dicksonia (Ogura, 1972), D. Barometz (Gwynne-Vaughan, 1903), Diellia (Wagner, 1952a), D. falcata (Bower, 1928), Diplazium Conilii, D. japonicum, D. lanceum, D. Wichurae (Ogura, 1921), D. esculentum (Ogura, 1927), Dryopteris africana, D. decursivopinnata, D. gracilescens, D. japonica, D. sophoroides, D. setigera (Ogura, 1921), Dryopteris sp. (Bower, 1928), D. cretica, D. Filix-Mas (Posthumus, 1936), D. cristata (Wardlaw, 1945), Grammitis (Tindale, 1961), Gymmogramme japonica, G. vestita (Gwynne-Vaughan, 1903), Hemionites (Nayar, 1962b), Hymenolepsis revoluta (Posthumus, 1936), Lastreopsis (Tindale, 1965), Lithostegia (Nayar and Kaur, 1966), Loxogramma avenia, L. grammitoides, L. involuta, L. lanceolata, L. malayaria, L. parallela, L. mexicana, L. perakense, L. Raciborskii (Posthumus, 1936), Matteucia orientalis (Ogura, 1921), M. Struthiopteris (Bower, 1928), Microsorium (Nayar, 1963b), Mohria (Posthumus, 1936), Monachosorum digitatum (Bower, 1928, as M. Bergiana; Posthumus, 1924, 1936, as Hypolepis Bergiana), Nephelea (Gastony, 1973; Lucansky, 1974), Nephrolepsis (Bower, 1928; Posthumus, 1936), Niphidium (Lellinger, 1972), Onoclea sensibilis (Ogura, 1921; Bower, 1928), Ophioglossum lusitanicum (Fahn, 1974), Peranema (Nayar and Kaur, 1963, 1966), P. cyatheoides (Bower, 1928), Phyllitis scolopendrium (Bower,

1928), Plagiogyria (Nayar and Kazui, 1962), P. adnata (Ogura, 1921), P. pyrrophylla (Bower, 1923; Stevensen, 1974), Platynerium (Tindale, 1961), P. alcicorne (Tansley, 1907; Bower, 1923; Stevensen, 1974), Polypodium digitatum, P. Feei, P. hemionitideum, P. lasiostripes, P. Mettenianum, P. peduncalatum, P. Wrightii (Posthumus, 1936; Stevensen, 1974), Polystichum aristatum (Ogura, 1921; Posthumus, 1936), P. aculeatum, P. falcatum, P. lepidocaulon (Ogura, 1921), P. tripterum (Posthumus, 1936), Pteris podophylla (Bower, 1928), Pyrrosia (Tindale, 1961), Sadleria (Posthumus, 1936), Scyphularia pentaphylla (Posthumus, 1936), Sphaeropteris (Lucansky, 1974), Stenochlaena sorbifolia (Bower, 1928), Stenosemia aurita (Posthumus, 1936), Trichipteris (Lucansky, 1974), Vittaria stipitata (Posthumus, 1936), Woodsia (Bower, 1928; Brown, 1964; Ogura, 1938) and Woodwardia radicans v. orientalis (Ogura, 1921).

RADIAL DICTYOSTELE: Acrophorus stipellatus (Posthumus, 1936), Adiantum aethiopicum, A. gracillima (Posthumus, 1936), A. lunulatum (Gwynne-Vaughan, 1903; Posthumus, 1924), A. nigrineense, A. philippense (Posthumus, 1936), Anogramma subdigitatum (Posthumus, 1936), Anopteris hexagona (Posthumus, 1936), Asplenium (Posthumus, 1924), A. germanicum, A. ruta-muraria, A. septentrionale (Posthumus, 1936), Athyrium alpestre, A. filix-femina, A. nipponicum, A. yokoscense (Posthumus, 1936), Blechnum attenuatum, B. brasiliense, B. capense, B. discolor, B. filiforme, B. integripinnulum, B. nipponicum, B. Patersoni, B. pennamarina, B. punctulatum, B. spicant, B. tabulare (Posthumus, 1936), Brainea insignis (Posthumus, 1936), Camptosorus sibiricus (Posthumus, 1936), Ceratopteris thalictroides (Bower, 1928), Ceterach officinarum (Posthumus, 1936), Cheilanthes persica (Posthumus, 1924, 1936; Bower, 1928), Coniogramma fraxinea, C. japonica (Posthumus, 1936), Cryptogramma

crispa (Allosorus crispus, Posthumus, 1924), Cyrtomium falcatum
 (Posthumus, 1936), Cystopteris fragilis, C. japonica (Posthumus, 1936),
Diacalpe (Posthumus, 1936), Dicksonia Barometz (Gwynne-Vaughan, 1903),
Didymochlaena truncatula (Posthumus, 1936), Diellia erecta, D. falcata
 (Posthumus, 1936), Diaplaziopsis japonica (Posthumus, 1936), Diaplazium
esculentum, D. japonicum, D. marginatum, D. proliferum, D. Pullingeri,
D. striatum, D. ultidifolium, D. Wichurae (Posthumus, 1936), Doodia
aspera Maxima (Posthumus, 1936), Dryopteris africana, D. cristata, D.
decomposita, D. decursive-pinnata, D. filix-mas, D. gongylodes, D.
gracilescens, D. hirtipes, D. japonica, D. Linneana, D. Miqueliana, D.
oreopteris, D. phegopteris, D. Robertiana, D. spinulosa, D. (Poly-
stichum) Standishii, D. thelypteris, D. tokyoensis, D. triphylla, D.
varia (Posthumus, 1936), Gymnogramme Calomelanos (Gwynne-Vaughan, 1903),
Hemigramma latifolia (Posthumus, 1936), Hemionites palmata (Gwynne-
 Vaughan, 1903; Posthumus, 1936), Lomaria semicordata (Plagiogyria
biserrata, Gwynne-Vaughan, 1903), Lomariopsis sorbifolia (Posthumus,
 1936), Matteuccia intermedia, M. japonica, M. orientalis, M. struthiop-
teris (Posthumus, 1936), Monachosorella flagellaris, M. Maximowiczii
 (Posthumus, 1936), Nephrolepis acutifolia, N. biserrata, N. cordifolia
 (Posthumus, 1936), Oleandra articulata, O. neriiformis (Posthumus, 1936),
Onoclea sensibilis (Posthumus, 1936), Peranema cyatheoides (Posthumus,
 1936), Phyllitis scolopendrium (Posthumus, 1936), Pityrogramma
Calomelanos, P. peruviana, P. tartarea, P. triangularis (Posthumus,
 1936), Plagiogyria adnata, P. pyenophylla, P. semicordata (Posthumus,
 1924), Polybotrya cervina, P. osmundacea, P. serratifolia (Posthumus,
 1936), Polystichum aculeatum, P. auriculatum, P. craspedosorum, P.
lepidocaulon, P. lobatum, P. lonchitis (Posthumus, 1936), Prosaptia

(Posthumus, 1924), P. alata, P. contigua (Posthumus, 1936), Pteris cretica, P. flabella, P. heterophylla, P. pellacida, P. tremula (Gwynne-Vaughan, 1903), Sadleria cyatheoides (Posthumus, 1936), Taenitis blechnoides (Gwynne-Vaughan, 1903; Posthumus, 1936), Tectaria chattagramica, T. irregularis, T. Moorei, T. macrodonta, T. tenerifrons (Posthumus, 1936), Woodsia ilvensis, W. obtusa (Posthumus, 1924), W. polystichoides (Posthumus, 1936) and Woodwardia radicans (Posthumus, 1936).

DORSIVENTRAL DICTYOSTELE: Adiantum macrophyllum, A. trapeziforme (Posthumus, 1924; Ogura, 1972), Aglaomorpha drynarioides, A. heraclea (Posthumus, 1936), Ananthacorus angustifolia (Posthumus, 1936), Anetium citrifolium (Posthumus, 1936), Anthrophyum (Bower, 1928), Araiostegia hymenophylloides, A. pulchra (Posthumus, 1936), Arthropteris altescandens, A. oblitterata, A. orientalis, A. tenella (Posthumus, 1936), Asplenium ikenoi (Ogura, 1972), Bolbitis aliena, B. hetero-clita, B. nicotianifolia, B. Quoyana (Posthumus, 1936; Ogura, 1972), Cheilanthes Feei (Posthumus, 1924, 1936), C. Fendleri, C. gracillima, C. lendigera, (Posthumus, 1936), Cyclophorus lanceolatus (Posthumus, 1936), Davallia bullata (Posthumus, 1924), D. canariensis, D. divaricata, D. Mariesi, D. pyxidata, D. solida, D. trichomanoides (Posthumus, 1936), Dendroglossae zeylanica (Ogura, 1972), Egenolfia (Nayar and Kaur, 1964b; Ogura, 1972), Elaphoglossum (Posthumus, 1924), E. brevipes, E. hybridum, E. latifolium, E. lingua, E. sieveri, E. simplex, E. tomentosa (Posthumus, 1936), Asplenium obtusifolium, E. unilaterale (Posthumus, 1936), Gymnopteris rufa, G. vestita (Posthumus, 1936), Humata heterophylla, H. parvula, H. repens, H. vestita (Posthumus, 1936), Hypodematium (Ogura, 1972), Hypoderis Brownii (Posthumus, 1924, 1936),

Leptochilus axillaris, L. decurrans (Posthumus, 1936), L. heteroclitus, L. nicotianifolius (Ogura, 1972), Lithostegia foeniculacea (Posthumus, 1936), Lomagramma guianensis (Posthumus, 1936), Merinthosorus drynarioides (Posthumus, 1936), Microgramma vacciniifolia, Notholaena ferruginea (aurea), N. Marantae (Posthumus, 1924, 1936), N. sinuata, N. triangularis (Posthumus, 1936), N. trichomanoides (Posthumus, 1924, 1936), Pellaea andromaedifolia, P. atropurpurea (Posthumus, 1924, 1936), P. cordata (Gwynne-Vaughan, 1903; Posthumus, 1924), P. rotundifolia (Tansley, 1907; Posthumus, 1936), Platyserium bifurcatum, P. stemaria (Posthumus, 1936), Polypodium accedens, P. angustifolium, P. aureum, P. Buergerianum, P. caespitosum, P. ciliatum, P. decurrens, P. fraxinifolium, P. fuscipunctatum, P. latipes, P. loriceum, P. lycopodioides, P. percussum, P. persicariaefolium, P. paradisae, P. piloselloides, P. pteropus, P. punctatum, P. sub-hastatum, P. subrostratum, P. squamulosum, P. sinuosum (Posthumus, 1936), Polystichum adiantiforme (Posthumus, 1936), Rhipidopteris pellata (Posthumus, 1936) and Vittaria lineata (Posthumus, 1936).

PERFORATED DICTYOSTELE: Adiantum (Ogura, 1972), Asplenium ensiforme (Ogura, 1972), Christopteris tricuspidis (Bower, 1928), Deparia (Athyrium) prolifera, D. concinna, D. Moorei (Bower, 1928), Diacalpe (Ogura, 1972), Drynaria heterophyllum, D. quercifolia (Posthumus, 1936), Neocheirop-teris palmato-pedata (Bower, 1928), Oleandra (Ogura, 1938), Polypodium lasiostipes (Ogura, 1972), Pteridium aquilinum (Posthumus, 1936) and Stenochlaena tenuifolia (Posthumus, 1936).

DAVALLIA DICTYOSTELE: Davallia (Ogura, 1972) and Humata (Ogura, 1972).

OLEANDRA DICTYOSTELE: Oleandra (Ogura, 1972).

ECTOPHLOIC DICTYOSTELE: Anthrophyum (Ogura, 1972), Pteridanetium (Ogura, 1972) and Vittaria (Ogura, 1972).

KALYMA TYPE DICTYOSTELE: Kalymma (Ogura, 1972).

OPHIOGLOSSACEAE DICTYOSTELE: Botrychium (Ogura, 1972), Cheiroglossa (Ogura, 1972), Ophioderma (Ophioglossum) pendulum (Ogura, 1972), Ophios-saceae (Ogura, 1972) and Rhizoglossum (Ogura, 1972).

The dictyostelic type is highly variable as witnessed by the extensive types of conditions noted from the literature. Problems of overlap of genera and species are once again encountered; a few of which will be noted. Diella falcata has been recorded as a radial dictyostele, a typical dictyostele, and a typical solenostele; Woodsia is described as being a typical dictyostele but W. ilvensis, W. obtusa and W. polystichiodes are described as radial dictyosteles; Adiantum has been described as a typical solenostele, transitional from solenostele to dictyostele, and a perforated dictyostele.

I. ONTOGENY - THE STELE

Tansley (1908) made the following reference as to the developmental stelar sequence:

We always find a protostelic structure in the first formed stem, and in the protostelic types, so far as evidence is available, this structure is retained throughout the stem, the stele merely increasing in size in relation to the larger and larger leaf traces that have to be supplied . . . Of the ontogenetic history of the Lindsaya-type of stele we know, unfortunately, nothing; but when we pass to the solenostele type we find that the first formed stele is again a protostele, giving off simple leaf traces, that it then passes through a Lindsaya-phase, in which an internal phloem, continuous with the inner phloem of the leaf trace, appears in the center of the stele.

The ontogenetic development of dictyostely through solenostely is

illustrated for Notholaena (Nothochlaea) sinuata and it clearly demonstrates protostely, solenostely and dictyostely. The developmental sequence of dictyostely in Polypodium aureum is illustrated and the original protostelic condition is obvious.

Thompson (1920) stated that: "By common consent protostely has been recognized as a primitive state . . . it figures universally in the juvenile plants of the Filicales, and is maintained in the adult stems of a number of their primitive genera." Specifically Thompson cited a number of examples: Schizaea malaccana has a protostele in the young portion of the stem. The ontogeny of Gleichenia pectinata is well known and it illustrates a progression from a protostele in the sporeling to a solenostele in the adult. Lindsaya adiantifolia illustrates a solid protostele stage (page 726) as does Loxsonoma Cunninghamii, although the solenostelic condition is delayed in this species until many leaves have been formed. In Acrostichum aureum the protostelic stage is very brief, but nevertheless, well illustrated (Figure 9, page 730). He continues, "The ontogenetic condensation thus shown for Acrostichum aureum appears also in Cheilanthes, and in Pteridium aquilinum, and Paesia podophylla and may be expected to figure generally for plants of Pterid affinity."

Ogura (1963) made the following statement:

It is well known that in species in Filicales, which show the solenostelic or dictyostelic system in the adult stems, the sporelings show a protostelic system. Such a protostelic system is small, consisting of a few elements, and if we trace the ontogeny of the stele, we will see the formation of parenchyma group, or the pith, within the xylem, so that the protostelic stage is seen in a very short distance.

Ogura (1972) made the following remarks regarding the ontogeny of the stelar system: "As described before, the youngest, that is, the

first formed part of the stem is small and its stele shows a very simple protostele, or the primitive protostelic type, consisting of a few tracheids and sieve tubes."

Esau (1965) contributed the following: "The simplest type of stele, and also the most primitive phylogenetically, contains a solid column of vascular tissue enclosing no pith. This is the protostele . . . Protosteles are most common in the lower vascular plants, but they occur also in the stems of some angiospermous water plants."

Fahn (1974) made the following statement: "Research on Ophioglossum lusitanicum (Gewirtz and Fahn, 1960) for instance showed that the stele of the rhizome of the sporophyte of this species that developed from the gametophyte (not as a result of vegetative reproduction) was protostelic at the base and siphonostelic (dictyostelic) in its upper portion."

Foster and Gifford (1974) state that many investigators have shown that the older portion of a fern stem is protostelic, but at a higher level (that is, younger portion) of the same stem the vascular cylinder may be solenostelic or dictyostelic.

Recently Webb (1975) makes these observations concerning the ontogeny of the stele in Ophioglossum petiolatum: "At the base of the stem is a protostele surrounded either partially or completely by phloem. Above this point pith develops, and the stele is an ectophloic siphonostele. The remainder of the stem contains a dictyostele of anastomosing collateral bundles with endarch xylem and no secondary vascular tissues."

Most recently Lucansky and White (1976) demonstrated the ontogenetic development of Sphaeropteris elongata and Lophosoria quadripinnata. It was shown that S. elongata progressed from, at the oldest

portion, a protostele, apically to a solenostele and then a dictyostele. Lophosoria quadripinnata progressed from a protostele, in its oldest portion, to a solenostele; the dictyostelic condition was not seen in this taxon.

J. ECOLOGY - THE STEM

In the Introduction the general habit and ecologic relationships of the Cheilanthoid ferns were described. In the Observation section more specific information regarding each taxon's growth habit and ecological niches will indicate a fairly high degree of specialization and adaptation.

To endure such a rigorous environment (xerophytic conditions) a perennial plant has to be able to withstand the dessication that results from high temperatures, high light intensities, low water supply and harsh edaphic conditions (Hevly, 1963).

Maximov (1929, 1931), Eames and MacDaniels (1947), Shields (1950) and Daubenmire (1959) noted many structural modifications important in controlling water loss in xerophytes, Hevly (1959, 1963) found these adaptations to exist in the Cheilanthoid ferns. Of particular interest to us is his description of the modifications of the rhizome. "Water loss in Cheilanthoid ferns may further be controlled by impregnation of the cell walls of the epidermis and cortex with suberin and lignin, particularly in the rhizome and stipe. The sclerification of the cell walls may extend to the stele in such ferns as N. sinuata and its close allies." These specialized cell layers probably play the same role in these ferns as in sclerophyllous plants where they are believed to prevent water loss through their impermeability to water (Eames and

MacDaniels, 1947). The effect of wall impregnations is heightened by the filling of the cells in the cortex by gum or tannin-like substances. It is also augmented by the sclerification of the epidermal appendages of the rhizomes and stipes in such species as N. californica Eaton, N. Standleyi Maxon, N. Galeottii Fee and N. Grayi Davenp. (Hevly, 1963). These features were noted in all specimens examined.

The presence or absence of some of these factors is thought by many to be controlled by environmental factors such as water deficit, high light intensity, nitrogen deficiency and temperature (Shields, 1950, 1951).

Hevly (1963) has demonstrated that when the Cheilantheid ferns are grown in greenhouses or transplanted to cooler regions, ". . . they retain their typical growth habit and associated anatomical and morphological alterations." He further stated that these characters were genetically fixed, and, if effective in controlling water loss, the characters should be considered true adaptations to xeric conditions.

Wardlaw's (1945) data and analysis indicated that the mode of distribution of metabolites and the development of mechanical stresses in the formative region may be factors in the morphological development of the stele, i.e. non-hereditary factors may play an important part in determining shoot organization.

MATERIALS AND METHODS

The following species of Notholaena were utilized in this study:
N. Aschenborniana Klotzsch, Garcia Caves, 36 mi. w. of Monterrey, Nuevo León, Mexico, Aug. 19, 1971, McCulloch 32-71; N. aurea (Poir) Desv., road from Monterrey to Saltillo, Coahuila, Mexico, Aug. 26, 1971, I. W. Knobloch 2483; N. brachypus (Kze.) J. Sm., Ahuacatlan Nayarit, July 18, 1960, I. W. Knobloch 1645; N. candida (Mart. and Gal.) Hook. var. candida, Tacuina, Chihuahua, Mexico, Aug. 12, 1967, I. W. Knobloch 2288; N. candida var. Copelandii (C. C. Hall) Tryon, Rio Elizondo, 5 mi. so. of Monterrey, Hwy. 85, Nuevo León, Mexico, Aug. 17, 1971, McCulloch 14-71; N. cochisensis Goodding, McKelligan Canyon, El Paso County, Texas, Sept. 9, 1971, I. W. Knobloch 2493; N. Galeottii Fée, 15 mi. so. of Huajuapán de León, Oaxaca, Mexico, Aug. 15, 1966, I. W. Knobloch 2198; N. Grayi Davenp., El Aguaje, 38 1/2 mi. w. of Chihuahua, Chihuahua, Mexico, Aug. 5, 1964, I. W. Knobloch 2078; N. interegerrima Hook., Garcia Caves, 36 mi. w. of Monterrey, Nuevo León, Mexico, Aug. 19, 1971, McCulloch 31-71; N. Lemmonei D. C. Eaton, Mexico, s.n.; N. limitanea Maxon var. mexicana (Maxon) Broun, Puerta el Chorro 3, Rt. 57 so. of Saltillo, Coahuila, Mexico, Aug. 21, 1971, McCulloch 59-71; N. neglecta Maxon, Huasteca Canon, so. of Santa Catarina, Nuevo León, Mexico, Aug. 24, 1971, McCulloch 85-71; N. Newberryi D. C. Eaton, garden of Dr. Hoover, San Diego County, California, I. W. Knobloch aq. no. 71-16; N. parvifolia Tryon, El Paso, Texas, Aug. 1, 1960, I. W. Knobloch

1687; N. rigida Davenp., Victoria-Jaumave Rd., Tamaulipas, Mexico, Sept. 9, 1966, I. W. Knobloch 2244; N. Schaffneri (Fourn.) Underw. ex Davenp. var. Schaffneri, Barranca Oblatos, Guadalajara, Jalisco, Mexico, Aug. 9, 1970, I. W. Knobloch 2478; N. sinuata (Lag. ex Sw.) Kaulf., rd. to Chipinque Mesa, Nuevo León, Mexico, Aug. 20, 1971, McCulloch 43-71; N. Standleyi Maxon, Puerta el Chorro 3, Rt. 57 so. of Saltillo, Coahuila, Mexico, Aug. 21, 1971, McCulloch 60-71.

