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THE FERN GENUS *ACROSTICHUM* IN THE EOCENE CLARNO FORMATION OF OREGON

BY

CHESTER A. ARNOLD and LYMAN H. DAUGHERTY

FROM THE

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CONTENTS

INTRODUCTION

Acrostichum is a genus of ferns that in the present era characterizes the vegetation along the borders of tropical mangrove swamps. Its typical habitat is the inshore reed marsh area which receives some salt water from high tides and some fresh water from inflowing streams. According to some authors (Thomas, 1905) *Acrostichum* is the only pteridophyte that grows in salty water. Though this generalization is not strictly true, it is the only fern that grows abundantly in brackish water at the present time. It

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can, however, grow where salt is absent, as along river banks at considerable distance inland and in places below high tide that are protected by dykes. The plants often form hummocks on mud flats.

Although *Acrostichum* grows mostly in swampy places near sea level, it is not restricted to this kind of habitat. A significant occurrence is in a marsh in a mountain valley at 6000 feet elevation in the Philippines that is watered by hot mineral springs. Apparently at this place a climate suitable for the establishment and development of this plant is produced on a small scale by the hot water, and whatever role salt usually plays in its existence is performed by the other minerals in solution. It is obvious that salt is not essential either nutritionally or otherwise. *Acrostichum* merely has greater tolerance for it than do other ferns, and there seems to be a similar degree of tolerance for certain other dissolved minerals. Small plants of *Acrostichum* have been observed rooted in shallow soil on rock ledges.

Depending mainly on how the genus is defined, opinions differ concerning the number of living species of *Acrostichum*. Some would limit the genus to *A. aureum* by merging certain species with it and transferring the remaining ones to different genera. Others would recognize three or more species.

The places where *Acrostichum* grows at present might seem to be ideal sites for preservation of plant fossils in large quantities. This, however, does not seem to be the case. As compared with some other plants, *Acrostichum* is quite rare in the fossilized condition, and when it is found the remains are seldom more than badly fragmented fronds that testify to the presence of the genus in ancient floras but furnish no additional information of significance.

The scarcity of *Acrostichum* remains in plant-bearing rocks may be the result of the same factors that restrict the entrance of herbaceous plants into fossiliferous deposits in general. Unlike the dicotyledonous trees, ferns and herbaceous flowering plants do not systematically shed their leaves. When a fern frond has finished its functional life it merely droops to the ground, where it may commence to decay while still attached. Warmth and moisture hasten the decaying process. Dispersal may take place only after it has undergone considerable fragmentation.

The present study deals with silicified material of *Acrostichum* that has been found in abundance in a chert bed in the Clarno formation of Late Eocene age in the John Day Valley in north-central Oregon. There is no evidence that the plants preserved in the Clarno chert grew in water containing salt. Whatever the role of salt may ordinarily be in the biology of *Acrostichum,* silica appears to have substituted for it in this particular instance. Silica is capable of preserving plant tissue to a degree sometimes approaching perfection, which salt does not do.

FOSSIL RECORDS OF *Acrostichum*

Acrostichum seldom receives much attention in the study of fossil floras. In the first place it is rare, and secondly, when it is found its remains are usually too fragmentary to yield much information of value. Of the 27 fossil species of *Acrostichum* listed by Jongmans (1954) in the *Fossilium Catalogus,* more than half are pre-Tertiary plants that von Ettingshausen and other authors had transferred to this genus many years ago from *Taeniopteris, Protorhippus, Glossopteris,* and *Sagenopteris.* Neither these, nor those plants that Goeppert named *Acrostichites,* and Fontaine called *Acrostichides* and *Acrostichopteris,* are evidence of the existence of *Acrostichum* or related plants before the Cenozoic era.

The oldest known *Acrostichum* is from the Paleocene of the Paris Basin (Fritel, 1910). Other authors have recorded it from the Eocene of Georgia, Alabama, Mississippi, Texas, Louisiana, Wyoming, Great Britain, and Italy; the Oligocene of Oregon, Spain, and Panama; the Miocene of Oaxaca and Mississippi; the Pliocene of Bolivia; and unspecified Tertiary horizons elsewhere. It is of interest to note that in western North America it has been reported only from the Green River formation in Wyoming (Newberry, 1883; Brown, 1934) and from an unnamed Oligocene formation in Oregon (Knowlton, 1900). None of the well-known Eocene floras west of the Rocky Mountains, such as the Goshen, Weaverville, Comstock, or La Porte, which contain palms and other tropical and near tropical plants, and where *Acrostichum* might be expected to occur, have as yet yielded a trace of it. The present account contains the first report of it in the Clarno flora.

ACKNOWLEDGMENTS

The plant-bearing Clarno chert was collected during two field expeditions from the Museum of Paleontology of The University of Michigan. During the summer of 1948 the late Mr. A. K. Chandler of Portland, Oregon, accompanied the senior author to the site. A larger collection was made in 1949 with the assistance of Richard A. Scott and Robert Lindsley. The laboratory study of the material was accomplished with equipment and technical assistance made available by a grant from the National Science Foundation for the project entitled "Investigations of Silicified Plants from Western North America" No. NSF-G19553. Laboratory space and living material of *Acrostichum* was furnished by the Botanical Gardens of The University of Michigan. Valuable suggestions were given by Dr. R. E. Holttum during his recent visit to the University, and by Dr. W. H. Wagner, Professor of Botany at The University of Michigan. Drs. L. B. Kellum and R. V. Kesling read the manuscript and gave helpful criticisms.

TAXONOMIC POSITION AND DISTINGUISHING FEATURES

Acrostichum, Neurocallis, and *Stenochlaena* are the so-called "acrostichoid" genera of the subfamily Pteridoideae, family Polypodiaceae, order Filicales. In manuals they are usually segregated from the other members of the subfamily but without being given formal taxonomic status. *Acrostichum* is distinguished from the other two genera of this group by the lack of definite sori. The sporangia are spread over the whole lower pinna surface. The fine reticulate venation pattern is another feature of distinction, though this is shared with a few other ferns.

With one exception the present authors are unaware of any structurally preserved plants described in paleobotanical literature that can be attributed to *Acrostichum*. The single exception is the fern petiole from the Green River formation that Arnold (1945) named *Eorhachis lomarioides*. The specimens that received this name are *Acrostichum* leaf stalks, and they are herewith transferred to that genus. All references in the literature to *Acrostichum* are concerned with compressions.

MATERIAL FROM THE CLARNO CHERT

Locality

The afore-mentioned chert containing the *Acrostichum* remains was discovered in the eastern part of Jefferson County, Oregon. As precisely as it can be specified the locality is in the extreme northwestern corner of sec. 27, T. 9 S., R. 18 E. It is about 9½ miles east and 1 mile north of Ashwood, and about 1½ miles northeast of Kilts Postoffice, which is marked on some maps, though nothing remains at the site of the postoffice which was abandoned several years ago.

