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A FOSSIL DENNSTAEDTIOID FERN FROM THE
EOCENE CLARNO FORMATION OF OREGON

BY

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A FOSSIL DENNSTAEDTIOID FERN FROM THE EOCENE CLARNO FORMATION OF OREGON

BY

CHESTER A. ARNOLD and LYMAN H. DAUGHERTY

ABSTRACT

Rhizomes and leaf stalks of a fern preserved in chert from the Eocene Clarno formation of Oregon show anatomical structures which indicate the subfamily Dennstaedtioideae of the Polypodiaceae. The distinguishing feature of this fern is the presence in the pith and cortex of the rhizomes of prominent layers of aerating tissue of the type common in aquatic plants. It has a stele and leaf trace similar to those in the living *Dennstaedtia cicutaria*, but the fossil form differs in its obvious aquatic habitat and in being associated with *Acrostichum*. The new genus and species, *Dennstaedtiopsis aerenchymata*, is created for it. The rhizomes are preserved *in situ* in a matrix which represents the silicified soil of a marsh.

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INTRODUCTION

THE FOSSIL fern described here is the "unidentified polypodiaceous fern" mentioned by the present authors (Arnold and Daugherty, 1963, p. 210) in their recent description of the *Acrostichum* remains in the Eocene age Clarno formation of Oregon. At the time that account was written, the new fern had not been thoroughly studied, and consequently a complete description could not be given.

Both of the ferns are preserved in chert, which was referred to as the Clarno chert. This chert represents the silicified soil of an Eocene marsh, and the two ferns are a part of the original vegetation of the marsh. There are some other plants in the chert, as *Ginkgo*, for example, which were apparently washed in from the surrounding terrain. Ferns, however, appear to have been the dominant vegetation in the marsh itself.

The fern that is described here has been identified as an extinct genus of the subfamily Dennstaedtiodeae of the family Polypodiaceae. It appears to differ from any known living members of the Dennstaedtiodeae in being an aquatic plant, which is most convincingly shown by the conspicuous aerating tissue in the pith and cortex of its rhizomes and leaf stalks (Pls. II, III, and V, Fig. 3). Its association in the marsh with *Acrostichum* is also a matter of interest because *Acrostichum* and ferns of the dennstaedtioid subfamily do not share common habitats today.

ACKNOWLEDGMENTS

The plant-bearing chert in the Clarno formation was discovered by the senior author in 1948 under the guidance of the late Mr. A. K. Chandler. More material was collected the following year with the help of R. A. Scott and Robert Lindsley. The final study was accomplished with equipment and technical assistance made available by grant No. NSF-G19553 from the National Science Foundation. Supplementary laboratory space was furnished by the Botanical Gardens of the University of Michigan, and valuable advice was received from Dr. Warren H. Wagner, Professor of Botany at the University of Michigan. Mr. P. C. Hutchinson, Senior Botanist at the Botanical Garden of the University of California, Berkeley, was instrumental in providing rhizome and frond material of *Dennstaedtia cicutaria* and other members of the Dennstaedtiodeae. To all the above-mentioned persons and institutions the authors are especially grateful for their co-operation. Dr. L. B. Kellum and Dr. R. V. Kesling read the manuscript and gave helpful suggestions.

THE CLARNO CHERT

Locality and occurrence.—The Clarno chert occurs in the eastern part of Jefferson County, Oregon, about 1½ miles northeast of a place shown

on some maps as Kilts Postoffice. The postoffice, however, is no longer there and no traces of it remain. As precisely as can be designated, the site is in the extreme northwestern corner of Sec. 27, T. 9S., R. 18E. The geology of this area has not been mapped and no sections have been measured in the vicinity where the chert occurs. During a second visit to the place in 1949 the chert outcrop was located beneath a lava bed that once covered the area, but which today exists only as remnants that cap the hilltops. The chert bed, which is about 2 feet thick, overlies an ash deposit with a maximum thickness of 400 feet.

Character and origin.—The plants were found in pieces of the chert that had broken away from the outcrop. When freshly broken the chert varies from medium to dark gray, but it becomes whitish when weathered. The plants show up most conspicuously on surfaces that have been slightly weathered (Pl. I). They are quite indistinct on dark freshly broken surfaces, and prolonged weathering usually bleaches most of the color from both plant and matrix.

The marsh in which the chert was formed had been fed by hot springs. The water issuing from them carried dissolved silica and probably other minerals in considerable quantities. The evaporation of moisture from the marsh caused the silica to accumulate in the black peaty soil, and with final expulsion of the free water, due presumably to the weight of a lava flow, the silica solidified into chert, and in so doing petrified the plants. The structure of the plants shows that they grew in thoroughly waterlogged soil, which at least part of the time was inundated, with only hummocks extending above the surface. The marsh also received some fresh volcanic ash directly from the air and by erosion of deposits that had been built up shortly before. This is indicated by considerable undecomposed ash in the chert.

Some of the plant remains are preserved *in situ* where they grew. These are mostly the roots and subterranean rhizomes of the fern described here. Most of the *Acrostichum* remains are parts of the large elevated fronds that had fallen into the marsh but were never-the-less preserved in the immediate vicinity of growth. As mentioned, a few plants came into the marsh from outside.

THE PROBLEM OF IDENTIFICATION

The rhizomes and the lower parts of the petioles of the fern under consideration are well preserved, but higher portions of the fronds had suffered considerable decay which became progressively worse in the finer frond subdivisions. In fact, the pinnules, sori, and sporangia have not been

recognized. This is in rather sharp contrast to the situation revealed by *Acrostichum* where all parts of the sporophyte body are preserved.

The lack of recognizable pinnules and sori renders positive identification difficult, and description of the fern was long delayed on this account. The expectation that more information might be obtained which would shed more light on its affinities has been only partially fulfilled. The accumulated evidence, incomplete though it is, does seem, however, to point quite convincingly to a place in the subfamily Dennstaedtioideae of the Polypodiaceae. Relationship with any particular genus is less certain, though there are unmistakable resemblances with certain species of *Dennstaedtia*. However, we know of no dennstaedtioid ferns in the Recent flora that grow in marshes or that show the internal adaptation to an aquatic habitat as revealed in the fossil. Furthermore, living dennstaedtioid ferns do not grow in the same intimate association with *Acrostichum*. Either the Clarno fern belongs to an extinct genus of the Dennstaedtioideae, or it has living members of limited distribution in remote tropical swamps. The former of the two possibilities is the one we are inclined to favor, partly because of the peculiar structure and partly because of its unique association with *Acrostichum*. The Clarno flora does contain extinct genera clearly referable to living families (Scott, 1955). On the assumption, therefore, that the fern is extinct, the new genus *Dennstaedtiopsis* is proposed for it.