The following species of Pellaea were used in this study:

P. allosuroides (Mett.) Hieron., Majalca, Chihuahua, Mexico, Aug. 4, 1964, I. W. Knobloch 2069; P. andromaedifolia (Kaulf.) Fée, Siskiyou Nursery, Medford, Oregon, I. W. Knobloch aq. no. 71-22; P. atropurpurea (L.) Link, Gardens of the Blue Ridge, North Carolina, 1971, I. W. Knobloch aq. no. 71-30, and Cañon de San Francisco above Villa Santiago, Nuevo León, Mexico, Aug. 23, 1971, McCulloch 78-71; P. brachyptera (Moore) Baker, Siskiyou Nursery, Medford, Oregon, 1965, I. W. Knobloch aq. no. 65-13; P. Breweri D. C. Eaton, Sierra Nevada Mountains, Fresno County, Sept. 1971, Taylor s.n., I. W. Knobloch aq. no. 71-29; P. Bridgesii Hook., Stanislaus National Forest at Pinecrest, California, Sept. 12, 1971, Rodin s.n., I. W. Knobloch aq. no. 71-26; P. dealbata (Pursh) Prantl, Colorado River below Miller Dam, Austin, Travis County, Texas, Jan. 8, 1969, Seigler 1034, I. W. Knobloch aq. no. 72-4; P. falcata (R. Br.) Fée, Antonelli Brothers, California, May, 1972, I. W. Knobloch aq. no. 72-7; P. intermedia Mett. ex Kuhn, Puerta el Chorro 3, Rt. 57 so. of Saltillo, Coahuila, Mexico, Aug. 21, 1971, McCulloch 57-71; P. longimucronata Hook., so. on a road to Madera Canyon, Arizona, July, 1971, Pinkava and Brown 615, McCulloch aq. no. 71-5; P. mucronata (D. C. Eat.) D. C. Eaton var. californica (Lemmon) Munz and Johnston,

near Redding, California at Slate Creek, June 14, 1971, Rodin, s.n., McCulloch aq. no. 71-18, and Siskiyou Nursery, Medford, Oregon, 1971, McCulloch aq. no. 21-21; P. notabilis Maxon, Cañon de San Francisco, above Villa Santiago, Nuevo León, Mexico, Aug, 23, 1971, McCulloch 79-71; P. pteroides (L.) Prantl, Univ. of Capetown, South Africa, Schelpe s.n., I. W. Knobloch aq. no. 73-6; P. Skinneri Hook., near Temoris station on Chihuahua al Pacifico R.R., Chihuahua, Mexico, Aug. 7, 1964, I. W. Knobloch 2089; P. viridis (Forsk.) Prantl var. viridis (as identified by Dr. E. Schelpe), Greenhill Nursery, loc. unknown, McCulloch aq. no. 71-33; P. X Wrightiana Hook., Malino Basin, Catalina Mountains, Arizona, July 8, 1960, I. W. Knobloch 1624.

Rhizomes were taken from collected plants by the author in 1971, from greenhouse grown plants of the author and Dr. I. W. Knobloch at Michigan State University, from plants purchased from various nurseries (identified, checked and corrected by the author and Dr. I. W. Knobloch) or from plants which had been given to the author or Dr. I. W. Knobloch by various individuals, as noted in the paragraphs above. Fronds were collected for the purpose of making voucher specimens and such specimens were deposited in the Michigan State University Herbarium (MSC).

Roots were removed as were most of the scales on the rhizomes. The rhizomes were killed and fixed in Formalin-acetic-alcohol (FAA).

Dehydration of the rhizomes was accomplished by using a tertiary-butyl-alcohol series (Table 2), modified from Sass (1958).

The dehydrated rhizomes were then placed in an aspirator to ensure that all the air was removed from the specimen for proper infiltration with paraffin. A minimum of two hours was used as a standard for evacuation, with as long as twenty-four not being unusual for some specimens.

TABLE 2. Dehydration series as modified from Sass (1958).

Solution number	Solution composition	Time in solution (hr.)
1	50 cc. distilled water 40 cc. 95% etoh 10 cc. tertiary-butyl- alcohol	24
2	30 cc. distilled water 50 cc. 95% etoh 20 cc. tertiary-butyl- alcohol	24
3	15 cc. distilled water 50 cc. 95% etoh 35 cc. tertiary-butyl- alcohol	24
4	5 cc. distilled water 40 cc. 95% etoh 55 cc. tertiary-butyl- alcohol	24
5	25 cc. 100% etoh 75 cc. tertiary-butyl- alcohol	24
6	100% tertiary-butyl- alcohol	2-3, with 3 changes

Following this procedure the specimens were infiltrated with Fisher's Tissue-mat paraffin at 60 degrees C. Table 3 outlines the infiltration process as was employed for each taxa, as modified from Sass (1958).

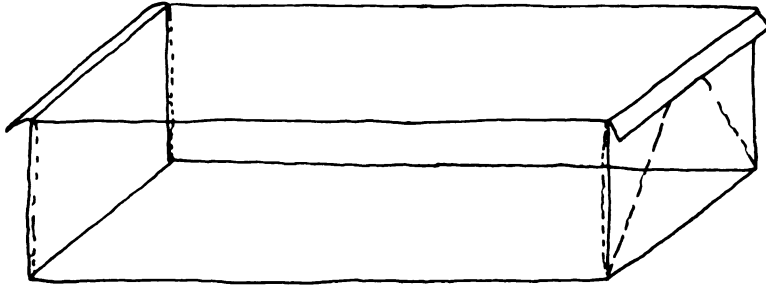
TABLE 3. Paraffin infiltration as modified from Sass (1958).

Infiltration medium	Time (hr.)	Temp. (C.)
25% paraffin 75% tertiary-butyl- alcohol	24	60
50% paraffin 50% tertiary-butyl- alcohol	24	60
75% paraffin 25% tertiary-butyl- alcohol	24	60
100% paraffin	2, 3 changes	60
100% paraffin	24	60

The rhizomes were then cast in paraffin. To accomplish this the following had to be assembled and ready for use: paper "boats," a slide warmer adjusted to 35 degrees C., an ice bath, a Bunsen burner, a needle probe and a supply of hot 100% paraffin. Paper boats are shown in Figure 1. The sides of the boats must be high enough to hold as much paraffin as will cover the specimens. Labels with the collection number or other identifying number are placed in the liquid paraffin. The paper boats are placed on the hot end of the slide warmer. The paraffin is allowed to harden a little on the bottom of the boat by gradually

Figure 1. Paper boat to hold paraffin and rhizomes.

moving the boat to the cooler end of the slide warmer, but the top is kept liquid by applying heat from the Bunsen burner. When the paraffin on the bottom has firmed up, about one-eighth of an inch, the rhizomes were poured into the boat. The rhizomes were arranged with their cross sectional surface parallel to the side of the boat. The specimens were arranged with a hot needle probe until their orientation was correct.



The paraffin was gradually cooled from the bottom up to ensure evenness throughout the block. As the top of the block began to cool, the boat was pushed under water in the ice water bath and the paraffin firmed up. After thirty seconds to a minute, the boat was removed from the ice water bath and the paper removed. The blocks were then placed in a refrigerator overnight to firm up the paraffin evenly and help prevent crystal formation. The block was then ready to trim into smaller blocks for sectioning. Blocks for sectioning were trimmed using a single-edged razor blade. After the blocks were cut and

trimmed, the cross sectional surface of those blocks to be sectioned was exposed. The blocks were placed in a jar with enough water in them to cover the specimen and placed in an incubator at about 40 degrees C. This was done to soften the tissues for sectioning in hopes that it would prevent tearing in highly sclerified specimens.

Paraffin blocks were mounted on specimen holders and thin paraffin sections were cut on an American Optical rotary microtome, model number 820. Tables 4 and 5 indicate the thickness at which the best sections for each taxa were obtained.

The thin sections were then adfixed to chemically clean microscope slides using either Weaver's solution or Mayer's egg albumin. The slides were placed on a slide warmer for approximately twenty-four hours. The slides with thin sections adfixed were then ready for staining.

A flow diagram for the decerating, staining, clearing and mounting of thin sections is outlined in Figure 2.

The prepared slides were left to dry for a minimum of twenty-four hours with weights placed on top of the coverslips to press out excess mounting media and air bubbles. The slides were then cleaned with xylene.

Tables 4 and 5 list the staining times best suited for the specimens used at the thickness indicated, other times were tried on many occasions, and the times listed are a matter of trial and error for the most part.

Photographs of the specimens were taken utilizing the following equipment: Nikon 70225 binocular microscope with a Microflex Model EFM, semi-automatic photomicrographic attachment with a reflex viewfinder

Figure 2. Flow diagram for decerating, staining, clearing and mounting.

100% xylene (5 minutes)-----100% xylene (3 minutes)-----
 ½100% xylene:½100% etoh (2 minutes)-----100% etoh (1 minute)
 95% etoh (1 minute)-----70% etoh (1 minute)-----50% etoh
 (1 minute)-----30% etoh (1 minute)-----15% etoh (1 minute)-----
 1% aqueous safranin (for times see Table 4 and 5)-----
 distilled water (wash)-----distilled water (wash)-----observe
 under microscope (restrain if necessary)-----15% etoh (time
 variable)-----30% etoh (time variable)-----50% etoh (time
 variable)-----70% etoh (time variable)-----0.5% fast green
 in 95% etoh (for times see Table 4 and 5)-----95% etoh
 (wash)-----95% etoh (wash)-----100% etoh (time variable)-----
 ½100% xylene:½100% etoh (time variable)-----Carbol-xylene
 clearing solution (30 sec.)-----100% xylene (30 sec.)-----
 100% xylene (30 sec.)-----add mounting media (Balsam or
 Clarite) and coverslip.

TABLE 4. Section thickness and staining times of Notholaena.

Species	Section thickness (u)	Staining times (sec.)	
		safranin	fast green
<u>N. Aschenborniana</u>	10-12	60	45
<u>N. aurea</u>	14	75	50
		90	60
		60	45
<u>N. brachypus</u>	20	90	60
<u>N. candida</u> v. <u>candida</u>	18	120	45
<u>N. candida</u> v. <u>Copelandii</u>	9	60	45
<u>N. cochisensis</u>	10	60	45
	12	75	50
<u>N. Galeottii</u>	12	60	45
<u>N. Grayi</u>	18	60	45
<u>N. integerrima</u>	12	65	45
<u>N. Lemmonii</u>	14	60	45
<u>N. limitanea</u> v. <u>mexicana</u>	12	60	45
<u>N. neglecta</u>	10	60	45
<u>N. Newberryi</u>	10	60	60
	16	65	60
<u>N. parvifolia</u>	12	60	45
<u>N. rigida</u>	14	60	45
		75	60
	18	100	60
<u>N. Schaffneri</u>	18	60	45
<u>N. sinuata</u>	10	60	60
<u>N. Standleyi</u>	11	65	60
	12	75	50
	16	80	55

TABLE 5. Section thickness and staining times of Pellaea.

Species	Section thickness (4)	Staining times (sec.)	
		safranin	fast green
<u>P. allosuroides</u>	12	60	45
<u>P. andromaedifolia</u>	18	60	45
	20	80	60
<u>P. atropurpurea</u>	10	60	50
<u>P. brachyptera</u>	16	60	45
<u>P. Breweri</u>	10	60	45
<u>P. Bridgesii</u>	10	60	45
<u>P. dealbata</u>	12	60	45
<u>P. falcata</u>	18	60	45
<u>P. intermedia</u>	9	55	45
<u>P. longimucronata</u>	10	60	60
<u>P. mucronata</u> v. <u>californica</u>	16	75	60
	18	75	60
<u>P. notabilis</u>	10	60	55
<u>P. ovata</u>	12	60	45
<u>P. pteroides</u>	18	75	50
<u>P. Skinneri</u>	14	100	60
<u>P. viridis</u> v. <u>viridis</u>	10	75	50
		90	60
<u>P. X Wrightiana</u>	16	75	55

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and coupled CdS exposure meter. The camera body was a Nikon M-35S dark box. Kodak Tri-X black and white film (ASA 400) was utilized for all photographs.

Due to the large diameter of most of the rhizome cross sections, it was impossible to include the complete section in one picture. Therefore, photographs of portions of the rhizome were put together for composite pictures. Photographs were taken at 40X with a shutter speed of 1/125 or 1/250th of a second. The composite pictures were trimmed to the outline of the rhizome cross section, placed on a gray mat-board background, covered with glare-proof glass and photographed.

In order to obtain more specific information about the nature of the xylem cells, Jeffrey's (1902) method for maceration was employed. Jeffrey's fluid consists of equal volumes of 10% chromic acid and 10% nitric acid. The tissues were treated for two days at 37 degrees C. Following treatment, the xylem tissue was washed and shaken with glass beads and the fluid decanted off. The tissue was then treated with 10% Chlorox which aided in bleaching the tissues. Chlorox treatment lasted about one-half hour. The Chlorox was decanted off and 1% aqueous safranin was added for a stain. The tissue was then placed on a microscope slide and viewed under 400X total magnification. Polaroid pictures were taken utilizing type 107 black and white Polaroid film on the Nikon photomicroscope as described before.

In an attempt to document the ontogeny of the stele in at least one species, thin sections of the rhizome from living Pellaea viridis were made. Living specimens of P. viridis were obtained from the greenhouse of Normandale Community College. The adventitious roots and fronds were removed from the rhizome by using a single-edged razor

blade. The most basal (the oldest area) portion of the rhizome was then examined. The old gametophyte was found to be still attached to the sporophyte. The last one-quarter of an inch of the rhizome, including the gametophyte, was cut off with a sharp, single-edged razor blade. The rhizome was mounted and then sectioned at 10 to 12 microns on an IEC model CTD Harris microtome cryostat. Wet mount slides were made of the sections, observed and photographed with the photomicrography equipment mentioned before. The Polaroid camera and type 107 black and white Polaroid film was used. Shutter speeds of 1/25 and 1/250th of a second were utilized.

OBSERVATIONS

The following observations will treat the species of each genera alphabetically and will include pertinent ecological and rhizome habit information. Photographs accompany the descriptions and illustrate the species in a mature anatomical condition which, in each case, was typical for the sections examined. Anatomical differences and similarities will be pointed out briefly, but in much more detail in the Discussion section.

Figure 3 illustrates a generalized rhizome cross section. The tissue layers and other features of the rhizome will be referred to by the letter key which is described with Figure 3. The plates throughout the text will include other rhizome features as they occur in some sections; these will be indicated and keyed in the text.

Notholaena Aschenborniana Klotzsh, McCulloch 33-71.

The rhizome habit of this species is stout, shortly-creeping, densely clothed with scales, ascending, branched and multicapital.

The habitat has been described as rocky slopes and ledges and in deep limestone canyons up to 1,600 m. and as dry rocks and cliffs preferring or perhaps confined to limestone, up to 1500-3000m.

The epidermis is one-celled thick and intact for the majority of the rhizome diameter.

Figure 3. Generalized rhizome cross section.
Key to symbols: e, epidermis; c, cortex; oen, outer endodermis; opc, outer pericycle; oph, outer sieve cells and phloem parenchyma; x, tracheids and xylem parenchyma when present; iph, inner sieve cells and phloem parenchyma; ipc, inner pericycle; ien, inner endodermis; pi, pith; lg, leaf gap; lt, leaf trace; art, adventitious root initiation; sc, rhizome scales.

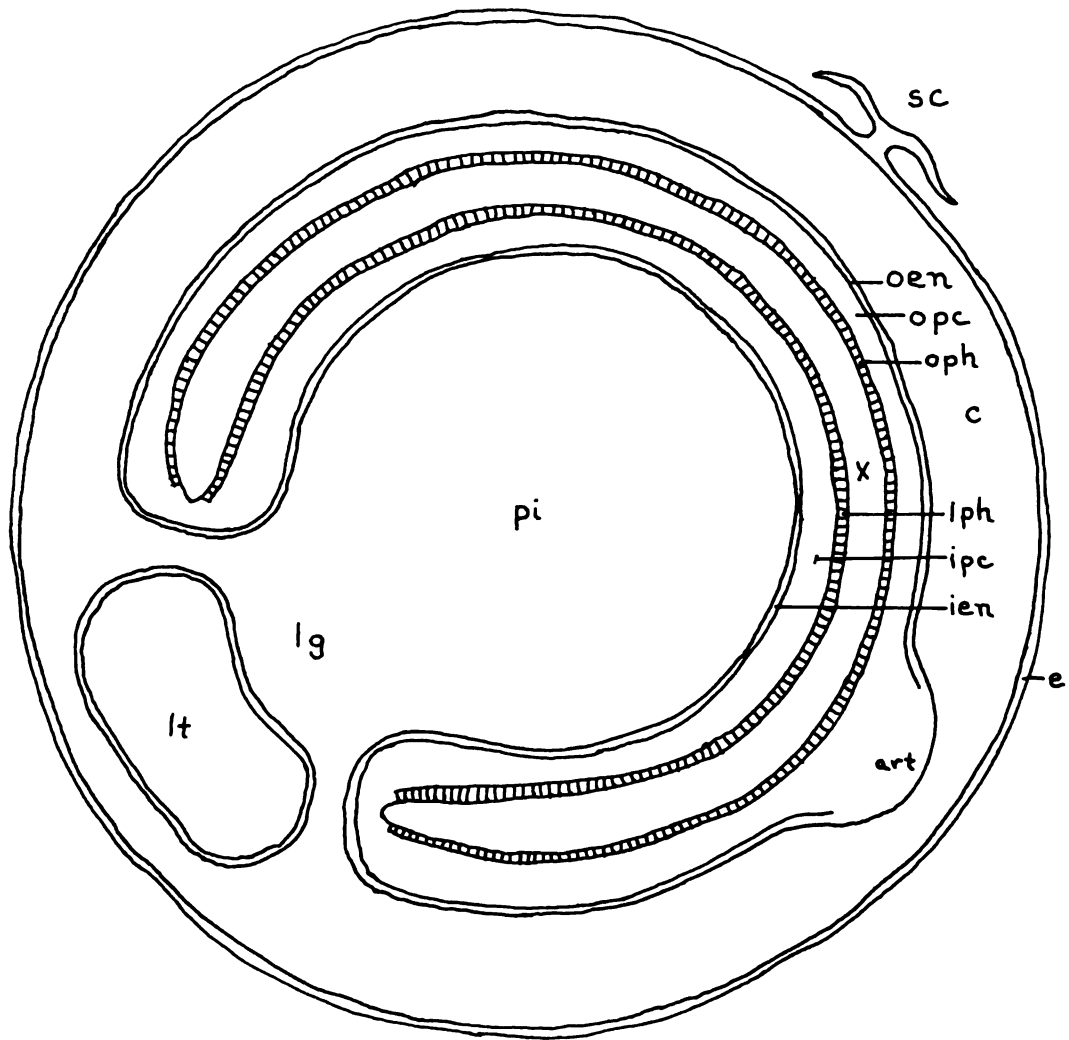
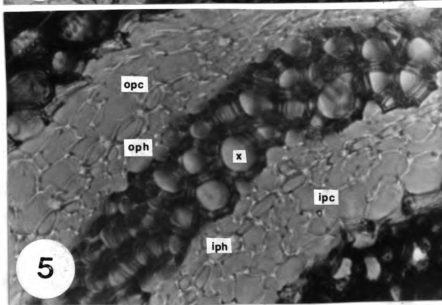
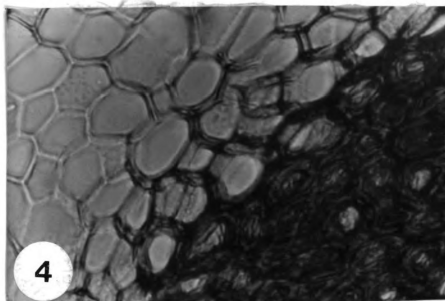


Figure 4. N. Aschenborniana. Cortex. Outer half to left. X100. Figure 5. N. Aschenborniana. Portion of vascular cylinder. Phloem, pericycle and xylem. X100.



The outer one half of the cortex is unsclerified (left area) and the inner portion heavily sclerified (right area) in Figure 4.

Both outer and inner endodermal areas are partially torn. The outer endodermis constitutes the innermost layer of the cortex.

The outer (opc) and inner (ipc) pericycle regions have two to three cell layers of thin walled parenchyma cells (Figure 5).

The outer (oph) and inner (iph) primary phloem are composed of narrow bands of sieve and parenchyma cells (Figure 5). The phloem parenchyma cells are smaller than those of the pericycle and can be seen in Figure 5. The sieve cells can be distinguished from the phloem parenchyma by their apparent lack of nuclei.

The primary xylem consists of scalariform tracheids (x) (Figure 5) and no xylem parenchyma is present. In cross section it is impossible to distinguish proto and metaxylem and the common practice of referring to the smaller of the cells as the protoxylem and the larger of the cells as the metaxylem will be adhered to in this paper; this will be discussed more fully under Discussion.

Notholaena Aschenborniana is considered to possess a solenostelic vascular system.

Notholaena aurea (Poir.) Desv., Knobloch 2483.

The rhizome habit is thick, shortly-creeping, ascending and densely scaly.

The habitat is talus slopes and in crevices of ledges and cliffs, on canyon walls and the base of boulders up to 2100 m.

Figure 6 illustrates a complete rhizome cross section of Notholaena aurea in which a solenostele is present. Two adventitious roots (art) can be seen arising from the outer pericycle. Two stipe cross-sections

Figure 6. N. aurea. Complete rhizome cross section, so Tenostele. X40. Figure 7. N. aurea. Portion of the vascular cylinder plus adjacent tissues. X100.

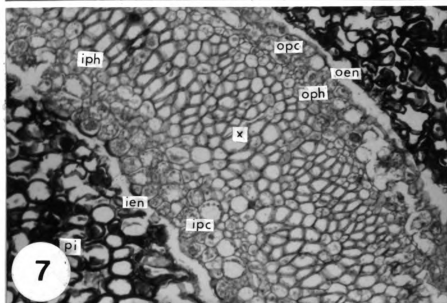
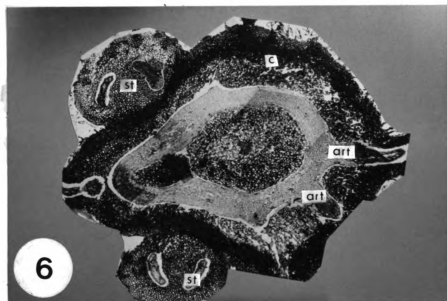
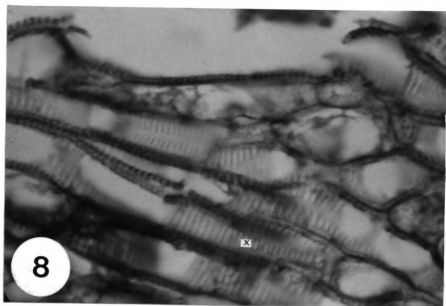


Figure 8. N. aurea. Longitudinal section of primary xylem showing scalariform tracheids. X400.



(st), each with two vascular bundles, can also be noted (Figure 6). In all of the sections examined (14) the solenostelic condition was seen.

The one-celled thick epidermis was intact. Immediately beneath the epidermis is a lightly sclerified area of cortex (c) followed interiorly by a heavier sclerified area and then an area of cortex very lightly sclerified (Figure 6).

Both outer (oen) and inner (ien) endodermal layers are adjacent to outer (opc) and inner (ipc) pericycle (Figure 7) which is three to four cells thick and characteristically stains for starch.

The sieve cells of both outer (oph) and inner primary phloem (iph) are few and scattered and interrupted by phloem parenchyma cells (Figure 7) and the xylem is composed exclusively of scalariform tracheids (x) and xylem parenchyma (Figure 7, 8).

The center of the solenostele is composed of parenchyma (pi) which is much more uniform in nature than the cortex (Figure 6).

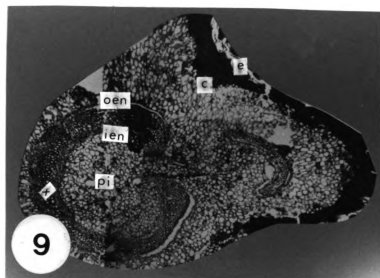
Notholaena brachypus (Kze.) J. Sm., Knobloch 1645.

