CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN

VOL. XXI, No. 8, pp. 139–203 (4 pls., 9 figs.) JUNE 30, 1967

EVOLUTION OF THE FERN GENUS *OSMUNDA*

BY
CHARLES N. MILLER, JR.

1817

MUSEUM OF PALEONTOLOGY
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EVOLUTION OF THE FERN GENUS *OSMUNDA*

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CONTENTS

ABSTRACT

The phylogenetic background of the living species of *Osmunda* is interpreted from seven species of fossil rhizomes, six of which are assigned to the genus in this account. *Osmunda pluma, O. precinnamomea,* and *O. arnoldii* are new species from the Paleocene of North Dakota that are described in the subgenera *Osmunda, Osmundastrum,* and *Plenasium* respectively. A fourth new species, *Osmunda nathorstii,* is based on a fossil from the Upper Tertiary of Spitsbergen that was previously included under the binomial *Osmundites spetsbergensis* (Nathorst) Kidston and Gwynne-Vaughan. This species is assigned to the subgenus *Osmunda. Osmundites schemnicensis* (Pettko) Unger, from the Miocene-Pliocene of Hungary, is transferred to the subgenus *Osmunda* under the new name *Osmunda iliaensis;* and *Osmundites oregonensis* Arnold, from the Eocene of Oregon, is placed in this subgenus as a new combination. The living *Osmunda claytoniana* L., which is usually treated in the subgenus *Osmundastrum,* is regarded as a member of the subgenus *Osmunda* because of its anatomical similarity to other members of this subgenus. *Osmundites chandleri* Arnold is treated as a synonym of *Osmunda dowkeri* (Carruthers) Chandler, a species in the subgenus *Plenasium* from the Eocene; and fossil rhizomes from the Upper Tertiary of Washington are identified as *Osmunda cinnamomea* L. Furthermore, *Osmundacaulis nom. nov.* is used in place of *Osmundites* Unger, which is invalid, and the species of this form genus are listed in groups according to their phylogenetic relationships.

The three subgenera of *Osmunda* have been well-defined lines of specialization since the Paleocene, and the subgenera *Osmunda* and *Plenasium* are in evidence in the Early and Late Cretaceous respectively. The Recent species evolved almost unchanged from their Tertiary ancestors with most modifications reflected in the various arrangements of petiolar sclerenchyma. An important exception to this is the development of the internal endodermis in *Osmunda cinnamomea* which occurred sometime between the Paleocene and the present.

Three of the living species of the subgenus *Osmunda* are the products of a line of development represented by *O. pluma, O. oregonensis,* and *O. iliaensis,* whereas *O. claytoniana* arose on a divergent branch of this line through *O. nathorstii* from a form similar to *O. iliaensis.* In the subgenus *Osmundastrum, Osmunda cinnamomea* is viewed as a more or less direct descendant of *O. precinnamomea.* The Recent species of *Plenasium* arose from *Osmunda arnoldii* or a similar form, and *O. dowkeri* represents an extinct line of specialization within *Plenasium* that converges with the main line in the Cretaceous.

Although it has not been possible to trace the origin of any of the subgenera to specific forms of *Osmundacaulis,* the subgenera *Osmunda* and *Osmundastrum* show greatest affinity with the *Osmundacaulis herbstii* group while *Plenasium* probably arose from an unknown form of the *Osmundacaulis skidegatensis* group. To recognize the probability that the genus *Osmunda* is polyphyletic and that its subgenera have been independent lines of specialization for at least 70 million years, it is recommended that *Osmunda, Osmundastrum,* and *Plenasium* be raised to genera.

INTRODUCTION

Structurally preserved remains of some thirty species of fossil Osmundaceae have been described from sediments ranging in age from Late Permian to Late Tertiary. About one-third of these are stems that demonstrate the probable evolution of the present osmundaceous stele—an ectophloic, dictyoxylic siphonostele—from protostelic ancestors by intrastelar origin of a pith and concurrent dissection of the xylem cylinder by leaf-gaps; and other stems show that the Osmundaceae had attained dictyostely during the Mesozoic. However important these forms are in illustrating the broad evolutionary trends in the family, they are either too simple or too specialized to have bearing on the immediate phylogenetic background of the present-day Osmundaceae. Species of *Osmundacaulis,* a *nomen novum* used here in place of *Osmundites* Unger which is invalid, show that the "modern" osmundaceous stele had evolved by Late Triassic time (Archangelsky and de la Sota, 1963). In all, thirteen of the previously described fossil species have steles that are similar to those of the extant species, and five of them occur in the Tertiary where closest resemblance to the living forms would be expected. Yet, all but one of these species are presently classified in a form genus indicating that they cannot be assigned to one of the three genera of living osmundaceous ferns.

There are no great differences between these more recent fossils and the living species; but *Leptopteris, Osmunda,* and *Todea* have nearly identical internal structures, and paleobotanists have lacked characters of rhizome anatomy that would enable them to distinguish between these genera in the fossil state. Thus, authors could not assign fossil species to these Recent genera because they were unable to determine which one of the three would best accommodate their material.

Recently, however, Hewitson (1962) surveyed thirteen of the sixteen commonly recognized species of the living Osmundaceae for anatomical characters useful in separating the taxa; and Chandler (1965), utilizing these features, has transferred *Osmundites dowkeri* Carruthers to the subgenus *Plenasium* of *Osmunda.*

In this account three new species are described in the genus *Osmunda.* They are based on new material of Paleocene age from the Fort Union Formation in North Dakota, and they show that the three subgenera of *Osmunda* were even then distinct lines of evolution. Two other fossil rhizomes from the Late Tertiary of central Washington are classified directly with *O. cinnamomea* L. Furthermore, four previously described species of petrified rhizomes have been reinvestigated and are assigned to the genus *Osmunda.* These fossil species and the new species are placed in phylogenetic series with the Recent members of *Osmunda.*

ACKNOWLEDGMENTS

Three of the four new species described in this treatment are based for the most part on materials from the private collection of Mrs. Pluma Spiss of Mandan, North Dakota. Mrs. Spiss has collected from areas near Mandan for several years and donated about fifty specimens of petrified rhizomes to the University of Michigan Museum of Paleontology for investigation. Her generosity and interest in paleobotany are commendable and one of the new species, *Osmunda pluma,* is named in her honor.

Several other Paleocene rhizomes were made available for study by Mr. John Bunting of Mandan, North Dakota. The two fossil rhizomes of *O. cinnamomea* were sent to the Museum by Mrs. Sam Kirkby of Riverside, California. My thanks go to these people for their contributions.

Many others are deserving of thanks for their help with this project. Dr. Walter Hewitson, College of the Pacific, Stockton, California, turned over to me the specimens remaining after his survey of the living Osmundaceae, and Dr. Shohei Kokawa, Osaka City University, Japan, sent additional living material. Dr. K. I. M. Chesters, Department of Paleobotany, British Museum (Natural History), London, and staff of the Department of Botany, University of Glasgow, Scotland, facilitated my investigation of preparations in the collections of these institutions. My appreciation is also extended to the staff of the University of Michigan Botanical Gardens where living materials were maintained prior to study.

Professor W. H. Wagner, Department of Botany, The University of Michigan, made many helpful suggestions regarding evolutionary relationships of living ferns, and Professor C. A. Arnold is deserving of special thanks for directing my work and providing encouragement during its progress. *Osmunda arnoldii* is named in his honor. Professors C. A. Arnold, R. V. Kesling, and E. C. Stumm critically reviewed the manuscript.

THE NORTH DAKOTA LOCALITY

Location and Occurrence of the Specimens

The petrified rhizomes from North Dakota occur in angular, siliceous boulders of various sizes which are scattered in wheat fields that occupy most of the land. The fields are located about five miles west of Glen Ullin, North Dakota, which in turn is about fifty miles west of the state capital, Bismark. These fields occur in Sections 7, 8, 17, and 18 of Township 138 North, Range 89 West and Sections 3, 4, 11, 12, 13, and 14 of Township 138 North, Range 90 West in Morton County, North Dakota. While there are similar boulders in other fields, fern stems have been found only in specimens from the above locations.

The angular shapes of these boulders suggest local origin rather than long-distance transport by glacial or other means, and Lloyd (1912) traced them to two or more thin beds of the Fort Union Formation, which he found in place near the tops of the higher hills and buttes in the county. Today, the region is relatively flat, but the boulders must have come from overlying strata that have since eroded almost completely away.

Although the majority of the boulders contain secondary wood of unidentified gymnospermous trees, only a few contain "ozzies," as these petrified osmundaceous rhizomes are locally called. A visit to the collecting localities with Mr. and Mrs. Spiss and Dr. H. F. Becker of the New York Botanical Gardens in June of 1962 produced only six of these fossils in a day of searching, so the "ozzies" are by no means abundant.

Most often the fern rhizomes are included between two or three flat pieces of petrified gymnospermous wood. It is possible that both plants were washed into the same basin of deposition and that the rhizomes were thus protected by the wood during fossilization. However, considerable erosion of the outer leaf-bases which surround the fern stems and random placement of the wood and fern axes would be expected under these conditions. On the contrary, the outer leaf-bases of many specimens are well preserved and the longitudinal axes of the slabs of wood are usually parallel to the longitudinal axes of the rhizomes so that transverse sections prepared of one organ result in transverse sections of the other. Most likely, then, the fern axes were directly associated with the wood in the living condition, and both were preserved more or less in place.

The wood associated with the fern rhizomes is poorly preserved, and all seems to be of one general type. The vertical system consists of tracheids with some xylem parenchyma, and the rays are uniseriate. No resin ducts were observed in the tissue. All cells appear to be thin-walled and pits are not visible. It is important to note that wherever a rhizome and the wood are associated in the same specimen, the rhizome lies next to the pelloderm and roots of the fern penetrate only into this layer. Annual rings are present in the xylem; but the yearly increments of growth are broad, and the areas of summer wood are narrow. Thus, the growing season of these trees must have been long.

The three present-day specimens of *Osmunda* that occur in North America, *O. cinnamomea, O. claytoniana,* and *O. regalis,* frequently grow in crevices in upright, partly decayed tree stumps, especially in habitats that are flooded during some part of the growth season. The physiography of North Dakota during deposition of the Fort Union Formation has been interpreted by several vertebrate paleontologists as a flat, swampy forest braided by many slow, meandering rivers which frequently flooded to produce numerous temporary lakes (Matthew, 1914; Jepson *in* Scott, 1937; Simpson, 1937). Such an environment would be ideal habitat for the Recent species; and if their ecological preferences can be extended to the Paleocene fossils, it would explain the association of these ferns with the wood.

Climatic Interpretation

The mean annual temperature during the Paleocene at 40° to 50° North Latitude in North America has been interpreted by Dorf (1959) as being between 47° F. and 54° F., and evidence from the osmundaceous ferns and associated wood supports his findings. The weakly-developed annual rings in the wood indicates a relatively long growing season with the probable absence of severe winters. Furthermore, the fern rhizomes do not show aborted petiole bases (cataphylls of Steeves and Wetmore, 1953) which in the living species serve as protective "bud scales." Thus, these Paleocene ferns must have enjoyed a mild climate without severe winters.

NOMENCLATURE

Use of Recent Taxa

All species described in this account are assigned to *Osmunda* Linneaus rather than to *Osmundites* Unger, a form genus that has traditionally been used for petrified osmundaceous stems in which the xylem is dissected by leaf-gaps. The form genus was used in the past because authors were unable to identify their material with *Osmuda, Todea,* or *Leptopteris;* but Hewitson (1962) showed that successful differentiation of these genera and the three subgenera of *Osmunda* could be made using characters of rhizome anatomy. According to his survey of the living Osmundaceae, members of *Osmunda* have long fibers making up the outer cortex of the stem, whereas in species of *Todea* and *Leptopteris* these cells occur only around the departing leaf-traces, the bulk of the outer cortex consisting of relatively short sclereids. Chandler (1965) also points out that in *Todea* and *Leptopteris* the stipular expansions of the petiole base are joined distally across the petiole by a transverse commissure, a feature absent in *Osmunda. Todea* differs from *Leptopteris* in having strands of sclerenchyma scattered in the inner cortex of the petiole base, while such strands are lacking in *Leptopteris*. Within the genus *Osmunda,* species of the subgenus *Plenasium* have leaf-traces that exhibit a pronounced adaxial curvature in transverse section as they separate from the stem xylem, and at this location each leaf-traces bears two protoxylem strands. Leaf-traces in the subgenera *Osmunda* and *Osmundastrum* are oblong or slightly curved as they separate from the stem xylem, and each trace bears one protoxylem at this point. The two species of *Osmundastrum* were thought to be unique among the living Osmundaceae in having both thick-walled and thin-walled fibers making up the sclerenchyma ring around the vascular strand of the petiole base; however, the ring is heterogeneous in all living species with the thick-walled fibers merely forming more conspicuous patterns in *O. cinnamomea* and *O. claytoniana* than in the other species. Further investigation of this character and others (explained in detail below) indicates that *O. claytoniana* has more structural features in common with members of the subgenus *Osmunda* than it does with *O. cinnamomea;* and for this reason *O. claytoniana* is treated as a member of the subgenus *Osmunda* in this account. While the leaf-traces of species of the subgenera *Osmunda* and *Osmundastrum* are similar, *Osmunda cinnamomea,* the only living member of *Osmundastrum,* differs in a number of respects from members of *Osmunda*. It has an internal endodermis, strands of thick-walled fibers axillary to each leaf-trace in the inner cortex of the stem, and three masses of thick-walled fibers in the sclerenchyma ring of the petiole base. The arrangement of sclerenchyma tissues in the base of the petiole is diagnostic for all living species; and other characters, such as the number of xylem strands or the number of leaf-traces in a given cross-section of the stem, are useful as correlative evidence but are not in themselves diagnostic (Hewitson, 1962).