No detailed study of the geology in the vicinity of the fossil locality has been published. Hodge (1942) in his *Geology of North Central Oregon* maps the Clarno and adjacent formations as far east as a north-south line that passes about 3 miles west of the fossil site. Some general observations made in 1949 revealed that the chert bed, which appears to be about 2 feet thick, outcrops beneath a lava sheet that caps the hilltops to the northwest of Muddy Creek which is a northeasterly flowing tributary of the John Day River. Beneath the chert is a light gray, at some places brecciated, ash deposit that contains chert and chalcedony beds and considerable silicified wood. The stems of *Osmundites chandleri* described by Arnold (1952) came from the upper part. There are few exposed outcrops: the silicified plants are found on the surface where they had accumulated following erosion. This ash bed is about 400 feet thick at places. It is underlain by white non-laminated ash that weathers to buff and forms large blocks and columns similar to those displayed at the type locality of the Clarno formation about 12 miles airline distance to the northeast (Merriam, 1901).

Character of the Chert and the Plant Remains

The fossiliferous chert breaks away from the outcrop as irregular blocks. These vary from medium gray to dark gray and the exposed surfaces take on a whitish color when weathered. Most of the chert is dense and hard, but scattered throughout are small pockets of lighter colored ash that consists mainly of sharp unweathered particles.

Plant material is abundant in the chert, consisting mostly of parts of those plants that grew in the marsh and a minor constituent derived from neighboring areas. *Acrostichum* is preserved in the chert only as fragments. None of the organs of the plant have been found connected, except the sporangia that are still attached to the pinna surfaces. All of the sporophyte body, however, is present, and the plant that is here named *Acrostichum preaureum* is one of the most completely known plants of any geological period.

The parts preserved in greatest numbers are petioles (Pl. I, Fig. 1; Pl. II, Fig. 2). Some are of considerable size, the largest one found being 5 cm in diameter. It must have supported a frond that was at least 2 m long. Small stem fragments are identifiable by the characteristic scales (Pl. IV, Fig. 1). Distal parts of fronds are represented by portions of midribs bearing pinnae (Pl. III, Fig. 3). Some of these that were cut parallel to the surface show the reticulate venation that is characteristic of the acrostichoid members of the Pteridoideae (Pl. V, Fig. 2). Certain of the preparations show the sporangia spread over the surface, and some of these contain spores (Pl. V, Fig. 5). Paraphyses are also visible. Since this material can be studied only in thin section, those characters commonly used in fern taxonomy are not advantageously displayed. There is no evidence, however, that more than one species of *Acrostichum* is present in the assemblage of fossilized remains in the chert, and all evidence points to close affinity with two living species, *A. aureum* and *A. danaefolium*.

Associated Plants

A complete account of the flora of the Clarno chert is postponed until some of the other plants have received more study. Besides *Acrostichum* the chert contains stems of *Equisetum,* twigs of herbaceous and woody dicotyledons, wood of *Ginkgo,* and several kinds of spores and pollen grains.

The plant present in largest quantities in the chert, rivaling even *Acrostichum* in abundance, is an unidentified polypodiaceous fern. It is represented by numerous slender solenostelic rhizomes a centimeter or less in diameter with conspicuous aerenchyma in the pith and cortex. These rhizomes ramify through the chert in all directions, lying mostly, however, in the plane of bedding. They are frequently seen within *Acrostichum* petioles, having penetrated them after burial of the latter. The obviously undisturbed condition, as shown by roots still attached, shows that these organs were preserved mostly *in situ.* Portions of petioles are still attached to some of them. There can be no question that this fern grew in the marsh among *Acrostichum* plants. It was a smaller plant, however, with horizontally growing subterranean rhizomes and its fronds, to judge from the size of the petioles, did not rise more than a few decimeters above the ground. Fertile parts of this fern have not been recognized.

Anatomical Structure of *Acrostichum*

The structure of a few of the species of *Acrostichum* has been dealt with by Thomas (1905) and by Schumann (1915), but no exhaustive and comprehensive anatomical study of the genus has been made. In studying the fossil material, it was found necessary to supplement the published treatments with observations on living plants. A complete plant of *Acrostichum danaefolium* supplied by the Botanical Gardens of The University of Michigan was dissected for comparison.

Stems.—Species of *Acrostichum* of the *A. aureum* type have large partly erect rhizomes (stems) of complicated structure. The upper part bears a cluster of fronds and a ramentum of rather distinctive flattened scales. Some of the individual fern plants in the Clarno swamp must have had large stems, to judge from the diameter of some of the petioles, but only small stems have been preserved, and these are few as compared with other parts of the plants.

One specimen appears to represent the upper part of a small stem (Pl. IV, Fig. 1) about 1 cm in diameter. The pith contains 2 accessory vascular strands that are about 0.50 mm in diameter. The main stele, which is about 5 mm across and slightly less than 1 mm thick, shows no leaf gaps, though a bulge on one side suggests that the section lies just below a departing trace. The xylem consists of closely packed tracheids which appear to be much contorted. Little can be seen of the tissues that lie between xylem and the sclerenchyma. The latter is a firm tissue of vertically elongated elements. The layer of sclerenchyma outside the stele constitutes the inner layer of the 3-layered cortex. The outermost part of the cortex is also sclerotic, but less so than the inner layer. The middle of the cortex is parenchymatous. There is less aerenchyma in the stem than in the roots and petioles.

The stem surface is covered by a ramentum of compactly placed scales. These scales are similar to those on living plants; but viewed in cross section, they present a rather distinctive appearance (Pl. IV, Fig. 2). Being tightly imbricated around the stem tip, they appear as spindle-shaped objects approximately a millimeter thick and twice as long. A conspicuous, flattened mass of dark sclerenchyma is located in the central part, and this is surrounded by radially elongated thin-walled cells. The length of the scales is unknown. Their superficial origin shows that these structures are emergences rather than appendages. The sclerenchyma of the scale is continuous with that in the outer part of the cortex.

The larger stems are fragmentary, and their original size is unknown. One specimen shows a pith that was originally about 3 cm wide and which contains numerous medullary strands (Pl. V, Fig. 1). Most of these strands are double, due to frequent branching. About 20 occupy an area 1 cm square, but the distribution is not regular throughout. Unbranched ones are round in cross section, and they range up to 1 mm or more in diameter. A thick sclerenchyma layer surrounds the vascular core (Pl. III, Fig. 4). The latter consists of a small mesarch xylem strand surrounded by phloem. Upon casual observation these medullary bundles may be mistaken for roots that had invaded the pith, but they differ from roots in structure and in relation to the surrounding tissue.

The main stele of the larger of the stems found in the Clarno chert is essentially like that in the living *A. aureum* as it is described and figured by Thomas, being a thin cylinder 1.5 to 2.0 mm thick, and enclosing the large pith. The sclerenchyma shows as two dark bands with the lighter colored vascular tissue sandwiched between. Little remains of the pericycle and phloem, and preservation is not adequate to show whether there is an endodermis. The xylem consists of a narrow layer of scalariform tracheids with considerable intermixed parenchyma. The cortex resembles that of the smaller stems, and only the bases remain of the surface scales. The amount and distribution of aerenchyma is similar to that mentioned in connection with the smaller stem.