The rhizome habit is short, thick and erect while the habitat is damp, shaded banks, rocky places, on rocks and occurring from 200-1600 m.

The epidermis is present but was badly torn. Internal to the epidermis (e) was a heavily-sclerified cortex (c) region. The abrupt change to thinner walled cells in the cortex layers adjacent to the outer endodermis (oen) (Figure 9) was distinct.

The outer endodermis (oen) is torn in this preparation, but the inner endodermis (ien) is, for the most part, intact (Figure 9). Internal to the endodermal layers are the outer and inner pericycle regions consisting of three to four cell layers.

Figure 9. N. brachypus. Complete rhizome cross section, solenostele. X40.



Scattered sieve cells and phloem parenchyma cells of both outer and inner primary phloem lie on opposite sides of the scalariform tracheids of the xylem (x) (Figure 9). The pith (pi) region shows no sclerification except in one isolated area (Figure 9). Notholaena aurea is interpreted to be a solenostele.

Notholaena candida (Mart. and Gal.) Hook. var. candida, Knobloch 2288.

The rhizome habit is short-creeping and branched, while the habitat of this species is on igneous rocks, found in sun or partial shade, from 500-1500 m. elevation.

In all sections examined, the most heavily sclerified regions of the cortex (c) are outermost and the sclerification gradually decreases as one progresses inward toward the outer endodermis (Figure 10). The one-cell thick outer (oen) and inner (ien) endodermis were torn in some preparations and not in others (Figure 11).

The outer pericycle (opc) is composed of three to four layers of large parenchyma cells (Figure 11). An adventitious root (art) can be seen originating in the outer pericycle (Figure 11) and the inner pericycle (ipc) is of a similar composition (Figure 11).

The outer and inner sieve cells are few in number and the phloem parenchyma cells are adjacent to the xylem, while the xylem (x) is composed of scalariform tracheids and xylem parenchyma is present (Figure 10, 12). Notholaena candida v. candida is considered to be solenostelic (Figure 10).

Notholaena candida (Mart. and Gal.) Hook. var. Copelandii (C. C. Hall) R. Tryon, McCulloch 14-71.

Figure 10. N. candida v. candida. Complete rhizome cross section, solenostele. X40.
Figure 11. N. candida v. candida. Portion of the vascular cylinder. X100.

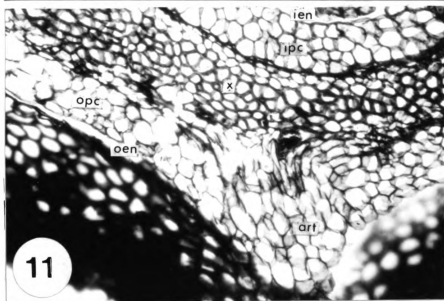
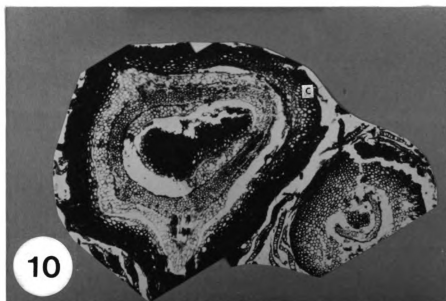


Figure 12. N. candida v. candida. Cross
section of primary xylem. X400.

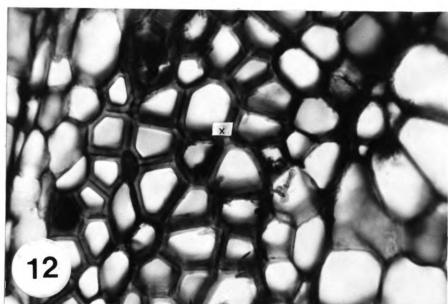
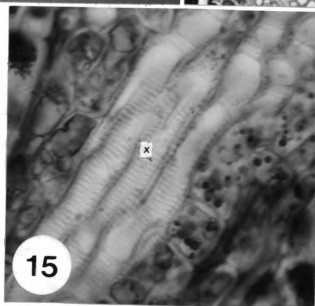
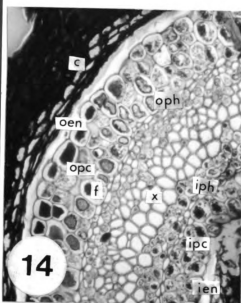
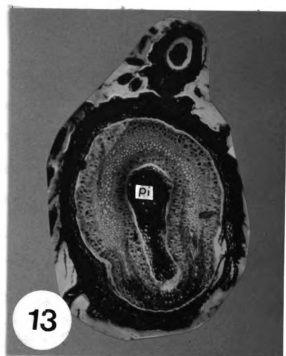


Figure 13. N. candida v. Copelandii. Complete rhizome cross section, solenostele. X40. Figure 14. N. candida v. Copelandii. Portion of the vascular cylinder. X100. Figure 15. N. candida v. Copelandii. Longitudinal section of primary xylem. X400.



The rhizome is short, compact, and multicipital. This variety of N. candida occurs on limestone ledges and in crevices of canyon walls and bluffs, on rocky slopes, at the base of cap rock and about boulders up to 1117.6 m.

The cortex (c) is heavily sclerified except the two-three cell layers adjacent to the outer endodermis (oen) (Figure 14). Both the outer (oen) and inner (ien) endodermal layers were torn in this preparation (Figure 14). Internal to the endodermal layers the outer (opc) and inner (ipc) pericycle were observed to consist of large parenchyma cells with some type of food storage (f) material retaining a stain (Figure 14).

The outer (oph) and inner (iph) sieve cells are scattered in a single, sometimes double row and the phloem parenchyma is adjacent to the xylem (x) (Figure 14). The xylem (x) is composed entirely of scalariform tracheids and small scattered areas of xylem parenchyma are visible (Figure 14, 15). The pith (pi) gradually increases in sclerification as one proceeds toward the center (Figure 13). Notholaena candida v. Copelandii exhibits a solenostele (Figure 13).

Notholaena cochisensis Goodding, Knobloch 2493.

The rhizome habit is short, thick, multicipital and densely clothed with scales, and the habitat is rock outcrops, rocky slopes of limestone, sandstone, lava and gypsum; usually found in full sunlight and occurring up to 2,300 m. altitude.

Unfortunately the rhizomes were not in a very good state of preservation for embedding and a high degree of tearing took place during sectioning. The best sections are described and illustrated.

Figure 16. N. cochisensis. Complete rhizome cross section, transitional. X40. Figure 17. N. cochisensis. Complete rhizome cross section, solenostele. X40. Figure 18. N. cochisensis. Longitudinal section of primary xylem. X400.

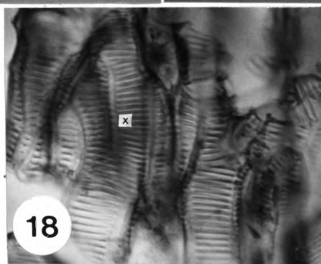
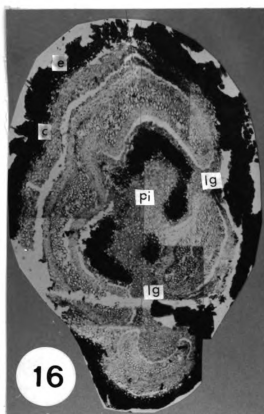
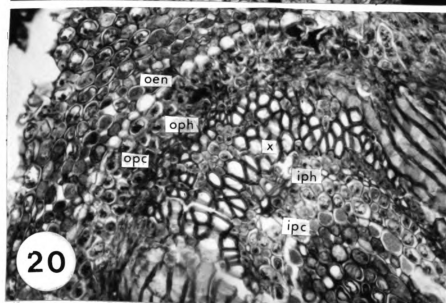
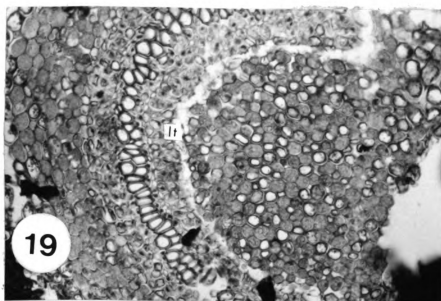


Figure 19. N. cochisensis. Stipe cross section. X100. Figure 20. N. cochisensis. Portion of the rhizome vascular cylinder. X100.



The epidermis (e) is partially intact in this species, and the outer cortex (c) area can be seen to be heavily sclerified, with the cells closest to the vascular cylinder being least sclerified (Figure 16). In a great many cases the cell lumens are entirely obscured.

Figure 17 is probably an older rhizome section than Figure 16, this would be indicated by the greater degree of cell wall thickness and a greater concentration of tannin-like substances.

In sections examined of this species the outer and inner endodermal layers were torn. In Figure 20 the outer (opc) and inner (ipc) pericycle tissues and an area where the outer endodermis (oen) is intact are all visible.

The sieve cells and parenchyma of the phloem are more easily discerned on the inner (iph) side of the xylem (x), while the outer sieve (oph) and parenchyma cells appear a bit compressed (Figure 20). The xylem (x) consists of scalariform tracheids (Figure 18, 20), xylem parenchyma can also be seen (Figure 20). The pith (pi) may be lightly or heavily sclerified. Figure 16 shows the former and Figure 17 shows the latter type.

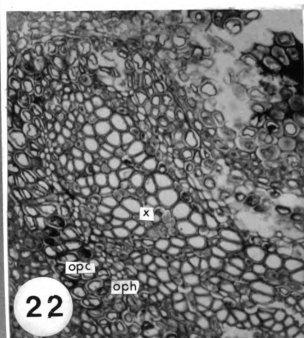
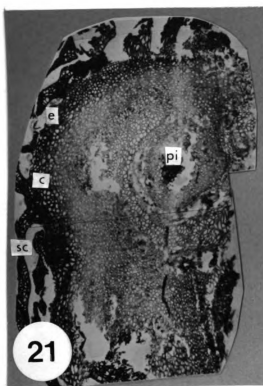
Figure 16 illustrates a section that has two leaf gaps (lg) occurring in it. One leaf trace (lt) is visible in Figure 19. Figure 17 shows the same tissue arrangements. The difference being the greater degree of sclerification and that a true solenostele is present.

Notholaena cochisensis is a transitional stele type.

Notholaena Galeottii Fée, Knobloch 2198.

The habit of the rhizome is sub-horizontal and/or short-creeping. The habitat is shaded or exposed rocks and rocky banks occurring from 1500-2200 m. elevation.

Figure 21. N. Galeottii. Complete rhizome cross section, solenostele. X40. Figure 22. N. Galeottii. Portion of the rhizome vascular cylinder. X100.



The epidermis (e) is partially torn off in the preparation, but is partially seen as are rhizome scales (sc) (Figure 21). Internal to epidermis the outer third of the cortex (c) can be seen as sclerified and the remainder of the cortex is less sclerified (Figure 21).

Figure 22 illustrates the three-four cell layered outer pericycle (opc), sieve cells and phloem parenchyma (oph) plus the xylem (x) which is composed of scalariform tracheids and xylem parenchyma cells. Figures 114, 115 illustrate isolated scalariform tracheids (x) and Figure 116 illustrates a helical protoxylem cell (px). The pith area is most heavily sclerified in the central portion (Figure 21).

This species is a solenostele. Even though the preparation of this species is not ideal, all 35 sections examined indicated the solenostele condition as being present.

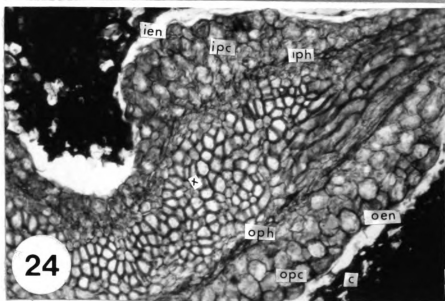
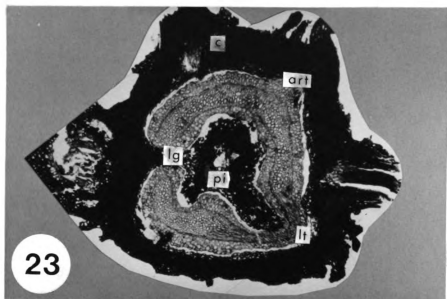
Notholaena Grayii Davenp., Knobloch 2078.

The rhizome is nodose, multicapital, sometimes short-creeping and densely scaly. The habitat is talus slopes in rock crevices, barrens of igneous rock and limestone occurring up to 1,900 m. altitude.

The epidermis and epidermal appendages are sclerified in this taxon. Internally from the epidermis the cortex (c) is heavily sclerified (Figure 23) with the exception of the innermost cell layers (Figure 24). Both outer (oen) and inner (ien) endodermal layers have been torn in this preparation (Figure 24), and the outer (opc) and inner (ipc) pericycle regions are composed of large parenchyma cells (Figure 24).

The sieve cells of both outer (oph) and inner (iph) primary phloem are partially compressed and the phloem parenchyma cells are adjacent to the xylem (Figure 24). The xylem (x) is composed of scalariform tracheids and xylem parenchyma is present (Figure 24). An examination

Figure 23. N. Grayi. Complete rhizome cross section, solenostele. X40. Figure 24. N. Grayi. Portion of the vascular cylinder. X100.



of all sections (14) of Notholaena Grayii indicate a solenostele (Figure 23). A partially closed leaf gap (lg), a new leaf trace (lt) originating, and an adventitious root (art) originating from the outer pericycle (Figure 23). The pith (pi) becomes more sclerified as one progresses toward the center (Figure 23).

Notholaena integerrima Hook., McCulloch 61-71 and 31-71.

The rhizome is short, thick, multicipital and densely clothed with hairs and the habitat is on calcareous substrates.

The epidermis (e) is intact in this preparation (Figure 25). Internal to the epidermis, the cortex (c) has a very definitive outer band of thickened cells and an inner region of relatively unsclerified cells in which large air spaces (as) occur (Figure 25).

The outer endodermis is partially torn but the inner endodermis is intact. The outer and inner pericycle areas are similar to other taxa examined, as are the sieve cells and phloem parenchyma cells of the outer and inner primary phloem.

The xylem (x) is scalariform tracheids and there is xylem parenchyma present (Figure 25).

All sections examined illustrated the transitional and solenostele condition. Figure 25 illustrates the solenostele condition, and three adventitious roots (art) can be seen emerging from the outer pericycle. The pith (pi) is uniform in composition with the same types of air spaces (as) present as seen in the cortex (Figure 25).

Notholaena Lemmonii D. C. Eaton, Cross s.n.

The rhizome habit of this taxon is multicipital, short, thick, and ascending.

Figure 25. N. integerrima. Complete rhizome cross section, solenostele. X40.

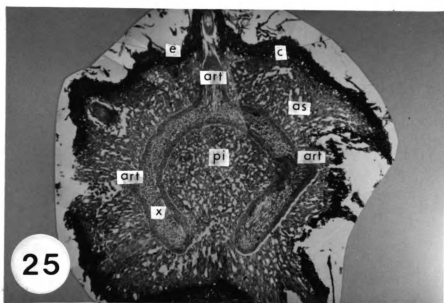
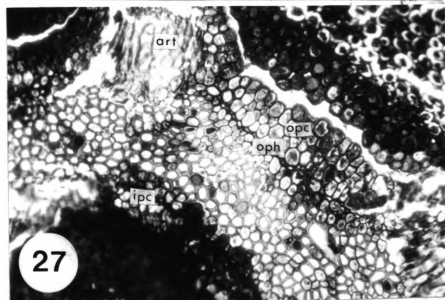
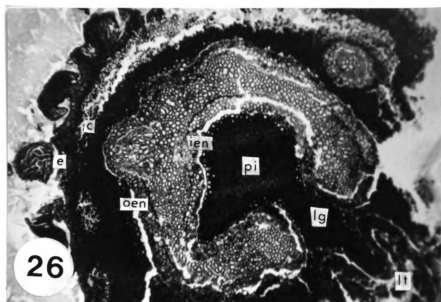
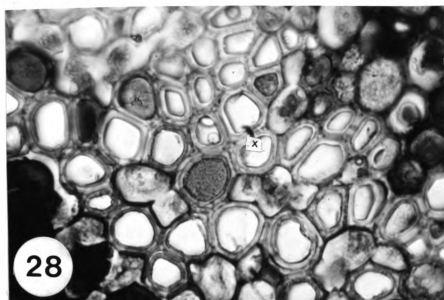


Figure 26. N. Lemmonii. Complete rhizome cross section, solenostele. X40. Figure 27. N. Lemmonii. Portion of the vascular cylinder. X100.



**Figure 28. N. Lemmonii. Cross section of
primary xylem. X400.**



The habitat of N. Lemmonii is the base of shaded rocks, pendent from crevices of old stone walls and igneous rocks from 1000-1500 m. elevation.

The epidermis (e) is partially torn in this preparation (Figure 26), while the cortex (c) exhibits a band of heavily sclerified cells, a band of lightly sclerified cells and a band of heavily sclerified cells as one progresses from the epidermis inward to the outer endodermis (oen) (Figure 26).

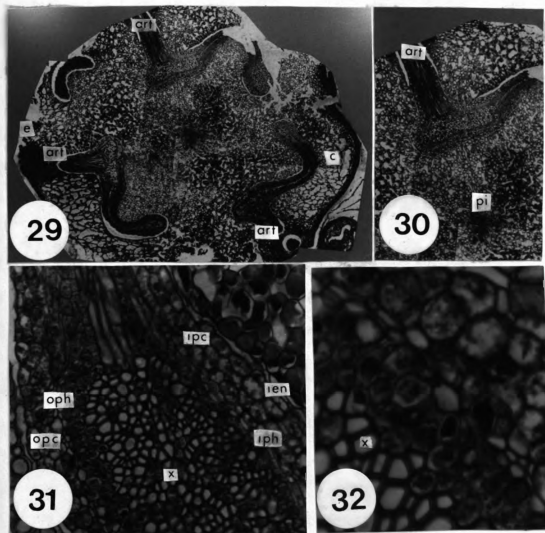
The outer (oen) and inner (ien) endodermal layers are both partially torn (Figure 26), and the outer (opc) and inner (ipc) pericycle consist of large parenchyma cells arranged in three to four cell layers (Figure 27). An adventitious root (art) can be seen originating from the outer (opc) pericycle in Figure 27. A leaf gap (lg) and leaf trace (lt) are noted in the lower right hand portion of Figure 26.

The sieve cells of the outer (oph) primary phloem forms a single layer that is almost uninterrupted (Figure 27), whereas the inner primary phloem is compressed. Phloem parenchyma separates the sieve cells from the xylem. The xylem (x) consists of scalariform tracheids, among which are scattered areas of xylem parenchyma (Figures 27, 28). The pith (pi) is uniformly heavily sclerified except for the outer one or two cell layers (Figure 26). Notholaena Lemmonii exhibits a solenostele.

Notholaena limitanea Maxon var. mexicana (Maxon) Broun, McCulloch 59-71.

The rhizome habit is described as decumbent to horizontal and compact and short. The habitat of this species is cliffs and rocky hillsides in calcareous or acidic soils occurring from elevations of 1700-3000 m.

Figure 29. N. limitanea v. mexicana. Complete rhizome cross section, transitional. X40. Figure 30. N. limitanea v. mexicana. Portion of the vascular cylinder, adventitious root. X40. Figure 31. N. limitanea v. mexicana. Cross section of the vascular cylinder. X100. Figure 32. N. limitanea v. mexicana. Outer endodermis to xylem. X400.



The epidermis (e) is partially torn in this taxa (Figure 29). The cortex (c) is uniform in its composition of large parenchyma cells which are for the most part not sclerified. In some areas toward the epidermis, two to three cell layers of cortex show some sclerification (Figure 29).

Both outer (oen) and inner (ien) endodermal areas are torn, except in a few specific areas (Figure 31). The outer (opc) and inner (ipc) pericycle areas consist of two to four cell layers of parenchyma cells (Figure 31). The cells of both pericycle regions are smaller than the parenchyma cells of the cortex. Adventitious roots (art) can be seen originating from the outer pericycle (Figure 29, 30).

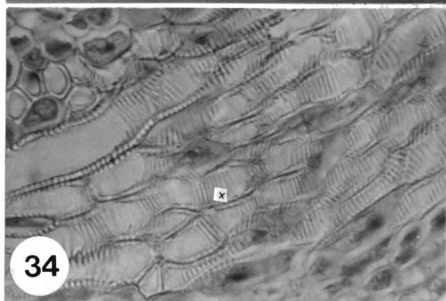
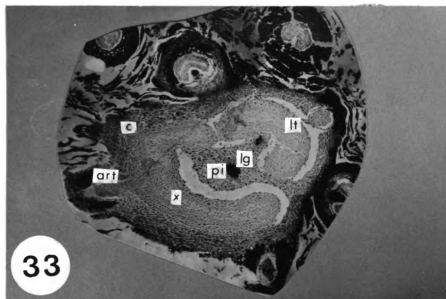
The primary phloem of both outer (oph) (Figure 31, 32) and inner (iph) (Figure 31) areas are sieve cells which occur in practically a continuous band in the vascular cylinder. The phloem parenchyma, both inner and outer, consist of cells smaller than the parenchyma of the pericycle. The xylem (x) consists of presumably scalariform tracheids and xylem parenchyma (Figure 31, 32). The pith (pi) is of similar composition to the cortex with little or no sclerification evident (Figure 30). All sections examined showed neither a true solenostele nor a true dictyostele. Therefore, N. limitanea v. mexicana is a transitional stele.

Notholaena neglecta Maxon, McCulloch 85-71.

The rhizome habit is short, multicipital, decumbent and densely scaly. The habitat is dry crevices in limestone ledges and cliffs and on rocky slopes and in canyons.

The epidermis is partially torn off from this preparation. The cortex (c) is uniform except for a few isolated areas that show some sclerified cells (Figure 33).

Figure 33. N. neglecta. Complete rhizome cross section, solenostele. X40. Figure 34. N. neglecta. Oblique section of primary xylem. X400.



The one cell thick outer and inner endodermal areas are partially torn in this preparation, while the pericycle, outer and inner, is a region of four to five cell layers in thickness. An adventitious root (art) is originating from the outer pericycle (Figure 33).

The sieve cells of the primary phloem (inner and outer) are scarce, as in most species, and do not form a continuous band of cells. The phloem parenchyma cells are scattered and adjacent to the xylem (x) (Figure 34). The xylem (x) is composed entirely of scalariform tracheids and xylem parenchyma (Figure 34). One leaf gap (lg) and its subtending trace (lt) can be seen in Figure 33. The pith (pi) is uniform except for some heavily sclerified cells in the center and an isolated pocket of cells (Figure 33). Notholaena neglecta is described as a solenostele.

Notholaena Newberryi D. C. Eaton, Knobloch accession 71-16,
Hoover s.n.

The rhizome habit is horizontal, branched and forming dense clumps, while the habitat is dry rocky places and crevices of rock, occurring up to 1300 m.

The epidermis (e) is, for the most part, still intact and is one cell layer (Figure 35). The cortex (c) in all sections examined (145) was practically all uniform and the cell walls were heavily sclerified (Figure 35, 36).