Since anatomical features that characterize the Recent genera and subgenera are known, there is no longer reason to arbitrarily place fossil axes in a form genus. However, even though it is now possible to identify structurally preserved rhizomes of the Osmundaceae to the level of the Recent subgenus or occasionally to the present-day species, a form genus is still needed to include fossil axes which have the general features of the living rhizomes but which defy classification with an extant taxon. In the past the form genus *Osmundites* Unger (1854) has served this purpose, but this name is invalid since Jaeger (1827) used it earlier for misidentified cycadophyte fronds. Furthermore, Unger's generitype, *Osmundites schemnicensis* (Pettko), belongs to *Osmunda* and is transferred to this genus in the present treatment. Thus, a *nomen novum* is required.

Osmundacaulis nomen nov., C. N. Miller

Diagnosis.—Structurally preserved rhizomes, roots, and (or) leaf-bases of plants resembling species of *Leptopteris, Osmunda,* or *Todea,* but which cannot be assigned to one of these genera. Stems containing a pith; xylem cylinder dissected by leaf-gaps; leaf-traces oblong or adaxially curved in transverse section; vascular strand of petiole base C-shaped in transverse section; xylem strand of root diarch.

Generitype.—*Osmundacaulis skidegatensis* (Penhallow) comb. nov., C. N. Miller.

List of species.—The species of *Osmundacaulis* are arranged below in phylogenetic groups which are given no taxonomic rank within the form genus.

Osmundacaulis skidegatensis group:
- *Osmundacaulis skidegatensis* (Penhallow) comb. nov., C. N. Miller.
  - *Osmundites skidegatensis* Penhallow. 1902.
- *Osmundacaulis natalensis* (Schelpe) comb. nov., C. N. Miller
  - *Osmundites natalensis* Schelpe. 1955.
- *Osmundacaulis atherstonei* (Schelpe) comb. nov., C. N. Miller
  - *Osmundites atherstonei* Schelpe. 1956.

Osmundacaulis herbstii group:
- *Osmundacaulis herbstii* (Archangelsky and de la Sota) comb. nov., C. N. Miller
  - *Osmundites herbstii* Archangelsky and de la Sota. 1963.
- *Osmundacaulis sahnii* (Vishnu-Mittre) comb. nov., C. N. Miller
  - *Osmundites sahnii* Vishnu-Mittre. 1955.
- *Osmundacaulis dunlopi* (Kidston and Gwynne-Vaughan) comb. nov., C. N. Miller.
  - *Osmundites dunlopi* Kidston and Gwynne-Vaughan. 1907.
  - *Osmundites aucklandicus* Marshall. 1924.
- *Osmundacaulis gibbiana* (Kidston and Gwynne-Vaughan) comb. nov., C. N. Miller.
  - *Osmundites gibbiana* Kidston and Gwynne-Vaughan. 1907.
- *Osmundacaulis patagonica* (Archangelsky and de la Sota) comb. nov., C. N. Miller.
  - *Osmundites patagonica* Archangelsky and de la Sota. 1962.
- *Osmundacaulis kolbei* (Seward) comb. nov., C. N. Miller.
  - *Osmundites kolbei* Seward. 1907.
- *Osmundacaulis kidstoni* (Stopes) comb. nov., C. N. Miller.
  - *Osmundites kidstoni* Stopes. 1921.

Osmundacaulis braziliensis group:
- *Osmundacaulis braziliensis* (Andrews) comb. nov., C. N. Miller.
  - *Osmundites braziliensis* Andrews. 1950.
- *Osmundacaulis carnieri* (Schuster) comb. nov., C. N. Miller.
  - *Osmundites carnieri* Schuster. 1911.

Discussion.—The description of *Osmundacaulis (Osmunda-caulis)* is necessarily general. Its future use should be restricted to structurally preserved stems, roots, and leaf-bases that are similar to those of the living Osmundaceae but which cannot be assigned to one of the extant genera for one or more of the following reasons: (1) the lack of preesrvation of sufficient diagnostic detail, (2) the presence of structural features that are not characteristic of the living species, and (3) the combination of features of the Recent genera in such a way that assignment to one of them cannot be made.

Osmundacaulis skidegatensis is selected as the generitype because of its priority and its unusual structure. With *Osmundites dowkeri* and *O. schemnicensis* removed to *Osmunda* (as *Osmunda dowkeri* and *O. ilianensis* respectively), *Osmundacaulis skidegatensis* has the next oldest date of description. Furthermore, its size and dictyostelic structure are not characteristic features of the living species; so regardless of how much may become known about Recent Osmundaceae, it is unlikely that this species can ever be assigned to one of the extant genera. Thus, *O. skidegatensis* is intended to serve as generitype of *Osmundacaulis* with some permanence.

Genus: *Osmunda,* Subgenus: *Osmunda*

Living Species

Three living species are generally recognized: *Osmunda lancea* Thunb., *O. japonica* Thunb., and *O. regalis* L., the latter being the type species. These ferns are distinct among those of the genus *Osmunda* in having bipinnate fronds. The first two species are restricted to eastern Asia while *O. regalis* is widespread in the northern temperate and tropical regions and extends as far south as India. Vegetatively, *O. regalis* and *O. japonica* are very similar. Their pinnules are asymmetrically subtruncate or auricled at the base while pinnule-bases of *O. lancea* are symmetrically accuminate. Fertile fronds of *O. regalis* have fertile pinnae at the apex with vegetative pinnae below; those of *O. japonica* usually follow this habit but may be completely dimorphic; and fertile fronds of *O. lancea* are most often completely dimorphic but may infrequently display the *O. regalis* condition. Anatomically, *O. lancea* tends to have fewer strands of stem xylem and more leaf-traces in the cortices, as observed in transverse stem sections, than *O. japonica* and *O. regalis,* but the arrangement of sclerenchyma tissues in the stipular petiole bases of these species is more diagnostic. An elongate strip of thick-walled fibers dominates the stipular expansions of *O. regalis* and *O. japonica,* while the largest group of these cells in stipular expansions of *O. lancea* is a relatively small rounded mass. Petiole bases of *O. lancea* and *O. japonica* have many small clusters of thick-walled fibers in the stipular expansions concentrated near the sclerenchyma ring but none in the inner cortex of the petiole base, while petiole bases of *O. regalis* have a few small clusters in the inner cortex but none in the stipular expansions.

The sclerenchyma ring of the petiole base in all three species of the subgenus *Osmunda* is heterogeneous (Fig. 1). Transverse sections of the petiole base near its point of attachment to the stem show an arch of thick-walled fibers occupying the entire abaxial semicircle of the ring with the remainder constructed of relatively thin-walled fibers. In slightly higher sections the arch of thick-walled cells is thinner abaxial to the vascular strand and thicker on each lateral side of the vascular strand. Eventually, all thick-walled sclerenchyma abaxial to the vascular strand disappears while the two lateral masses remain. This pattern occurs at a level that is about one-third of the distance from the point of attachment of the petiole base to the stem to the top of the stipular region, and the arrangement of ring sclerenchyma here is identical to that in *O. claytoniana* as figured by Hewitson (1962, Fig. 7E) and Kidston and Gwynne-Vaughan (1907, Plate VI, Fig. 12). Slightly higher the two lateral concentrations of thick-walled fibers diminish in size and thick-walled fibers extend from them around the adaxial side of the ring. Finally, sections in the upper one-half of the stipular region show only a narrow, inconspicuous band of thick-walled fibers on the adaxial side and at the outer edge of the sclerenchyma ring (Fig. 1a).

Since the occurrence of two lateral concentrations of thick-walled fibers in sclerenchyma rings of *O. lancea, O. japonica,* and *O. regalis* is similar to the pattern that is generally figured for *O. claytoniana,* the arrangement of ring sclerenchyma in the latter species was reexamined. The pattern of thick-walled ring fibers in the lower one-third of the *O. claytoniana* petiole base is like that in *O. regalis, O. japonica,* and *O. lancea.* However, the two lateral masses of fibers, once formed, extend upward for the remaining length of the stipular region (Fig. 13).

O. claytoniana is generally treated as a species of the subgenus *Osmundastrum* because of the similarity of its vegetative fronds to those of *O. cinnamomea* (Copeland, 1947) and because it was previously thought that only these two species had heterogeneous sclerenchyma rings in their petiole bases (Hewitson, 1962). In *O. cinnamomea* three separate masses of thick-walled fibers occur in the sclerenchyma ring and extend throughout the vertical length of the stipular region. Furthermore, stems of *O. cinnamomea* characteristically have an internal endodemris and a mass of

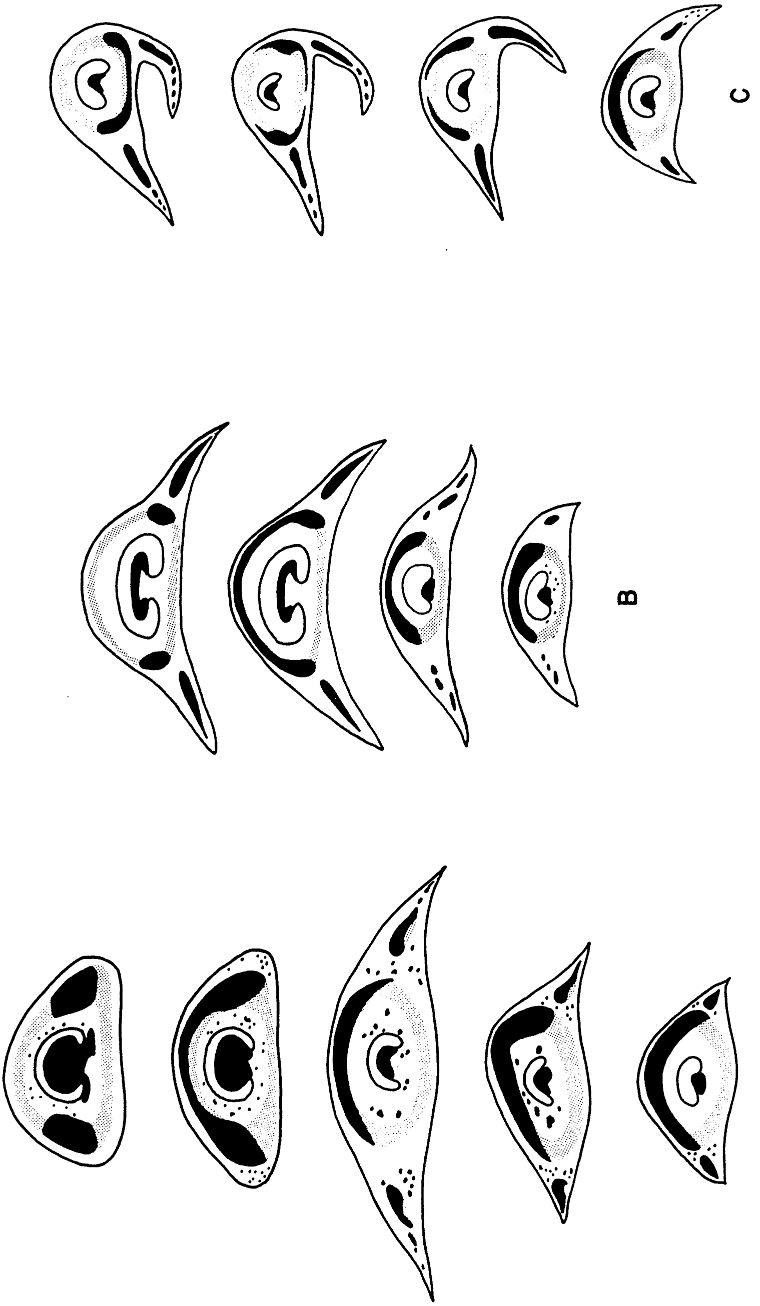

FIG. 1. Transverse sections of stipular petiole bases showing sclerenchyma arrangement in *A. Osmunda pluma* sp. nov., *B. Osmunda claytoniana*, and *C. Osmunda regalis;* thin-walled fibers, gray; thick-walled fibers, black.

thick-walled fibers axillary to each leaf-trace. These two tissues are lacking in stems of *O. claytoniana*. In both *O. cinnamomea* and *O. claytoniana* the protoxylem of the leaf-trace initially bifurcates in the base of the petiole, while in *O. regalis, O. japonica,* and *O. lancea* this protoxylem branching occurs while the leaf-trace is in the inner or outer cortex of the stem. In most other anatomical respects *O. claytoniana* is more similar to species of the subgenus *Osmunda* than it is to *O. cinnamomea.* Furthermore, O. X. *ruggii* Tryon (1940), a presumed hybrid between *O. regalis var. spectabilis* and *O. claytoniana* shows that a combination of characters of these two parental types is possible, while no such hybrid between *O. cinnamomea* and *O. claytoniana* is known. Therefore, *O. claytoniana* is considered a member of the subgenus *Osmunda* in this treatment.