Roots.—The roots of *Acrostichum* are abundant in the Clarno chert.

Ofttimes they can be seen as having grown through the partly disintegrated tissues of other plants, or even through the entombed petioles of the same plant.

Thomas has compared the *Acrostichum* root with an insulated wire. The analogy is an excellent one. The central cylinder with its tough sclerenchymatous sheath (Pl. VI, Fig. 1) is surrounded by a thick but soft cortex that in many specimens is quite aerenchymatous (Pl. VI, Fig. 2). In a living root the cortical sheath can be slipped off the central cylinder like a sleeve. The xylem strand is triarch in a small root, but in the larger ones it is hexarch with 3 broad protoxylem poles alternating with 3 smaller ones. The phloem bays are shallow, so in cross section there is some resemblance to a protostelic stem (Pl. VI, Figs. 1, 2).

Petioles and midribs.—Petioles (leaf stalks) that range up to 5 cm in diameter (Pl. I, Fig. 1; Pl. II, Fig. 2), and small pieces of midribs with lamina attached (Pl. II, Fig. 1; Pl. III, Fig. 2) are abundant in the Clarno chert. The petioles are rarely found intact. Most of them had been shredded or split and, rather paradoxically, strips torn from larger petioles often show better tissue preservation than do the more complete specimens. This is probably due to the internal tissues having had more direct exposure to dissolved silica. Where the hypodermal sclerenchyma was unbroken, the inner tissues were shielded, which delayed infiltration and allowed decay to advance before it was halted by deep burial.

In spite of the usual fragmentary condition, the essential characters of *Acrostichum* fronds are adequately revealed in the material preserved in the chert. The petioles are rounded or slightly angular and most of them show a conspicuous adaxial groove (Pl. I, Fig. 1), which seems to be both wider and deeper than in most typical living specimens.

In transverse section the *Acrostichum* petiole shows a distinctive arrangement of the vascular bundles, which is complex and not well understood. At places, a cyclic plan is suggested (Pl. II, Fig. 2), but careful examination indicates that the cyclic appearance may be illusory, and that a modified horseshoe or *omega* form best describes the pattern. It is decidedly more complicated in the larger petioles where there may be several hundred vascular bundles than in the smaller ones where there may be as few as a dozen. What may appear locally to be two or more cycles may simply be a deep infold of a single series. Also at places there often appear to be small closed cycles that are separated from the others. One feature stands out clearly, and that is a transverse series of bundles along the sloping sides of the adaxial groove in which the protoxylems are directed outwardly, which is in contrast to the other peripherally placed bundles with their protoxylems directed inwardly. This outer range of bundles probably had a different ontogenetic origin from the others. In the larger specimens the median vascular bundle of this row, which lies directly inward from the bottom of the median groove (Pl. I, Fig. 1) is about twice as wide as the others. To the left and to the right of this median bundle, the bundles of the adaxial row diminish progressively in size out to the extremities where the smallest ones are located. Observations of midrib sections with pinnae attached show that the bundles at the two extremities of this range supply the strands that enter the pinnae (Pl. II, Fig. 1).

In the large median vascular bundle, especially in the larger petioles, the protoxylem may be on either side. The bundle may even have two or more protoxylems located opposite each other. In the smaller petioles the protoxylem seems to be external, as in the other bundles of the adaxial row.

Except for those nearest the periphery, the vascular bundles in the petiole are embedded in an aerenchymatous matrix with large air spaces. The spaces are small near the surface where the thin-walled tissue gives way to a layer of supporting cells.

Each petiole bundle of *Acrostichum* is surrounded by a well-developed sclerenchymatous sheath (Pl. I, Fig. 2). Inside is an endodermis with Casparian strips (Pl. III, Figs. 1, 2). This is followed by a pericycle of a single layer of rather large "squarrish" cells. The flanks of the transversely placed xylem mass usually touch the pericycle (Pl. I, Fig. 2; Pl. III, Fig. 2), thus separating the phloem into two masses, one lying on the side with the protoxylem, and the other on the opposite side (Pl. I, Fig. 2). Occasionally, however, a row of phloem cells may intervene between the flanks of the xylem mass and the pericycle, though the complete separation of the phloem into two masses is complete in most instances. The petiole bundles therefore appear to be bicollateral (Pl. III, Fig. 2). The xylem shows one or two protoxylem points, depending on the size of the bundle. The protoxylem lies completely to one side of the xylem mass, thus not revealing the mesarch condition commonly present in fern axes (Pl. I, Fig. 2).

The number of vascular bundles varies with the size of the petioles. One specimen that is 2.5 cm in diameter contains about 200 bundles (Pl. I, Fig. 1), and there may be as many as 1000 in the largest observed specimen. However, since only smaller petioles are preserved whole, the number of bundles in the larger ones can only be estimated. Midribs with attached pinnae may contain as few as 5 bundles, but usually there are more. A midrib 3 mm in diameter will ordinarily contain 12 to 17 (Pl. II, Fig. 1). Distribution of the bundles in the midribs seems to be similar to that in the petioles though the pattern may be less complex due to the smaller size. The bundles in the adaxial row with the outwardly directed protoxylem are the ones that supply the pinnae with vascular strands. The median bundle is conspicuous.

The midribs contain much supporting tissue with few air spaces in the interior as compared with the petioles. The sclerenchymatous sheath surrounding each bundle extends from the petioles into and through the midrib.

Pinnae.—Some details of the structure of the pinnae are revealed in sections cut transversely and parallel to the surface. The range in pinna width is undetermined, but a complete transverse section shows a midrib about 1.3 mm in diameter supporting a laminar portion 10 mm wide on each side (Pl. III, Fig. 3). Some of the larger midribs probably supported correspondingly wider laminae. In size, the pinnae seem to correspond closely to those of the related living species.

Pinnae fragments cut parallel to the surface reveal the netted venation pattern (Pl. V, Fig. 2). The meshes are 0.5–1.5 mm wide, and of variable lengths. The internal structure is not well preserved, though the bifacial arrangement of the palisade and spongy mesophyll layers is distinctly visible.

Sporangia and spores.—A distinguishing feature of the genus *Acrostichum* is the absence of definite sori: the sporangia are spread over the lower pinna surface without receptacle or indusium. Some of the fossilized sporangia have retained their spores (Pl. V, Fig. 5). Numerous isolated ones are scattered amongst the disorganized plant debris in the chert. Paraphyses similar to those of the living species occur among the sporangia.

The sporangia, which are 0.30–0.45 mm long, are evidently nearly sessile (Pl. V, Figs. 3–5). No cells of an attachment stalk remain on any specimen so far observed. The vertical annulus of 22 to 27 cells extends two-thirds of the distance around the sporangium. The stomial region contains 4 transversely elongated cells which are separated from the extremity of the annulus and the stalk region by about 5 cells (Pl. V, Figs. 3, 4). Dehiscence took place between the pair of cells in the middle of the stomium.

The spores are 30–40 microns in diameter, and have smooth walls and a distinct tetrad scar (Pl. V, Fig. 6). Not having been much flattened by compression, the spores are difficult to photograph under magnifications sufficiently high to show all details.