Both outer (oen) and inner (ien) endodermal layers were usually torn in preparation but some sections did have intact endodermal layers (Figure 35). The outer (opc) and inner (ipc) pericycle regions consist of four to five layers of parenchyma cells (Figure 36).

The outer (oph) and inner (iph) phloem areas are one to two layers of cells wide and seem to form almost a continuous band around the stele,

Figure 35. N. Newberryi. Complete rhizome cross section, solenostele. X40. Figure 36. N. Newberryi. Portion of the vascular cylinder. X100.

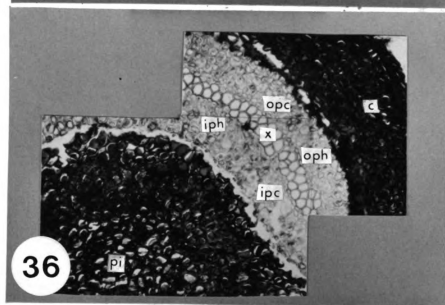
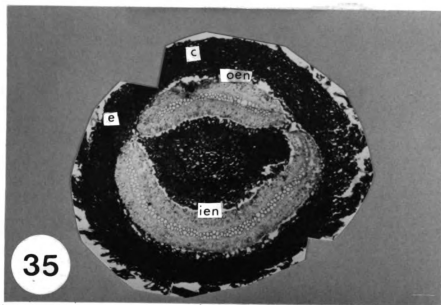
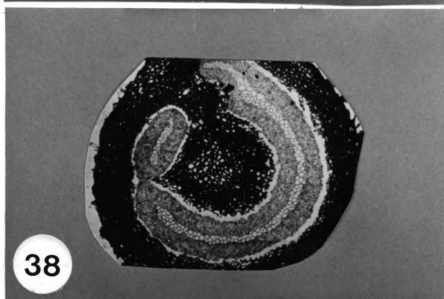
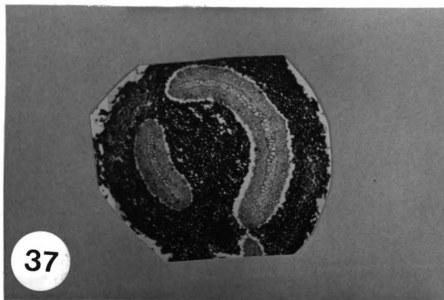


Figure 37. N. Newberryi. Complete rhizome cross section, transitional. X40. Figure 38. N. Newberryi. Complete rhizome cross section, solenostele. X40.



except where gaps occur. There are not as many phloem parenchyma cells in this species and the sieve cells appear closer to the xylem than in other taxa. The xylem (x) is not as massive as in previous species and there is no xylem parenchyma present (Figure 36). The pith (pi) area is heavily sclerified, with the least sclerified cells seeming to occur in the central portion of the pith (Figure 36). Figures 35 and 38 indicate that this taxon is a solenostele with some indication that it may be transitional (Figure 37) in some portions of its habit.

Notholaena parvifolia R. M. Tryon, Knobloch 1687 and 1687-1.

The rhizome habit is short, thick and scaly. The habitat of this species is limestone ledges in gorges and canyons, high on limestone hills and talus slopes, faces of cap rock, and in shaded or exposed situations.

The epidermis (e) of the preparation is partially intact (Figure 39). 1687-1 illustrates a high degree of tissue disintegration in the cortex (c) and pith (pi) regions (Figure 40). It still can be noted, however, that two distinct areas exist in the cortex (c): an outer band (4-5 cells in thickness), the cells of which have definitely more sclerified walls and are smaller in area than those of the remaining inner area (Figure 40). Figure 39 of collection 1687 shows the same arrangement, but in this specimen there is no disintegration.

Endodermal areas are partially torn in 1687-1 and 1687, while pericycle areas are most obvious in collection 1687, in which adventitious roots (art) can be seen (Figure 39).

The sieve cells in the phloem areas, both outer and inner, are similar to other taxa described, that is, they are few in number and scattered in a ring surrounding the xylem. Figure 41 illustrates the

Figure 39. N. parvifolia. Complete rhizome cross section, transitional. X40. Figure 40. N. parvifolia. Complete rhizome cross section, transitional. X40.

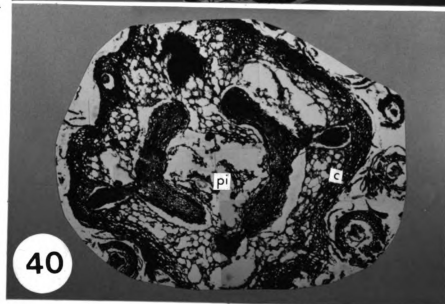
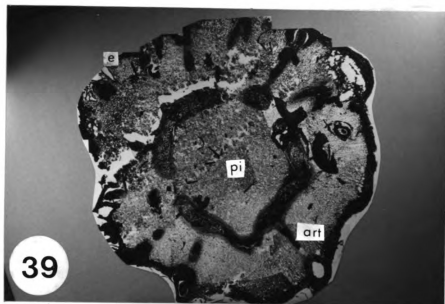
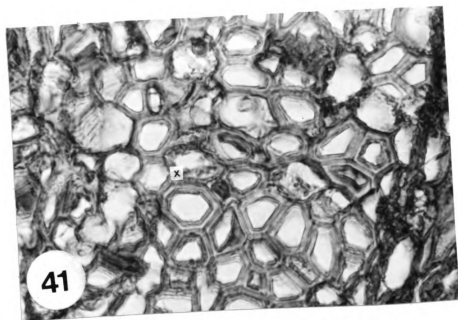


Figure 41. N. parvifolia. Cross section of primary xylem. X400.



scalariform tracheids (x) and the xylem parenchyma. The pith (pi) is homogenous throughout with no indication of sclerified cells (Figure 39).

Figures 39, 40 illustrate a good section that is transitional in nature, therefore, N. parvifolia is considered to be transitional.

Notholaena rigida Davenp., Knobloch 2244.

The rhizome habit is horizontal and rather slender, and the habitat is limestone ledges.

The one-celled layer of epidermis (e) is intact in this preparation and several scales can be seen in Figures 42 and 43. The cells of the cortex (c) appear to be equally sclerified, but with smaller cells toward the epidermis and inner endodermis (Figure 42, 44). All cells are impregnated by suberin and lignin. The effect of the wall impregnations is heightened by the filling of the cells in the cortex and pith in this case, with gums and tannin-like substances.

Both outer (oen) and inner (ien) endodermal layers are torn in this preparation (Figure 42). Both outer (opc) and inner (ipc) pericycle regions are from one to four cells thick and consist of variously shaped, thin-walled parenchyma cells and enclose food (f) reserve materials (starches and oils) in addition to the normal cell contents (Figure 44).

The outer (oph) and inner (iph) primary phloem is readily visible in Figure 44 and consists of a narrow band of sieve and phloem parenchyma cells. The phloem parenchyma cells are smaller than those of the pericycle but also contain reserve foods (f) (Figure 44). The xylem (x) consists of scalariform tracheids and xylem parenchyma is present (Figure 45). The pith (pi) cells have the same type of cell wall impregnations and cell content as the cells of the cortex, the most heavily sclerified area being the central mass of cells (Figure 42).

Figure 42. N. rigida. Complete rhizome cross section, solenostele, internode. X40.

Figure 43. N. rigida. Complete rhizome cross section with leaf trace at node. X40.

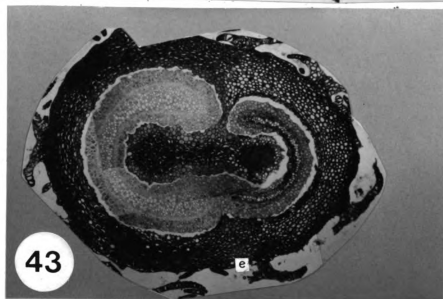
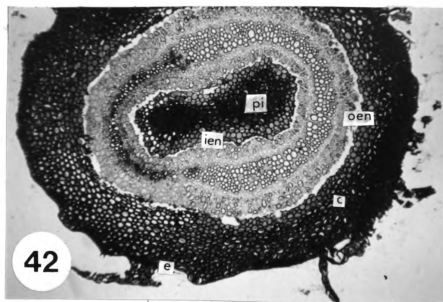
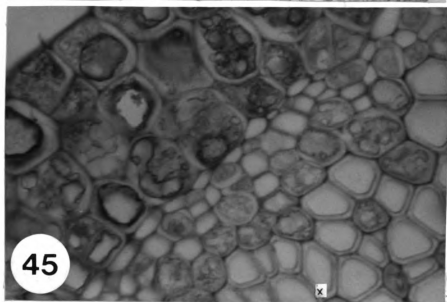
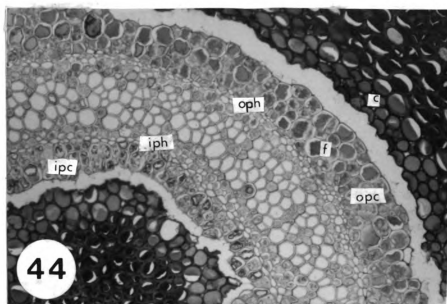


Figure 44. N. rigida. Portion of the vascular cylinder. X100. Figure 45. N. rigida. Cross section from outer pericycle to primary xylem. X400.



In all sections examined a solenostelic condition was noted, and therefore, N. rigida is considered to be solenostelic.

Notholaena Schaffneri (Fourn.) Underw. ex Davenp. var. Schaffneri, Knobloch 2478.

The rhizome is short, branched and ascending, and the habitat is shaded ledges and rocky places from 100-1700 m. elevation.

The one-celled thick epidermis of this species is still intact and a portion of a rhizome scale (sc) can be seen in Figure 46. In this species the thickest-walled cells of the cortex occur in a central band in the cortex bounded on the inside and outside by thinner-walled cells. In many cases the lumen of the cells has been occluded by the cell content (c) (Figure 47).

Both outer (oen) and inner (ien) endodermal layers are torn in this preparation (Figure 46). The root traces (art) can be seen originating from the outer pericycle (opc) in Figure 46. The leaf gap (lg) is still present from the origin of a leaf trace (lt) and a second trace (lt) appears to be forming (Figure 46). The outer (opc) and inner pericycles are from three to four cells thick (Figure 47).

The sieve cells of the outer (oph) and inner (iph) primary phloem were compressed in sectioning and appear as a thin dark line bordering a large xylem (x) area consisting of scalariform tracheids and xylem parenchyma cells (Figure 47). The pith (pi) of this species has the same cellular banding arrangement as the cortex (Figure 46). N. Schaffneri is solenostelic.

Notholaena sinuata (Lag. ex Sw.) Kaulf., McCulloch 43-71.

The rhizome of this species is short, thick, multicipital and densely clothes with scales, while the habitat is dry, gravelly slopes,

Figure 46. N. Schaffneri. Complete rhizome cross section, three adventitious roots, solenostele. X40. Figure 47. N. Schaffneri. Portion of the vascular cylinder. X100.

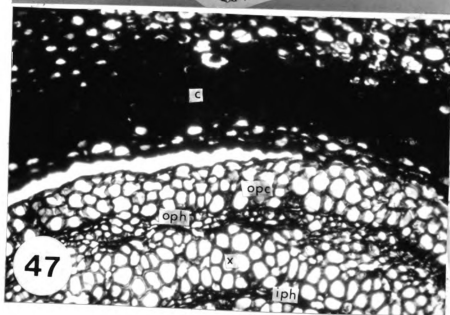
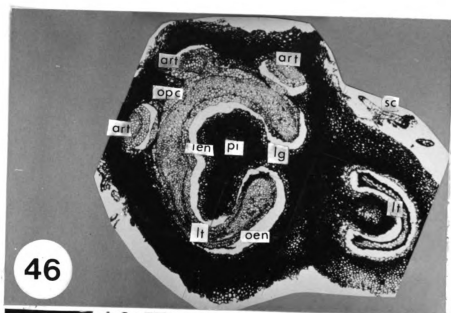
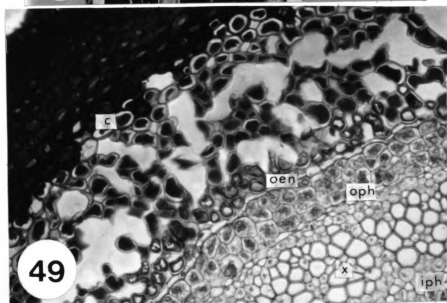
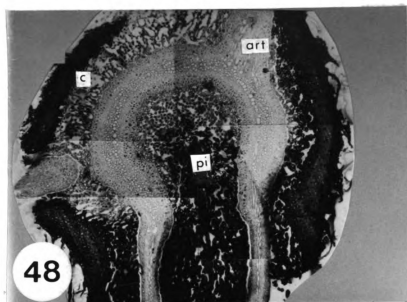


Figure 48. N. sinuata. Complete rhizome cross section, adventitious root and leaf trace. X40. Figure 49. N. sinuata. Portion of the vascular cylinder at lower right. X100.



with the plants being found on or about boulders, ledges and canyon walls and in crevices of lava cliffs, in full sunlight or in partial shade and up to 2000 m. altitude.

The epidermis (e) is intact in this preparation as evidenced by the sclerified rhizome scales (sc) (Figure 48). The cortex (c) is divided into two distinct areas; an outer region which is heavily sclerified and the cells filled with tannin-like substances and an inner region, in which the cells are not nearly or not sclerified and seem to have intracellular air spaces (Figure 48, 49).

The outer (oen) and inner endodermis are for the most part intact (Figure 49). Starches and oils are visible in both the inner and outer parenchyma cells of the pericycle and a root trace (art) can be seen originating from the outer pericycle in Figure 48.

Sieve cells and parenchyma cells of the outer (oph) and inner (iph) primary phloem are alike in appearance and visible in Figure 49. The xylem (x) consists of scalariform tracheids and xylem parenchyma is present (Figure 49). The pith (pi) resembles the cortex in cell types, but not in arrangement. The more heavily sclerified cells seem to occur at points of leaf trace origins (Figure 48). In all sections examined a solenostele was observed.

Notholaena Standleyi Maxon, McCulloch 60-71.

The rhizome of N. Standleyi is short, multicipital and densely covered with scales. The habitat is one of dry rock ledges and crevices, on talus slopes, cliffs, canyon walls and on and among boulders, on sandstone, limestone, rhyolite and lava, occurring up to elevations of 2,200 m.

Figure 50. N. Standleyi. Complete rhizome cross section, adventitious root and leaf gap. X40. Figure 51. N. Standleyi. Vascular cylinder. X40.

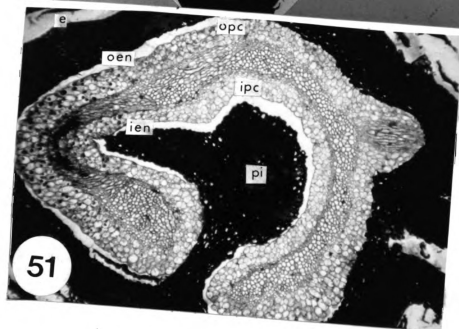
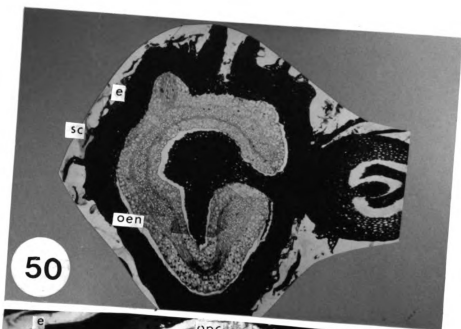
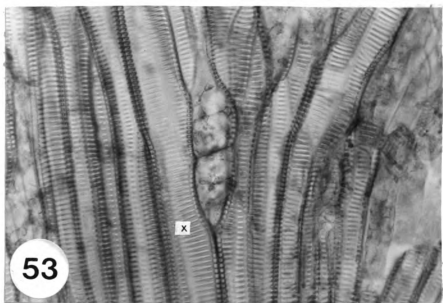
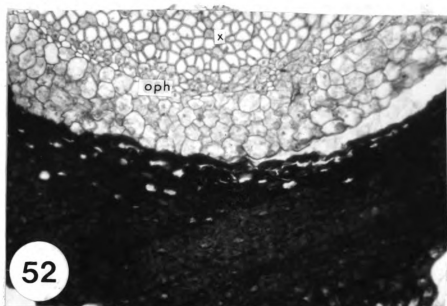


Figure 52. N. Standleyi. Portion of the vascular cylinder, at top. X100. Figure 53. N. Standleyi. Longitudinal section of primary xylem showing scalariform tracheids. X400.



The epidermis (e) in N. Standleyi is still intact and several rhizome scales (sc) can be seen in Figure 50. The cortex is very heavily sclerified from the epidermis (e) to the outer endodermis (oen) (Figure 50, 51). The cortical cells closest to the epidermis and outer endodermis are the most heavily sclerified and the middle area of the cortex has cells that are slightly less sclerified. In most cases the cortical cell lumens are completely obscured (Figure 51).

The outer (oen) and inner (ien) endodermal layers were both torn in this preparation (Figure 51). The outer (opc) and inner (ipc) pericycle areas are alike, consisting of large, thin-walled parenchyma cells (Figure 51).

Sieve cells and phloem parenchyma cells of both outer (oph) and inner primary phloem areas are alike (Figure 52). The xylem (x) consists of scalariform tracheids and xylem parenchyma is present (Figure 52). Figure 53 illustrates the scalariform tracheids (x) in longitudinal section and Figure 117 shows them (x) isolated after maceration. The pith (pi) is evenly sclerified with most of the cell lumen areas obscured (Figure 51).

This species is a solenostele with some areas that show a transitional nature.

Table 6 is a list of Notholaena species that have had the rhizome described in the literature by various authors but were not available for sectioning by this investigator.

TABLE 6. Stele types of unsectioned Notholaena rhizomes.

Species	Stele	Source
<u>N. Marantae</u> R. Br.	transitional	Gwynne-Vaughan (1903)
<u>N. Marantae</u> R. Br.	transitional	Ogura (1972)
<u>N. Marantae</u> R. Br.	dorsiventral soleno- stele	Tansley (1907)
<u>N. Marantae</u> R. Br.	dorsiventral dictyo- stele	Posthumus (1924, 1936)
<u>N. trichomanoides</u> (L.) R. Br.	transitional	Gwynne-Vaughan (1903)
<u>N. trichomanoides</u> (L.) R. Br.	transitional	Ogura (1972)
<u>N. trichomanoides</u> (L.) R. Br.	transitional to solenostele	Posthumus (1936)
<u>N. trichomanoides</u> (L.) R. Br.	dorsiventral dictyo- stele	Posthumus (1924)

Table 7 summarizes the stele type and the presence or absence of xylem parenchyma in the Notholaena species examined. Table 8 summarizes the number of sections examined and the stem diameter of the rhizomes.

Pellaea allosuroides (Mett.) Hieron, Knobloch 2069.

The rhizome of P. allosuroides is rather stout, short-creeping and densely scaly, and the habitat is cliffs, boulders and humus on rocky slopes up to 2,600 m. elevation.

The epidermis (e) is partially sloughed off in these preparations (Figure 54, 55). The cortex (c) is heavily sclerified with the outer few cell layers being less so than the inner regions (Figure 55).

Both outer (oen) and inner (ien) endodermal layers have been torn in preparation (Figure 55). The outer and inner pericycle regions are thin-walled, parenchyma cells. Adventitious roots (art) can be seen as

TABLE 7. Stele type and xylem parenchyma of Notholaena.

Species	Xylem parenchyma	Stele
<u>N. Aschenborniana</u>	no	solenostele
<u>N. aurea</u>	yes	solenostele
<u>N. brachypus</u>	yes	solenostele
<u>N. candida</u> v. <u>candida</u>	yes	solenostele
<u>N. candida</u> v. <u>Copelandii</u>	yes	solenostele
<u>N. cochisensis</u>	yes	solenostele-transitional
<u>N. Galeottii</u>	yes	solenostele
<u>N. Grayi</u>	yes	solenostele
<u>N. integerrima</u>	yes	solenostele-transitional
<u>N. Lemmonii</u>	yes	solenostele
<u>N. limitanea</u> v. <u>mexicana</u>	yes	transitional-solenostele
<u>N. neglecta</u>	yes	solenostele
<u>N. Newberryi</u>	no	solenostele-transitional
<u>N. parvifolia</u>	yes	transitional
<u>N. rigida</u>	yes	solenostele
<u>N. Schaffneri</u>	yes	solenostele
<u>N. sinuata</u>	yes	solenostele
<u>N. Standleyi</u>	yes	solenostele

TABLE 8. Number of sections examined and stem diameter of Notholaena.

Species	Sections examined	Rhizome diameter (mm.)
<u>N. Aschenborniana</u>	14	2.50 - 3.50
<u>N. aurea</u>	41	3.75 - 5.00
<u>N. brachypus</u>	1	3.50 - 5.00
<u>N. candida</u> v. <u>candida</u>	77	2.00 - 3.50
<u>N. candida</u> v. <u>Copelandii</u>	13	1.10 - 1.25
<u>N. cochisensis</u>	42	2.50 - 4.00
<u>N. Galeottii</u>	35	2.00 - 2.25
<u>N. Grayi</u>	14	2.00 - 3.00
<u>N. integerrima</u>	18	3.00 - 4.25
<u>N. Lemmonii</u>	3	1.25 - 2.25
<u>N. limitanea</u> v. <u>mexicana</u>	8	3.50 - 4.50
<u>N. neglecta</u>	6	1.50 - 2.00
<u>N. Newberryi</u>	145	1.25 - 2.00
<u>N. parvifolia</u>	99	5.50 - 6.00
<u>N. rigida</u>	97	1.50 - 1.75
<u>N. Schaffneri</u>	44	2.00 - 3.00
<u>N. sinuata</u>	3	3.00 - 4.00
<u>N. Standleyi</u>	10	2.00 - 2.75

Figure 54. P. allosuroides. Complete vascular cylinder with leaf gap, leaf trace and adventitious root, solenostele. X40.

Figure 55. P. allosuroides. Complete vascular cylinder, leaf gap and two adventitious roots, solenostele. X40.

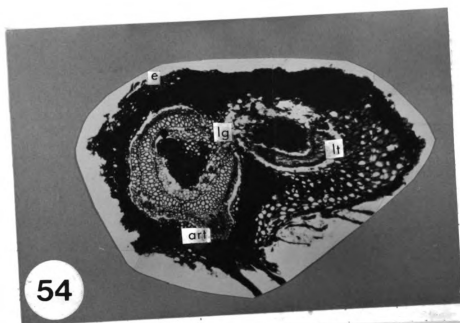
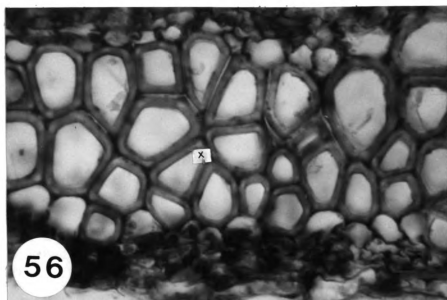


Figure 56. P. allosuroides. Cross section
of primary xylem. X400.



originating from the outer pericycle area in Figure 54, 55 and a leaf gap (lg) and leaf trace (lt) are visible in Figure 54.