SYSTEMATIC DESCRIPTION

Family: Osmundaceae
Genus *Osmunda* Linneaus
Subgenus *Osmunda* Linneaus
Osmunda pluma sp. nov. C. N. Miller
(Figs. 1c, 2; Pl. I, Figs. 1–4)

Diagnosis.—Petrified rhizomes about 2–4.5 cm. in diameter, consisting of a stem about 7.0 mm. in diameter surrounded by a mantle of closely adhering petiole bases; xylem cylinder of stem about 2.5 mm. in diameter, 0.75 mm. thick, and consisting of 7–12 strands as observed in transverse section; leaf-gaps high and wide, formed immediately opposite each departing leaf-trace; phloem a continuous cylinder around the xylem; endodermis external only; cortex consisting of a thin inner parenchymatous zone and a thick outer fibrous zone, together including 6–11 departing leaf-traces in a given transverse section; leaf-trace endarch, separating from stem xylem with a single protoxylem which bifurcates as leaf-trace passes through inner cortex; petiole base stipular, sclerenchyma ring heterogeneous, containing an abaxial arch of thick-walled fibers which splits just above stipular region to form two lateral clusters; inner cortex of petiole base containing scattered clusters of thick-walled fibers; stipular expansions containing an elongate strip of thick-walled fibers near base of stipular region, and separate patches of fibers in linear series above; roots with diarch xylem strand, separating from leaf-trace as latter diverges from stem xylem.

Locality and Horizon.—Morton County, North Dakota; Paleocene, Fort Union Formation.

Holotype and paratypes.—University of Michigan Museum of Paleontology 52157 and 52158 respectively.

Introduction.—This new species is based on rhizomes that occur in silicified boulders from the Fort Union Formation in central North Dakota. Rhizomes of *Osmunda pluma* make up the majority of those found in the boulders. The species is represented in twenty-seven specimens, and several rocks contain more than one axis. The position of certain rhizomes indicates that they arose as branches of others, but actual branching regions are present in only three specimens. About one-half of the rhizomes are too poorly preserved to warrant sectioning for microscopic examination, so the following description is based on polished pieces and petrologic sections from fifteen rhizomes which are adequately preserved.

The rhizome structure of the new species is basically like that in the Recent osmundas (Pl. I,Fig. 1). The stem consists of an ectophloic-dictyoxylic siphonostele which is surrounded by a cortex. The latter is sharply differentiated into an inner layer of parenchyma and an outer layer of sclerenchyma. Petiole bases adhere closely around the stem and their stipular expansions overlap to form a thick mantle. Indeed, much of the bulk of the rhizome is due to these stipular petiole bases, the stem being relatively small in diameter.

Stem.—In *Osmunda pluma* the pith is 0.5–1.0 mm. in diameter and may be constructed of parenchyma cells, sclerenchyma cells, or both. The sclereids are stone cells which have a cell wall thickness of 10–16 microns, and the walls of the parenchyma cells are 1–2 microns thick. The two cell types differ only in this respect. Walls of neither type of cell show pitting, and both kinds of cells are 35–85 microns in diameter and 85–155 microns in length. The two cell types are polygonal in cross-sectional outline. They are arranged in irregular axial rows, and they may have either transverse or oblique end walls. Where both sclerenchyma and parenchyma cells occur in the pith, the tissue generally has sclereids at the center and changes gradually, through cells of medium wall thickness, to thin-walled parenchyma cells at the periphery of the tissue. Furthermore, sections in which the pith is entirely sclerotic appear to have come from older regions of the rhizome as indicated by the compression and decay of tissues constructed of thin-walled cells and the invasion of roots into the stelar region. On the other hand, preservation of tissues is generally good throughout in transverse stem sections having only parenchyma in the pith suggesting a more apical placement. Thus, the stone cells probably formed from pith parenchyma by an increase in cell wall thickness some distance behind the shoot apex as a part of the normal ontogenetic sequence in this species.

There have been numerous reports of sclerenchyma in the pith regions of Recent Osmundaceae but only a few cases in fossil species. Among the living members of this family, *Osmunda regalis, O. cinnamomea, O. javanica, O. vachellii, Todea barbara, Leptopteris frazeri, L. superba,* and *L. hymenophylloides* may have sclerenchyma cells in the pith (Faull, 1901; Seward and Ford, 1903; Hewitson, 1962). Kidston and Gwynne-Vaughan (1910) mention the occurrence of thick-walled parenchyma cells in the pith of their material of *Osmundites schemnicensis* and Arnold (1952) observed thick-walled cells scattered singly or in groups in the pith of his material of *O. dowkeri* but said that they may be due to mineral matter adhering to the cell walls. However, the occurrence of similar thick-walled parenchyma cells in the pith of type specimen and other materials in the British Museum (Natural History) indicates that Arnold's first impression was most likely correct. Thick-walled cells also occur in the pith regions of *Osmundicaulis skidegatensis* (Kidston and Gwynne-Vaughan, 1907), *O. atherstonei* and *O. natalensis* (Schelpe, 1955 and 1956 respectively).

The xylem of *Osmunda pluma* consists of seven to eleven strands of primary xylem tracheids which are arranged in a circle around the pith (Pl. I, Fig. 2). These strands anastomose above and below a given transverse section to form a cylinder which is broken by vertically overlapping leaf-gaps and give the impression of separate xylem strands when viewed in a transverse section. Each strand is of 10–15 tracheids thick in radial dimension. The metaxylem tracheids are 27–70 microns in diameter and have one to three, but mostly two, vertical series of scalariform pits on each wall. Protoxylem tracheids, which are 10–25 microns in diameter, have only one vertical series of scalariform pits on each wall or have helical wall thickenings. These tracheids occur in some, but not all, strands of xylem. Their presence or absence depends on the position of a given strand in relation to the formation of the leaf-trace.

The parenchymatous sheath around the xylem is inconspicuous. Cells of the tissue are thin-walled, about 15 microns in diameter and about 85 microns in length. These cells occur between the pith and xylem but only as a single layer which is interrupted in places. They also extend between the xylem strands, through leaf-gaps, forming a ground tissue for the xylem. The sheath cells can be seen in places between the xylem and phloem, but the region just outside the xylem is too transparent to allow identification of a continuous tissue at this location.

Cells of the metaphloem, porose layer, protophloem, and pericycle also occur locally within this transparent zone. Sieve cells of the metaphloem are 25–40 microns in diameter and are situated mainly in wedges opposite leaf-gaps where they may extend for a short distance between adjacent xylem strands. Sieve cells also occur in places between these wedges and probably formed a complete cylinder of metaphloem around the xylem though this condition cannot be observed in any one specimen. Thin-walled, tabular cells occur in places between the endodermis and metaphloem and no doubt represent the remains of the protophloem, porose layer, and pericycle.

The endodermis is one or two cells thick and completely surrounds the phloem-pericycle region. The endodermal cells measure 15 microns radially and 25 microns tangentially with respect to the stem. Casparian strips cannot be seen, but the tissue stands out because of the darkly colored contents of the cells. Furthermore, endodermal cells are smaller than cells of the inner cortex and are more regular in shape than the slightly flattened cells of the pericycle.

The inner cortex is made up of parenchyma cells whose walls are 1–2 microns thick. These cells are 50–150 microns long and 35–55 microns in diameter. Unlike the cells of the pith which are polygonal in transverse outline, cells of the inner cortex are oval and form a loose tissue with conspicuous intercellular spaces. The tissue is 0.5–1.0 mm. in breath and includes 1–3 departing leaf-traces in a given transverse section (Pl. I, Figs. 1–2).

In comparison, the outer cortex is a dense tissue that is 0.5–1.5 mm. thick and consists of elongate fibers. These cells are 280 microns and more in length and taper to a fine point at each end. Cell diameter varies from 10–50 microns with the smaller measurements representing the cut tips of cells above and below the plane of section. The cell walls are 5–6 microns thick, and the fibers fit closely together without conspicuous intercellular spaces. The outer cortex includes 6–10 leaf-traces in a given transverse section (Pl. I, Fig. 1).

Leaf-trace.—Formation of the leaf-trace in *Osmunda pluma* is much like that in living members of the subgenera *Osmunda* and *Osmundastrum* of the genus *Osmunda* (Hewitson, 1962). The xylem of the leaf-trace separates from a strand of stem xylem dividing the latter into two strands which continue upward in the stele on either side of the leaf-gap (Fig. 2). Some distance below the leaf-gap, the strand of stem xylem is oval in transverse outline and consists entirely of metaxylem tracheids. Slightly closer to the leaf-gap, however, the strand becomes mesarch with the appearance of a small cluster of protoxylem tracheids near its center but somewhat closer to the phloem than to the pith. Just above this point a small group of parenchyma cells of the xylem sheath appears immediately adaxial to the protoxylem elements. This cluster of parenchyma cells increases in size upward toward the pith replacing metaxylem tracheids adaxial to the protoxylem and giving the strand an "O" shape in transverse section. Eventually, these parenchyma cells connect with the pith, and the resulting xylem strand is endarch having a "U' 'shape in transverse outline with the protoxylem in medial position on the concave surface. The curved portion of the strand then breaks away as the xylem of the leaf-trace. Its transverse outline is oblong with a slight adaxial curvature, and the single cluster of protoxylem tracheids is in medial position on the concave surface.

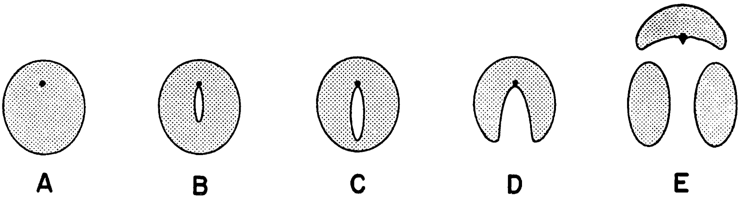

FIG. 2. *Osmunda pluma* sp. nov., transverse sections of xylem strands through a leaf gap, the letters A to E indicate an acropetal series.

As the xylem of the leaf-trace passes through the ploem, pericycle, and endodermis, the protoxylem elements spread out on the concave surface of the strand; and, as the leaf-trace becomes surrounded by cells of the inner cortex, the protoxylem tracheids reorganize in two distinct clusters, one to either side of the medial position. The exact location of protoxylem branching is not fixed. In some cases the protoxylem elements disperse prior to the separation of the leaf-trace from the stem xylem, while certain leaf-traces that have passed out as far as inner cortex have only one cluster of protoxylem elements. Yet, all leaf-traces in the outer part of the inner cortex have at least two protoxylems, and no traces separate from the stem xylem with two discreet clusters.

As the xylem of the leaf-trace passes into the inner cortex, it carries with it encircling layers of phloem, pericycle, and endodermis. No gaps are left in these tissues because they fill in immediately behind the leaf-trace to maintain their continuity. Similarly, as the leaf-trace moves into the outer cortex, it is accompanied by a surrounding layer of cells of the inner cortex. Concurrent with these changes is a slight increase in size and curvature of the leaf-trace.