GEOLOGICAL HISTORY OF THE DENNSTAEDTIOIDEAE

The geological history of the Dennstaedtioideae is short, as is also the history of the family Polypodiaceae of which it is a part. Lack of recognizable polypodiaceous ferns below the Upper Cretaceous, and their apparent confinement to Upper Cretaceous and later deposits, leads us to conclude that the whole group must have taken form rather late in geologic time. Even in Tertiary floras polypodiaceous ferns are seldom abundant, though actually they are about as prevalent as other ferns. But ferns are always subordinate to angiosperms in these floras, and their paucity is due in part to the fact that when the latter began their rapid spread during the middle part of the Cretaceous period, the lower groups (which include the ferns) diminished accordingly. The result was a great reduction in number of ferns as compared with angiosperms. Then the usual habits of ferns with their fragile fronds have not been such as to favor preservation in large numbers. Even the fact that many of them grow in moist places lessens the chances of preservation because of the rapid decay, especially in warm climates. At the end of the growing season fern fronds fall to the ground while still attached, and prompt decay usually sets in. About the only

means of transport to sites of deposition that are at all favorable to preservation are chance dispersal of accidentally detached fragments by wind, or by water where the ferns grow beside streams. In case of polypodiaceous ferns with finely divided fronds, as many are, the chances of preservation in large numbers are relatively slight. Also in this family the sori with their sporangia borne on separate stalks in loose clusters are too fragile to retain their characters well in compressions. If preserved at all, the frond fragments seldom retain a significant number of characters of the type that are commonly relied upon for precise identification.

With few exceptions the literature on fossil dennstaedtioid ferns consists of scattered references to *Dennstaedtia*, *Hypolepis*, and *Microlepia*. The two dennstaedtioids most often cited in American literature are *Dennstaedtia americana* (Knowlton, 1910) and *D. blomstrandii* (Hollick, 1936). The former name applies to Paleocene material from Saskatchewan, North Dakota, and Wyoming, and from the Miocene of Japan. The latter is a Tertiary form (presumably Eocene) from Greenland, Spitzbergen, and Alaska. In addition to these, Knowlton (1930) grouped a few pinnule fragments from the Upper Cretaceous of Colorado into *D. crossiana*, but emphasized the questionable nature of the remains. A more probable fossil *Dennstaedtia* is *D. adamantea* from the Oligocene of Montana (Becker, 1961). The material consists of one pinna which resembles figures of *D. blomstrandii*. *Hypolepis coloradensis*, from the Oligocene at Florissant, Colorado, was transferred to *Dryopteris* by MacGinitie (1953).

None of the fossil material that has been identified as *Dennstaedtia* or any other genus of the Dennstaedtioideae is free of doubt. Some of the compressions show marginal sori only suggestive of a genus or subfamily. One might, if so inclined, repudiate all of the supposed fossil Dennstaedtioideae on grounds that none of them are trustworthy, and that we possess no reliable knowledge of the geologic history of the group. If, on the other hand, all published accounts are to be accepted at face value, the Dennstaedtioideae have been in existence since Early Cretaceous times and maybe even longer. The truth probably lies somewhere between, and there is scarcely any doubt but the subfamily thrived during the Eocene epoch.

The Clarno chert happens to constitute an extremely favorable medium for the preservation of ferns that under most conditions would have left no remains. The underground rhizomes were infiltrated and petrified *in situ* along with the basal parts of the attached leaf stalks. The marsh environment, however, was much less favorable for preservation of the finely divided frond portions which mostly decayed before they could become entombed in sediments. Consequently the sori and sporangia have

not been found, and identification of the fern in question as a member of the Dennstaedtioidae rests wholly on structure of the rhizomes and leaf stalks, and on certain inferences concerning other features as revealed by the structure of the parts.

SYSTEMATIC DESCRIPTION

Order FILICALES

Family Polypodiaceae

Subfamily Dennstaedtioidae

Genus *Dennstaedtiopsis* nov.

Diagnosis.—Ferns with solenostelic subterranean rhizomes and single leaf trace strands similar to those of *Dennstaedtia*.

Generitype.—*Dennstaedtiopsis aerenchymata* Arnold and Daugherty, sp. nov.

Dennstaedtiopsis aerenchymata Arnold and Daugherty, sp. nov.

Diagnosis.—Aquatic ferns with horizontally oriented, cylindrical, hairy rhizomes up to 12 mm in diameter, with leaf gaps not overlapping. Prominent aerenchymatous tissue in cortex and pith characterized by large, radially elongated air spaces. Petiole with single leaf trace strand which in cross section has the shape of an inverted bowl with bulbous base and flaired rim. Pinnæ alternately arranged and distant.

Locality and horizon.—Northeastern corner of Sec. 27, T. 9S., R. 18E., Jefferson County, Oregon. Clarno formation, Upper Eocene.

Holotype.—No. 48297 UMMMP.

ANATOMICAL DESCRIPTION

The reasons for identifying this fern as a member of the Dennstaedtioidae will be explained after the anatomical features are described.

Rhizomes.—These are slender, horizontally oriented, branched organs that exhibit slight dorsi-ventrality. The stele in most specimens is slightly flattened, but that this is natural and not the result of pressure is amply shown by the nearly circular outline of the whole axis (Pl. III). Furthermore, there are structural features associated with the oval form of the stele. The rhizomes range up to 12 mm in the broadest dimension, though most of them are smaller. The petiole bases are attached at intervals of several centimeters along the slender axes. Branching is frequent. A branch may be larger or smaller than the parent axis and is seldom exactly the same size (Pl. VII, Fig. 3). Though the rhizomes ramify through the chert in all directions, a given rhizome portion may follow a straight course for a considerable distance. On the surface of one block a rhizome was traced for more than 10 cm before it left the plane of the cut.

Some of the distinctive and characteristic features of the rhizomes can be seen on the surfaces of the chert blocks with no visual aid other than a low-power lens. The vascular cylinder, which is interrupted only by widely spaced leaf gaps stands out conspicuously around the pith (Pls. II and III). In the cortex and pith there are large radially elongated air spaces (the aerenchyma mentioned before) that form zones of lighter color than the tissues that flank them. The layer of firm pith tissue that lies between the aerenchyma and the inner endodermis is a thin dark-colored band. Likewise, the narrow innermost cortex immediately outside the outer endodermis is similarly darkened, as is also the outer cortex, which is about as wide as the aerenchyma. Darker still is a thin layer of weakly developed sclerenchyma, which in many specimens constitutes the surface layer (Pl. IV, Fig. 1).

The innermost pith is a compact core of vertically elongated cells with slightly thickened walls. It resembles the outer cortex in color and cell characteristics. The aerenchyma that surrounds the pith is similar to that in the cortex. In both places it consists of air spaces that are elongated radially and separated by partitions that are one cell thick. The cells composing the partitions are thin-walled and are slightly smaller than those of the solid tissue. They are nearly equidimensional, appearing rounded in transverse section and rectangular in radial view. The air spaces are up to 0.75 mm long in the radial direction. Some extend the entire width of the aerenchyma band whereas others are divided by oblique or tangentially placed partitions. The aerenchyma is thickest along the dorsal and ventral sides of the axis and thinnest laterally, the difference being more pronounced in the pith than in the cortex. It appears to have originated schizogenously. The thin layer of solid cortex external to the aerenchyma is composed of cells of about the same size as those composing the partitions.