Ecological Relations, and Conditions Under Which the Clarno Plant-bearing Chert Developed

The Clarno formation, which is about 3000 feet thick, is a massive accumulation of erupted material, some of which accumulated on land and some in water. Most of the water-lain material was deposited in shallow lakes. Some of this consists of ash that fell directly into the lakes, and some is reworked material derived by erosion of ash beds that had accumulated first on land.

The presence in the Clarno formation of a well-preserved and distinctive flora has been known for a long time. It is the lowermost of a succession of floras in north-central Oregon that range in age from Eocene to Pliocene. Usually dated as Late Eocene, the Clarno flora is succeeded by the Oligocene Bridge Creek, the Miocene Mascall, and The Dalles Pliocene floras. These reflect progressive climatic changes from tropical to temperate. The Clarno flora has never been as thoroughly described as the Bridge Creek and Mascall floras, but it has long been of major interest because of its tropical or subtropical character. Chaney (1948) mentions the presence in it of cycads, palms, and subtropical dicotyledons (members of the Lauraceae in particular), and he compares it with similar floras in Panama today. Scott (1954) has identified seeds and fruits of Juglandaceae, Menispermaceae, Lauraceae, Icacinaceae, Vitaceae, Nyssaceae, and Cornaceae. Some of these find their closest relatives in the tropics, others in warm, temperate climates. Only one fern, an undescribed species of *Lygodium,* has been reported from the Clarno flora.

Unless there is other evidence to the contrary, the presence of *Acrostichum* in a fossil flora would be interpreted as an indication of deposition at or near sea level in water that probably contained some salt. The climate could have been either tropical or subtropical. Somewhat different conditions, however, seem to have prevailed at the place where the Clarno chert was formed. There is no evidence that deposition took place in salty water, and moreover, it probably occurred some distance from the coast. The climate probably exhibited considerable local variation. On the whole it must have been essentially a subtropical climate, or maybe even a warm temperate one, though the former seems more in accord with available data. Locally, however, and probably in the marshes kept moist by hot springs, conditions approximating tropical developed on a small scale. Such developments could take place only at low elevations at the latitude of the Clarno chert locality which is close to 45 degrees north. A climate free from occasional severe frosts could hardly have been maintained if the marsh lay more than a few hundred feet above sea level.

The plant-bearing chert obviously represents the indurated soil of a marsh in which the plants grew. The chief inorganic constituent of the soil was fresh and reworked volcanic ash, and to this was added the usual complement of organic matter supplied by the decay of plants that grew in the marsh. It was probably a grayish muck, owing its color to the mixture of light and dark material.

The marsh in which the chert formed evidently existed in a valley surrounded by hills. Instead of one major stream flowing through the valley, several small ones probably entered from different directions, and, after a lava flow impounded the main outflowing one, the valley was flooded. The resulting lake began to fill, and marsh conditions developed when it was shallow enough for plants to become rotted on the bottom.

The small streams that fed first the open lake and then the marsh may have carried water from numerous hot springs. This hot water performed two important roles. One was that it carried great quantities of dissolved silica obtained from the thick ash deposits in the region into the marsh. The other role was that of raising the temperature of the soil in the marsh and the atmosphere in the immediate vicinity to the point where tropical conditions were maintained on a local scale. This amelioration of the local climate was effective the year around because of the constant supply of heat. It prevented frosts in, and very near, the marsh, and produced a habitat in which *Acrostichum* and other warmth-loving plants could thrive.

The high evaporation rate coupled with the impeded outflow of the water in the marsh resulted in a buildup of silica in the mucklike soil, leading to development of silica gel. The silica had also infiltrated the undecomposed plant fragments mixed with the muck as well as those rhizomes and roots already underground. Solidification of the mineral-saturated soil and plant parts was the final stage of the process of fossilization which was brought about by the weight of a sheet of lava which finally covered the marsh. This resulted in expulsion of enough water to precipitate and harden the siliceous residue into chert, and at the same time effectively protect the deposit from erosion. Tissues and cells of the plants were preserved to a high degree, especially in those organs formed beneath the ground and thereby protected from much decay.

The uncompressed rhizomes of the ferns associated with *Acrostichum* still have attached roots that extend out into the chert in various directions, and this, coupled with the fact that they lie mostly in the plane of bedding, are all evidence that these rhizomes were preserved in place, having been essentially undisturbed during buildup of the deposit. The roots of *Acrostichum,* and possibly some of its stems, are the only parts of this particular plant to be preserved in place. As already explained, the fronds, which in some instances probably stood at considerable height above the ground (to judge from the diameter of some of the petioles), are badly fragmented. The disassociation of the parts of these different plants therefore reflects to some degree their habit and manner of growth.

Some interesting parallelisms are seen between the Clarno chert with its silicified plants and the well-known Rhynie chert of Scotland. The site of each is envisaged as having been an intermontane marsh in which the environment owed much of its distinctive character to local volcanic activity and numerous hot springs. In each the water discharged into the marsh from the hot springs carried large quantities of dissolved mineral matter, principally silica. These minerals in turn were responsible for the formation of the chert and the petrifaction of the plants. In each, some of the plants were preserved *in situ*. There are some differences, the most important being the difference in age (Devonian *versus* Eocene). Then there is the difference in the kinds of plants present in each. One may note, however, that in both instances, the dominant vascular plants are homosporous cryptograms.

When cooler climates developed in post-Eocene time, the particular set of conditions disappeared which had made possible the growth of *Acrostichum* in Oregon. The fern then retreated to the low latitudes where it became established on the borders of the mangrove swamps where we find it mostly today.

SYSTEMATIC DESCRIPTION

Order FILICALES
Family Polypodiaceae
Subfamily Pteridoideae
Genus *Acrostichum* Linnaeus

Acrostichum preaureum nom. nov. Arnold and Daugherty

Eorhachis lomarioides Arnold, 1945, p. 11, Fig. 1A; Pl. II, Figs. 1, 2.

Diagnosis.—Petioles rounded or angular in cross section, with broad adaxial groove, up to 5 cm in diameter. Bundles numerous, bicollateral, surrounded by sclerenchymatous sheath, arranged according to modified horseshoe or *omega* form, those on abaxial side with protoxylem inward, those on adaxial side reversed. Supported externally by layer of hypodermal sclerenchyma that partially surrounds bundles adjacent to the outer surface. Intervascular tissue aerenchymatous.

Midribs similar to petioles, but with attached winglike lamina, generally lacking aerenchyma and with fewer bundles, 4 mm or less in diameter. Pinnae bifacial, with netted venation.

Sporangia .30–.45 mm long with annulus of 22 to 27 cells, stomial region of 4 transversely elongated cells and separated from stalk and extremity of annulus by about 5 cells.

Spores 30–40 microns in diameter, round-triangular, smooth except for distinct tetrad scar.

Stem siphonostelic with numerous medullary bundles. Stele amphiphloic. Ramentum of flattened scales.

Roots adventitious with hard core and soft sheathlike cortex which is parenchymatous or aerenchymatous, hexarch, phloem bays shallow.