Petiole base.—Hewitson (1962) found that of all anatomical characters useful in distinguishing between the living members of the Osmundaceae the arrangement of sclerenchyma tissues in the stipular region of the petiole base is the most reliable. This character is particularly important in defining *O. pluma* and interpreting its relationships with other species. The sclerenchyma tissues change in form and composition throughout the length of the stipular region, so their arrangement at any one level is not representative of the whole.

Two types of sclerenchyma cells occur in the petiole base; but they are both varieties of the type of fiber making up the outer cortex of the stem, having the same size and shape but differing in cell wall thickness. Certain fibers have walls that are only slightly thicker than those of the cortical fibers (8–10 microns), while the walls of others are so thick (12–18 microns) that their cell lumina are nearly filled.

Leaf-traces and surrounding cortical tissues near the periphery of the stem form a ridge on the stem surface that appears as a distinct bulge in transverse stem sections (Pl. I, Fig. 1). All fibers of the outer cortex abaxial to the leaf-trace are thick-walled while those on each tangential side and on the adaxial side of the leaf-trace are of the thin-walled type. The bulge increases in size upward and finally diverges from the stem into the petiole base as a unit consisting of the leaf-trace, a surrounding layer of parenchyma cells that are continuous downward with those of the inner cortex of the stem, and a layer of fibers that are continuous downward with those of the outer cortex of the stem. In transverse sections these fibers appear as a ring of sclerenchyma around the inner cortex of the petiole base. In addition, a thin tissue of parenchyma surrounds this unit and extends from it tangential to the stem forming stipular expansions which are very short near the point of attachment of the petiole to the stem. Transverse secions at this level show a triangular mass of thick-walled fibers in each stipular expansion, a rounded cluster of these cells in the concavity of the vascular strand, and an arch of thick-walled fibers occupying the entire abaxial semicircle of the sclerenchyma ring (Fig. 1c; Pl. I, Fig. 4). Petiole bases at this lowermost level measure about 5 mm. tangential to the stem and 1.5 mm. radial to the stem. Their sclerenchyma rings are about 0.3 mm. thick and have an elliptical transverse outline that is 1.5 mm. by 2.5 mm.

The petiole base increases in size upward mainly by lateral extension of the stipular expansions; the vascular strand becomes C-shaped, but there is only slight enlargement of other tissues. Near the middle of the stipular region, the abaxial arch of thick-walled fibers in the sclerenchyma ring is somewhat thinner apparently due to the replacement of thick-walled fibers at the inner edge of the sclerenchyma ring by thin-walled fibers. Further, the cluster of thick-walled fibers in the concavity of the vascular strand is in the form of a narrow band that lines the concavity. The triangular mass of fibers in each stipular expansion extends nearly to the tip of the expansion, and additional small clusters of thick-walled fibers occur in the inner cortex of the petiole base (Fig. 1c).

At the upper part of the stipular region, where the stipular expansions have their greatest lateral extent, the arrangement of sclerenchyma tissues in the petiole base is the most complex. The tips of the vascular strand recurve slightly, and the band of thick-walled fibers in its concavity conforms to this shape. Additional small clusters of thick-walled fibers appear in the inner cortex of the petiole base and also in the stipular expansion where they are concentrated near the sclerenchyma ring. The elongate strip of thick-walled cells in the stipular wing extends from a position near the sclerenchyma ring to a point about two-thirds the distance to the tip of the wing; it is thickest near the sclerenchyma ring and tapers toward the tip of the expansion, in some cases breaking into separate small clusters near the wing tip (Fig. 1c). Petiole bases at this level are about 2 mm. thick, measured radial to the stem, and about 10 mm. from wing-tip to wing-tip. The sclerenchyma rings are about 0.3 mm. thick and about 1.5 mm. by 3.0 mm. in over-all size.

In transverse sections of some rhizomes, petiole bases occur at the periphery of the mantle whose stipular expansions are smaller than those of petiole bases just inside them. These sections represent a position on a given petiole base a short distance above the stipular region where the expansions diminish into the rachis of the frond. At this location the abaxial semicircle of the sclerenchyma ring consists dominantly of thin-walled fibers at the middle of the arch with the thick-walled fibers in two lateral concentrations. Initially these clusters are connected across the abaxial sector of the ring by a narrow bridge of thick-walled fibers, and in higher sections they are separate (Fig. 1c; Pl. 1, Fig. 3). Such a configuration is suggestive of the pattern occurring in petiole bases of *O. claytoniana* (Kidston and Gwynne-Vaughan, 1907; Hewitson, 1962).

Stem branching.—Branching of the stem in *O. pluma,* as in the Recent species, is by more or less dichotomous bifurcation of the axis (Faull, 1901). Below the fork, the stem is somewhat flattened. The xylem cylinder is as thin as five tracheids in radial thickness, and the xylem strands are more confluent than in unbranched portions of the stem. Leaf-gaps occur opposite certain leaf-traces, but gaps of other leaf-traces indent the xylem cylinder without piercing it. Flattening of the stem is followed by the constriction of the tissues across the narrow diameter of the axis and the separation of two stems, each of which is about one-half the diameter of the original stem. No leaf-traces occur between the two xylem cylinders until they are several millimeters apart. Throughout the branching region there is no production of anomalous tissues as in certain stems of *O. cinnamomea* (Faull, 1901; Hewitson, 1962).

Roots.—Root-traces separate singly or in pairs from leaf-traces just above the point of divergence of the latter from the stem xylem. Normally, this separation occurs when the leaf-trace is in the ploem-pericycle region of the stem, but in some cases divergence of the root-trace is not complete until the leaf-trace is in the inner cortex. The xylem of the root is diarch and becomes surrounded by layers of phloem, pericycle, endodermis, inner cortex, and outer cortex as it passes through each of these respective stem tissues. Roots vary in the relative thickness of their cortical tissues; but the inner cortex is usually about two cells thick, while the thick-walled cells occupy the outer two to four cell layers.

Discussion.—Rhizomes of *Osmunda pluma* are similar in their general arrangement of tissues to those of the present-day Osmundaceae. Characters such as the number of leaf-traces in the cortex and the number of strands of stem xylem as seen in a given transverse section of the rhizome are within the limits of variation observed by Hewitson (1926) in the living members of the family. Since the outer cortex in the fossils is constructed of elongate fibers rather than short sclereids, the new species is more closely related to *Osmunda* than to *Leptopteris* or *Todea,* and the arrangement of sclerenchyma tissues in petiole bases of *Osmunda pluma* is also indicative of a close relationship to *Osmunda.*

Within the genus *Osmunda,* species of the subgenus *Plenasium* have leaf-traces that separate from the stem xylem bearing two protoxylem strands. Thus, the fossil species must belong to either the subgenus *Osmunda,* the subgenus *Osmundastrum* or to some extinct subdivision of the genus. The pattern of thick-walled fibers in the sclerenchyma ring in the fossil appears in a condensed version in the lower one-half of the stipular region in petiole bases of all living species of the subgenus *Osmunda.* It is on this basis and because of the similar numbers of stem xylem strands and cortical leaf-traces that *O. pluma* is assigned to the subgenus *Osmunda.* The relationship of this new species to other members of the subgenus *Osmunda* will be treated in a later section which is concerned with the phylogeny of the subgenus.

Genus: *Osmunda* Linneaus

Subgenus: *Osmunda* Linneaus

Osmunda oregonensis (Arnold) comb. nov., C. N. Miller

(Pl. I, Fig. 5)

Osmundites oregonensis Arnold. 1945, pp. 5–7, Pl. I, Figs. 1–2.

Diagnosis.—Dichotomously branched stems surrounded by a thick mantle of leaf bases and adventitious roots. Stems about 10 mm. in diameter; pith about 0.5 mm. in diameter, decomposed, tissue construction unknown; xylem cylinder about 0.5–1.0 thick, decomposed, estimated to consist of about 16–20 strands; leaf-trace with one endarch protoxylem which bifurcates as leaf-trace passes through inner cortex; inner cortex parenchymatous, 0.5–1.0 mm. thick, containing 0–2 leaf-traces in a given transverse section; outer cortex fibrous, 2.0–4.5 mm. thick, containing about 15 leaf-traces in a given transverse section; leaf-bases stipular, containing a C-shaped vascular strand; single mass of thick-walled fibers in concavity of petiolar bundle near point of attachment to stem, extending upward as band lining concavity; abaxial arch of thick-walled fibers in sclerenchyma ring of petiole occurring throughout stipular region, bifurcating just above stipular region to form two lateral masses; inner cortex of petiole base containing numerous, small clusters of thick-walled fibers scattered throughout; stipular expansions containing an elongate strip of thick-walled fibers and several small clusters of thick-walled fibers in linear series between the strip and the tip of the expansion.

Locality and Horizon.—Crook County, Oregon; Upper Eocene, Clarno Formation.

Holotype.—UMMP 23389.

Discussion.—*Osmunda oregonensis* is similar to *O. pluma* in all important respects and differs from the Paleocene species mainly in being larger (Table 1). An arch of thick-walled fibers occupies the abaxial sector of the sclerenchyma ring throughout the length of the stipular region in both species. In *O. oregonensis,* as in *O. pluma,* this arch becomes divided just above the stipular region forming two lateral strands (Pl. I, Fig. 5). Furthermore, the method of formation of the leaf-trace is similar in the two species, and bifurcation of the leaf-trace protoxylem occurs at about the same location in the stems of both forms.

Rhizomes of *O. oregonensis* are generally larger than those of *O. pluma.* They have more strands of stem xylem and a higher number of leaf-traces in transverse sections of the cortices. The angle between the stem xylem and the departing leaf-trace in *O. oregonensis* is 25°–30° while this angle is 5°–10° in *O. pluma.* Furthermore, in stipular expansions of *O. pluma* there are many small strands of sclerenchyma between the elongate strip and the sclerenchyma ring, while such strands are lacking in *O. oregonensis.* Thus, *O. oregonensis* and *O. pluma* are separate species; but because of their over-all similarity, the reasons for allying *O. pluma* to the subgenus *Osmunda* also apply to *O. oregonensis.* The two species are close geologically and geographically, and it is evident that they exist on the same phylogenetic line.

Genus: *Osmunda* Linneaus
Subgenus: *Osmunda* Linneaus
Osmunda iliaensis nom. nov., C. N. Miller

Osmundites schemnicensis (Pettko) Unger. 1954, p. 1, Pl. I.
Asterochlaena schemnicensis Pettko. 1849, p. 163, Pl. 20, Figs. 1–10.

Diagnosis.—Stems surrounded by a thick mantle of petiole bases and adventitious roots. Stems about 11.0 mm. in diameter; stele an ectophloic-dictyoxylic siphonostele 4.0 mm. in diameter; pith about 1.0 mm. in diameter, consisting entirely of parenchyma; xylem cylinder about 1.0 mm. thick, consisting of 17–18 strands in a given transverse section; leaf-trace with one endarch protoxylem which bifurcates as leaf-trace enters inner part of outer cortex; inner cortex parenchymatous, 0.5–0.7 mm. thick, and including 2–5 leaf traces in a given transverse section; outer cortex fibrous, 1.0–3.5 mm. thick, including 13–15 leaf traces in a given transverse section; single mass of thick-walled fibers in concavity of petiolar bundle, extending upward to form a band lining concavity; abaxial arch of thick-walled fibers occurring in sclerenchyma ring of petiole bases; inner cortex of petiole base consisting entirely of parenchyma; stipular expansions containing an elongate strip of thick-walled fibers and numerous small clusters of thick-walled fibers, some between the strip and the tip of the expansion but most concentrated near the sclerenchyma ring.

Locality and Horizon.—Illia, near Schemnitz, Hungary; at or near contact of Miocene and Pliocene.

Holotype.—Present location unknown; neotype in Kidston Collection, Department of Botany, University of Glasgow, Scotland.

Discussion.—This species was first named *Asterochlaena schemnicensis* by Pettko (1850), but Unger (1854) recognized its relationship to the Osmundaceae and created *Osmundites* to receive it. He was apparently ignorant of the prior use of this name by Jaeger (1827) for misidentified cycadophyte foliage. Material of this species in the Kidston Collection does not include preparations of the holotype; but Kidston and Gwynne-Vaughan (1910) mention that their specimens came from Pettko's locality, and their fossils agree with his and Unger's figures and descriptions. The sclerenchyma rings of many petiole bases appear homogeneous, because of peculiar preservation (Kidston and Gwynne-Vaughan, 1910), but a few petiole bases show a distinct arch of thick-walled fibers making up the adaxial semicircle of the ring (Kidston and Gwynne-Vaughan, 1910, Pl.