The vascular cylinder is a solenostele with external and internal endodermis, pericycle, and phloem (Pl. IV, Fig. 2). Of these tissues, the endodermis is the most difficult to identify because its cells are small, filled with black substance, and generally not well preserved. It has been recognized with certainty only where the phloem and pericycle had decayed leaving only the Casparian strips standing free as two series of minute, black, regularly spaced, radially elongated dots, one inside the cortical cylinder and the other outside the pith. Often, especially where the pericycle is preserved, the endodermis shows only as a thin black line between the surface cells of the vascular cylinder and the pith and the cortex.

The pericycle (both inner and outer) is a single layer of small, regu-

larly arranged cells. It is distinct from the endodermis because of the larger cells and lack of Casparian strips, and from the phloem because of its darker cell contents. The phloem is mostly a single layer of cells, though locally, especially along the dorsal and ventral sides of the rhizome, it may consist of a double cell layer. The larger more regularly arranged cells are evidently the sieve cells, and the smaller, more irregularly distributed ones appear to be phloem parenchyma. No sieve areas have been identified on the supposed sieve cells, due to failure to secure longitudinal sections through sufficiently well-preserved portions of rhizomes.

In transverse section the xylem consists of tracheids and small-celled parenchyma which fills numerous spaces where the tracheids are not in contact. The xylem band may be six or seven tracheids wide where it is thickest, but it is only one to three cells wide along much of its circumference. At the lateral margins it is very thin, along with increasing amounts of parenchyma. There it may consist of a single row of tracheids which at places becomes discontinuous.

At the outer surface of the xylem one may see a dozen or so clusters of small tracheids. These are evidently the protoxylem, and it is outward from these groups that the adventitious roots arise. The stele therefore appears to be exarch.

The scalariform type of wall thickening appears to prevail in the tracheids throughout the xylem. Spiral thickenings are rare, though they do exist. A few tracheids bearing spiral elements probably occur in each mass of small tracheids at the periphery of the xylem, though most of the small tracheids are scalariform. Some of the smallest tracheids that have been observed bear scalariform markings, so there seems to be no consistent correlation between tracheid size and type of wall sculpturing. In one instance a few spiral elements were observed on the inner face of the xylem. Annular elements have not been seen.

The external phloem, pericycle, and endodermis are similar to their counterparts on the inside. The extreme innermost cortex resembles the outermost pith in extent and cellular characteristics. The aerenchyma is also of similar construction except for being slightly wider, occupying about one half of the total cortical area.

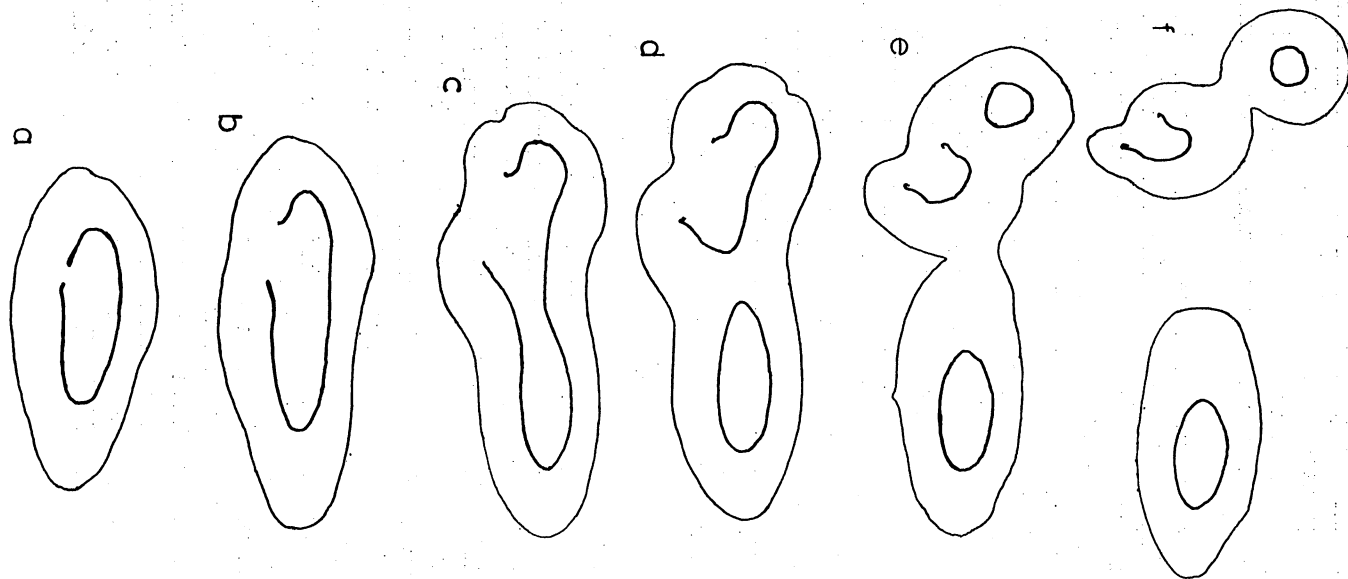
The sclerenchyma zone in the outer cortex is only a few cells thick (Pl. IV, Fig. 1). In some rhizomes, presumably young ones, it is weakly developed and often scarcely discernible. Where it is fully developed, its cells are much like the other cortical cells except for their slightly thicker and darker walls. In many rhizomes this sclerenchyma constitutes the surface layer. It is quite apparent, however, that in such instances a delicate outermost layer has been removed because in some specimens it

has been preserved. Where it is present it is only a few cells thick, and is composed of compactly placed thin-walled cells. The outermost tier of this layer is clearly the epidermis. It resembles the epidermis of many hydrophytic stems and of most roots in the complete lack of cuticle or thickened walls (Pl. IV, Fig. 1).

Epidermal hairs are numerous at places on the rhizomes (Pl. IV, Fig. 1). They are simple, multicellular, tapering, and as much as 2 mm long. They are broadened at the base where there are two or more cells. At places the hairs are crowded; elsewhere they are scattered.

Branching, and leaf trace formation.—Branching was accomplished by simple dichotomy and from budding from the bases of the petioles. Conard (1908) has described similar phenomena in the living *Dennstaedtia punctilobula*. The first intimation of rhizome branching by bud formation, as revealed in serial sections progressing toward the apex (Fig. 1a-f), is a noticeable flattening of the rhizome and assumption of a broadly oval form. Further along an opening appears in the vascular ring through which the cortex and pith merge. This opening is the lower extremity of the wedge-shaped leaf gap (Fig. 1a). At levels taken successively toward the apex the gap widens (Fig. 1b) and instead of presenting the oval form, it becomes dumbbell shaped from a median constriction (Fig. 1c). Further constriction separates the stele into two parts, one forming a complete solenostele without a gap; the other containing the previously formed gap (Fig. 1d; Pl. VII, Fig. 3). The gapless stele supplies one of the branches. On the other stele, a bulge appears at one side of the gap (Fig. 1d). At a higher level this bulge forms a second complete branch stele (Fig. 1e; Pl. VII, Fig. 3). The remaining strand, which is deeply curved or U-shaped, is the frond trace. It is here situated between the two branches but slightly lateral to them. The gap, which was initiated lower down, continues upward and forms the concavity of the trace. One branch then separates completely from the rhizome (Fig. 1f), leaving the other connected to the petiole by a narrow isthmus of tissue but which itself separates farther along.