Holotype: No. 23390, UMMP. *Paratypes* Nos. 23391–23395, UMMP. Hypotypes No. 47111, UMMP.

Horizon and locality.—Green River formation, Sweetwater County, Wyoming; Clarno formation, Jefferson County, Oregon.

Discussion.—The fern petiole from the Green River formation of Wyoming that Arnold (1945) described as *Eorhachis lomarioides* belongs to *Acrostichum.* The original description was based upon several silicified petiole fragments collected in the Eden Valley region in the northern part of Sweetwater County. The specimens had weathered out of the formation and were not found in place, hence the stratigraphic position of the source has not been determined. It is probable, however, that they came from the Tipton tongue or the Morrow Creek member of the Green River formation, both of which are known to contain petrified plants (Bradley, 1925, p. 126).

The objects had been collected by amateur rock collectors who called them fossil bamboo stems, sugar cane, and other things. They range from 1–3 cm in diameter. They are rounded or angular in cross section, but have a wide groove along one side (the adaxial side), hence the fancied resemblance to large stems of the grass family. In the same area where the petioles abound, there are numerous silicified limbs and logs, some of which are surrounded by thick crusts of limey material formed by the algal species *Chlorellopsis coloniata.*

These fossils were recognized as fern petioles when the genus *Eorhachis* was proposed, but a more precise identification was not made. However, the resemblance was noted of the similar bundle distribution in this petiole and one figured by Thomae (1886) as *Blechnum zamioides.* Thomae's figures were merely diagrams, and since no additional information on *Blechnum zamioides* was obtained, no further comparisons were made. It is now clear, however, that the petiole that Thomae figured belonged to *Acrostichum* or *Stenochlaena.* The Green River petioles represent *Acrostichum,* and because of this the genus *Eorhachis* may be abandoned, and the name of the living genus used instead. A new trivial epithet must be proposed, however, because the binomial *Acrostichum lomarioides* had been used previously for a living plant.

The silicified petioles probably represent the same plant that was earlier described as *Acrostichum hesperium* (Newberry, 1883; Knowlton, 1923). This name, however, is not suitable for the structurally preserved material because the type specimens are merely compressions of frond fragments without sporangia, and identity can therefore only be surmised.

Brown (1934) lists Newberry's species as one of the recognizable species of the Green River flora. He neither figures nor embellishes the previously published brief description of *A. hesperium*, but says that it is one of the species which substantiates previously expressed opinions about a warm-temperate climate during Green River time. *Acrostichum* would seem to indicate conditions somewhat warmer than merely warm-temperate. There were certainly climatic fluctuations during the interval of Green River deposition, and *Acrostichum* probably indicates the warmer phases of the climatic cycles. Further, the presence along with *Acrostichum* of fishes with teeth resembling those of marine species indicates deposition might have taken place in sites where there was some salt water. The situation may have been different from the *Acrostichum* swamps in Oregon where there is no evidence of salt water and where some of the heat necessary for growth of the plant possibly came from hot springs.

The silicified *Acrostichum* remains from Oregon and Wyoming appear to be specifically identical. At least there is no evident basis for separation. Consequently, they are considered to belong to one species. None of the fossilized material shows any significant differences from the living *Acrostichum aureum* and *A. danaefolium*, although, as already explained, those characters on which living species are distinguished, are not well revealed in the silicified material.

SUMMARY

Abundant material of *Acrostichum*, a fern genus that, at present, characterizes the flora of brackish parts of tropical mangrove swamps, has been found in chert from the Clarno formation of Late Eocene age in the John Day Valley of Oregon. The fossil species, *Acrostichum preaureum* nom. nov. Arnold and Daughtery, is very similar to the living *A. aureum* and *A. danaefolium*. Roots, stems, frond parts, and sporangia containing spores are preserved. Parts present in greatest abundance are petioles, some of which are of considerable size. The numerous bundles in the petioles appear to be bicollateral, and are arranged in a complex pattern. Scales characteristic of the genus are preserved on the short stems.

The plant-bearing chert is apparently the indurated soil of a marsh that was fed by hot water bearing large quantities of silica in solution. The hot water is believed to have raised the temperature of the immediate area sufficiently to produce tropical conditions on a local scale, which made possible the establishment of *Acrostichum* in the marsh.

The fern petiole from the Green River formation that was earlier described as *Eorhachis lomarioides* is an *Acrostichum* leaf stalk.

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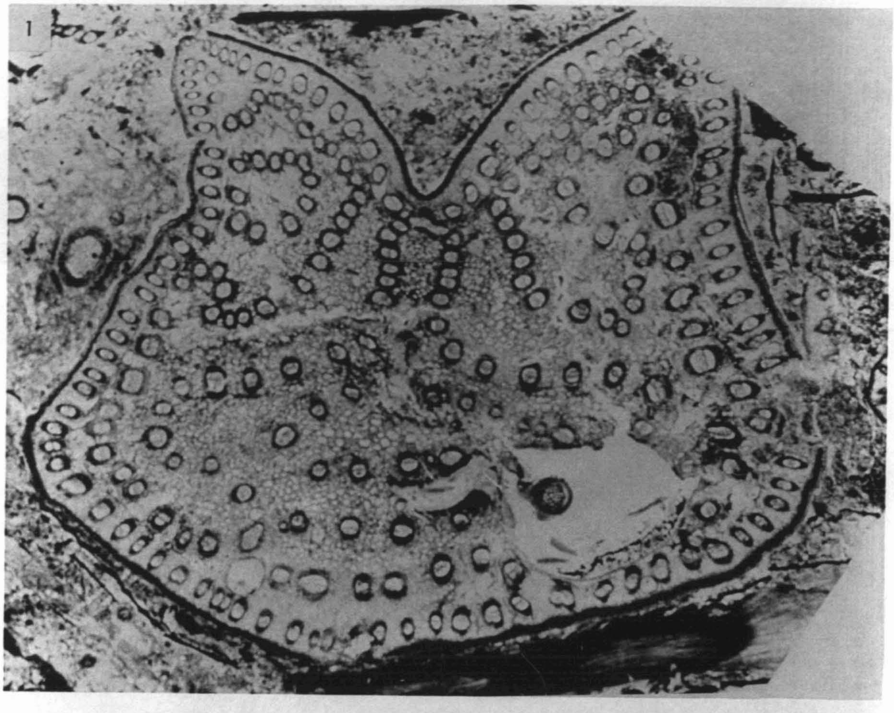
PLATES

EXPLANATION OF PLATE I

FIG. 1. Transverse section of medium-sized petiole showing the characteristic complex bundle arrangement and the conspicuous adaxial groove. × 4.5.

FIG. 2. Group of 3 bundles from petiole shown in Figure 1. The phloem tissue has mostly disappeared leaving the transversely placed xylem masses arranged crosswise within sclerenchyma-enclosed cavities. × 60.