III, Fig. 22). As observed in transverse sections of the mantle the arch occurs both in petiole bases near the stem which represent a position near the base of a given petiole, and near the periphery, which represent a position near the top of the stipular region of a given petiole base. The tissue was presumably continuous between these two positions. Leaf-traces of this species separate from the stem xylem bearing a single endarch protoxylem which bifurcates as the leaf-trace passes through the inner part of the outer cortex. The arrangement of sclerenchyma tissues in stipular expansions of this species is like that in *O. regalis,* but the presence of numerous small strands of fibers between the elongate strip and the sclerenchyma ring suggests a closer relationship of *O. iliaensis* to *O. japonica.*

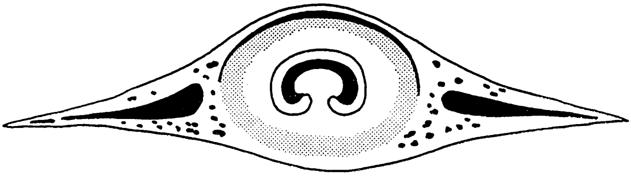

FIG. 3. *Osmunda iliaensis* nom. nov., transverse section of stipular petiole base showing sclerenchyma arrangement; thin-walled fibers, gray; thick-walled fibers, black; modified from Kidston and Gwynne-Vaughan, 1910, p. 463, by permission of the Royal Society of Edinburgh.

The petrified rhizomes are treated under a *nomen novum* because the binomial *Osmunda schemnicensis* is preoccupied by foliage impressions described by Stur (1857) from the type locality of the stems. While these pinnules are similar to those of *O. regalis* and *O. japonica* and probably represent foliage of *O. iliaensis,* proof of organic attachment to the rhizomes is lacking, and the two organs must be treated as separate species.

Genus: *Osmunda* Linneaus

Subgenus: *Osmunda* Linneaus

Osmunda nathorstii sp. nov., C. N. Miller

(Fig. 4)

Osmundites spetsbergensis (Nathorst) Kidston and Gwynne-Vaughan. 1914, pp. 469–474, Pls. XLI–XLIII, Text-figs. 1 and 2 (*in part*).

Osmunda spetsbergensi Nathorst. 1910, p. 382 (*in part*).

Diagnosis.—Portion of mantle of petrified petiole bases, stem and remainder of mantle missing; petiole bases stipular, each containing a reniform to C-shaped vascular strand with endarch xylem; vascular strands of innermost petiole bases of mantle with one protoxylem, number of protoxylems increasing in outer petiole bases; stipular expansions containing elongate strip of thick-walled fibers; sclerenchyma rings of some petiole bases with two lateral masses of thick-walled fibers; thick-walled sclerenchyma also forming one or two rounded masses in concavity of vascular stand and a few scattered clusters in the inner cortex of the petiole base.

Locality and Horizon.—Spitzbergen; Tertiary, horizon No. 6 of Nathorst (1910).

Holotype.—Specimen in the Geology Annex, British Museum (Natural History), London, England; preparation in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

Discussion.—This new species is based on part of a mantle of leaf-bases that is presently included under *Osmundites spetsbergensis* (Nathorst) Kidston and Gwynne-Vaughan but which was originally treated as *Osmunda spetsbergensis* Nathorst. The specimen containing the petiole bases is one of several pieces of peaty material that were collected from two localities in Spitzbergen by members of two expeditions (Kidston and Gwynne-Vaughan, 1914). Exactly where and by whom the specimen containing the leaf bases was found is not known. Most of the specimens bear surface impressions of fern pinnules similar to those of *O. regalis* (Kidston and Gwynne-Vaughan, 1914, Text-Fig. 2), and these fossils no doubt prompted Nathorst (1910) to include the material in the genus *Osmunda.* When Kidston and Gwynne-Vaughan sectioned the specimen containing the petiole bases, they found, in addition, several layers of foliage, isolated sporangia, and solenostelic rhizomes of a fern they tentatively named *Solenostelopteris radiculata.* Except for the latter, they were able to demonstrate the osmundaceous affinity of these organs and assumed that they belonged to the same species whose foliage appears as surface impressions. While this foliage clearly resembles that of *O. regalis,* Kidston and Gwynne-Vaughan believed the petiole bases to be more similar to those of *O. claytoniana.* Lacking a stem for additional characters and unable to resolve the inconsistency between the foliage and petiole bases, they treated all osmundaceous organs under the binomial *Osmundites spetsbergensis* (Nathorst).

The assumption that all these organs belong to the same species is untenable because there is no organic attachment between them. It is not unusual to find plants of *O. regalis* and *O. claytoniana* growing near one another today, and fossil ancestors of these two species could have grown in sufficient proximity to have contributed remains to the same basin of deposition, thereby accounting for the inconsistency in the Spitzbergen material. Thus, each organ must be considered separately.

While the pinnule impressions are referable to the subgenus *Osmunda* under the original binomial O. *spetsbergensis* Nathorst, the morphology and thus the subgeneric relationship of the foliage preserved within the matrix is unknown. The isolated sporangia can only be assigned with accuracy to the family (Hewitson, 1962). While affinities of *Solenostelopteris radiculata* are not in question here, a reinvestigation of these rhizomes in light of the description of *Dennsteadtiopsis aerenchymata* by Arnold and Daugherty (1964) might lead to a clarification of the affinities of this Spitzbergen fern.

Despite the poor preservation of the mantle of petiole bases, Kidston and Gwynne-Vaughan (1914) were able to describe the major structural features of this fossil. Each stipular expansion contains a tissue of fibers which appears as a triangular mass in sections near the base of the petiole but which at higher levels forms an elongate strip that extends from a point near the sclerenchyma ring almost to the margin of the wing. A single mass of fibers occurs basally in the concavity of the vascular strand and bifurcates upward to produce two groups above, one against each recurved tip of the petiolar strand. In addition, a few small clusters of thick-walled fibers are scattered in the inner cortex of the petiole base (Fig. 4).

The most striking feature of the fossil is the occurrence of two lateral masses of thick-walled fibers in the sclerenchyma ring. Kidston and Gwynne-Vaughan (1914) mention that the ring is homogeneous at the base of the petiole and that the masses of specialized fibers appear at higher levels. However, the mantle is poorly preserved, and the construction of the basal part of the sclerenchyma ring may have been altered by decay prior to preservation. It is nonetheless clear that the mantle belongs to the subgenus *Osmunda* because of the known species of the Osmundaceae only those of this subgenus have two lateral masses of thick-walled fibers in the sclerenchyma ring.

The affinities of the fossil within this subgenus are more problematic. The two masses of thick-walled fibers in the sclerenchyma ring of *O. pluma* and *O. oregonensis* occur only at levels that are slightly above the stipular

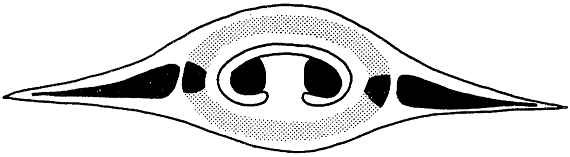

FIG. 4. *Osmunda nathorstii* sp. nov., transverse section of stipular petiole base showing sclerenchyma arrangement; thin-walled fibers, gray; thick-walled fibers, black; modified from Kidston and Gwynne-Vaughan, 1914, p. 471, by permission of the Royal Society of Edinburgh.

region, and in *O. iliaensis* no such specialized masses have been observed. In *O. regalis, O. japonica, O. claytoniana,* and *O. lancea,* however, the two masses of thick-walled fibers do occur within the stipular region, and all of these living species except for the latter also have an elongate strip of thick-walled fibers in their stipular expansions.

In the Spitzbergen fossil the petiolar strand has only one protoxylem at its base. This feature indicates that *O. nathorstii* is more closely related to *O. claytoniana,* the only species of the subgenus which is similar in this respect. In *O. regalis* and *O. japonica* the protoxylem bifurcates in the stem, so petioles of the species have at least two protoxylems in their vascular strands. The fossil differs from *O. claytoniana* in apparently lacking the abaxial arch of thick-walled fibers in the sclerenchyma ring near the base of the petiole. Furthermore, in the concavity of the petiolar strand *O. claytoniana* has an elongate strip of fibers while *O. nathorstii* has two groups of these cells, and there are fewer strands of fibers in the inner cortex of the petiole in *O. nathorstii* than in *O. claytoniana.* For these reasons, the sheath of petiole bases is treated as representing a species that is similar to but separate from *O. claytoniana,* and the association of *O. spetsbergensis* foliage, which is like that of *O. regalis,* further supports that distinction.

Phylogeny of the subgenus *Osmunda*

The fossil species of the subgenus *Osmunda* provides a series of known points on the lines of development leading to the living species. While no species-by-species evolution of the living representatives from fossil ancestors can be demonstrated at this time, it is evident that these present-day ferns are the products of two lines of specialization, one a divergent branch of the other. The development of *O. regalis, O. japonica,* and *O. lancea* through *O. iliaensis, O. oregonensis,* and *O. pluma* represents the main phylogenetic line within the subgenus, while the divergent branch is indicated by *O. claytoniana* and *O. nathorstii.* It should be kept in mind that the fossil record of the subgenus is far from complete. Other similar species, as yet undiscovered, probably existed contemporaneously with the known forms.

Stelar characters in members of *Osmunda* have remained basically the same throughout the recorded history of the subgenus, but the phylogenetic lines are well indicated by changes in the arrangement of petiolar sclerenchyma and differences in the point of first branching of the leaf-trace protoxylem. The line involving *O. regalis, O. japonica, O. lancea, O. iliaensis, O. oregonensis,* and *O. pluma* is characterized by the initial bifurcation of the leaf-trace protoxylem in the cortex of the stem, while in *O. claytoni-*

ana and *O. nathorstii* this branching first occurs in the base of the petiole.

Differences in the arrangement of petiolar sclerenchyma agree with the trends indicated by protoxylem ramification and also suggest a possible point of divergence of the *O. claytoniana* line of specialization. In both *O. pluma* and *O. oregonensis* the arch of thick-walled fibers in the abaxial part of the sclerenchyma ring continues upward from the base of the petiole to a point just above the stipular region where it bifurcates to form two lateral masses. The condition in *O. iliaensis* is somewhat uncertain because an abaxial arch of thick-walled fibers has only been observed in the basal and distal part of the stipular region but probably the arrangement of this tissue was similar to that in *O. oregonensis* and *O. pluma.* If bifurcation of the arch did occur in *O. iliaensis,* it must have been in the upper part of the stipular region or just above it. In *O. claytoniana,* and presumably also in *O. nathorstii,* the arch forks in the lower one-half of the stipular region with the resulting two lateral masses of thick-walled fibers extending upward throughout the remaining length of the winged part of the petiole base. In *O. regalis, O. japonica,* and *O. lancea* bifurcation of the arch of thick-walled fibers similarly occurs in the lower one-half of the stipular region; but the two lateral clusters extend around the adaxial side of the sclerenchyma ring forming an inconspicuous band of thick-walled fibers, and this narrow strip of tissue then extends upward throughout the remaining length of the stipular region as the only indication of the thick-walled tissue.

Thus, *O. pluma* and *O. oregonensis* represent ancestors from which both the *O. claytoniana* line and the *O. regalis* line developed. Most likely, the *O. claytoniana* line diverged from the *O. regalis* line in Late Teriary from a form similar to *O. iliaensis.* The latter species is slightly divergent in having bifurcation of the leaf-trace protoxylem in inner part of the outer cortex while the other species of the *O. regalis* line have the forking in the inner cortex. Thus, *O. iliaensis* is somewhat closer to *O. claytoniana* in this respect, but it is more like *O. regalis* in other features.

Many species of compressed foliage from the Cretaceous and Tertiary have been assigned to the subgenus *Osmunda,* but some of them may have been borne by non-osmundaceous ferns. The form and venation of pinnules of *O. regalis, O. japonica,* and *O. lancea* are general and occur in whole or in part in many other ferns. Pinnules of *Llavea cordifolia* Lag., *Plagiogyria japonica* Nakai, *Polybotrya appendiculata* (Willd.) Bl., or *Polystichum juglandifolium* (H.B.K.) Diels are quite similar to those borne by members of the subgenus *Osmunda,* and pinnae lobes of *Matonia* and *Lygodium* have the same form and venation as the pinnule tips of the aforementioned osmundaceous ferns. Any of these other ferns could be mistaken for a species of the subgenus *Osmunda* if only fragments of the foliage were preserved.