Leaf stalks.—Portions of leaf stalks that had become separated from rhizomes and higher portions of the fronds are scattered throughout the chert. They are generally round with a groove along the adaxial side (Pl. VI, Figs. 2-5). The smaller ones are flattened abaxially (Pl. VI, Figs. 2 and 3). The largest petioles are slightly more than 5 mm in diameter. Preservation is seldom as complete as in the rhizomes, apparently the result of having been borne above the ground. The best preservation is in the largest petioles (Pl. V, Fig. 3). In the small midribs the



EXPLANATION OF TEXT FIGURE 1a-f

FIG. 1. *Dennstaedtiopsis aerenchymata* Arnold and Daugherty, sp. nov. Series of tracings showing (a) transverse elongation of rhizome preparatory to departure of leaf trace and branch and lowest appearance of leaf gap; (b) widening of leaf gap and appearance of bulge preparatory to branch formation; (c) constriction of stele preparatory to departure of trace; (d) separation of trace (left) and parent stele (right); (e) separation of rhizome branch from side of trace strand; and (f) complete separation of parent rhizome (right) from trace and its branch.

form of the vascular strand may be recognizable but the cells are usually indistinct (Pl. VI, Figs. 2, 3, and 4).

In cross section the shape of the xylem strand of the petiole is quite distinctive (Pl. V, Fig. 3) and the same form is retained along the length of the frond (Pl. VI, Figs. 1-4). The strand is always in one piece. Nowhere does it separate into two. Near its point of origin from the stem it is U-shaped, but in the free petiole it acquires rather deep lateral indentations and flared extremities, resembling an inverted bowl with a bulbous base and flared rim (Pl. VI, Fig. 1). It is a thin band of tissue which at many places, is only one cell thick. Its ends, however, are sharply flexed inward and lie alongside the ventral surface (Pl. VI, Figs. 1, 5, 6). Several (8-10) groups of small tracheids, evidently protoxylem, are distributed along the band. The phloem is not distinct, but it appears to surround the xylem. Aerenchyma, similar to that in the rhizomes, occupies part of the inner cortical region and part of the pocket formed by the curvature of the strand. Aerenchyma is abundant in some of the larger petiolar axes and disappears completely from the distal parts. The outer cortical tissues intergrade with a layer of hypodermal sclerenchyma. No epidermal hairs have been seen on the petioles.

The pinnules apparently were not preserved as no midribs with attached pinnules have been found. No sporangia attributable to this fern have been recognized in the chert matrix.

AFFINITIES

The Clarno fern has been assigned to the Dennstaedtioideae only after much deliberation. All of the facts that can be assembled which bear upon probable habit and external form have been taken into consideration. Some of them have been adduced from the internal structure and form of the rhizomes and leaf stalks. The sori, which are heavily relied upon in classification and identification of Recent ferns have not been seen. It is not inconceivable, therefore, that discovery of fertile parts could change our present concept of the taxonomic status of this fern. In the meantime, however, it is classified according to the available evidence.

Several characters seem to focus on the Dennstaedtioideae. The most obvious of these, and the first to be considered, is the solenostelic rhizome with its rather distantly placed foliar gaps. On this basis alone, the fern might be referable to the Dicksoniaceae, the Loxsomaceae, to any one of several polypodiaceous genera, or even to the Marsileaceae.

The simple, pointed, multicellular hairs on the rhizomes constitute an important character which eliminates all ferns with scaly rhizomes. According to Bower (1926, p. 268) *Hypolepis*, *Microlepia*, *Leptolepia*, and

Dennstaedtia, those genera which are currently assembled into the subfamily Dennstaedtiodeae, were long ago grouped together on the basis of the rhizome hairs.

Those characters that appear to ally the fossil fern most specifically with the Dennstaedtiodeae are frond characters. Some are directly depicted by the structure; others are inferred. The front trace is a single curved strand, which, according to Bower (1926, p. 268), is the type of strand shown by all species of *Dennstaedtia*.

It was noted early in the course of the investigation that, among the numerous petioles observed, branched leaf stalks were rare. This, along with the lack of pinnules attached to even the smallest front subdivisions led to the surmise that these were naked rachises or leafstalks that bore pinnules only at the summit after the manner of the Marsileaceae. This interpretation was abandoned after it had become evident that the pinnules had merely decayed. Rarity of branched midribs simply indicates long internodal regions.

Since the pinna traces never depart from the main rachis in pairs, the pinnae were obviously alternately arranged (Pl. VI, Fig. 4). Then the distances between departing pinnae traces show that the pinnae were not close together. The lack of preserved pinnules is taken to be evidence that these organs were small and delicately constructed like those of many living dennstaedtioid ferns. The finely divided and openly constructed fronds of *Dennstaedtiopsis* thus stood in marked contrast to the large, coarse, leathery fronds of the *Acrostichum* plants with which *Dennstaedtiopsis* was associated, and parts of which are present in large numbers in the chert. The fronds of most living members of the Dennstaedtiodeae are open with small pinnules, and the frond of the fossil fern appears to have been similar.

COMPARISONS WITH OTHER FERNS

As heretofore explained, lack of preserved pinnules and sori are major obstacles in identification. Another difficulty arises from the fact that most of its stelar characters are similar to those of a considerable number of ferns. Then there are many ferns that are not well known anatomically, and this restricts those with which the fossil form may be compared. Among the most useful sources of information are the papers on *Loxsonia* and a few other ferns by Gwynne-Vaughan (1901, 1903) and one on *Dennstaedtia punctilobula* by Conard (1908).

Loxsonia and *Loxomopsis* constitute the Loxsomaceae of authors. Vegetatively and anatomically they resemble the Dennstaedtiodeae. Gwynne-Vaughan (1901, Pl. III, Figs. 7a-e) figures a series of cross

sections of a trace strand of *Loxsonia* (a genus with one species) that is strikingly like that in the smaller rachises of *Dennstaedtiopsis* (Pl. VI, Figs. 2, 3). The resemblance even extends to the two hooks at the extremities of the xylem (Pl. VI, Fig. 6). There are also some differences. The *Loxsonia* xylem strand shows masses of sclerotized fibrous elements close to the xylem but apparently not a part of it. These do not show in *Dennstaedtiopsis*. Gwynne-Vaughan could locate no spiral elements in the stipe or rhizome, but these are present in small numbers in our fern. Trace departure seems to be simpler in *Loxsonia*, because nothing is said about branch buds arising from the petiole bases.

Gwynne-Vaughan comments upon certain similarities in structure between *Loxsonia* and *Marsilea*, and similar resemblances may be noted between *Marsilea* and *Dennstaedtiopsis*. A conspicuous resemblance is the presence of large air spaces in the cortex of *Marsilea* that are figured by Haupt (1953, p. 294). Gwynne-Vaughan (1901) says that the protoxylem in *Loxsonia* is exarch, and Smith (1938, p. 329) shows an identical feature in *Marsilea*. *Dennstaedtiopsis* resembles both of these in this respect. *Marsilea*, however, has a smaller pith than either *Dennstaedtiopsis* or *Loxsonia*, and the pith contains no aerenchyma. *Marsilea* also has a layer of supporting tissue immediately inside the aerenchyma zone in the cortex, which is noticeably lacking in *Dennstaedtiopsis*.