PLATE I



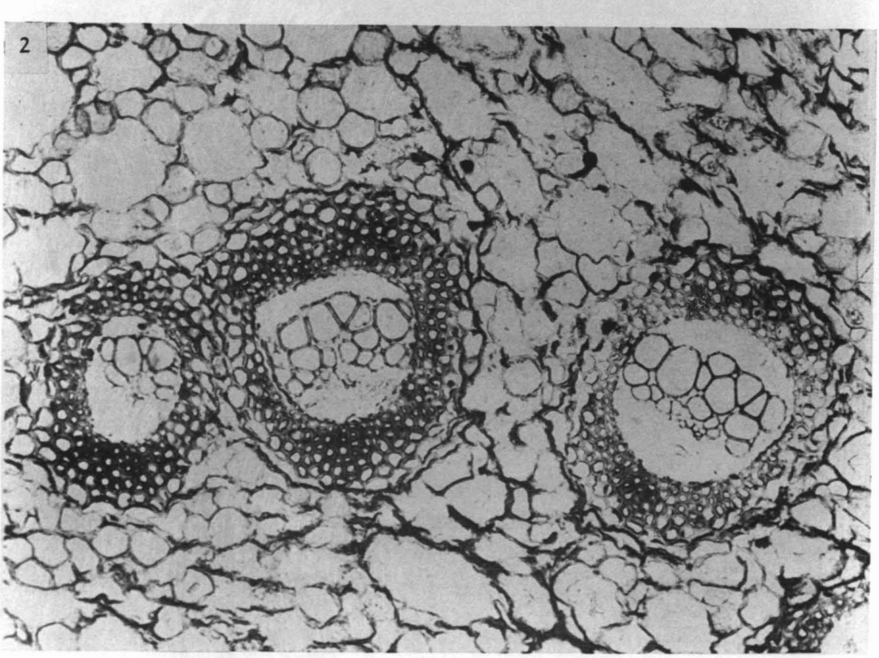
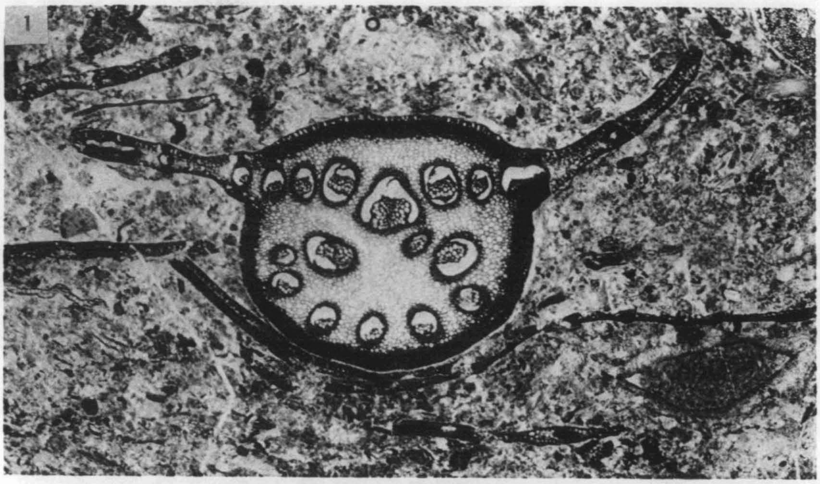
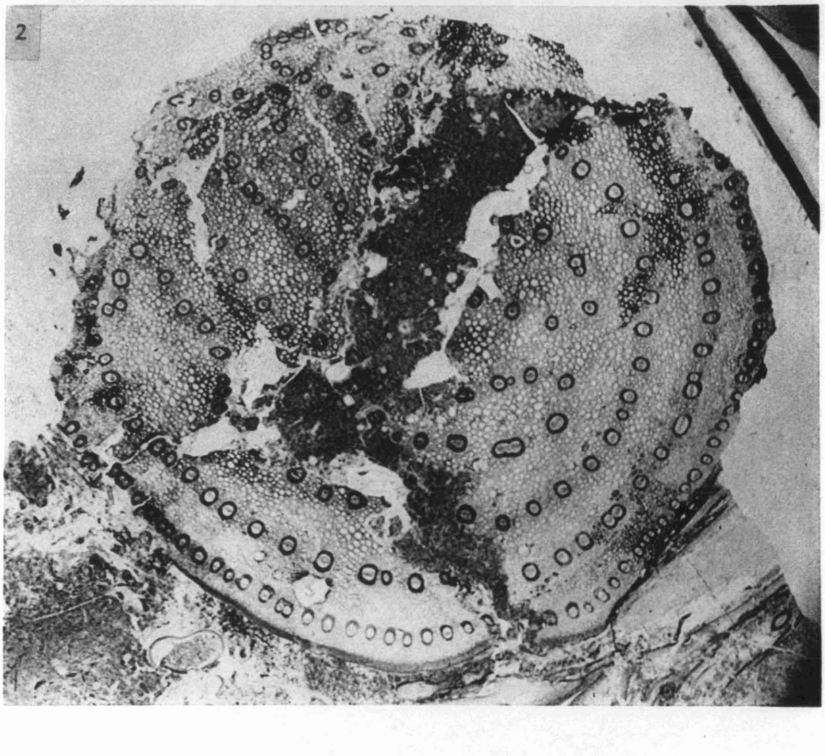


PLATE II





EXPLANATION OF PLATE II

PAGE

Acrostichum preaureum nom. nov. Arnold and Daugherty 217

FIG. 1. Transverse section of midrib showing distribution of bundles and portions of pinna lamina attached. × 12.

FIG. 2. Cross section of incomplete petiole showing illusory cyclic arrangement. × 4.5.