On the other hand, a number of fossil pinnules bear a convincing similarity to those of *O. regalis, O. japonica,* and *O. lancea* (Table I). Most important of these are: *O. petiolata* Heer, from the Lower Cretaceous of Greenland; *O. asuwensis* Matsuo, from the Upper Cretaceous of Japan; *O. montanensis* Knowlton, from the Upper Cretaceous of the northern Rocky Mountain states, and *O. oebergiana* Heer, from the Upper Cretaceous of Greenland and the Potomac Formation of the eastern United States. The species provide ample evidence of the presence of the subgenus *Osmunda* in the Cretaceous. Furthermore, these pinnule compressions display the two dominant conditions that occur in the Tertiary and Recent species. *O. asuwensis, O. oebergiana,* and the majority of the other species are sessile as are pinnules of *O. regalis* and *O. japonica,* while *O. petiolata* and *O. montanensis* are attached to the rachis by a distince petiole as are pinnules of *O. lancea.* The size of the pinnules varies from species to species, but their form and venation do not differ significantly from that displayed by the living species. Thus, while foliage is generally regarded as one of the most plastic of all organs subject to profound modification by paleoecologic conditions, that of the subgenus *Osmunda* has been stable since Early Cretaceous time.

Although the subgenus can be traced back to the Early Cretaceous, its origin is not clear. There is a possibility affinity of the group with *Osmundacaulis kidstoni* (Stopes), which like the species of *Osmunda* has a distinct arch of thick-walled fibers in the abaxial part of the sclerenchyma ring of the petiole base. This fossil comes from Queensland, and its age was designated as "probably Cretaceous" (Stopes, 1921). Stopes (1921) thought that its stem, which contains a protostele with secondary xylem represented the "missing link in Osmundites" as was postulated by Kidston and Gwynne-Vaughan (1910). However, Posthumus (1924) demonstrated that the stele was in fact a foreign axis which had grown into the cavity left by the decay of the fern stem. Since then little importance has been attached to the remains. Edwards (1933) mentions that the pattern of stipular sclerenchyma in this fern is similar to that in *Osmundacaulis dunlopi* and suggested a Jurassic age for *O. kidstoni* on that basis. However, the resemblance is superficial, and comparison with the arrangement of these tissues with those in *Osmunda lancea* would have been more accurate since petiole bases of both these species have an abaxial arch of thick-walled fibers in the sclerenchyma ring. The arch in *Osmundacaulis* *kidstoni* is well defined by its dark color in the outer petiole bases of the mantle; but petiole bases at the inner edge of the mantle appear to have homogeneous rings of sclerenchyma. These petiole bases are oblique to the plane of section, so the cell wall thickness of the fibers cannot be accurately determined. For this reason and because there is no information about the structure of the stem, the species was not assigned to the subgenus *Osmunda*. Other than the similarity of the arch in *Osmundacaulis kidstoni* to that in species of *Osmunda*, there is no indication of the origin of this subgenus.

TABLE I.

Fossil Foliage of the Subgenus Osmunda

Mesozoic:

Osmunda asuwensis Matsuo. 1962. Science Reports of the Kanazawa Univ., Vol. XIII, No. 1. Late Cretaceous, Japan.

Osmunda haldemiana Hosius and V. D.Marck. 1880. Palaeontographica XXVI, 5, 6, p. 140 (16), pl. 25, f. 18. Cretaceous, Germany.

Osmunda hollicki Knowlton. 1917. U.S.G.S. Prof. Pap. 101, p. 246, pl. 30, f. 6. Cretaceous, Colorado.

Osmunda major Lesquereux. 1883. Rept. U. S. Geol. Surv. Terr. VIII, Cret. and Tert. Fl., p. 121, t. 18, f. 5. Upper Cretaceous, Colorado.

Osmunda montanensis Knowlton. 1905. U.S.G.S. Bull. 257, p. 129, pl. 14, f. 6. Upper Cretaceous, Montana.

Osmunda petiolata Heer. 1874. Flora foss. arctica, III, 2, Kgl. Sv. Vet. Ak. Handl., XII, 6, p. 57, t. 3, f. 1c, 2b. Lower Cretaceous, Greenland.

Osmunda oebergiana Heer. 1874. Flora foss. arctica, III. p2, Kgl. Sv. Vet. Ak. Handl., XII, 6, p. 98, t. 26, f. 9, 9b; t. 32, f. 7a. Upper Cretaceous, Greenland, also U. S. A.

Cenozoic:

Osmunda affinis Lesquereux. 1878. Tertiary Flora, Hayden's Rept. U. S. Geol. Surv. Terr., VII, p. 60, t. 4, f. 1. Miocene, Western U. S. A.

Osmunda bilinica (Ettingshausen) Saporta and Marion. Bull. Soc. Geol., (3) II, p. 278, Pliocene, Germany.

Osmunda doroschkiana Goeppert. 1861. Tertiärfl. d. Polargegenden, p. 457. Oligocene ?, Alaska.

Osmunda macrophylla Penhallow. 1907. Trans. Roy. Soc. Canada, 3d. Series I, p. 332. Paleocene, Alberta.

Osmunda occidentalis Brown. 1940. Jour. Wash. Acad. Sci. XXX, p. 344, f. 1. Oligocene, Western U. S. A.

Osmunda regalis var. ? Endo. 1961. Trans. Proc. Palaeont. Soc. Japan, N.S., No. 44, pp. 157–160, f. 2, 3. Eocene, Japan.

Osmunda schemnicensis Stur. 1867. Jahrb. d. K. K. geol. Reichsanst. vol. XVII., p. 136, pl. iii, figs. 1–3.

Osmunda spetsbergensis Nathorst. 1910. Bull. Geol. Instit. Upsala, Vol. X, p. 382. Upper Tertiary, Spitzbergen.

Osmunda strozzii Gaudin and Strozzi. 1862. Contr. a la flora fossile italienne, VI, p. 9, t. 1, f. 1–4. Miocene and Pliocene, Europe.

TABLE II.

SALIENT FEATURES OF RHIZOMES OF THE SUBGENUS *Osmunda*

	O. regalis	*O. japonica*	*O. lancea*	*O. claytoniana*	*O. nathorstii*	*O. iliaensis*	*O. oregonensis*	*O. pluma*
Age:	Recent	Recent	Recent	Recent	Late Tertiary	Miocene-Pliocene	Eocene	Paleocene
Number of strands of stem xylem in an X-section:	4–11*	4–11*	6–8*	7–16*	not preserved	17–18	16–20	7–12
Number of leaf-traces in an X-section of the cortex:								
Inner cortex:	2–3*	2–4*	1–5*	4–7*	not preserved	2–5	0–2	1–3
Outer cortex:	5–11*	5–11*	11–15*	7–15*		13–15	15	6–10
Point of basal forking of leaf-trace protoxylem:	Inner Cortex	Inner Cortex	Inner Cortex	Petiole Base	Petiole Base	Outer Cortex	Inner Cortex	Inner Cortex
Nature of thick-walled fibers in sclerenchyma ring of petiole base at positions indicated below:								
Point of attachment of petiole to stem:	Abaxial Arch	Abaxial Arch	Abaxial Arch	Abaxial Arch	Unknown	Abaxial Arch	Abaxial Arch	Arch Abaxial
Slightly above point of attachment of petiole to stem:	Lateral Masses	Lateral Masses	Lateral Masses	Lateral Masses	Unknown	Unknown	Abaxial Arch	Arch Abaxial
Midway between point of attachment and top of stipular region:	Adaxial Strip	Adaxial Strip	Adaxial Strip	Lateral Masses	Lateral Masses	Unknown	Abaxial Arch	Abaxial Arch
Top of stipular region:	Adaxial Strip	Adaxial Strip	Adaxial Strip	Lateral Masses	Unknown	Abaxial Arch	Abaxial Arch	Abaxial Arch
Just above stipular region:	Adaxial Strip	Adaxial Strip	Adaxial Strip	Lateral Masses	Unknown	Unknown	Lateral Masses	Lateral Masses

* Data from Hewitson (1962) confirmed by my investigation.

Genus: *Osmunda*
Subgenus: *Osmundastrum*
Living Species

With *Osmunda claytoniana* treated in the subgenus *Osmunda, O. cinnamomea* remains as the only living member of the subgenus *Osmundastrum.* This fern has once-pinnate vegetative fronds with pinnatifid pinnae. Fertile fronds consist entirely of specialized pinnae that lack a lamina. Reddish-brown hairs occur on both sterile and fertile fronds and give this species its common name, the Cinnamon Fern.

O. cinnamomea is distinguished anatomically from another living member of the family by two characters which are unique to this species, the occurrence of three masses of thick-walled fibers in the sclerenchyma ring of the petiole base and the nearly constant presence in the stele of an internal endodermis. Internal phloem is also produced in this species, but it is restricted to branching regions of certain stems. A third important character, a strand of thick-walled fibers axillary to each leaf-trace in the inner cortex of the stem, is shared by one other species, *Todea barbara* (L.) Moore.

Osmunda cinnamomea L., Fossil Rhizomes
(Pl. II, Figs. 1–2)

Introduction.—The occurrence of *O. cinnamomea* in the Late Tertiary flora of central Washington is established by two fossil rhizomes which are in the collection of the Museum of Paleontology of The University of Michigan. Precise collection data is lacking, but they were labeled by their contributor, Mrs. Sam Kirkby of Riverside, California, as coming from the vicinity of Yakima, Washington. Pleistocene glacial deposits and volcanic sediments from the Eocene and Oligocene occur locally within a 40-mile radius of this city, but volcanic sediments from the Miocene and Miocene-Pliocene dominate the region, and the fossils are assumed to have come from these strata.

Although both specimens were silicified, the result was quite different. One rhizome is typically embedded in a siliceous block, while the other had eroded from its matrix becoming almost completely decorticated in the process. This fossil consists mostly of a naked stele with leaf- and root-traces projecting from its surface. (Pl. II, Fig. 2). Cortical tissues and petiole bases remain only around the lower part of the axis and they only encircle half the stele. Since this specimen was too fragile to be placed in the vise of a saw, it was embedded in a rectangular block of Turtox "Bioplastic," after which the plastic and the fossil were sawed and ground into petrologic sections in the usual manner.

Preservation of thin-walled tissues in both rhizomes is poor. Only xylem remains in the stele of the fully embedded specimen; all other tissues had been replaced by mineral matter. Similar crystalline material adheres to the cell walls of the central tissues in the decorticated fossil obscuring much of their detail. However, all features observed in these rhizomes indicate that they are fossil representatives of *O. cinnamomea.* Since the anatomy of this species is described in detail elsewhere in the literature (Faull, 1901, 1910; Hewitson, 1962), description of the fossils is restricted to their more general features.

Description.—The stems are 7–12 mm. in diameter. The xylem cylinder, which is about 3.0 mm. in diameter and 1.0 mm. thick, is divided by leaf-gaps into 12–14 strands in transverse section each of which is surrounded by a distinct sheath of parenchyma. The pith is 0.5–1.0 mm. in diameter and consists of parenchyma cells though mineral matter adhering to the cell walls gives them the appearance of stone cells. Sieve cells form a continuous layer of phloem around the xylem cylinder, but they are more concentrated opposite leaf-gaps and extend for a short distance between adjacent xylem strands. Several layers of small, tabular cells outside the phloem represent the protophloem, porose layer, and pericycle. The endodermis, which would be expected to occur just outside the pericycle, cannot be located. Mineral matter obscures the cell wall morphology making it impossible to distinguish Casparian strips, and there is no color differentiation to aid in the location of this tissue. For the same reason, no internal endodermis is visible between the pith and the xylem cylinder, nor can endodermal cylinders be seen around each leaf- and root-trace. No doubt, endodermal tissues occurred at least around the stele and root- and leaf-traces during the life of the plants, but the state of preservation does not allow their identification.

The cortex is differentiated into an inner layer of parenchyma cells that is 0.5–1.5 mm. thick, and an outer layer of fibers that is 0.5–3.0 mm. thick. Six to nine leaf-traces occur in the inner cortex in a given transverse section, and axillary to each leaf-trace is an oblong cluster of thick-walled fibers. This mass of fibers merges upward with and is replaced by thin-walled fibers of the outer cortex as its associated leaf-trace enters this tissue. The outer cortex as its associated leaf-trace enters this tissue. The outer cortex includes 9–12 leaf-traces in a given transverse section.