Although *Marsilea* is solenostelic, the xylem ring is somewhat uneven in thickness at places and there is considerable parenchyma interspersed between concentrically placed bands of tracheids. While this may be an important difference, the resemblances should not be ignored or their importance minimized. Almost nothing is known of the geologic history of the Marsileaceae or of the phylogenetic relationships of the family. Although the aerenchyma in *Marsilea* and *Dennstaedtiopsis* may be merely a reflection of the aquatic environments, some of the other resemblances may have some meaning.

Dennstaedtia punctilobula, the eastern American species, is a solenostelic fern with a rhizome about half the diameter of that of *Dennstaedtiopsis aerenchymata*. Cross sections show a nearly circular stele of even thickness on all sides (Conard, 1908, Fig. 67). While no aerenchyma is present, the inner cortex and outer pith are composed of cells that are filled with starch, and between the cells there are rather large intercellular spaces. In an aquatic habitat, aerating tissue could conceivably develop there. Conard (1908, Fig. 82) shows a small stem stele departing from the margin of the trace strand, similar to that in *Dennstaedtiopsis*. Though in Conard's figure the departing stem is some distance from the leaf axil, the trace strand shows the same relation to the gap. The similarities between

the fossil and living forms are obvious: differences pertain only to details.

The trace strand of *Dennstaedtia punctilobula* resembles that of *Loxsonia* more than *Dennstaedtiopsis*. Its simpler form is probably related to smaller petiole diameter.

Conard says that only the bases of hairs are present on mature parts of the rhizomes, but he shows hairs on leaves of young sporophytes which are similar to those on mature rhizomes of *Dennstaedtiopsis* (Conard, 1908, Fig. 258).

Among living ferns that have been available for comparison, *Dennstaedtiopsis* bears the closest resemblance to *Dennstaedtia cicutaria* (Pl. V, Figs. 1, 2), material of which was kindly supplied by the Botanical Garden of the University of California. The most conspicuous difference as regards rhizome and petiolar structure, is the absence from the latter of medullary and cortical aerenchyma, which, as previously explained, is the characteristic feature of *Dennstaedtiopsis*.

Aerenchyma of the type displayed by the fossil indicates an aquatic habitat, and the marked similarity to that in the rhizomes of *Marsilea* apparently reflect similar or identical habitats. The living *Dennstaedtia*s are in no sense aquatic plants, and although some of them do grow in moist places, their rhizomes are of the usual terrestrial fern type.

Kershaw's *Solenostelepteris*, from the Cretaceous of Japan (Kershaw, 1910), shows stelar structure similar to that of the Clarno fern, though the limited amount of material of the former renders a thorough comparison impossible. The cortex of *Solenostelepteris* was not preserved, but the outermost pith shows large-celled parenchyma located near the site of the medullary aerenchyma in *Dennstaedtiopsis*. A striking similarity between the two is shown in the relation of the lateral branch to the leaf trace (Kershaw, 1910, Pl. LVIII, Fig. 6). In both, the branch is initiated by a lateral bulge of the stele at one side of the leaf gap, with the branch separating below the point where the trace leaves the stele. Kershaw does not assign *Solenostelepteris* to any extant fern group, though a number of resemblances to *Microlepia* are noted.

ECOLOGICAL IMPLICATIONS

In our paper describing the *Acrostichum* remains in the Clarno chert, an intermontane marsh that was watered by hot mineral springs was briefly described. We know nothing of the size of the marsh, as the chert has so far been found in the Clarno formation only at this one place. Because chert of this kind had previously not been reported in the formation, marsh conditions apparently did not prevail widely over the area of deposition, but were localized in rather small lowland areas. However,

there could have been, and no doubt were, others scattered over the region at the same time. The individual marshes were apparently of short existence.

The chert appears to consist of the silicified soil of the marsh, which seems to have had the character of muck rather than peat. The plant remains show a noticeable lack of compaction, which one would expect in peat. Conditions apparently were not favorable for it to form. Aside from the numerous and well-preserved roots and rhizomes of *Dennstaedtiopsis* and the somewhat less well-preserved *Acrostichum* fragments, the bulk of the cherty matrix is made up of a heterogeneous mixture of comminuted plant tissue that is mostly unidentifiable.

The two ferns, *Acrostichum preaureum* and *Dennstaedtiopsis aerenchymata*, are the plants that dominated and apparently characterized the flora of the marsh. So far, no remains of Sphagnum or other bryophytes have been recognized. However, whether the ferns contributed the bulk of the organic substance of the soil is not known, as there are other and as yet unidentified plants in the chert.

The size of some of the silicified *Acrostichum* petioles suggest that this fern had fronds that were at least 2 m long. These large plants probably grew on hummocks in the marsh, with the much smaller *Dennstaedtiopsis* plants occupying the partly shaded areas between. The smaller fern must have formed a dense undergrowth, as indicated by the abundance of *in situ* rhizomes in the chert. Thin sections often show these rhizomes inside *Acrostichum* petioles, obviously having grown into them after burial of the latter. Conversely, roots of *Acrostichum* are occasionally seen within the rhizomes of the other fern. This provides conclusive evidence that both ferns grew together within the same area.

Acrostichum, being the only one of the two ferns of the marsh flora that has survived to the present day, furnishes better testimony than does the other concerning climatic conditions at the time the marsh was in existence. At present its characteristic habitat is along the margins of mangrove swamps, and is one of the few ferns that can grow in water containing salt. It has been claimed that it is the only pteridophyte that grows in salty water, but this is not strictly true. In spite of its tolerance for salt, however, *Acrostichum* is not restricted to salt or brackish water habitats, because it grows along river banks several miles inland from the sea coast. It seems to show more tolerance for high mineral concentrations than do most ferns, and its prevalence in salty habitats may be due to its ability to establish itself in places where other ferns cannot grow. Whatever its mineral relations are, year-round warmth is a requisite. Estimates of Eocene climates in Oregon have ranged from temperate to tropical,

with the balance of opinions favoring warm temperate or subtropical. These climates, like those elsewhere, probably varied with time and place. Though the prevailing climate in north-central Oregon during the interval of Clarno deposition might have been warm temperate or subtropical, tropical climates could have existed locally as the result of the heat held in the spring fed marshes. These marshes could have supported tropical plants such as *Acrostichum*, provided the heated areas were sufficiently large. Thus the occurrence of tropical swamp plants in a marsh deposit may reflect local conditions which could be different from those generally prevailing in the region.

The aerenchyma in the rhizomes of *Dennstaedtiopsis* shows that it had developed into a true aquatic plant that is not known to have a living relic in the Recent flora. Such tissue is not common in ferns. The best examples of its occurrence in living ferns are probably *Acrostichum* and *Marsilea*. It did develop in roots of the Paleozoic *Psaronius*. It could well exist in some living ferns in which it has not been recognized. As far as we know, it is not present, or at least not as well developed, in any living members of the Dennstaedtiodeae.