EXPLANATION OF PLATE III

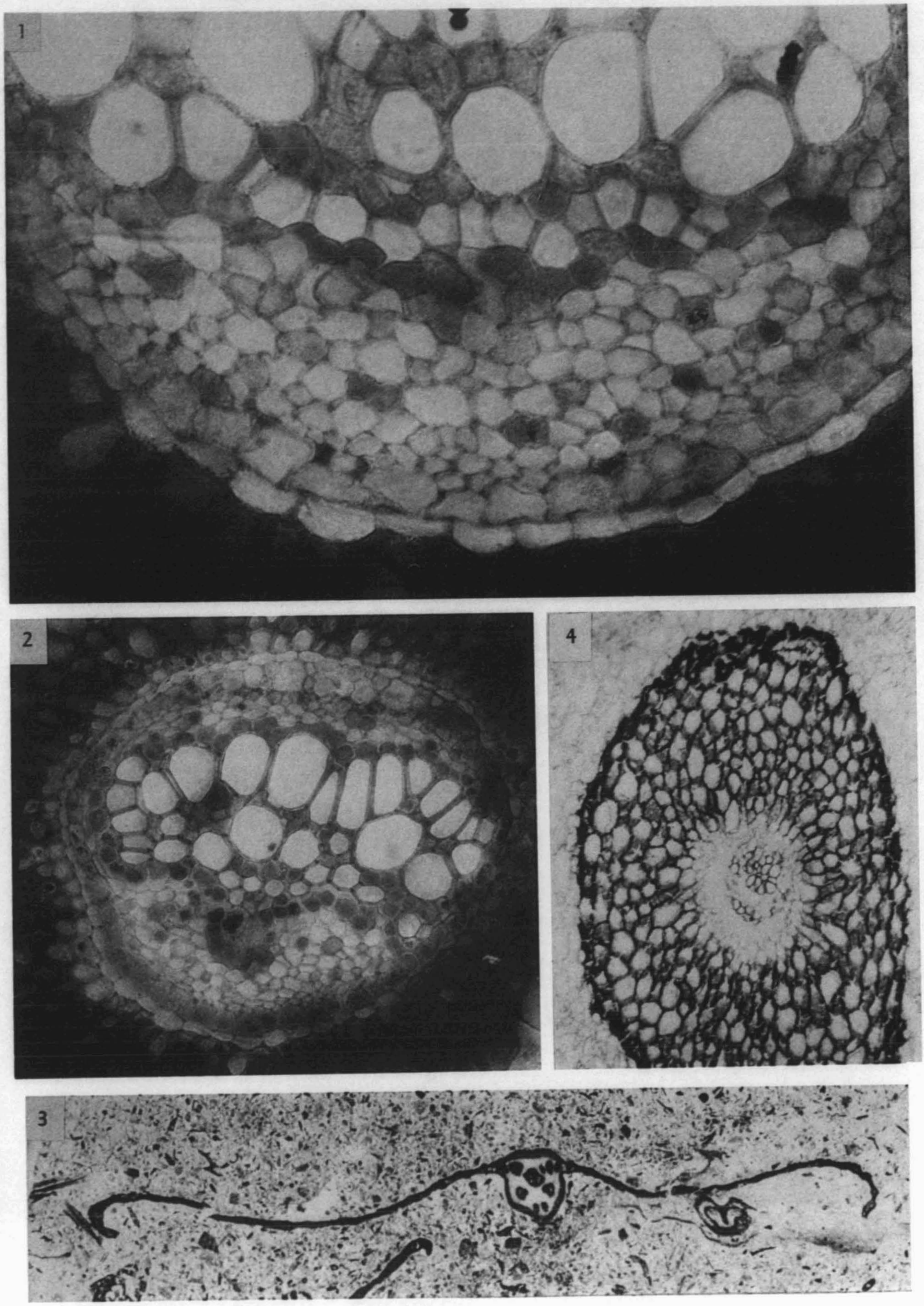
FIG. 1. Portion of petiole bundle showing endodermis (lower row of cells), pericycle (row of large cells in contact with endodermis), mass of phloem cells, and portion of xylem consisting of tracheids and intermined parenchyma. × 300.

FIG. 2. Cross section of complete petiole bundle similar to that shown in part in Figure 1. Phloem appears both above and below the xylem mass in which the protoxylem is on the lower side. × 100.

FIG. 3. Transverse section of pinna showing midrib and lamina. × 7.

FIG. 4. Transverse section of medullary strand in large stem. × 60.

PLATE III



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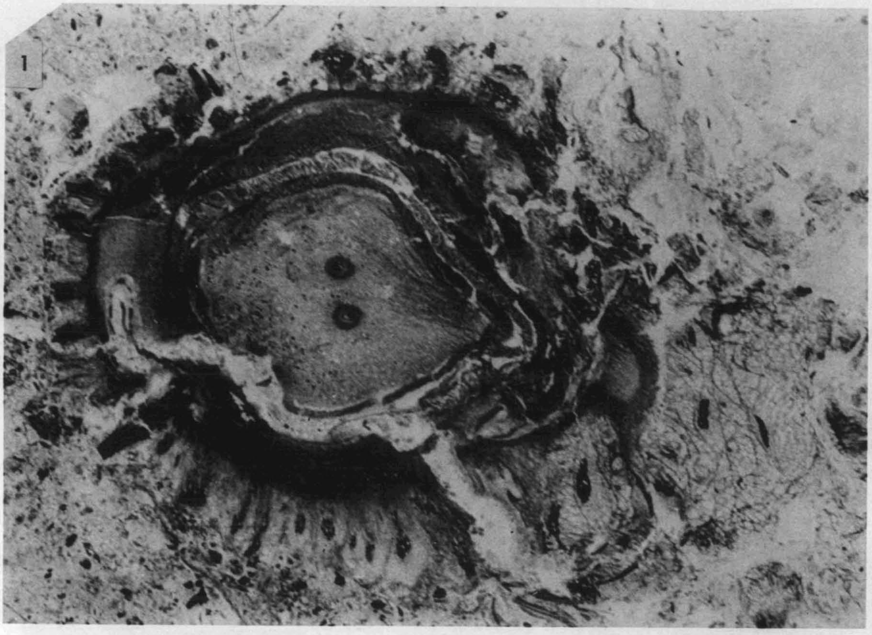
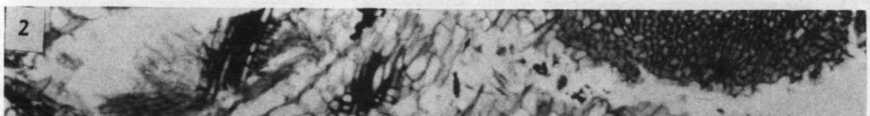




EXPLANATION OF PLATE IV

PAGE

Acrostichum preaureum nom. nov. Arnold and Daugherty 217

Fig. 1. Transverse section through small stem showing surface ramentum, the complete solenostele (broken), and large pith containing two medullary bundles. × 5.5.

Fig. 2. Portion of ramentum shown at right of stem in Figure 1. The transversely cut scales show the internal sclerenchyma mass and surrounding thin-walled radially elongated cells. × 30.

EXPLANATION OF PLATE V

PAGE

Acrostichum preaureum nom. nov. Arnold and Daugherty 217

Fig. 1. Transverse section of portion of large stem showing pith with numerous vascular strands, the stele (to left) flanked internally and externally by sclerenchyma, thin cortex, and (on surface) compact layer composed of bases of scales of ramentum. × 6.

Fig. 2. Portion of pinna cut nearly parallel to surface showing *Acrostichum* type of venation. × 10.

Figs. 2–5. Longitudinal sections of sporangia showing the annulus and stomial regions. Figure 5 contains spores. × 185.

Fig. 6. Single spore. × 400.