A leaf-gap occurs in the xylem cylinder immediately opposite each leaf-trace. Formation of a leaf-trace, as observed in a series of transverse sections, is first noted by the appearance of a small cluster of mesarch protoxylem elements within an oval metaxylem strand. A small group of parenchyma cells forms immediately adaxial to the protoxylem, enlarges toward the pith in higher sections, and finally connects with parenchyma cells of the xylem sheath bordering the pith. The xylem strand at this level appears U-shaped with the endarch protoxylem in medial position on the concave surface. The curved portion of the xylem strand then breaks away as the xylem of the leaf-trace. While there is slight enlargement of the leaf-trace as it passes through the cortex, it retains its reniform shape until it enters the base of the petiole. At this location, the curvature of the xylem increases, its protoxylem bifurcates, and the vascular strand of the petiole becomes C-shaped.

The xylem of a root diverges from the xylem of a leaf-trace just below the point of attachment of the latter to the stem xylem. As the root-trace passes through the cortical layers, it gains encircling layers of these tissues. The xylem strand of the root is diarch; but since no roots were preserved outside the stem in either specimen, the relative proportion of inner cortex to outer cortex in mature roots is unknown.

Petiole bases of the fossil *O. cinnamomea* rhizomes are stipular and contain sclerenchyma tissues that are arranged as they are in petiole bases of living plants of this species. Near the point of attachment of the petiole to the stem, the stipular expansions are short and each contains a rounded mass of thick-walled fibers. The three clusters of thick-walled fibers in the sclerenchyma ring that are characteristic of *O. cinnamomea* are visible in the petiole base as it becomes separate from the stem, and they occur throughout the length of the stipular region. At levels where the vascular strand is somewhat curved a single group of fibers forms adaxial to it. More distant from the stem the vascular strand is C-shaped, and two masses of fibers occur in the concavity, one against each recurved tip of the strand. At this level there are additional small clusters of thick-walled fibers in the stipular expansions between the rounded mass and the tip of the wing. The resulting pattern is, for all practical purposes, identical to the arrangement of tissues in petiole bases of Recent plants as figured by Kidston and Gwynne-Vaughan (1907) and Hewitson (1962).

Discussion.—The arrangement of sclerenchyma tissues in the petiole bases and the clusters of fibers associated with leaf-traces in the fossils are characters which provide sufficient evidence for the classification of the specimens with *O. cinnamomea.* The latter character occurs only in *O. cinnamomea* and *Todea barbara,* while the former condition is unique to *O. cinnamomea.*

It is unfortunate that the presence or absence of endodermal tissues cannot be established. An internal endodermis in the fossils would provide additional support to the classification, for this species is the only living member of the Osmundaceae to regularly produce such a tissue (Hewitson, 1962). On the other hand, the absence of an internal endodermis in the fossils is not necessarily detrimental to the diagnosis because a stem of *O. cinnamomea* lacking this tissue was reported by Hewitson (1962). All of the 150 plants of *O. cinnamomea* included in Faull's (1901) study had an internal endodermis, but the morphology of the tissue is variable. In some cases the internal endodermis forms a regular cylinder at the periphery of the pith; in other cases it is irregular, extending for a short distance into leaf-gaps; and in still other cases, the internal endodermis connects with the external endodermis through certain leaf-gaps breaking the stele into "vascular units." Internal phloem occurs in some stems but is restricted to the branching region and usually vanishes once bifurcation of the axis is complete (Hewitson, 1962). Connection of the internal and external endodermal cylinders in some stems of this species has led to the misconception that they are dictyostelic. According to strict definition (Esau, 1953), dictyostely requires that internal and external phloem cylinders connect through leaf-gaps dividing the vascular cylinder into a series of concentric vascular units. There are no reports of this condition in *O. cinnamomea.* The vascular cylinder of these stems is nonetheless dissected, and it is best to describe the tissue arrangement as a "dissected ectophloic or amphiphloic siphonostele" depending on the presence or absence of internal phloem.

The variability of the stele of *O. cinnamomea* suggests that the origin of the internal endodermis was recent, and that a constant state has not yet evolved. The Paleocene fossils treated next have bearing on this question, so further discussion is deferred until after their description.

SYSTEMATIC DESCRIPTION

Family: Osmundaceae
Genus: *Osmunda* Linneaus
Subgenus: *Osmundastrum* Presl
Osmunda precinnamomea sp. nov., C. N. Miller
(Fig. 5; Pl. III, Figs. 1–3)

Diagnosis.—Petrified rhizomes about 1.8–2.0 in diameter, consisting of a stem about 6.0 mm. in diameter surrounded by a mantle of closely adhering petiole bases; xylem cylinder of stem about 1.5 mm. in diameter, 0.5 mm., and consisting of 3–7 strands as observed in transverse section;

leaf-gaps high and narrow, formed immediately opposite each departing leaf-trace; phloem a continuous cylinder around the xylem; endodermis external only; cortex consisting of a thin inner parenchymatous zone and a thick outer fibrous zone, together including 11–13 leaf-traces in a given transverse section; leaf-trace endarch, separating from the stem xylem with a single protoxylem which bifurcates as leaf-trace enters petiole base; strand of thick-walled fibers axillary to leaf-trace in inner cortex of stem; petiole base stipular, sclerenchyma ring containing one abaxial and two lateral clusters of thick-walled fibers in each stipular expansion, inner cortex of petiole base containing many small clusters of fibers; roots with diarch xylem strand, diverging from leaf-trace as latter separates from stem xylem.

Locality and Horizon.—Morton County, North Dakota; Paleocene, Fort Union Formation.

Holotype.—UMMP 52159.

Introduction.—This new species is based on three specimens which were collected by Mrs. Spiss at the Paleocene locality in Morton County, North Dakota. The ring of sclerenchyma around the vascular strand in petiole bases of these fossils is like that in *O. cinnamomea,* but the arrangement of sclerenchyma tissues in the stipular expansions and inner cortex of the petiole bases in the Paleocene material is more complex than that in the Recent species. Thus, the fossils are considered representatives of a species that is separate from, but ancestral to, *O. cinnamomea.*

The stem of *O. precinnamomea* is about 6.0 mm. in diameter and consists of an ectophloic, dictyoxylic siphonostele surrounded by a thick cortex (Pl. III, Fig. 1). The stele has a central pith of parenchyma cells, 3–7 strands of xylem arranged in a ring around the pith, and layers of phloem, porose cells, and pericycle respectively surrounding the xylem cylinder. A distinct endodermis encircles the stele, but there is no indication of such a tissue between the pith and the xylem (Pl. III, Fig. 2). The cortex consists of an inner parenchymatous zone and an outer fibrous zone which together contain 11–13 departing leaf-traces in a given transverse section. A leaf-gap occurs in the xylem cylinder immediately opposite the point of separation of each leaf-trace. The xylem of the leaf-trace is an endarch strand that is oblong and slightly concave on the adaxial side. A single cluster of protoxylem elements occurs in medial position on the concave surface and continues with the leaf-trace into the base of the petiole where it bifurcates. The petiole bases are stipular; and the arrangement of sclerenchyma tissues in them is like that in *O. cinnamomea,* but the fossils have, in addition, small clusters of fibers in the inner cortex of the petiole base.

Stem.—The pith is 0.5 mm. in diameter and consists entirely of parenchyma cells that are 25–70 microns in diameter and 110–165 microns in length. The walls of these cells are 1–2 microns thick and show no pitting. There is only slight decrease in cell size at the periphery of the pith; large and small cells are mixed throughout, but a few more of the smaller diameter cells occur near the xylem sheath.

The xylem sheath consists of parenchyma and is only 1–2 cells thick between the pith and the xylem, but the tissue extends through leaf-gaps and forms a layer 2–3 cells thick between the xylem and phloem. The cells that make up this tissue are about as long as the pith cells (130 microns average) and are 15–27 microns in diameter. They are thin-walled and do not exhibit pitting.

The xylem cylinder is about 1.5 mm. in diameter and about 0.5 mm. thick. It is made up of 3–7 strands in transverse section each of which is about 10 tracheids in radial depth. The metaxylem tracheids are 25–60 microns in diameter and have one to four, but mostly two, vertical series of scalariform pits on each wall. Protoxylem tracheids, which are 10–25 microns in diameter and have only one vertical series of scalariform pits on each wall, appear within metaxylem strands that are below leaf-gaps. Such strands are initially mesarch but become endarch closer to the point of divergence of a leaf-trace.

A continuous layer of phloem surrounds the xylem cylinder. The sieve cells are 20–45 microns in diameter and have thin-walls. Most of them show the effects of crushing, and no sieve areas can be distinguished. The tissue is 2–3 cells thick for the most part, but sieve cells are more concentrated opposite xylic gaps where they extend for a short distance between adjacent xylem strands.

The protophloem, porose layer, and pericycle are represented by a cylinder of flattened cells two to three cells thick outside the metaphloem. The tissues are preserved only in places, and it is impossible to distinguish between them. Each tissue probably formed a continuous cylinder in the living condition.

Outside the pericycle is an endodermis. The tissue is one or two cells thick and forms a complete ring around the stele. The endodermal cells are darker than cells of tissues to either side; and they are more oval than the flattened cells of the pericycle and smaller than the cells of the inner cortex. While the radial dot characteristic of endodermal cells is not visible, the aforementioned characters are sufficient to demonstrate the presence of the endodermis in these fossils. No such tissue occurs between the pith and the xylem (Pl. III, Fig. 2).

The inner cortex is made up of parenchyma cells that are 30–60 microns in diameter and 65–100 microns long. The cell walls are 1–2 microns thick and show no pitting. The cells are oval in transverse section making up a loose tissue with wide intercellular spaces. The inner cortex may contain 4–5 departing leaf-traces in a given transverse section; and, because of the presence of these traces, the tissue varies in thickness from 0.25–0.75 mm. As in *O. cinnamomea* an oblong cluster of thick-walled fibers occurs axillary to each leaf-trace in the inner cortex. It connects with, and is eventually replaced by, thin-walled fibers of the outer cortex as the leaf-trace enters this tissue.

The outer cortex consists of fibers whose walls are 5–8 microns thick. These cells are 10–50 microns in diameter, the smaller measurements representing the pointed ends of cells lying above and below the plane of section. The fibers are polygonal in cross-sectional outline and fit together tightly forming a dense tissue without intercellular spaces. The outer cortex includes 6–9 leaf-traces in a given transverse section and is 0.75–1.5 mm thick.

Leaf-trace.—Formation of the leaf-trace in *O. precinnamomea* follows the same sequence of changes as in *O. pluma* (Fig. 2). In the lowermost of a series of transverse sections a small cluster of protoxylem elements appears within a metaxylem strand, and an island of parenchyma cells develops immediately adaxial to it. Upward, the island enlarges toward the pith and, in connecting with it, leaves the protoxylem in medial position on the concave surface of a U-shaped strand. The curved portion of the strand then breaks away as the endarch xylem of the leaf-trace.

Passing outward, the xylem of the leaf-trace acquires surrounding layers of all peripheral stem tissues, each of which fills in immediately behind the trace to maintain its continuity around the stem. The leaf-trace retains an elliptical shape until it enters the petiole base where is protoxylem bifurcates and its adaxial curvature increases.

As the leaf-trace approaches the periphery of the stem, certain of the thin-walled fibers of the outer cortex abaxial to the trace are replaced thick-walled fibers as in *O. pluma*. However, in *O. precinnamomea* the thick-walled fibers extend into the petiole base as a large cluster that occupies only about half of the abaxial semicircle of the sclerenchyma ring. In addition, two small masses of thick-walled fibers appear, one of which occurs on each lateral side of the ring. These lateral clusters appear to arise *de novo* rather than as ramifications of the abaxial mass.

Petiole base.—The characteristic one abaxial and two lateral clusters of thick-walled fibers of the sclerenchyma ring occur at all levels in the stipular region of the petiole (Pl. III, Fig. 3). Near the point of attachment of the petiole to the stem the leaf-bases have short stipular expansions each of which contain a rounded mass of thick-walled fibers (Fig. 3). At this level petiole bases are 3.5 mm. from wing-tip to wing-tip, and their greatest radial thickness is 1.25 mm. The sclerenchyma ring is about 1.0 mm. in diameter and 0.25 mm. thick.