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PLATES

EXPLANATION OF PLATE I

	PAGE
<i>Dennstaedtiopsis aerenchymata</i> Arnold and Daugherty, gen. et sp. nov.	70
FIG. 1. Block of the Clarno chert showing rhizomes and leaf stalks exposed on slightly weathered surface. $\frac{1}{2}$ Natural size.	
FIG. 2. Portion of surface shown in Fig. 1. Natural size.	

PLATE I

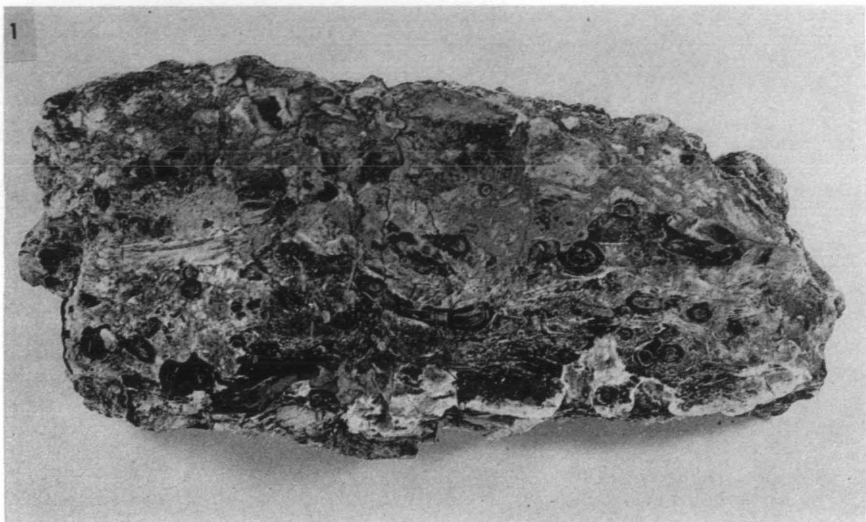
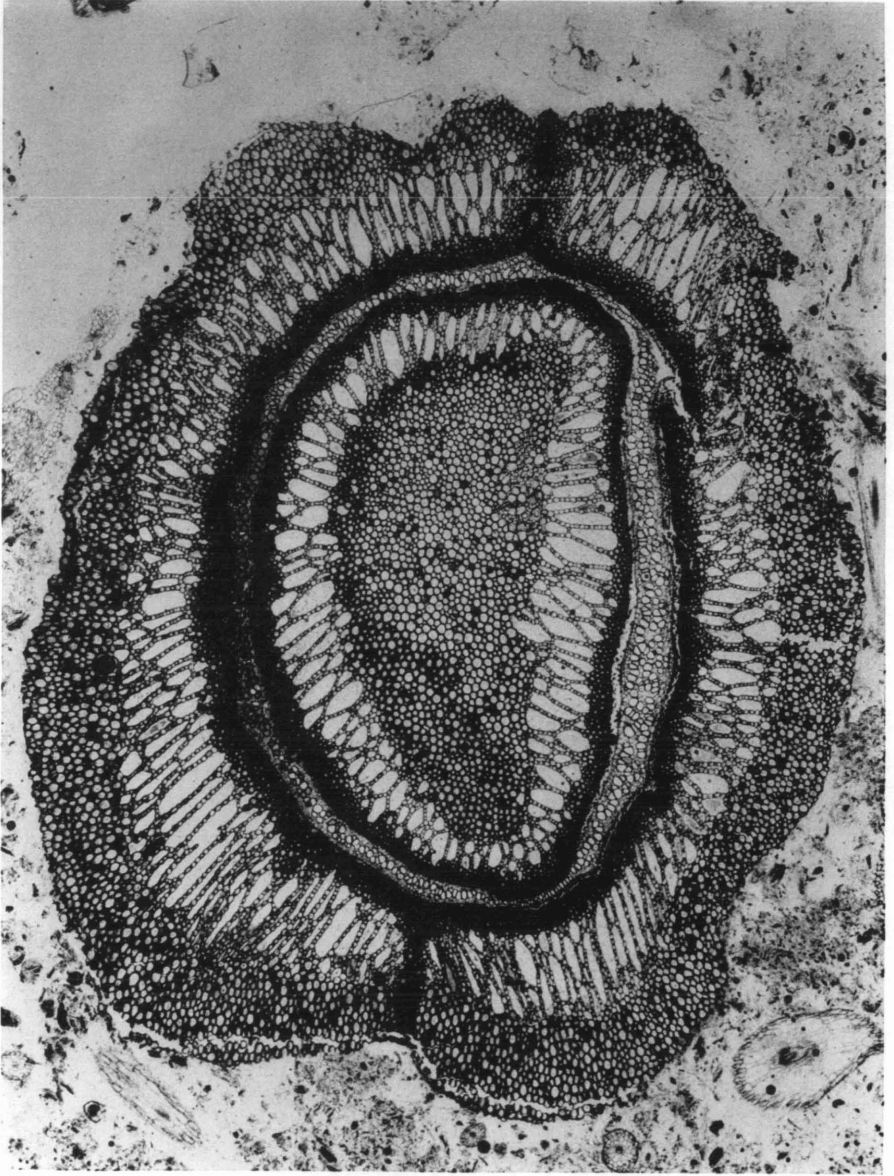


PLATE II



EXPLANATION OF PLATE II

	PAGE
<i>Dennstaedtiopsis aerenchymata</i> Arnold and Daugherty, gen. et sp. nov.	70
Cross section of rhizome. $\times 9$. Holotype No. 48297 UMMP.	

EXPLANATION OF PLATE III

	PAGE
<i>Dennstaedtiopsis aerenchymata</i> Arnold and Daugherty, gen. et sp. nov.	70
Cross section of rhizome. $\times 9$. Paratype No. 48298 UMMP.	