PLATE V

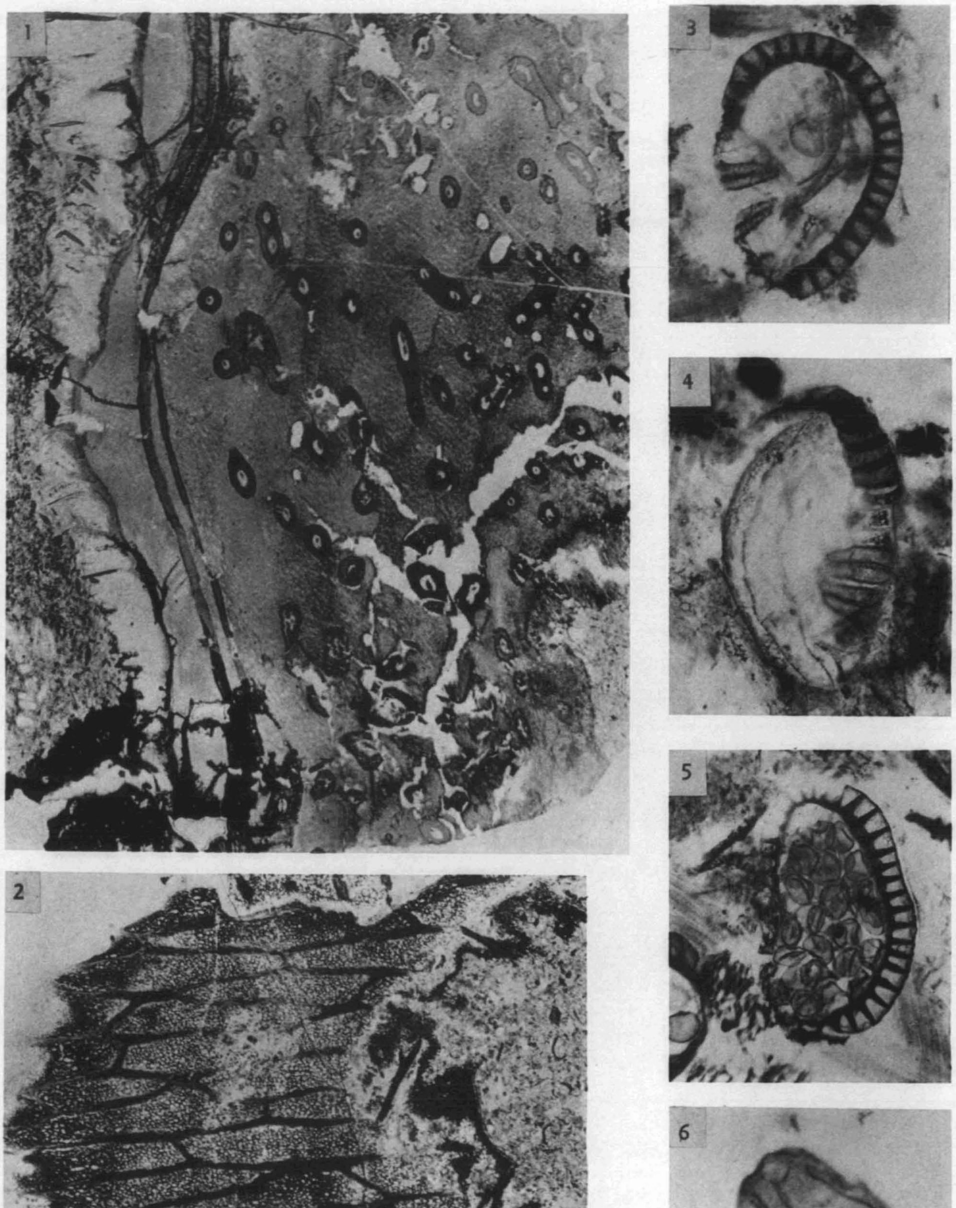
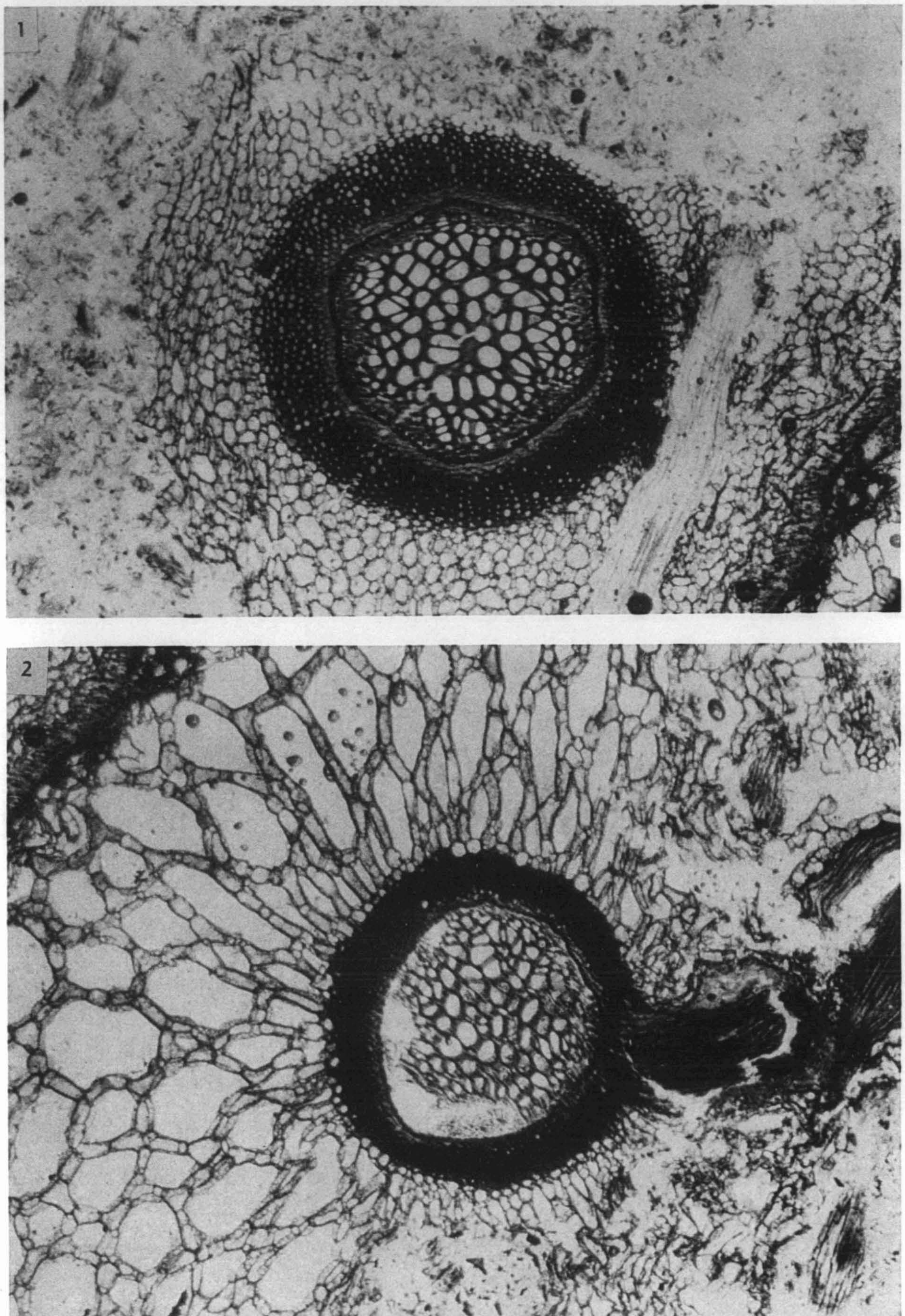


PLATE VI



EXPLANATION OF PLATE VI

FIG. 1. Cross section of hexarch root showing stelar portion surrounded by sclerenchyma and parenchymatous outer cortex without conspicuous aerenchyma. × 30.

FIG. 2. Root similar to that shown in Figure 1, but with well-developed aerenchyma in middle cortex. × 30.