The sieve cells and parenchyma cells of the outer and inner primary phloem have been compressed in preparation and appear as a thin, dark line in both outer and inner areas. The xylem (x) is scalariform tracheids and it should be noted that no xylem parenchyma is present (Figure 55, 56). The pith (pi) is very highly sclerified and the cell contents occlude the lumens as it does in the majority of cells in the cortex (Figure 55). All sections examined illustrated a solenostele (Figure 54, 55).

Pellaea andromaedifolia (Kaulf.) Fée, Knobloch accession 71-22.

The rhizome is slender, cord-like, dichotomously branched, long-creeping and rarely compact. The habitat of this fern is dry, rocky ravines, ledges or along moist shaded stream banks between 60-100 m. elevation.

The epidermis (e) is intact (Figure 57, 58) and numerous rhizome scales (sc) are visible in this preparation (Figure 57). The cortex (c) illustrates a distinct banding pattern: in the outer region a layer, 8-10 cells thick, that are unsclerified with tannin-like substances present in their cells; the middle region consisting of a layer eight cells in thickness that are rather heavily sclerified with tannin-like substances in their cells; and an inner 3-5 cell layer of cells similar to the outermost region (Figure 57, 58).

The outer (oen, Figure 58) and inner (ien, Figure 57) endodermis can be discerned as intact in many areas of the rhizome. Outer (oph) and inner (iph) sieve cells and phloem parenchyma cells are readily seen (Figure 58) and the xylem (x) consists of scalariform tracheids (Figure

Figure 57. P. andromaedifolia. Complete rhizome cross section with leaf gap, solenostele. X40. Figure 58. P. andromaedifolia. Portion of rhizome from cortex to inner primary phloem. X100.

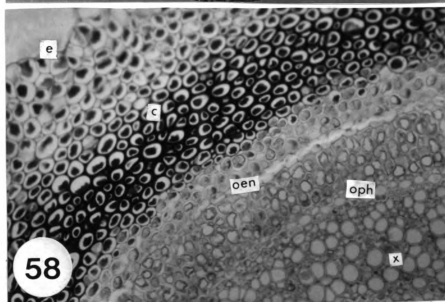
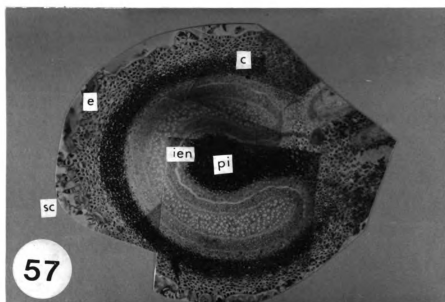
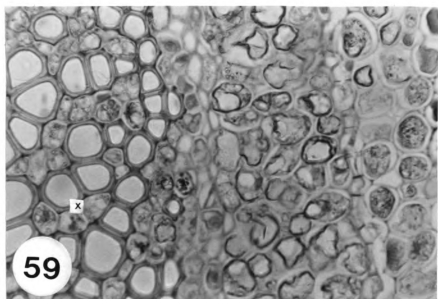


Figure 59. P. andromaedifolia. Inner cortex
to primary xylem. X400.



58, 59). Xylem parenchyma is present (Figure 58, 59). All sections examined illustrated a solenostelic condition, with some tendency toward a transitional condition in a few sections.

The pith (pi) consists of an outer region of non-sclerified cells and a large central mass of sclerified cells (Figure 57).

Pellaea atropurpurea (L.) Link, Knobloch accession 71-30, McCulloch 78-71.

The rhizome is short, densely clothed with long-attenuate, tortuous rusty scales. The habitat is a rocky loam forest floor, rock ledges, among rocks, on cliffs, canyon walls, banks and talus slopes of limerock, occurring in partial shade and up to 2000 m. elevation.

The epidermis (e) is partially intact in this preparation (Figure 60). The cortex (c) shows no marked sclerification pattern in that all cells seem to be unlignified (Figure 60). They contain some tannin-like substances.

The outer (opc) and inner (ipc) pericycles are thin-walled parenchyma cells two to four cell layers thick (Figure 62). The sieve cells and phloem parenchyma cells of the outer (oph) and inner (iph) primary phloem are evident (Figure 62).

The xylem (x) consists of scalariform tracheids (Figure 62, 63) and xylem parenchyma is present (Figure 62). An isolated scalariform tracheid (x) can be seen in Figure 118. Figure 119 illustrates a helical protoxylem (px) cell. The pith (pi) has the same cellular composition as the cortex (Figure 60, 61, 62). The majority of sections examined illustrated a solenostele (Figure 60) with some sections being transitional (Figure 61).

Figure 60. P. atropurpurea. Complete rhizome cross section, one leaf gap, one leaf trace and adventitious root. X40. Figure 61. P. atropurpurea. Vascular cylinder, two leaf gaps, transitional. X40.

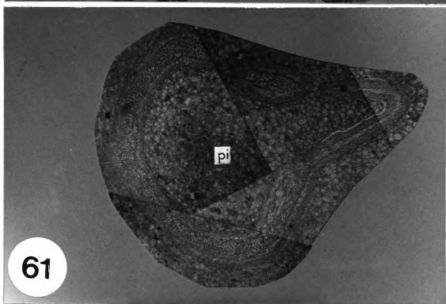
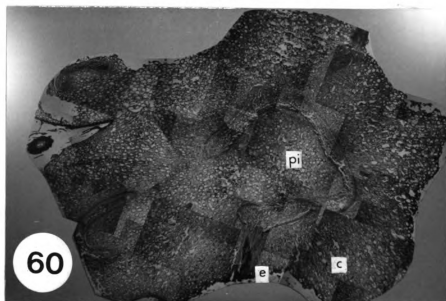
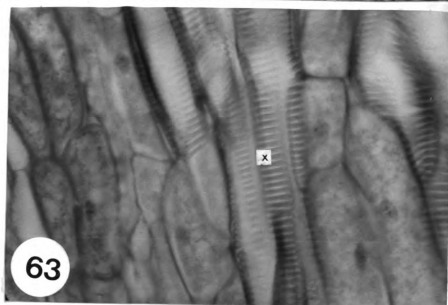
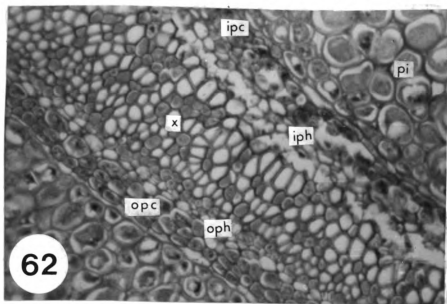


Figure 62. P. atropurpurea. Portion of the vascular cylinder in center. X100.
Figure 63. P. atropurpurea. Longitudinal section of primary xylem, scalariform tracheids. X400.



Pellaea brachyptera (Moore) Baker, Knobloch accession 65-13.

The rhizome is moderately stout, elongate, decumbent and/or multicapital, while the habitat of this species is talus slopes, basalt or serpentine rock outcrops from 800-2900 m. elevation.

The epidermis (e) of this species is intact (Figure 64, 65). The cortex (c) consists of two distinct regions: the outer region is three to four cell layers thick and are very sclerified, with the cell lumens obscured by tannin-like substances; the inner region is much less sclerified but the tannin-like substances are still present (Figure 64, 65).

Both the outer (oen) and inner (ien) endodermis are partially torn in this preparation (Figure 64, 65). The outer and inner pericycle, sieve cells and phloem parenchyma cells, both outer and inner, are partially or wholly disrupted and/or compressed.

The xylem (x) consists of the usual scalariform tracheids and xylem parenchyma is present (Figure 66). The pith (pi) is loosely organized, especially in its center, some cells are, however, sclerified (Figure 64, 65).

This specimen was interesting because of the high degree of variation in the vascular cylinder. This species is described as being solenostelic (Figure 64), with Figure 65 illustrating the transitional condition which was found in some sections. Two leaf gaps (lg) and two leaf traces (lt) are readily seen in Figure 65.

Pellaea Breweri D. C. Eaton, Knobloch accession 71-29, E. Taylor S.n.

The rhizome of this specimen is compact, ascendent, massive and with many compressed bases of articulated stipes and a habitat of usually granite rocks or basalt, but also on limestone and occurring at elevations from 1600-3800 m.

Figure 64. P. brachyptera. Complete rhizome cross section, adventitious root, solenostele. X40. Figure 65. P. brachyptera. Complete rhizome cross section, two leaf gaps, two leaf traces, adventitious root, transitional. X40.

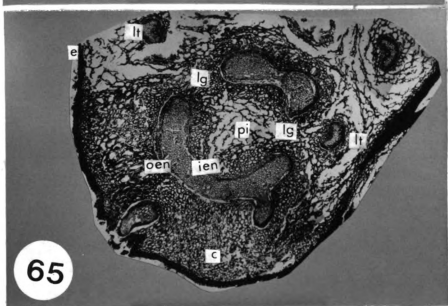
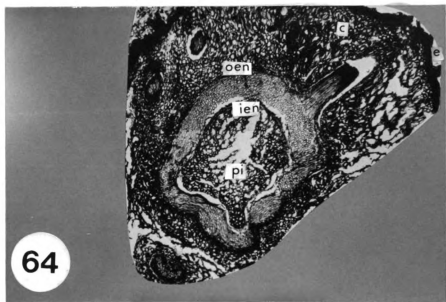
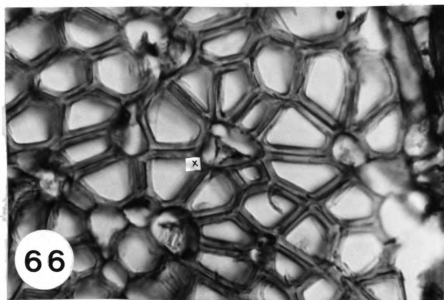


Figure 66. P. brachyptera. Cross section of
primary xylem. X400.



The one-cell thick epidermis (e) in this taxa is for the most part intact (Figure 67). The cortex (c) (Figure 67, 68), except for the outermost one, two or three cell layers, is uniform in sclerification. The parenchyma cells of the cortex retain a food storage material besides the normal cell contents.

Figure 69 illustrates the intact outer (oen) and inner (ien) one-celled thick endodermal areas. Because of the fragility of the tissue it is often torn in sectioning as seen in some areas.

The outer (opc) and inner (ipc) pericycle (Figure 69) areas are both composed of thin-walled parenchyma cells that retain food (f) storage materials. Both pericycle tissue areas are from two to four cells thick and the cells are generally smaller than the cells of the cortex.

The sieve cells, both outer (oph) and inner (iph), of the primary phloem are readily visible in Figure 69. Primary phloem areas can generally be distinguished in cross section because the sieve cells are angular in cross section and usually lack any stainable cell contents. For the most part the sieve cells form a continuous band in the vascular system. The outer and inner phloem areas also consist of parenchyma cells which are smaller than the pericycle cells.

The xylem (x) consists of scalariform tracheids (Figure 69, 70) and xylem parenchyma. The pith (pi) is similar, in cell composition and uniformity, to the cortex. There are no sclerified areas in the pith (Figure 67). Figure 67 illustrates a transitional type stele where four gaps (lg) and four leaf traces (lt) are visible. An adventitious root (art) can be seen originating from the outer pericycle in Figure 67, 68.

Most sections examined were solenostelic. Therefore, P. Breweri is considered to be solenostelic with some portions of the rhizome being transitional.

Figure 67. P. Breweri. Complete rhizome cross section, four leaf gaps, four leaf traces, adventitious root, transitional. X40.
Figure 68. P. Breweri. Portion of the vascular cylinder, adventitious root, xylem. X40.

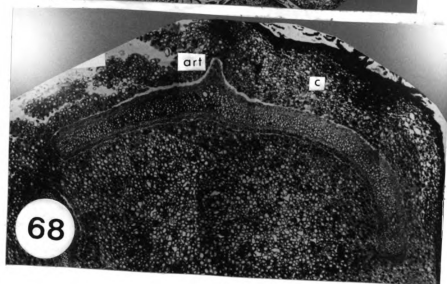
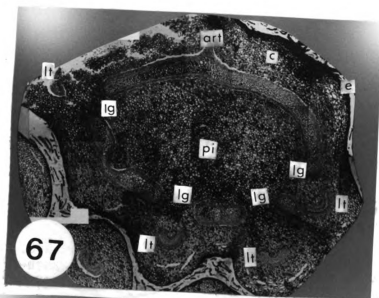
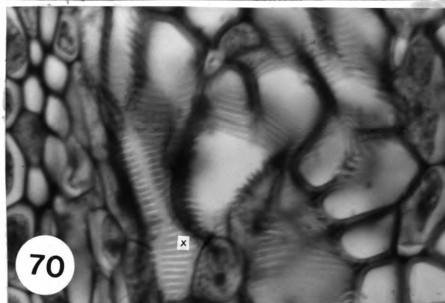
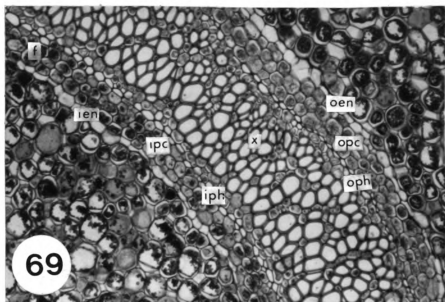


Figure 69. P. Breweri. Portion of the vascular cylinder in center. X100. Figure 70. P. Breweri. Oblique section of primary xylem. X400.



Pellaea Bridgesii Hooker, Knobloch accession 71-26, R. Rodin s.n.

The rhizome is short-creeping, often massive and with the divisions short and close.

The epidermis (e) is intact and remains of the rhizome scales are present (Figure 71). The cortex (c) region is unsclerified except for the outermost two-three layers (Figure 71). Tannin-like substances are easily visible in the cells of both the cortex (c) and pith (pi) (Figure 71, 72, 74).

Both endodermal areas (outer, oen and inner, ien) are intact except for small tears in the outer endodermis (Figure 72). The outer (opc) and inner (ipc) pericycle are composed of thin-walled parenchyma cells (Figure 72). An adventitious root can be seen in Figure 74.

The outer (oph) and inner (iph) sieve cells and phloem parenchyma are readily visible in Figure 72. The xylem (x) presumably consists of scalariform tracheids and xylem parenchyma (Figure 72, 73). The pith (pi) is similar to the cortex except there are no sclerified cells (Figure 74). This species would be considered to be a solenostele (Figure 71) but with some sections transitional. In Figure 74 two leaf gaps (lg) are visible and one leaf trace (lt).

Pellaea dealbata (Pursh) Prantl, Knobloch accession 72-4, Seigler 1035.

The rhizome is short and ascending, and the habitat is dry crevices on cliffs and boulders of limestone and other calcareous rocks and usually occurring in partial shade.

The epidermis (e) is intact in this preparation as can be seen in Figure 75, 76. The cortex (c), directly beneath the epidermis, has three-five layers of cells that are filled with tannin-like substances

Figure 71. P. Bridgesii. Complete rhizome cross section, one leaf gap, solenostele. X40. Figure 72. P. Bridgesii. Portion of the vascular cylinder in the center. X100.

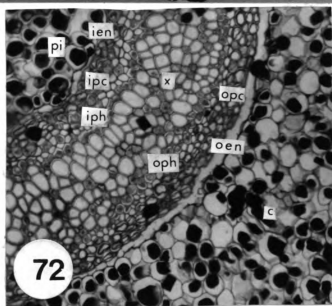
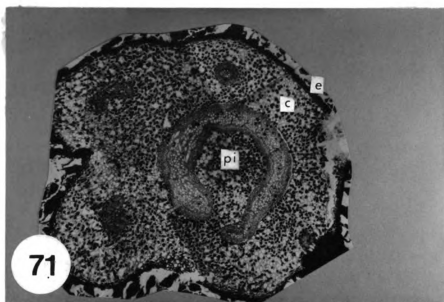


Figure 73. P. Bridgesii. Cross section of primary xylem. X400. Figure 74. P. Bridgesii. One leaf gap, leaf trace, adventitious root, solenostele. X40.

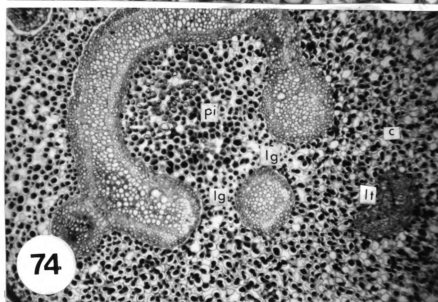
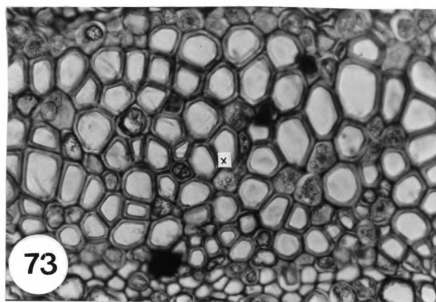


Figure 75. P. dealbata. Complete rhizome cross section, dictyostele. X40. Figure 76. P. dealbata. Portion of the rhizome from epidermis to pith. X100.

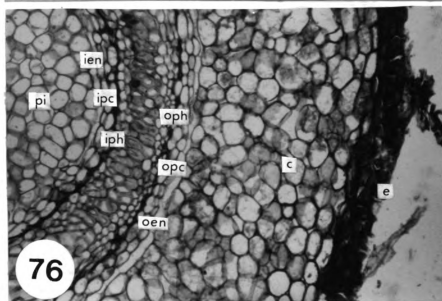
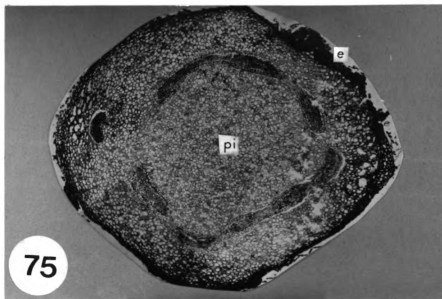
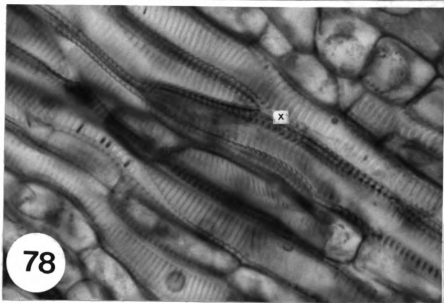
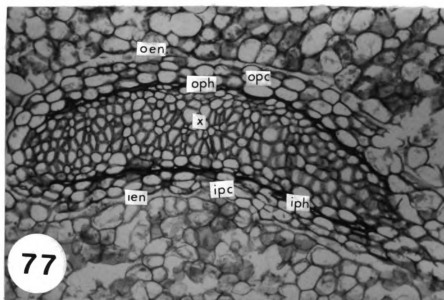


Figure 77. P. dealbata. Portion of vascular cylinder or meristele. X100. Figure 78. P. dealbata. Longitudinal section of primary xylem, prominent scalariform tracheids. X400.



with the remainder of the cortex being composed of large, unsclerified cells (Figure 76).

Both outer (oen) and inner (ien) endodermal layers consist of rectangular cells and they are torn in some areas in this preparation (Figure 76, 77). The outer (opc) and inner (ipc) pericycles are two-three cells in thickness and are smaller than the cortical cells but have the same shape (Figure 76, 77).

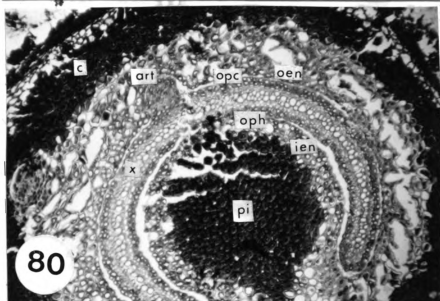
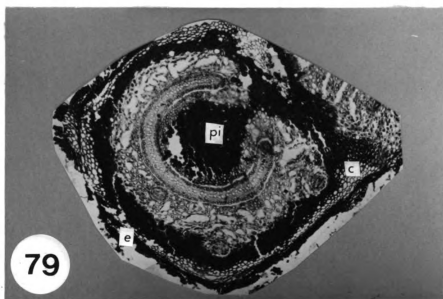
The outer (oph) and inner (iph) sieve cells and phloem parenchyma are similar in their distribution and occurrence to previous taxa and can be seen in Figure 76, 77. The xylem (x) consists of scalariform tracheids (Figure 77, 78) and xylem parenchyma (Figure 77). The pith (pi) is of the same general composition as the cortex, except that there are no distinct areas of tannin-filled cells (Figure 75, 76). This species is considered to be a dictyostele (Figure 75).

Pellaea falcata (R. Br.) Fée, Knobloch accession 72-7.

The epidermis (e) is partially intact in this preparation (Figure 79). The cortex (c) has a band of several layers of highly sclerified cells in the central region. The cell lumens are completely obscured with tannin-like substances in most cases. The thick cell walls are impregnated with lignin and suberin. The layers of cells outward from the central band appear to have very little sclerification (Figure 79, 80). The cell layers inward appear to have some degree of sclerification, but lack the large amounts of tannin-like substances (Figure 80).

Both outer (oen) and inner (ien) endodermal layers are torn in most areas (Figure 80). There is very little pericycle in this species, usually two-three cell layers in both outer (opc) and inner (ipc) regions (Figure 80). Figure 80 illustrates an adventitious root (art) originating at the arrow.

Figure 79. P. falcata. Complete rhizome cross section, one leaf gap, solenostele. X40. Figure 80. P. falcata. Vascular cylinder and adventitious root. X40.



The outer and inner sieve cells of the primary phloem and phloem parenchyma cells are similar to other taxa examined. The xylem (x) consists of scalariform tracheids (Figure 80), and no xylem parenchyma is present. The majority of the pith (pi) is composed of highly sclerified cells with a band of three-four cells toward the inner endodermis that are not sclerified (Figure 79, 80).

This species exhibits a true solenostele.

Pellaea intermedia Mett. ex Kuhn, McCulloch 57-71.

The rhizome is elongate, slender, widely-creeping, wirey, scaly and about 1.5 cm. in diameter. The habitat is dry and rocky slopes and ledges, cliffs and about boulders of igneous and limestone.

The epidermis (e) of this species is intact and some partial rhizome scales (sc) can be identified in Figure 81, 82. The cortex (c) region becomes more sclerified as one advances inward, with the exception of the last one or two cell layers that are adjacent to the outer endodermis (oen) (Figure 82). No tannin-like substances can be observed.