PLATE III

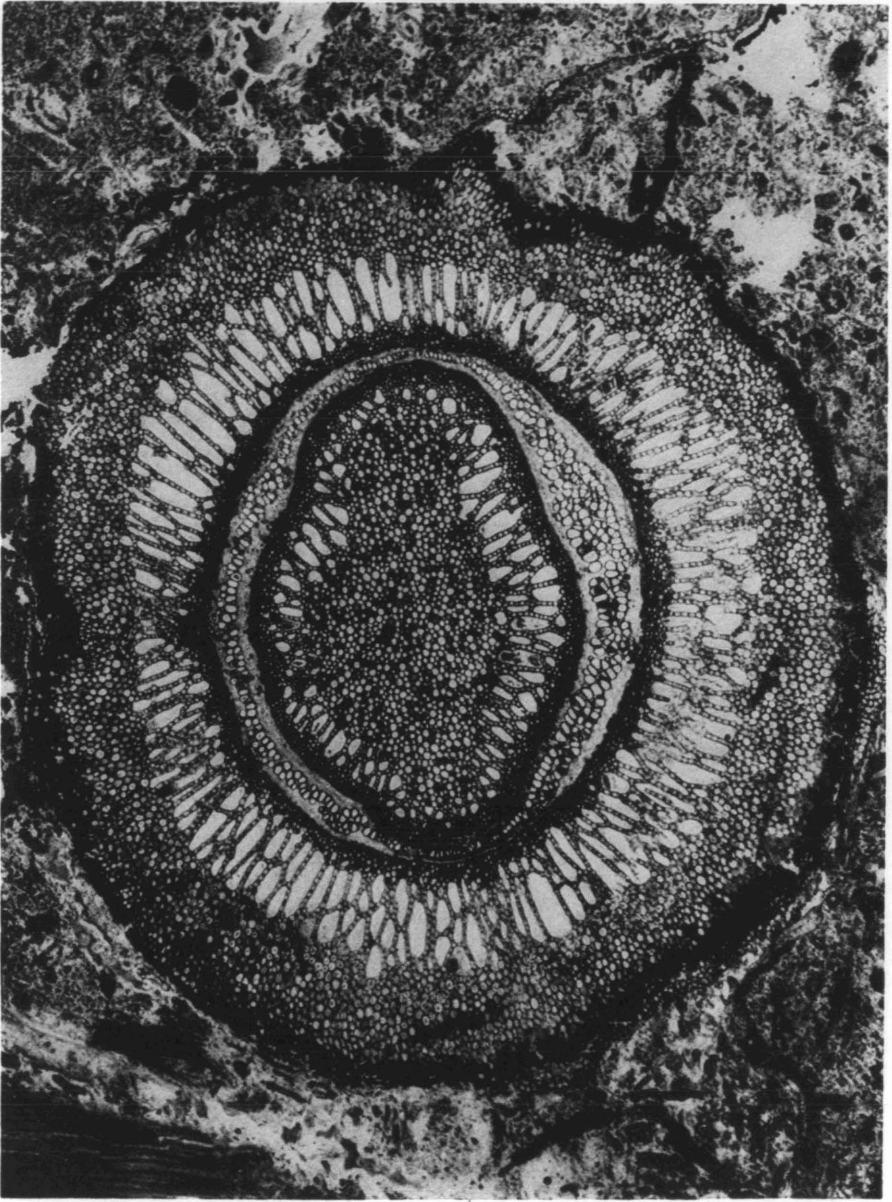
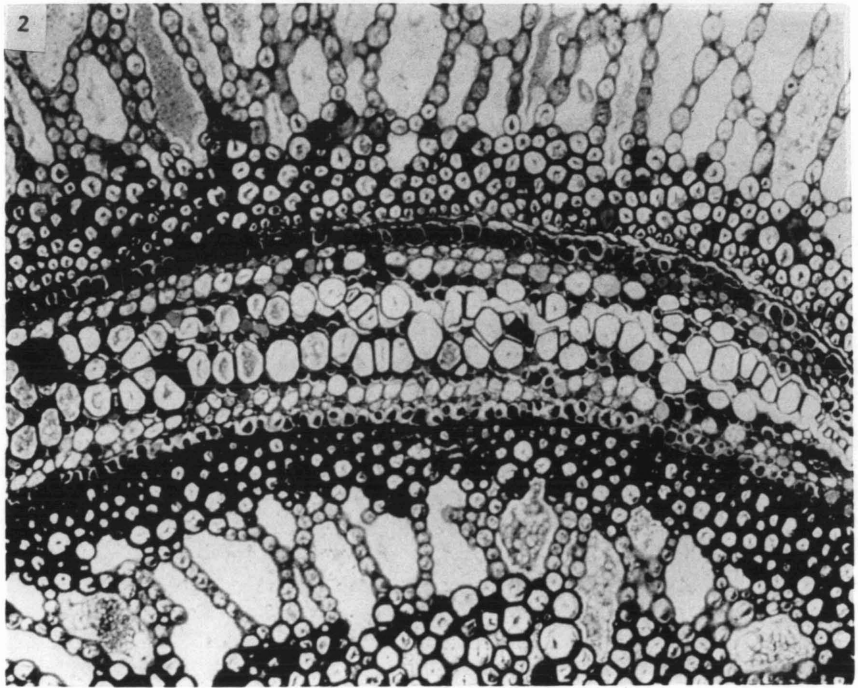
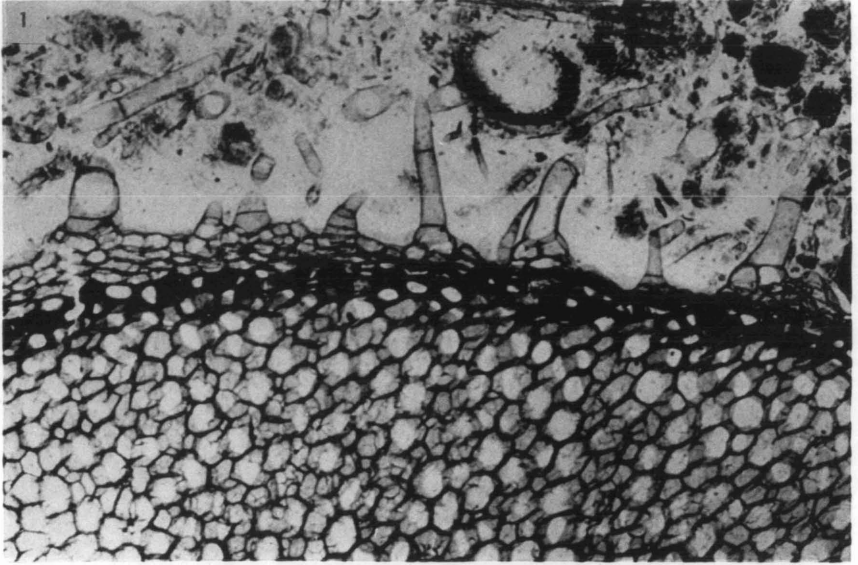


PLATE IV



EXPLANATION OF PLATE IV

	PAGE
<i>Dennstaedtiopsis aerenchymata</i> Arnold and Daugherty, gen. et sp. nov.	70

FIG. 1. Portion of outer part of rhizome showing multicellular hairs and thin sclerenchyma band near surface. $\times 35$.

FIG. 2. Portion of the solenostele of the rhizome, and portions of adjacent cortex and pith. Flanking the xylem is the external and internal phloem, the external and internal pericycle (each a single row of cells with black contents), and the external and internal endodermis (each represented by the contact line with the cortex and pith respectively). The cortical aerenchyma shows at the top of the photo, and the medullary aerenchyma below. $\times 25$.

EXPLANATION OF PLATE V

	PAGE
<i>Dennstaedtia cicutaria</i> (Swartz) Moore	78
FIG. 1. Unstained, freehand section of rhizome, introduced for comparison with rhizome of <i>Dennstaedtiopsis aerenchyma</i> . $\times 12$.	
FIG. 2. Unstained, freehand section of leaf stalk, introduced for comparison with leaf stalk of <i>Dennstaedtiopsis aerenchyma</i> . $\times 12$.	
<i>Dennstaedtiopsis aerenchymata</i> Arnold and Daugherty, gen. et sp. nov.	70
FIG. 3. Cross section of leaf stalk showing shape of vascular strand and aerenchyma similar to that of the rhizome. $\times 7\frac{1}{2}$.	