The outer (oen) and inner (ien) endodermis are torn in this preparation (Figure 82). The outer (opc) and inner (ipc) pericycle are similar to each other in composition, both consisting of thin-walled parenchyma cells that stain for a food reserve substance in the cell along with the normal cell content (Figure 82, 83).

Both outer (oph) and inner (iph) sieve cells of the primary phloem and the phloem parenchyma are readily visible in Figure 83. The xylem (x) consists of scalariform tracheids and xylem parenchyma is present (Figure 83). An isolated scalariform tracheid can be seen in Figure 120. The pith (pi) becomes more sclerified as you move toward the center (Figure 82). In all sections examined, this species demonstrated a solenostele (Figure 81).

Figure 81. P. intermedia. Complete rhizome cross section, internode, solenostele. X40.
Figure 82. P. intermedia. Portion of the rhizome. X100.

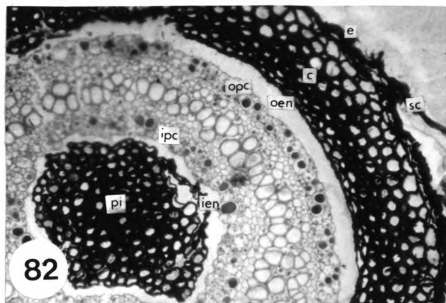
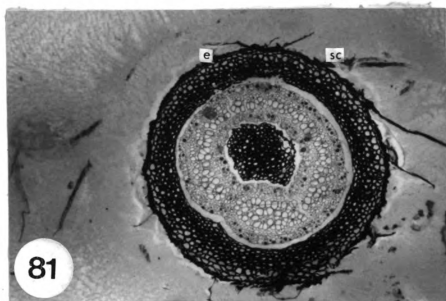
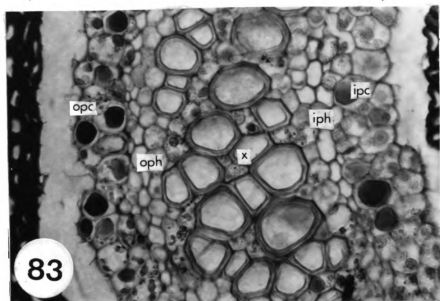


Figure 83, P. intermedia. Portion of vascular cylinder, note xylem parenchyma. X400.



Pellaea longimucronata Hook., McCulloch 89-71.

The rhizome of this species is described as being moderately stout, elongate, decumbent and multicipital. This species occurs in clefts of igneous rocks, among granite boulders in open sun, and in gravelly soil, from 600-2000 m. elevation.

The epidermis (e) is partially intact, although it is difficult to determine because of the heavy sclerification that is present in the outer portion of the cortex (c) (Figure 87).

The outer (oen) and inner (ien) endodermis in Figure 84 are visible even though they are partially torn. The outer (opc) and inner (ipc) pericycle regions can be seen in Figure 84 and are from two to three cells in thickness.

The outer (oph) and inner (iph) sieve cells and phloem parenchyma as well as scalariform tracheids (x) and xylem parenchyma are easily seen in Figure 84. Figure 85 shows a longitudinal section of the xylem (x) area, in which the scalariform nature of the tracheids can be seen. The cells of the pith (pi) in this specimen are unsclerified (Figure 87).

In Figure 86 a rare occurrence was noted. It appears that an adventitious root (art) was growing through the pith (pi) area. This was noted in all sections from this particular block and was not noted in other blocks of the same species.

Figure 87 illustrates a solenostelic condition with an adventitious root (art) originating from the outer pericycle, and Figure 88 illustrates a transitional condition in which two leaf gaps (lg) and two leaf traces (lt) can be seen. This species is considered to be solenostelic with scattered areas being transitional.

Figure 84. P. longimucronata. Portion of the vascular cylinder with adventitious root. X100. Figure 85. P. longimucronata. Longitudinal section of primary xylem, showing scalariform tracheids. X400.

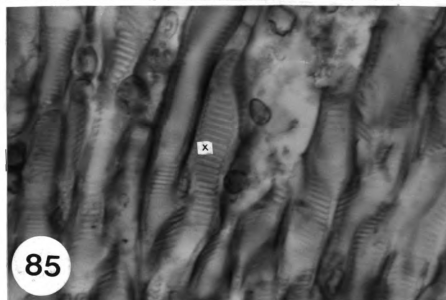
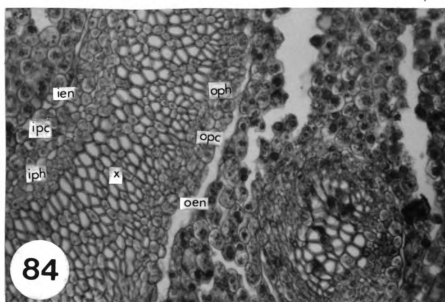


Figure 86. P. longimucronata. Vascular cylinder with adventitious root in pith area. X100. Figure 87. P. longimucronata. Complete rhizome cross section, one leaf gap, adventitious root, solenostele. X40.

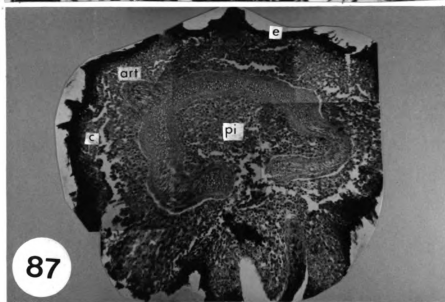
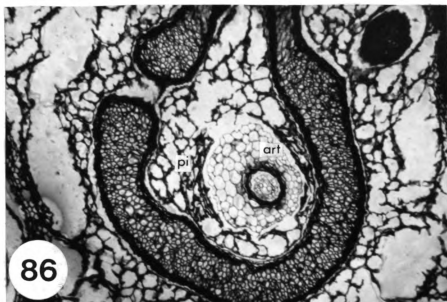
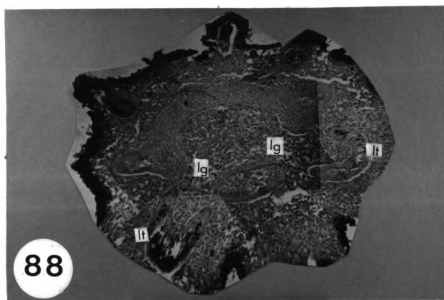


Figure 88. P. longimucronata. Complete rhizome cross section, two leaf gaps, two leaf traces, adventitious root, transitional. X40.



Pellaea mucronata (D. C. Eaton) D. C. Eaton var. californica
(Lemmon) Munz and Johnston, Knobloch accessions 71-18 and 71-21, Rodin
s.n.

This species occurs on talus, among loose rocks or in rocky woods, in shade or open sun and from 1800-3000 m. elevation.

The epidermis (e) in Figure 89 is partially intact. The specimen in Figure 90 taken from another rhizome of the collection has a more poorly preserved epidermis, but both illustrate the same cortex (c) structure. In both Figure 89 and 90 the sclerified layers of cortex cells occur toward the outside and the remaining cells of the cortex are not sclerified, or at least not sclerified to the same degree. Both specimens show tannin-like substances within the cells.

In both preparations the outer and inner endodermis is, for the most part, intact. Figure 91 illustrates the vascular cylinder in which the outer (opc) and inner (ipc) pericycle regions are present and the outer (oph) and inner (iph) sieve cells and phloem parenchyma cells of the phloem. Specifically, the phloem area and pericycles show some degree of compression from sectioning.

The xylem (x) consists of scalariform tracheids and xylem parenchyma is present (Figure 91). The pith (pi) shows little or no sclerification (Figure 92). This species illustrates a great deal of variation in the vascular cylinder. Very few sections examined illustrated a true solenostele, the majority of sections being transitional in nature (Figure 89, 90, 91, 92). No sections illustrated a true dictyostele, where the vascular cylinder was completely dissected into meristeles. Figure 92 comes closest to resembling a dictyostele, where a number of meristeles and leaf gaps (lg) can be seen on the upper right half of the vascular

Figure 89. P. mucronata v. californica. Complete rhizome cross section, four leaf gaps, transitional. X40. Figure 90. P. mucronata v. californica. Complete rhizome cross section, three leaf gaps. transitional. X40.

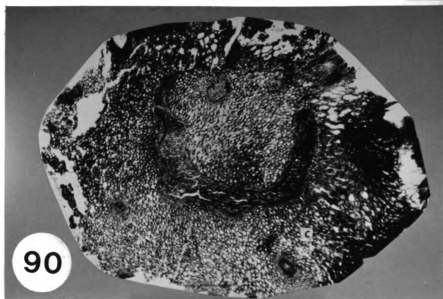
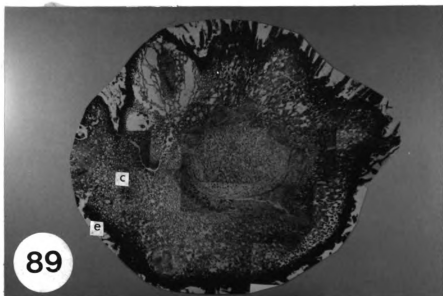
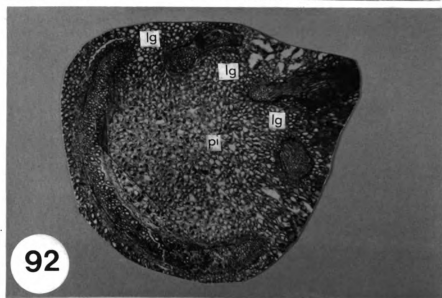
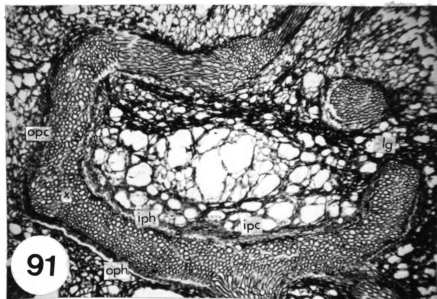


Figure 91. P. mucronata v. californica. Vascular cylinder, two leaf gaps, transitional. X100. Figure 92. P. mucronata v. californica. Vascular cylinder, four leaf gaps, transitional. X100.



cylinder. The leaf traces are not visible. A number of sections illustrated two meristeleles.

Pellaea notabilis Maxon, McCulloch 79-71.

The rhizome is moderately stout, compact, decumbent and multicipital and occurs among limestone rocks, along the banks of a stream and in shaded areas.

The epidermis (e) is intact (Figure 93), and the cortex (c), excluding the outermost one-four layers of cells, is unsclerified (Figure 93, 95). Very little tannin-like substances appear in the parenchyma cells of the cortex.

The outer (oen) and inner (ien) endodermis is intact (Figure 94). Both outer and inner pericycle regions, sieve cells and phloem parenchyma are present but hard to distinguish. An adventitious root (art) can be seen in Figure 94.

The xylem (x) contains scalariform tracheids and xylem parenchyma (Figure 94). The vascular cylinder for this taxon would be described as transitional (Figure 93, 94) with some solenostelic sections (Figure 95). The pith (pi) is unsclerified and resembles the cortex in composition (Figure 94).

Pellaea ovata (Desv.) Weatherby, McCulloch 76-71.

The rhizome is slender, dichotomously branched, creeping or compact, clothes with scales and enveloped by matted roots. P. ovata may be found on dry ledges and talus slopes of limestone, calcareous rocks or granite, at the base of cliffs, in rich soil, brushy savanah, oak forests in open sun or shaded banks.

The epidermis (e) in this species is partially intact and can be seen in Figure 96, 97, and the cortex (c) is for the most part heavily

Figure 93. P. notabilis. Complete rhizome cross section, three leaf gaps, adventitious root. X40. Figure 94. P. notabilis. Vascular cylinder, transitional, leaf traces not visible. X100.

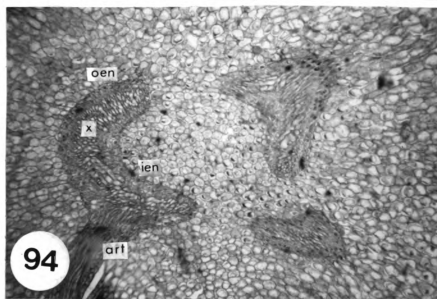
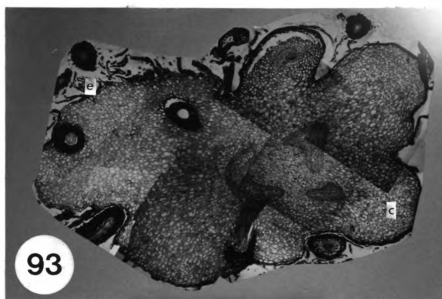


Figure 95. P. notabilis. Complete rhizome cross section, one leaf gap, solenostele. X40.

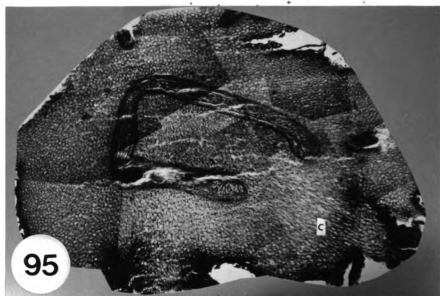


Figure 96. P. ovata. Complete rhizome cross section, one leaf gap, adventitious root, solenostele. X40. Figure 97. P. ovata. Portion of rhizome. X100.

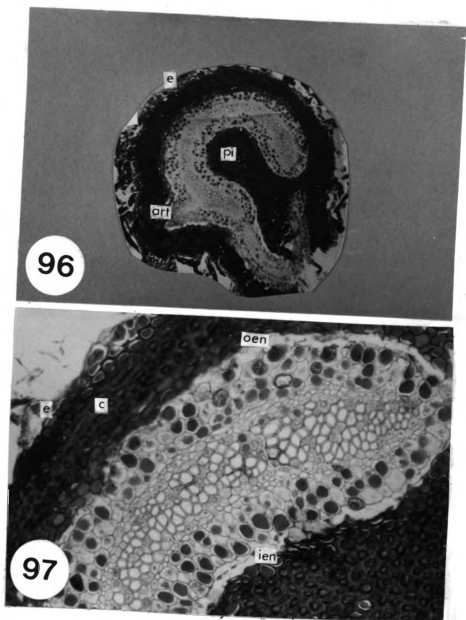
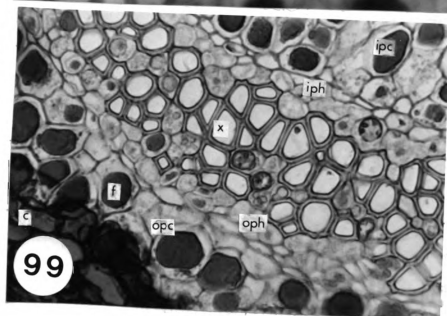
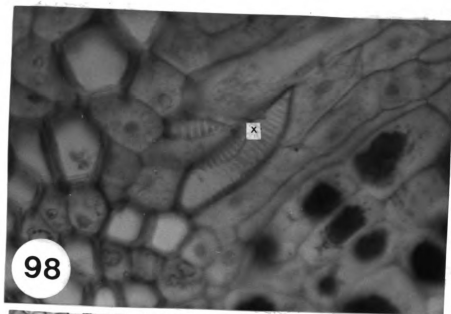


Figure 98. P. ovata. Oblique section of
primary xylem. X400. Figure 99. P. ovata.
Portion of the vascular cylinder. X100.



sclerified, except directly below the epidermis (Figure 97) and near the outer endodermis (Figure 97, 99). The cell walls are impregnated with suberin and lignin. The cell lumens are partially or totally obscured in many areas of the cortex.

The outer (oen) and inner (ien) endodermal regions are partially torn as can be seen in Figure 97. In Figure 99 the outer (opc) and inner (ipc) pericycle, the sieve cells (oph, iph) and phloem parenchyma cells, tracheids (x) and xylem parenchyma are all clearly visible. Food (f) storage material can be seen in the pericycle in Figure 99, and an adventitious root is originating in the outer pericycle in Figure 96.

Figure 98 illustrates an oblique section through the xylem area and the scalariform nature of the tracheids (x) can be seen. All sections examined illustrated a solenostele (Figure 96). The pith (pi) follows the same general pattern of sclerification as the cortex (Figure 96).

Pellaea pteroides (L.) Prantl, Knobloch accession 73-6, Schelpe
S.n.

The epidermis (e) is mostly sloughed off in this preparation (Figure 100). The outermost five-six layers of cortex (c) are highly sclerified, the remainder of the cortex is uniform in terms of cell wall thickness and tannin-like substances are easily visible (Figure 100).

The outer (oen) and inner (ien) endodermis are partially intact (Figure 101). The outer (opc) and inner (ipc) pericycle bear a distinct resemblance to the cortical cells, as they also contain tannin-like substances and the cells are of similar size (Figure 101).

Outer (oph) and inner (iph) sieve cells and phloem parenchyma are readily distinguished (Figure 101). The phloem parenchyma cells also contain what appear to be tannin-like substances (Figure 102).

Figure 100. P. pteroides. Complete rhizome cross section, two leaf gaps, adventitious root. X40. Figure 101. P. pteroides. Portion of rhizome. X100.

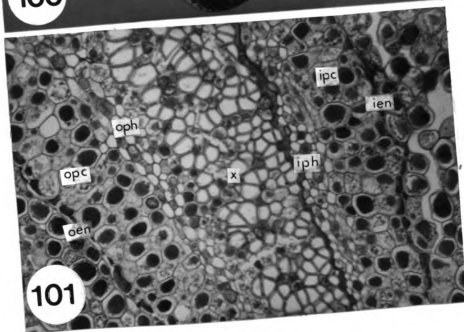
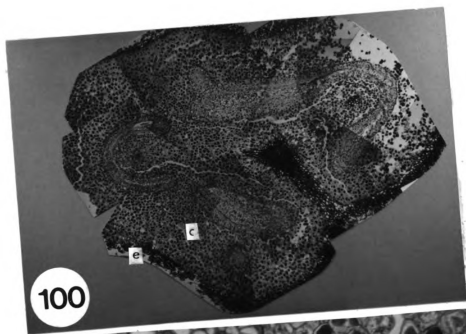
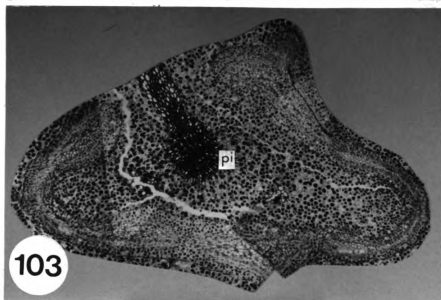
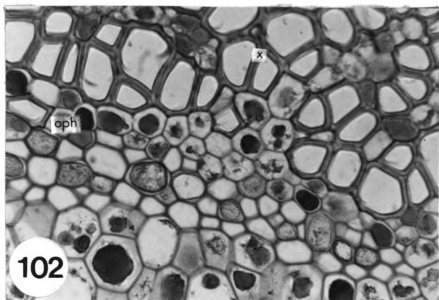


Figure 102. P. pteroides. Portion of the
vascular cylinder. X100. Figure 103. P.
pteroides. Vascular cylinder. X100.



The xylem (x) consists of scalariform tracheids and xylem parenchyma (Figure 101, 102). In no sections was a true solenostele observed, so this species is described here as a dictyostele (Figure 100, 103). The pith (pi) has a composition similar to the cortex but with the most heavily sclerified cells occupying the central area (Figure 103).

Pellaea Skinneri Hook., Knobloch 2089.

The rhizome of P. Skinneri is short and stout with a widespread root system and the habitat is deep shade at the base of rhyolitic cliffs.

The epidermis (e) in this preparation is partially sloughed off (Figure 104). The cells of the cortex (c) seem to be evenly sclerified for the most part (Figure 104).

The outer (oen) and inner (ien) endodermis is torn (Figure 104), and the outer (opc) and inner (ipc) pericycle contain some tannin-like substances (Figure 104).

The sieve cells and phloem parenchyma are present as is usual but the outer primary phloem area is more extensive than the inner primary phloem area.

The xylem (x) consists of supposed scalariform tracheids. There is no xylem parenchyma present in this species (Figure 104). All sections that were examined had a solenostele (Figure 104). The pith (pi) seems to be uniformly sclerified with the exception of the outermost one or two cell layers (Figure 104).

Pellaea viridis (Forsk.) Prantl var. viridis, Knobloch accession number 71-33.

The epidermis (e) (Figure 105) is one-celled thick and intact for the majority of the rhizome diameter. No stomata were noticed in our preparations. The outer third to one-half of the cortex (c) is heavily

Figure 104. P. Skinneri. Complete rhizome
cross section, internode, solenostele. X40.

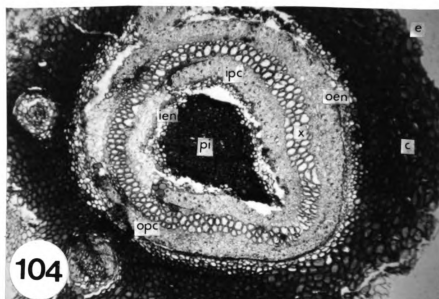


Figure 105. P. viridis. Complete rhizome cross section, adventitious roots, three leaf gaps. X40. Figure 106. P. viridis. Complete rhizome cross section, adventitious roots, two leaf gaps. X40.

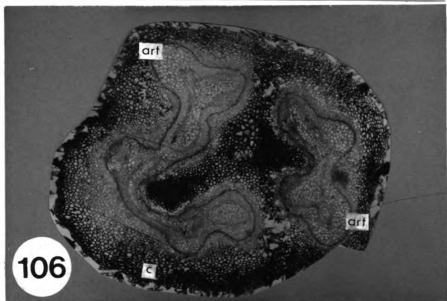
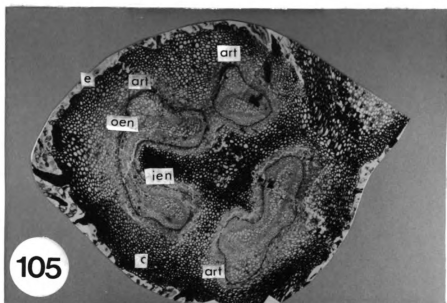


Figure 107. P. viridis. Portion of rhizome,
cross section. X100. Figure 108. P. viridis.
Meristele, note prominent endodermis. X100.

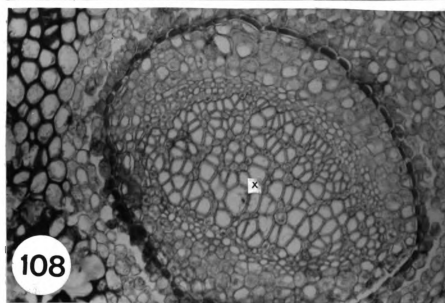
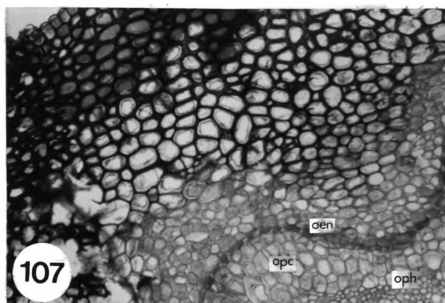
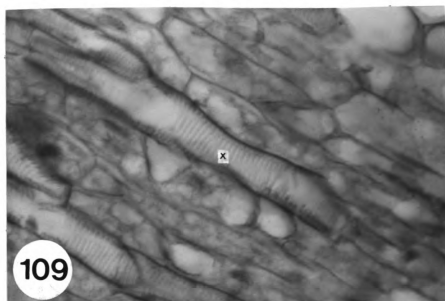


Figure 109. P. viridis. Longitudinal section of primary xylem, with scalariform tracheids. X400.



sclerified and the inner portion is less sclerified or unsclerified (Figure 105, 106). The degree of sclerification seems to vary with the age of the specimen.

The endodermis (oen, ien) is readily seen in this preparation as de-limiting the stele in Figure 105. The endodermis is seen to be composed of a one-celled wide layer with Casparian strips (Figure 107) on the radial walls. The outer endodermis constitutes the innermost layer of the cortex.

The outer and inner pericycles have several layers of thin-walled parenchyma cells. The cells are of various shapes. The outer (opc) pericycle can be seen in Figure 107. In Figure 105, 106 adventitious roots (art) can be seen originating from the outer pericycle.

The outer (oph) and inner primary phloem is composed of narrow bands of sieve and parenchyma cells (Figure 107). The phloem parenchyma cells are smaller than those of the pericycle and can be seen in Figure 107.

The primary xylem (x) consists of scalariform tracheids (Figure 108, 109) and xylem parenchyma is present (Figure 108). In Figure 121 an isolated scalariform tracheid (x) is visible. This species is considered to be a dictyostele (Figure 105, 106). Figure 108 illustrates a meristele.

Pellaea X Wrightiana Hook., Knobloch 1624.

The epidermis (e) is partially intact and scales are visible (Figure 110). The cortex (c) consists of an outer region of compact cells four or five layers in thickness (Figure 110). The inner region of the cortex consists of loosely arranged parenchyma cells (Figure 110, 113). The cells of the cortex do not appear to show any sclerification.

Figure 110. P. X Wrightiana. Complete rhizome cross section, solenostele. X40.
Figure 111. P. X Wrightiana. Vascular cylinder, one leaf gap, solenostele. X40.

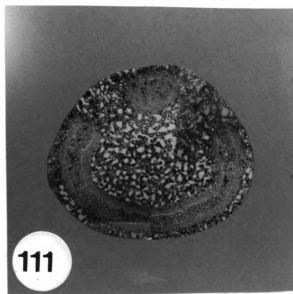
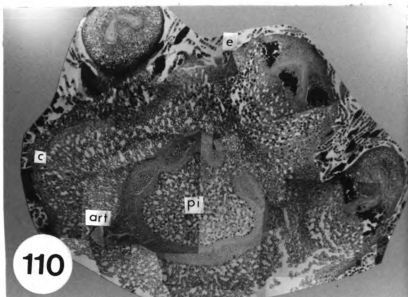
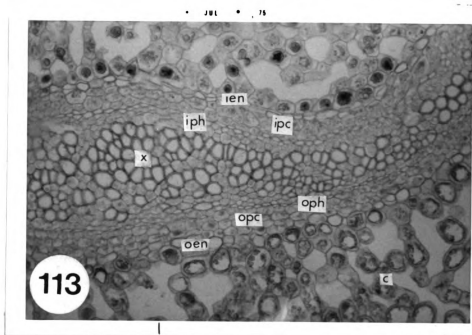
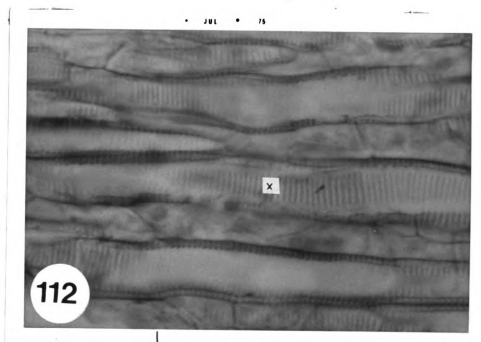


Figure 112. P. X Wrightiana. Longitudinal section of primary xylem. X400. Figure 113. P. X Wrightiana. Portion of the vascular cylinder. X100.



Both the outer (oen) and inner (ien) endodermal layers are intact (Figure 113). The outer (opc) and inner (ipc) pericycle regions consist of two to three layers of parenchyma cells which are smaller in size than the parenchyma cells of the cortex, yet larger than the phloem parenchyma (Figure 113). An adventitious root (art) can be seen originating from the outer pericycle in Figure 110.

The sieve cells of both outer (oph) and inner (iph) primary phloem are readily visible, as in other taxa examined, and are few in number (Figure 113). The outer (oph) and inner (iph) phloem parenchyma cells are visible in Figure 113.

The xylem (x) consists of scalariform tracheids and xylem parenchyma (Figure 112, 113). This species is considered to be solenostelic (Figure 110) with indications of being transitional in some sections. The pith (pi) is of similar structure and composition as the inner region of the cortex (Figure 110).

The vascular cylinders of three Notholaena and three Pellaea species were treated with Jeffrey's maceration liquid and observations made on the xylem components.

Table 9 summarizes the stele type and the presence or absence of xylem parenchyma in the Pellaea species examined.

Table 10 represents the number of sections of Pellaea examined and the stem diameters.

Three samples of N. Galeotti illustrate scalariform tracheids (x) (Figure 114, 115) and what appears to be a helical protoxylem (px) tracheid (Figure 116). Two samples of N. rigida illustrate scalariform tracheids, while three samples of N. Standleyi illustrate scalariform tracheids (x) (Figure 117).

Pellaea atropurpurea, in three samples, illustrate scalariform tracheids (x) (Figure 118) and what appears to be a helical protoxylem (px) tracheid (Figure 119).

Figure 114. N. Galeottii. Scalariform tracheid. X400. Figure 115. N. Galeottii. Scalariform tracheid. X400.

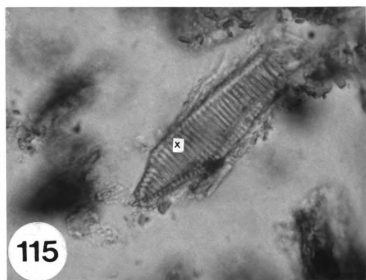
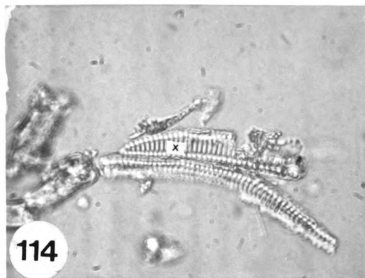


Figure 116. N. Galeottii. Helical proto-
xylem tracheid. X400. Figure 117. N.
Standleyi. Scalariform tracheid. X400.

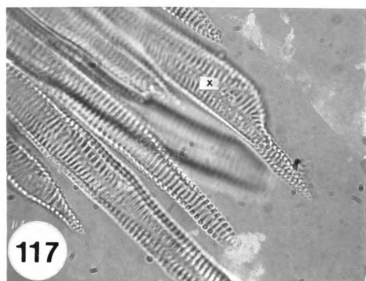
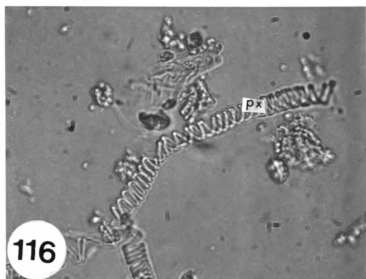


Figure 118. P. atropurpurea. Scalariform
tracheid. X400. Figure 119. P. atropur-
purea. Helical protoxylem tracheid. X400.

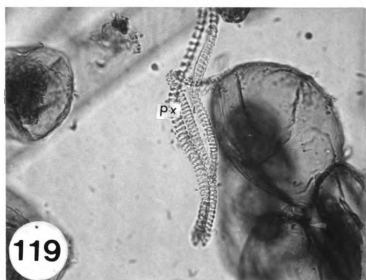
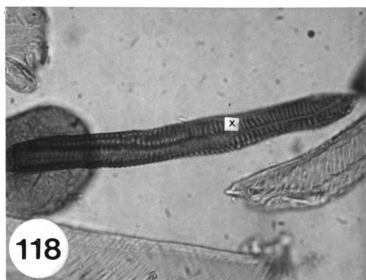


TABLE 9. Xylem parenchyma and stele type of Pellaea.

Species	Xylem parenchyma	Stele
<u>P. allosuroides</u>	no	solenostele
<u>P. andromaedifolia</u>	yes	solenostele
<u>P. atropurpurea</u>	yes	solenostele
<u>P. brachyptera</u>	yes	solenostele
<u>P. Breweri</u>	yes	solenostele
<u>P. Bridgesii</u>	yes	solenostele
<u>P. dealbata</u>	yes	dictyostele
<u>P. falcata</u>	no	solenostele
<u>P. intermedia</u>	yes	solenostele
<u>P. longimucronata</u>	yes	solenostele
<u>P. mucronata</u> v. <u>californica</u>	yes	transitional
<u>P. notabilis</u>	yes	transitional
<u>P. ovata</u>	yes	solenostele
<u>P. pteroides</u>	yes	dictyostele
<u>P. Skinneri</u>	no	solenostele
<u>P. viridis</u> v. <u>viridis</u>	yes	dictyostele
<u>P. X Wrightiana</u>	yes	solenostele

TABLE 10. Number of sections examined and stem diameter of Pellaea.

Species	Sections examined	Rhizome diameter (mm.)
<u>P. allosuroides</u>	24	1.25 - 1.50
<u>P. andromaedifolia</u>	33	1.50 - 1.75
<u>P. atropurpurea</u>	51	5.25 - 9.00
<u>P. brachyptera</u>	71	3.50 - 3.75
<u>P. Breweri</u>	67	4.00 - 5.00
<u>P. Bridgesii</u>	5	2.10 - 3.00
<u>P. dealbata</u>	39	3.00 - 3.50
<u>P. falcata</u>	21	2.00 - 2.50
<u>P. intermedia</u>	13	0.80 - 0.90
<u>P. longimucronata</u>	19	2.00 - 2.25
<u>P. mucronata</u> v. <u>californica</u>	18	4.00 - 4.50
<u>P. notabilis</u>	29	2.50 - 7.50
<u>P. ovata</u>	14	2.50 - 3.50
<u>P. pteroides</u>	95	3.00 - 5.50
<u>P. Skinneri</u>	5	2.25 - 2.30
<u>P. viridis</u> v. <u>viridis</u>	104	2.50 - 3.00
<u>P. X Wrightiana</u>	97	3.75 - 4.00

Pellaea intermedia, in two samples, illustrate all scalariform tracheids (x) (Figure 120).

Pellaea viridis, in two samples, illustrate all scalariform tracheids (x) (Figure 121).

In order to document the ontogeny of the stele in at least one species, and to confirm the past literature, observations of the stele were made with P. viridis. It should be noted that in the mature condition P. viridis is considered to be dictyostelic. We would expect to find in P. viridis then, a sequence that would include the solenostelic and then protostelic condition, as one progressed to older and older portions of the rhizome. Indeed, this is what was observed in this taxon. Observations made in younger portions of the rhizome, near the basal end, clearly indicate the solenostelic condition in three different sections (Figure 122 - 124). The protostelic condition is evident, in older portions of the rhizome (the most basal part) and is illustrated in Figure 125, 126).

Figure 120. P. intermedia. Scalariform tracheid. X400. Figure 121. P. viridis. Scalariform tracheid. X400.

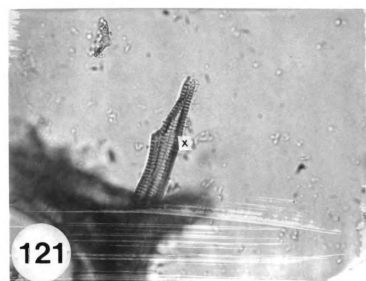
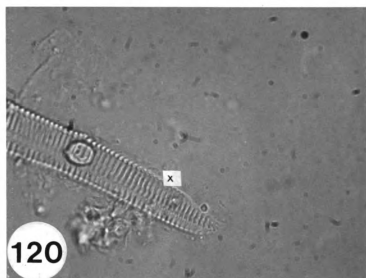


Figure 122. P. viridis. Solenostelic condition. X40. Figure 123. P. viridis. Solenostelic condition. X40.

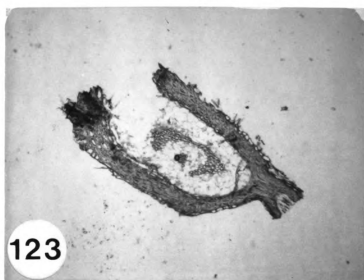
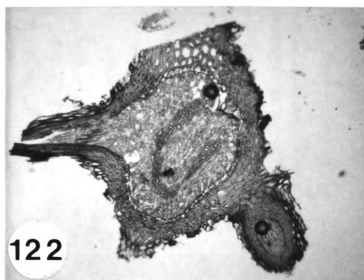


Figure 124. P. viridis. Solenostelic condition. X40. Figure 125. P. viridis. Protostelic condition. X40.

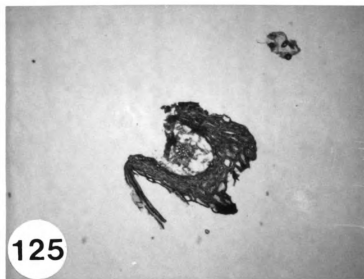
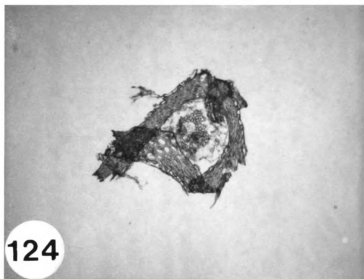
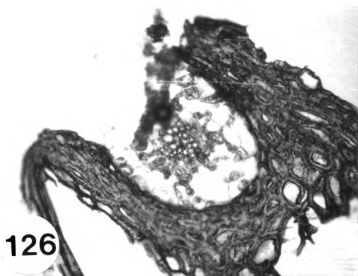


Figure 126. P. viridis. Protostelic condition. X100.



DISCUSSION AND SUMMARY

The first formed xylem is protoxylem and has helical markings (Figure 116, 118) at least for some species of Notholaena and Pellaea. Marsh (1914) was unable to find any protoxylem in the rhizomes of Cheilanthes (C. gracillima, C. persica, C. Feei (as lanuginosa), C. Wootonii (as Fendleri) that he examined.

Gwynne-Vaughan (1903) noted that in some ferns the protoxylem of the stipe was continuous with that of the stem, whereas in other ferns, the protoxylem in the stipe never connected with the stem. In the latter case, Gwynne-Vaughan (1903) believed that the first formed primary xylem on the periphery of the stem could be called "exarch protoxylem" even though the cell walls were scalariformly pitted. McCulloch et al. (1974) agree with that point of view and surmise that fern rhizomes, especially those of xeric species (as investigated here), grow very slowly and the stretchable type of protoxylem cannot be distinguished, at least in cross section. This may have to be modified in light of the evidence that some protoxylem has been found and further research is conducted. Helical protoxylem cells were demonstrated to occur in N. Galeottii and P. atropurpurea, in mature rhizomes. It should be noted that these protoxylem cells were rare and infrequent and that of the six species examined, in only two taxa were typical protoxylem cells found. This certainly does not limit the existence of protoxylem to N. Galeottii and P. atropurpurea, nor does

it imply that a statement as to the universal occurrence of protoxylem in Notholaena and Pellaea is appropriate.

Gwynne-Vaughan (1908) stated that the metaxylem of the Filicales consisted of typical scalariform tracheids; the typical scalariform tracheid possessing elongated pits arranged parallel to each other so as to form a ladder-like pattern. He noted that the departure, in ferns, from the tracheid type of element had been noted in only two cases: Pteris (Pteridium) aquilina and Nephrodium (Dryopteris) filix-mas (in the root), where true perforations occurred in the end walls of the "tracheids" and they, therefore, had to be regarded as vessels.

Bancroft (1911) concluded that the xylem elements of the Pteridophytes were typically tracheids.

Bliss (1939) did a comprehensive survey on the tracheal elements of ferns which incorporated some twenty-four genera from eight families as classified by Eames (1936). Pellaea was one of the genera analyzed. Bliss (1939) concluded that true vessels did exist in Pteridium latiusculum (Desv.) Maxon and P. esculentum (Forst.) Nakai, and that the water and mineral conducting elements of all other ferns investigated were tracheids. The tracheids were, in general, scalariform, but some showed a tendency to serial and irregular pitting on the lateral walls.

Bierhorst (1960) conducted an extensive survey on tracheary elements in plants. A large section of his work was devoted to the ferns. Without going into the detailed terminologies and the ontogenic sequences as illustrated by him, suffice it to say that he stated that scalariform elements seemed to be of general occurrence among the higher ferns.

White (1963) stated that, with two exceptions (the Ophioglossaceae and Marratiaceae), scalariform lateral pitting of tracheids was recognized as the most common type occurring in ferns and that numerous variations of the basic scalariform pattern had been noted in the literature.

Typical fern tracheids are elongate, tapered at both ends and have scalariform pits on all walls. In the rhizome and petiole, these cells typically overlap along the greater proportion of their length, rather than having relatively short oblique terminal overlaps like those of vessel members. As a consequence, it is not usually possible to distinguish an "overlap" area between two tracheids from the lateral walls of the tracheids.

Tracheids are traditionally considered to differ from vessel members in at least two ways: (1) in vessel members, there is a distinct end plate present which represents the area of articulation between vertically contiguous cells; no such specialization occurs in typical tracheids; (2) there are true perforations in the end plates of vessel members which allow for direct and uninterrupted vertical flow of water between cells; in tracheids the middle lamella and primary wall constitute a barrier through which water must pass when flowing from one tracheid to the next.

White made this interesting observation:

With the presence of vessel members in Pteridium aquilinum and, possibly in Woodsia ilvensis, both dry habitat species, it seemed reasonable that this character might be related to the xerophytic habitat. Even Marsilea in many of its ecological niches is a functional xerophyte for long periods during each year. In view of this, species typical of dry areas were checked, including Pellaea, Cheilanthes, Ceterach and Notholaena, and of these, vessel-like members were uncovered only in the roots of Notholaena sinuata. . . . In view of the taxonomic position of these species, plus the fact that other species of their genera and closely related genera do not have tracheary elements of this character, the presence of apparent vessel members in Notholaena sinuata and Woodsia ilvensis points to the possible sporadic occurrence of this cell type still to be found in other species, genera, and perhaps even in families.

White (1964), in summing up, stated that concerning the condition of presumptive vessels in the roots of Notholaena sinuata; "This condition appears to be a random occurrence and at present I am unable to correlate it with anything common to all species."

In examining the photographs of the xylem areas, the tracheids examined all appear to be of scalariform type, with no good criteria for establishing and distinguishing protoxylem and metaxylem when seen in cross section, as mentioned before.

The redundancy of the same genera being listed with several stelar conditions in the past literature is not unusual (for example; Azolla listed under typical protostele or haplostele and reduced protostele; Lygodium found under both typical protostele or haplostele and protostele with mixed pith). Another problem found in the past literature is that of not mentioning the species under a specific stelar type. This incomplete data presents a problem because it is known that the members of a genus can exhibit several different stelar conditions (McCulloch et al., 1974). One is at a loss then, to assign a particular species with a specific stelar condition, if such an assignment can be made or is even desirable to make. The past investigators themselves are at fault for not providing sufficient information when reporting their data. Not only are species' names missing in reports but such important information as the growth habit, rhizome morphology, the age or estimated age, number of sections examined and the portion of the rhizome examined, are in most cases completely absent from the literature. Furthermore, authorities in taxonomy are not in total agreement, and in the catalogue presented in the literature review will be found the same taxon under different names. For example, Stenoloma chusanum is now Sphenomeris chusana and Vandenboshia radicans has been lately called Trichomanes radicans. Much of the older work is also defective in that voucher specimens of the species described were not always made for later comparisons.

The analysis of the stelar systems as pointed out above and in the literature review has served to identify the taxonomic difficulties in trying to research the genera Pellaea and Notholaena and to compare them to the rhizome condition of Cheilanthes.

An analysis of the past interpretations of Notholaena, Pellaea and Cheilanthes as to their stelar conditions was conducted with the results presented in tabular form. Table 11 illustrates the stelar condition of the three genera before this research on Pellaea and Notholaena was initiated. The research by McCulloch et al. (1974) on Cheilanthes is included in Table 11. The occurrence of Cheilanthes Fendleri, C. lendigera, C. microphylla, Notholaena Marantae, N. sinuata, Pellaea atropurpurea and P. rotundifolia, which are found in two or more stele type categories, is particularly striking. The large number of Cheilanthes species placed under typical solenostele was in large part based on McCulloch et al. (1974).

Utilizing the same format as Table 11 the taxa from this research on Pellaea and Notholaena can be added, and the stelar types reduced for generalization to: solenostele, transitional and dictyostele, in Table 12. This may be the best method for a comparative study of the three genera, even though a more complete description and analysis would be necessary for each taxa.

It would be additionally beneficial to eliminate from the solenostelic and dictyostelic columns any taxa that appears to be transitional. The transitional condition describes more fully and accurately the stelar condition found in many of the taxa.

It has been pointed out by Stevensen (personal correspondence, June, 1976) that within the same taxon a solenostele or a dictyostele

might be found. With this in mind and with the frequency of the transitional stele in some species the above method of description seems the most logical in light of the present evidence. Table 13 represents a further refinement of the rhizome conditions of the three genera with this concept in mind.

The dictyostelic condition is seen as the exception in Cheilanthes, Notholaena and Pellaea, with no representatives (thus far) in Notholaena, one in Cheilanthes, and only three in Pellaea. The transitional stele type is frequent in representatives of Cheilanthes, Notholaena and Pellaea. The dominant stele type, however, in all three genera is the solenostele.

The placement of taxa previously reported that were examined in this research, and found to be of a stele type different from previous reports, were changed to reflect this research.

In an attempt to compare past interpretations of stelar ontogeny, as noted in the literature review, with our research, sections of Pellaea viridis were made, starting with the upper portion of the young rhizome and proceeding to the basal portion (oldest region).

The mature stelar condition of P. viridis is a dictyostele. As one proceeds basally then, it would be expected that the solenostelic and then the protostelic condition would be encountered. Observations made confirm this pattern of development in Pellaea viridis (Figure 122 - 126). The exact mode of origin of the pith and developmental changes that occur from the protostelic to solenostelic stage are still in question in this taxa as they are in most ferns. The Figures 122 - 126 were sent to Dr. Richard White, Department of Botany, Duke University, at the suggestion of Dr. Irving Knobloch, for his comments and

interpretations. Dr. White confirmed our opinions of the sections (personal communication, July, 1976). The results of this investigation confirm the past literature in that the youngest portion of the stele was protostelic.