PLATE V

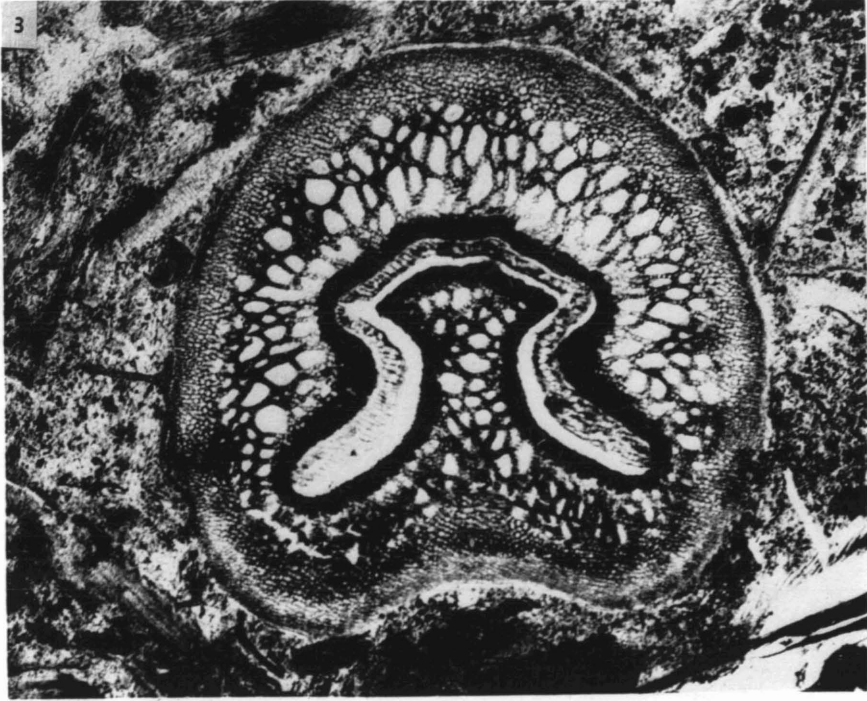
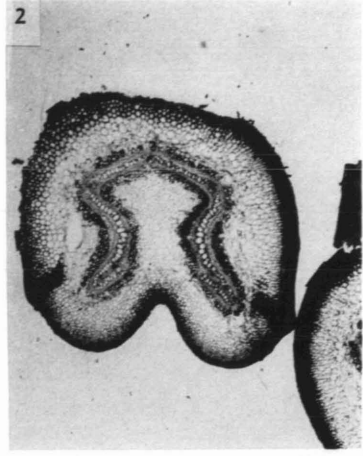
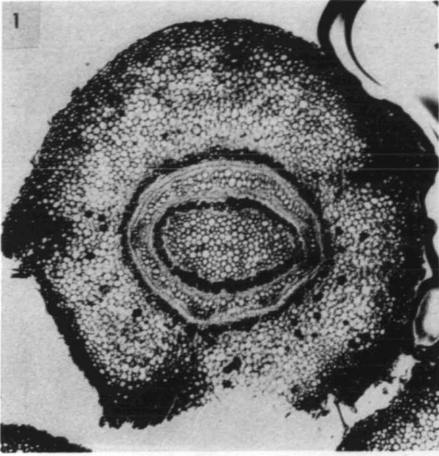
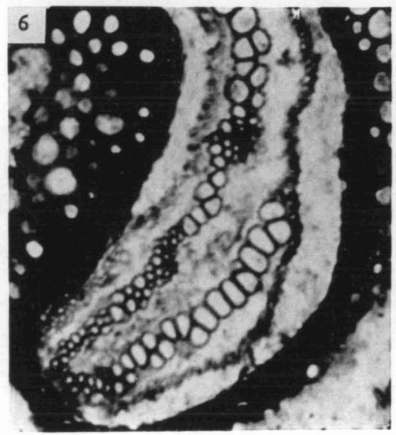
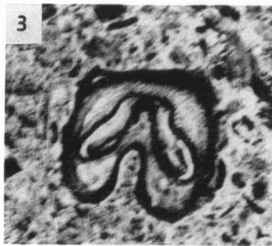
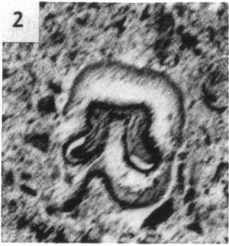
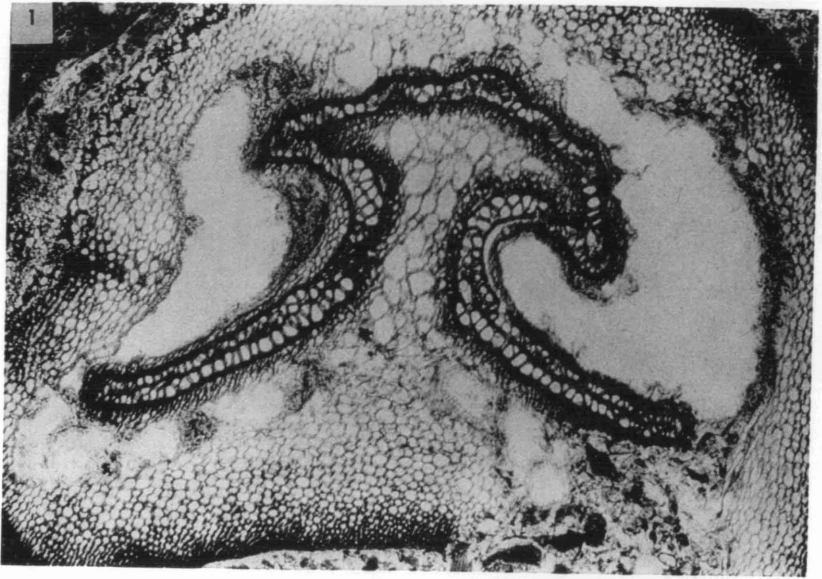


PLATE VI



EXPLANATION OF PLATE VI

	PAGE
<i>Dennstaedtiopsis aerenchymata</i> Arnold and Daugherty, gen. et sp. nov.	70
FIG. 1. Cross section of large leaf stalk. $\times 25$.	
FIG. 2. Cross section of small midrib from distal part of frond. $\times 15$.	
FIG. 3. Cross section of midrib slightly below that shown in Fig. 2. $\times 15$.	
FIG. 4. Cross section of midrib from which a pinna trace has departed. $\times 15$.	
FIG. 5. Cross section of midrib intermediate in position on the frond, and showing well-preserved xylem strand. $\times 20$.	
FIG. 6. Portion of midrib shown in Fig. 5 showing inwardly flexed margin of the xylem strand. $\times 50$.	

EXPLANATION OF PLATE VII

	PAGE
<i>Dennstaedtiopsis aerenchymata</i> Arnold and Daugherty, gen. et sp. nov.	70

FIG. 1. Section taken below level of complete separation of branch (left) from petiole (right) above level of departure of trace from parent rhizome. Equivalent to text. fig. 1f. $\times 10$.

FIG. 2. Section taken slightly below (in direction of base of parent rhizome) that shown in Fig. 1 above, and corresponding to text fig. 1e. Evidence of attachment to parent rhizome shows at upper right. $\times 10$.

FIG. 3. Section showing parent rhizome (right) and departing trace (left) from which a rhizome branch, shown in Figs. 1 and 2 above, is forming. Section corresponds to that shown in text fig. 1d. $\times 5$.

PLATE VII