Esau (1965) observed that in the botanical literature the question has often been raised as to how much of the vascular system of the stem is foliar by origin and how much is cauline by origin.

Some workers consider that, at least in some ferns, all the vascular tissue in the stem is foliar in origin (Schoute, in Verdoorn, 1938). Campbell (1921) believed that the stelar system of the stem was simply an aggregate of leaf traces, implying that the stelar system of the stem was, in fact, initially absent.

This is seemingly the case in the Marattiaceae and Ophioglossaceae where the leaf traces are extremely large and they assemble as if to form a central stele (Ogura, 1972).

McAlpine and White (1974) have stated that it is the sheathing leaf bases that are most significant in the organization of the upright shoot in the Ophioglossaceae. In this case no sharp anatomical differences delimit the cells of a leaf and its sheath from the cells of the stem during the primordial stages.

A contemporary proponent of this theory is Stevensen, as related by White (personal correspondence, July, 1976); Stevensen's opinion also being that the stem protostele develops from a fusion of leaf traces.

The opposing theory is one in which the stele is cauline in origin. White (personal correspondence, July, 1976) states that:

There is considerable distance of protostele in some young fern sporophytes between the transition from root

to shoot and before the departure of a leaf trace. When a leaf trace does join to the shoot stele, it is much smaller than the total stele in area - in other words there is more vascular tissue than can be ascribed to the leaf trace alone - even when only a single leaf is present in the sporophyte . . . I think, based on my observations of ontogenetic series and some of Wardlaw's work, that there is a cauline vascular system independent of leaf traces in the ferns. Hence I would see the traces going out to leaves from the stele, and I do not believe the mature siphonostele, etc. to be the result of merged leaf traces. Wardlaw showed that by continual puncturing of leaf primordia at the shoot tip, the stelar pattern became protostelic, but that a protostele remained despite the absence of leaf traces, etc. Therefore, a cauline system is retained even after the loss of the foliar system.

Pellaea viridis (Figure 126) illustrates a portion of the protostele in which no leaf traces can be observed, yet there is a discernable amount of xylem; this observation would tend to support White's concept as well as Lucansky and White (1976) concerning the cauline nature of the stele. It must be stated that much more research needs to be conducted in this area, in particular as it relates to Leptosporangiate ferns and a comparison of them to conditions in the Eusporangiate ferns. This research, furthermore, does not negate the research of those who find that the stele originated by a fusion of leaf traces.

From the literature as it relates to the ecology of the rhizome, two points become increasingly clear. First, the growth habits as expressed in the Cheilantheid ferns are highly specialized and the stelar condition is probably not genetically fixed on a rigid basis, but is partly a response on the part of the plant to the environment that it is in. This fact is reflected in the varying stelar conditions and the numerous taxa occurring in a "transitional" category. The unevenness of the terrain could account for the variety of

interpretations of stelar conditions found in the literature. For example, a creeping habit might illustrate a solenostelic condition, but an ascending semi-erect portion of the same rhizome might illustrate a transitional or dictyostelic condition. The stelar condition as reported in the past literature most likely depended heavily on what portion(s) of the rhizome(s) were sectioned and how many sections were made. Because this kind of data is lacking in one-hundred percent of the cases, a good deal of interpretation has had to take place in analyzing the information. The following Tables 14 and 15 compare the growth habit of the taxa (Correll, 1952; Hevly, 1963; Knobloch and Correll, 1962; Munz, 1959; Shreve and Wiggins, 1964; Tryon, A., 1957; Tryon, R., 1956) and their stelar condition. From Tables 14 and 15 it can be observed that the growth habit for the most part is reflected in the stelar condition, i.e. a slender horizontal growth habit has a solenostele, e.g. N. rigida, a short ascending growth habit has a dictyostele, e.g. P. dealbata.

Secondly, genetically fixed characters might possibly serve for identification and taxonomic purposes. Supporting this statement was the observation that the taxa examined expressed a range of sclerification patterns in the cortex and pith that seemingly might be an appropriate diagnostic character. Tables 16 and 17 illustrate the sclerification pattern of the cortex in the taxa and their stelar condition. These Tables (16 and 17) seem to indicate that there does not appear to be any intergeneric or intrageneric relations between stelar taxa that have uniform sclerification (N. neglecta, N. Newberryi, P. atropurpurea and P. ovata). It also appears that there are no correlations between growth habit (Tables 14 and 15) and sclerification pattern (Table 16 and 17).

In summary, this research has attempted to ascertain a number of points. This research has: (1) provided detailed descriptions of the rhizome anatomy of selected species of eighteen members of the genus Notholaena (seventeen species of which had not been previously described), and seventeen species of the genus Pellaea (none of which have been previously described); (2) provided a logical systematic method for describing the rhizome anatomy in a consistent fashion by using the terms solenostele, transitional stele and dictyostele; (3) determined that scalariform tracheids (as examined in the macerated xylem tissue of N. Galeottii, N. rigida, N. Standleyi, P. atropurpurea, P. intermedia and P. viridis) are the dominant water and mineral conducting cells of the xylem; (4) determined that in both genera there is at least one species (P. atropurpurea and N. Galeottii) that has helical protoxylem cells; (5) documented the ontogenetic development of the stele type in at least one species (P. viridis); (6) determined that the major stele type in Notholaena and Pellaea is a solenostele, with some species being transitional and only Pellaea exhibiting the dictyostelic condition; (7) determined that in general the rhizome growth habit described as horizontal to semi-erect is likely to be a solenostele or transitional stele, and that the rhizome growth habit that is described as erect is likely to be transitional or dictyostelic; (8) determined that the presence of xylem parenchyma is predominant in both genera (Notholaena and Pellaea) and in all stele types; this is in contrast to Cheilanthes, where a correlation was found between the solenostelic condition and no xylem parenchyma and the transitional and dictyostelic condition and the presence of xylem parenchyma; (9) determined that distinctive sclerification banding patterns are found to occur in the cortex, but

there is no correlation of genera and banding patterns; and (10) determined that the rhizome anatomy will not serve as a diagnostic character to effectively separate Cheilanthes, Notholaena and Pellaea, at least at the present.

Further research in the following areas would be beneficial in elucidating anatomical problems in the Cheilanthoid ferns and furthering the quest for diagnostic characters that might be used to illustrate the complex relationships that seem to exist in this group of ferns:

(1) more species of the genera Cheilanthes, Notholaena and Pellaea need to have their rhizome anatomy described; (2) experiments involving the ontogeny of the stele should be done on a large number of taxa; (3) more species need to be analyzed for the presence of protoxylem in the rhizome; (4) taxa need to be examined for the possible occurrence of vessels in both rhizome and roots; and (5) further standardization of stelar terminology needs to be accomplished.

TABLE 11. Stele types as reported in the previous literature.

		GENUS		
		CHEILANTHES	NOTHOLAENA	PELLAEA
STELE TYPE	RADIAL DICTYOSTELE	<u>C. persica</u>		
	DORSIVENTRAL DICTYOSTELE	<u>C. Feei</u> <u>C. Fendleri</u> <u>C. gracillima</u> <u>C. lendigera</u>	<u>N. ferruginea (aurea)</u> <u>N. Marantae</u> <u>N. sinuata</u> <u>N. trichomanoides</u>	<u>P. andromaedifolia</u> <u>P. atropurpurea</u> <u>P. cordata</u> <u>P. rotundifolia</u>
	TRANSITIONAL	<u>C. Feei</u> <u>C. Fendleri</u> <u>C. gracillima</u> <u>C. Kaulfussii</u> <u>C. lanosa</u> <u>C. lendigera</u> <u>C. Parryi</u> <u>C. viscida</u>	<u>N. ferruginea (aurea)</u> <u>N. Marantae</u> <u>N. sinuata</u> <u>N. trichomanoides</u>	<u>P. andromaedifolia</u> <u>P. atropurpurea</u> <u>P. rotundifolia</u>
	DICTYOXYLIC SOLENOSTELE	<u>C. lendigera</u> <u>C. microphylla</u>		
	DORSIVENTRAL SOLENOSTELE	<u>C. microphylla</u>		
	TYPICAL SOLENOSTELE	<u>C. aemula</u> <u>C. angustifolia</u> <u>C. Brandegii</u> <u>C. castanea</u> <u>C. Clevelandii</u> <u>C. Cooperae</u> <u>C. Covillei</u>		

TABLE 11 (cont'd.)

		GENUS		
		CHEILANTHES	NOTHOLAENA	PELLAEA
TYPICAL SOLENOSTELE	C. <u>Eatonii</u>		N. <u>Marantae</u>	P. <u>atropurpurea</u>
	C. <u>Fendleri</u>		N. <u>sinuata</u>	P. <u>falcata</u>
	C. <u>gracillima</u>			P. <u>rotundifolia</u>
	C. <u>horridula</u>			
	C. <u>intertexta</u>			
	C. <u>lindigera</u>			
	C. <u>Lindheimeri</u>			
	C. <u>mexicana</u>			
	C. <u>microphylla</u>			
	C. <u>myriophylla</u>			
	C. <u>notholaenoides</u>			
	C. <u>Pringlei</u>			
	C. <u>tomentosa</u>			
	C. <u>Wootonii</u>			
	C. <u>Wrightii</u>			

TABLE 12. Stele types in previous literature reduced to basic conditions (solenostele, transitional, dictyostele).

		GENUS		
		CHEILANTHES	NOTHOLAENA	PELLAEA
STELE TYPE	SOLENOSTELE	<u>C. aemula</u> <u>C. angustifolia</u> <u>C. Brandegii</u> <u>C. castanea</u> <u>C. Clevelandii</u> <u>C. Cooperae</u> <u>C. Covillei</u> <u>C. Eatonii</u> <u>C. Fendleri</u> <u>C. gracillima</u> <u>C. horridula</u> <u>C. intertexta</u> <u>C. Lendigera</u> <u>C. Lindheimeri</u> <u>C. mexicana</u> <u>C. microphylla</u> <u>C. myriophylla</u> <u>C. notholaenoides</u> <u>C. Pringlei</u> <u>C. tomentosa</u> <u>C. Wootonii</u> <u>C. Wrightii</u>	<u>N. Aschenborniana</u> <u>N. aurea (ferruginea)</u> <u>N. brachypus</u> <u>N. candida v. candida</u> <u>N. candida v. Copelandii</u> <u>N. cochisensis</u> <u>N. Galeottii</u> <u>N. Grayi</u> <u>N. Lemmonii</u> <u>N. Marantae</u> <u>N. neglecta</u> <u>N. Newberryi</u> <u>N. rigida</u> <u>N. Schaffneri</u> <u>N. sinuata</u> <u>N. Standleyi</u>	<u>P. allosuroides</u> <u>P. andromaedifolia</u> <u>P. atropurpurea</u> <u>P. Breweri</u> <u>P. Bridgesii</u> <u>P. falcata</u> <u>P. intermedia</u> <u>P. Tongimucronata</u> <u>P. ovata</u> <u>P. rotundifolia</u> <u>P. Skinneri</u> <u>P. X Wrightiana</u>
	TRANSITIONAL	<u>C. Feei</u> <u>C. Fendleri</u> <u>C. gracillima</u> <u>C. Kaulfussii</u> <u>C. lanosa</u> <u>C. Lendigera</u> <u>C. Parryi</u>	<u>N. aurea (ferruginea)</u> <u>N. intergerrima</u> <u>N. limitanea v. mexicana</u> <u>N. Marantae</u> <u>N. parvifolia</u> <u>N. sinuata</u> <u>N. trichomanoides</u>	<u>P. andromaedifolia</u> <u>P. atropurpurea</u> <u>P. brachyptera</u> <u>P. mucronata v. californica</u> <u>P. notabilis</u> <u>P. rotundifolia</u>
	DICTYOSTELE	<u>C. Feei</u> <u>C. Fendleri</u> <u>C. gracillima</u> <u>C. Lendigera</u> <u>C. persica</u>	<u>N. aurea (ferruginea)</u> <u>N. Marantae</u> <u>N. sinuata</u> <u>N. triangularis</u> <u>N. trichomanoides</u>	<u>P. andromaedifolia</u> <u>P. atropurpurea</u> <u>P. cordata</u> <u>P. dealbata</u> <u>P. pteroides</u> <u>P. rotundifolia</u> <u>P. viridis</u>

TABLE 13. Refined stele types.

		GENUS		
		CHEILANTHES	NOTHOLAENA	PELLAEA
STELE TYPE	SOLENOSTELE	<u>C. aemula</u> <u>C. angustifolia</u> <u>C. Brandegii</u> <u>C. castanea</u> <u>C. Clevelandii</u> <u>C. Cooperae</u> <u>C. Covillei</u> <u>C. Eatonii</u> <u>C. horridula</u> <u>C. intertexta</u> <u>C. Lindheimeri</u> <u>C. mexicana</u> <u>C. microphylla</u> <u>C. myriophylla</u> <u>C. notholaenoides</u> <u>C. Pringlei</u> <u>C. tomentosa</u> <u>C. Wootonii</u> <u>C. Wrightii</u>	<u>N. Aschenborniana</u> <u>N. aurea</u> <u>N. brachypus</u> <u>N. candida</u> v. <u>candida</u> <u>N. candida</u> v. <u>Copelandii</u> <u>N. cochisensis</u> <u>N. Galeottii</u> <u>N. Grayi</u> <u>N. Lemmonii</u> <u>N. neglecta</u> <u>N. Newberryi</u> <u>N. rigida</u> <u>N. sinuata</u> <u>N. Standleyi</u>	<u>P. allosuroides</u> <u>P. andromaedifolia</u> <u>P. atropurpurea</u> <u>P. Breweri</u> <u>P. Bridgesii</u> <u>P. falcata</u> <u>P. intermedia</u> <u>P. longimucronata</u> <u>P. ovata</u> <u>P. Skinneri</u> <u>P. X Wrightiana</u>
	TRANSITIONAL	<u>C. Feei</u> <u>C. Fendleri</u> <u>C. gracillima</u> <u>C. Kaulfussii</u> <u>C. lanosa</u> <u>C. Tendigera</u> <u>C. Parryi</u>	<u>N. intergerrima</u> <u>N. limitanea</u> v. <u>mexicana</u> <u>N. Marantae</u> <u>N. parvifolia</u> <u>N. trichomanoides</u>	<u>P. brachyptera</u> <u>P. mucronata</u> v. <u>californica</u> <u>P. notabilis</u> <u>P. rotundifolia</u>
	DICHYOSTELE	<u>C. persica</u>		<u>P. dealbata</u> <u>P. pteroides</u> <u>P. viridis</u>

TABLE 14. Notholaena rhizome habit and stele type.

Species	Habit	Stele
<u>N. Aschenborniana</u>	stout, short creeping	solenostele
<u>N. aurea</u>	thick, short creeping	solenostele
<u>N. brachypus</u>	short, thick, erect	solenostele
<u>N. candida</u> v. <u>candida</u>	short creeping, branched	solenostele
<u>N. candida</u> v. <u>Copelandii</u>	short, compact	solenostele
<u>N. cochisensis</u>	short, thick	solenostele
<u>N. Galeottii</u>	short creeping	solenostele
<u>N. Grayi</u>	short creeping	solenostele
<u>N. integerrima</u>	short, thick	transitional
<u>N. Lemmonii</u>	short, thick ascending	solenostele
<u>N. limitanea</u> v. <u>mexicana</u>	horizontal	transitional
<u>N. neglecta</u>	horizontal, short creeping	solenostele
<u>N. Newberryi</u>	horizontal	solenostele
<u>N. parvifolia</u>	compact, short creeping	transitional
<u>N. rigida</u>	horizontal, slender	solenostele
<u>N. Schaffneri</u>	short ascending	solenostele
<u>N. sinuata</u>	short, thick, horizontal	solenostele
<u>N. Standleyi</u>	short, horizontal	solenostele

TABLE 15. Pellaea rhizome habit and stele type.

Species	Habit	Stele
<u>P. allosuroides</u>	stout, short creeping	solenostele
<u>P. andromaedifolia</u>	slender, cord-like	solenostele
<u>P. atropurpurea</u>	stout, compact	solenostele
<u>P. brachyptera</u>	moderately stout, elongate	transitional
<u>P. Breweri</u>	compact, massive, ascendent	solenostele
<u>P. Bridgesii</u>	short creeping	solenostele
<u>P. dealbata</u>	short ascending	dictyostele
<u>P. falcata</u>	short creeping to erect	solenostele
<u>P. intermedia</u>	elongate, slender	wolenostele
<u>P. longimucronata</u>	moderately stout, elongate	solenostele
<u>P. mucronata</u> v. <u>californica</u>	erect	transitional
<u>P. notabilis</u>	moderately stout, compact	transitional
<u>P. ovata</u>	slender, creeping or compact	solenostele
<u>P. pteroides</u>		transitional
<u>P. Skinneri</u>	short, stout	solenostele
<u>P. viridis</u>	erect	dictyostele

TABLE 16. Notholaena: stele type and sclerification pattern.

Species	Stele	Sclerification
<u>N. Aschenborniana</u>	solenostele	none-heavy
<u>N. aurea</u>	solenostele	light-heavy-light
<u>N. brachypus</u>	solenostele	heavy-light
<u>N. candida</u> v. <u>candida</u>	solenostele	heavy-light
<u>N. candida</u> v. <u>Copelandii</u>	solenostele	heavy-light
<u>N. cochisensis</u>	solenostele	heavy-light
<u>N. Galeottii</u>	solenostele	heavy-light
<u>N. Grayi</u>	solenostele	heavy-light
<u>N. integerrima</u>	transitional	heavy-light
<u>N. Lemmonii</u>	solenostele	heavy-light-heavy
<u>N. limitanea</u> v. <u>mexicana</u>	transitional	heavy-light
<u>N. neglecta</u>	solenostele	uniform
<u>N. Newberryi</u>	solenostele	uniform
<u>N. parvifolia</u>	transitional	heavy-light
<u>N. rigida</u>	solenostele	heavy-light
<u>N. Schaffneri</u>	solenostele	light-heavy-light
<u>N. sinuata</u>	solenostele	heavy-light
<u>N. Standleyi</u>	solenostele	heavy-light-heavy

TABLE 17. Pellaea: stele type and sclerification pattern.

Species	Stele	Sclerification
<u>P. allosuroides</u>	solenostele	light-heavy
<u>P. andromaedifolia</u>	solenostele	light-heavy-light
<u>P. atropurpurea</u>	solenostele	uniform
<u>P. brachyptera</u>	transitional	heavy-light-heavy
<u>P. Breweri</u>	solenostele	heavy-light
<u>P. Bridgesii</u>	solenostele	heavy-light
<u>P. dealbata</u>	dictyostele	heavy-light
<u>P. falcata</u>	solenostele	light-heavy-light
<u>P. intermedia</u>	solenostele	light-heavy
<u>P. longimucronata</u>	solenostele	heavy-light
<u>P. mucronata</u> v. <u>californica</u>	transitional	heavy-light
<u>P. notabilis</u>	transitional	heavy-light
<u>P. ovata</u>	solenostele	uniform
<u>P. pteroides</u>	transitional	heavy-light
<u>P. Skinneri</u>	solenostele	uniform
<u>P. viridis</u>	dictyostele	heavy-light

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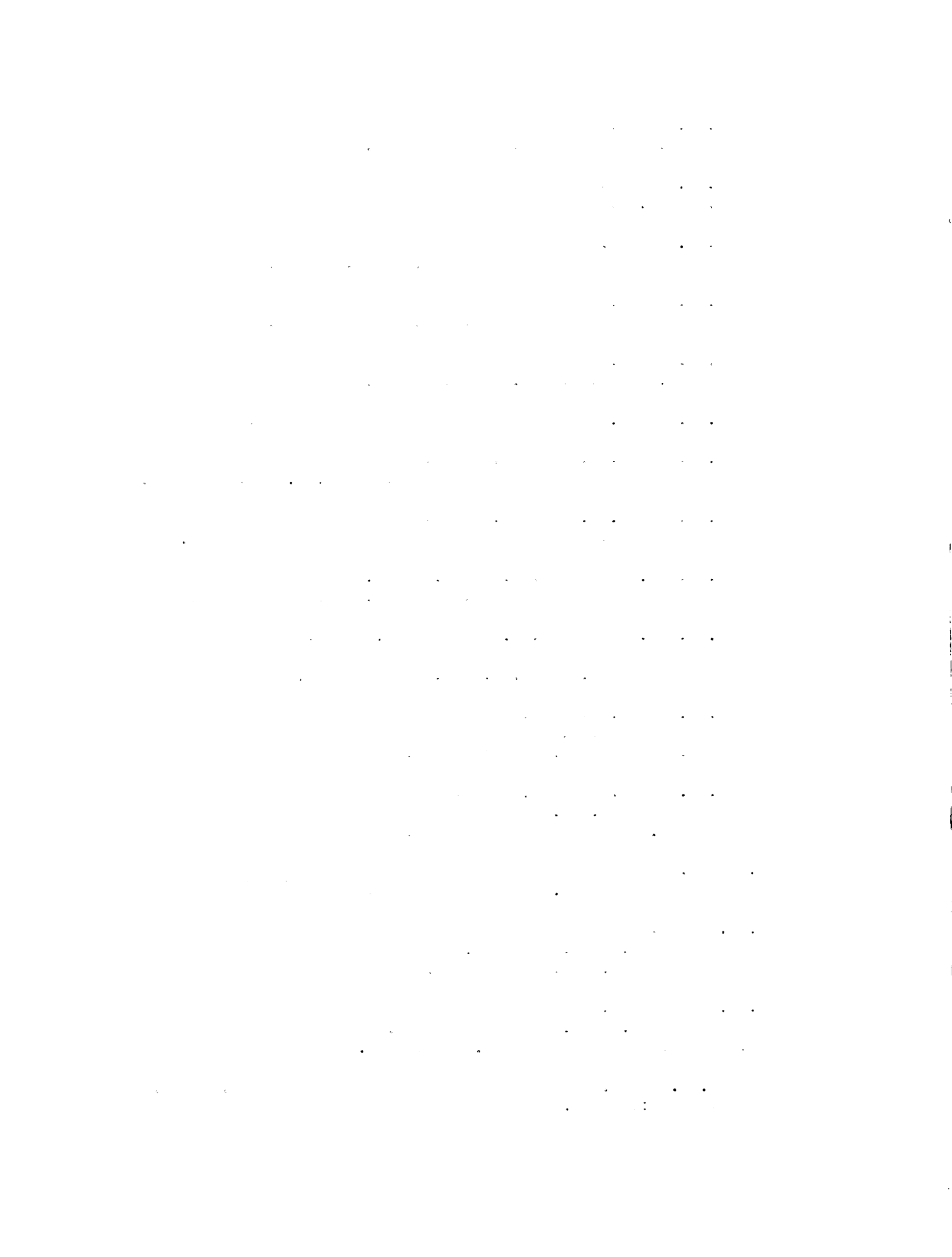
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