Upward, the stipular expansions extend laterally, and the vascular strand increases in curvature (Fig. 3). A small cluster of thick-walled fibers appears in the concavity of the vascular strand; and, as the tips of the strand recurve, the mass of fibers bifurcates, one branch lying against each tip. A few small clusters of thick-walled fibers appear in the inner cortex of the petiole base and increase in number upward. The mass of fibers in each stipular expansion continues upward occupying the center of the wing, and numerous smaller clusters occur without definite relationship to the dominant mass (Fig. 5). In crushed petiole bases, the sclerenchyma in each wing is compressed, and the strands appear to be in linear series; but where no crushing is evident, the large mass is at the center of the wing with smaller groups of fiber scattered throughout. Where the stipular expansions are the most extended, the petiole base measures 9.0 mm. from wing-tip to wing-tip, and its greatest radial thickness is 1.75 mm. The thickness of the sclerenchyma ring is about 0.25 mm., but its diameter at this level is about 1.5 mm.

Roots.—At least one root-trace, and in some cases two, connect to each

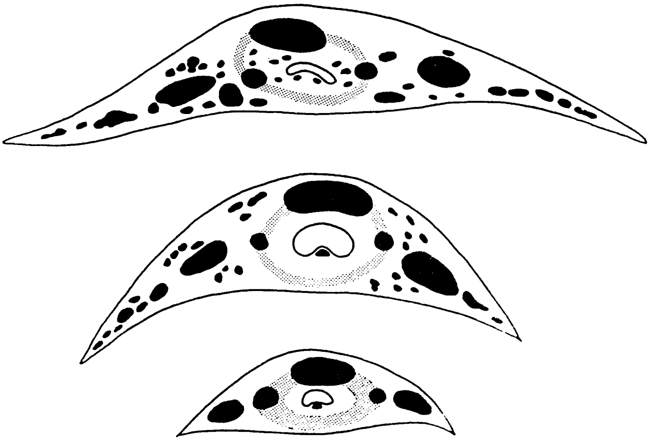

FIG. 5. *Osmunda precinnamomea* sp. nov., transverse sections of stipular petiole base at three levels showing sclerenchyma arrangement; thin-walled fibers, gray; thick-walled fibers, black.

leaf-trace. Actual separation of the xylem of the root from that of the leaf-trace occurs just below the point where the connection between the latter and the stem xylem is broken. The xylem strand of the root is diarch, and narrow cylinders of phloem, pericycle, and endodermis surround it. The inner cortex of the root is parenchymatous and is only a few cells thick; while thick-walled cells form the outer cortex, and this tissue may be as many as ten cells thick.

Discussion.—Close relationship between *O. precinnamomea* and *O. cinnamomea* is most effectively demonstrated by the similar clusters of thick-walled cells in sclerenchyma rings of their petiole bases. This pattern occurs in no other known species, and Hewitson's (1962) wide geographic sampling of *O. cinnamomea* showed great uniformity of this character. In both species bifurcation of the leaf-trace protoxylem occurs in the base of the petiole, and in these two species and in *Todea barbara* an adaxial cluster of fibers accompanies each leaf-trace in its passage through the inner cortex of the stem.

One of the main differences between *O. precinnamomea* and *O. cinnamomea* is the nearly constant presence of an internal endodermis in stems of the latter and its absence in stems of the former. Of the 150 or more stems of *O. cinnamomea* that were studied by Faull (1901, 1910), all that were mature had an internal endodermis. While one of the specimens included in Hewitson's (1962) investigation lacked this tissue, the combined sample is sufficient to demonstrate a high frequency of the occurrence of an internal endodermis in this species. On the other hand, two of the three specimens of *O. precinnamomea* lack an internal endodermis; and its presence or absence in the third fossil cannot be determined because none of the central tissues are preserved. It is remotely possible that the two stems in which central tissues are preserved were too young to have produced an internal endodermis. Faull (1910), in his study of *O. cinnamomea* sporelings mentions that the internal endodermis first appears when there are three or four overlapping leaf-gaps in the xylem cylinder. While some transverse sections of *O. precinnamomea* show only three overlapping leaf-gaps, others show seven, and one would expect an internal endodermis to have appeared by this time in the life of the plant. Thus, it is likely that the production of an internal endodermis was not a common feature in this new species, if it happened at all.

Another difference between *O. cinnamomea* and *O. precinnamomea* is the arrangement of sclerenchyma tissues in their petiole bases. *O. precinnamomea* has nearly the same distribution of these tissues as *O. cinnamomea,* but there are more clusters of thick-walled cells in the stipular expansions

TABLE III

Salient Features of Rhizomes of *Osmundastrum*

	O. cinnamomea	*O. cinnamomea*	*O. precinnamomea*
Age:	Recent	Miocene-Pliocene	Paleocene
Number of strands of stem xylem in an X-section:	7–22*	12–14	3–7
Number of leaf-traces in an X-section of the cortex:			
Inner cortex:	4–12*	6–9	4–5
Outer cortex:	7–15*	9–12	6–9
Angle of leaf-trace divergence:	18°–24°	10°–16°	10°–15°
Internal endodermis:	present	not visible	absent
Strand of fibers axillary to leaf-trace:	present	present	present
Strands of thick-walled fibers in sclerenchyma ring of petiole base:	3	3	3
Strands of fibers in stipular expansions:	few	few	many

* Data from Hewitson (1962) confirmed by my investigation.

of the Paleocene fern, and the small groups of fibers that are scattered in the inner cortex of petiole bases of *O. precinnamomea* are absent in *O. cinnamomea.* Thus, the distribution of these supporting tissues in petiole bases of the Recent species is a reduction of that in the fossil form.

For these reasons, *O. precinnamomea* is considered a taxon distinct from, and ancestral to, *O. cinnamomea,* and the fossil species is assigned to the subgenus *Osmundastrum* of the genus *Osmunda.*

Phylogeny of the subgenus *Osmundastrum*

Jeffrey (1899, 1902) and Faull (1901, 1910) considered *Osmunda cinnamomea* to be the most primitive member of the living *Osmundaceae.* They believed that the ectophloic, dictyoxylic siphonostele typical of the living species was reduced from an amphiphloic siphonostele which had previously been derived from a protostele by "intrusion" of extrastelar tissues and that the internal endodermis and local internal phloem in *O. cinnamomea* were remnants of the former condition. On the other hand, Seward and Ford (1903) contended that the modern osmundaceous stele was derived from a protostele by intrastelar development of a pith and subsequent dissection of the xylem cylinder by leaf-gaps. Thus, they felt that the internal endodermis and internal phloem of *O. cinnamomea* were specialized modifications of the ectophloic, dictyoxylic siphonostele found in other living Osmundaceae. The fossil species described by Kidston and Gwynne-Vaughan (1907–1914) and by Zalessky (1924, 1931a, 1931b, 1935) document several stages of the intrastelar evolution of the pith in this family. However, the problem of whether the stele of *O. cinnamomea* is primitive or specialized has never been solved since dictyostelic Osmundaceae of Mesozoic age could have given rise to one or more of the Recent species by reduction of their stelar tissues. The lack of an internal endodermis and internal phloem in *O. precinnamomea,* however, indicates that the occurrence of these tissues in *O. cinnamomea* represent specializations, and the stele of this Recent species must therefore be regarded as the most advanced of those of the living Osmundaceae.

While the stele of *O. cinnamomea* is specialized over that in *O. precinnamomea,* the arrangement of sclerenchyma tissues in its petiole bases is reduced from that in the Paleocene species. The loss of some small strands of sclerenchyma in the stipular expansions and all such strands in the inner cortex of the petiole must have occurred between the Paleocene and the Late Tertiary since the sclerenchyma distribution in the Miocene-Pliocene fossils of *O. cinnamomea* is like that in living plants of this species. Concurrent development of the internal endodermis cannot be demonstrated with as much accuracy since the presence or absence of this tissue in the fossil rhizomes of *O. cinnamomea* cannot be determined. The instability of the internal endodermis in living plants of this species suggests that the stele of this species may be evolving toward dictyostely and that the internal endodermis is probably of recent origin.

While *O. precinnamomea* and the fossils of *O. cinnamomea* show that the subgenus *Osmandastrum* has been a distinct line of evolution for about 60 million years, evidence concerning the origin of this group is lacking. Several speculative points regarding the relationships of the subgenus may be raised, however. Since *O. precinnamomea* lacks an internal endodermis, this tissue was probably absent in its ancestors. Thus, even though the stele of *O. cinnamomea* is specialized, *Osmundastrum* converges toward an ancestor having a vascular cylinder that is essentially similar to that in the subgenus *Osmunda* and in the genera *Leptopteris* and *Todea.* Secondly, the three masses of thick-walled fibers in sclerenchyma rings of species of *Osmundastrum* is like the abaxial arch of similar cells in petiole bases of *Osmunda.* It is presently impossible to demonstrate from known species of *Osmundastrum* that the two lateral clusters are in any way derived from the larger abaxial mass, and thus no homology of these sclerenchyma tissues in the subgenera *Osmunda* and *Osmundastrum* can be postulated. The similarity of these respective tissues is nonetheless interesting and may indicate relationship. Finally, the strand of thick-walled fibers that is axillary to leaf-traces in the inner cortex in *Osmundastrum* is a peculiar feature that also appears in *Todea barbara.* While the latter species bears no other close resemblances to *O. cinnamomea* and *O. precinnamomea,* the occurrence of such an unusual character in these species suggests that they may have had a common origin. Such evidence of the origin of the subgenus, however speculative, is the best our present fossil record offers.

Genus: *Osmunda*
Subgenus: *Plenasium*
Living Species

Four living species are generally recognized in the subgenus *Plenasium: Osmunda javanica* Blume, *O. vachellii* Hook., *O. bromeliaefolia* (Pr.) Copel., and *O. banksiaefolia* (Pr.) Kuhn. All of them have once-pinnate fronds, and all have fertile fronds that are incompletely dimorphic. In *O. vachellii* the fertile pinnae are borne at the base of the fertile frond, while fertile pinnae are attached near the middle of the fertile frond in other species. Pinnae are alternate in *O. banksiaefolia,* alternate to subopposite to opposite in *O. bromeliaefolia* and *O. javanica.* Pinnae margins are generally entire in *O. vachellii,* serrate to entire in *O. javanica,* shallowly serrate in *O. bromeliaefolia,* and deeply serrate in *O. banksiaefolia.* Hewitson (1962) was able to differentiate between these ferns on the basis of pinnae venation; but the only anatomical means of identifying these species is by the arrangement of sclerenchyma tissues in their petiole bases, and this character is not distinct (Hewitson, 1962). *O. javanica* and *O. vachellii* are very similar and were considered to be conspecific by Posthumus (1942b) and Hewitson (1962).

While the four living species of this subgenus are very similar to one another, they differ structurally from other Recent Osmundaceae with respect to the method of formation and the resulting cross-sectional shape of their leaf-traces (Hewitson, 1962; Chandler, 1965). In species of *Plenasium* a leaf-trace is derived from two adjacent strands of stem xylem. The gap between the two strands is closed by the curving of the outer tip of each strand toward the other followed by their fusion. Just below the point of merging of the two strands, each appears crosier- or query-shaped in transverse outline and each generally bears an endarch group of protoxylem tracheids. The fused combination of these strands, which is horseshoe-shaped in transverse outline, bears two protoxylems. The curved portion then breaks away forming the xylem of the leaf-trace; and because of the nature of its formation, it has a pronounced curvature at the point of its divergence (Fig. 4). Hewitson (1962) noted certain exceptions to this general procedure in which the leaf-trace was derived from only one strand of stem xylem. It nonetheless had two protoxylems which were ramifications of a single strand below the point of divergence of the trace. Further variations may occur in which the symmetry ascribed to the general method of formation is lacking. The changes in each strand of stem xylem are the same as in the general method, but one strand of the adjacent pair may be larger or more curved than the other in a given transverse section. Most often, however, a given section of a stem of *Plenasium* displays one or more crosier-shaped xylem strands (Hewitson, 1962), and this feature combined with the pronounced curvature of the leaf-traces is characteristic of the subgenus.

The arrangement of petiole sclerenchyma in species of *Plenasium* is not as diagnostic as it is in other members of the genus *Osmunda.* Thick-walled fibers commonly occur in scattered strands and do not form elongate strips of tissue in the stipular expansions as in most species of the subgenus *Osmunda* (Hewitson, 1962, Fig. 7F, G, H, and I). While the sclerenchyma ring of the petiole base appears homogeneous in species of *Plenasium,* there is a very thin abaxial arch of thick-walled fibers visible in transverse sections near the stem. In sections more distant from the stem, the ring is completely surrounded by a narrow layer of these cells, and this situation persists throughout the stipular region. The tissue of thick-walled fibers is only two to four cells thick and is not conspicuous. Leaf-bases of *Todea barbara* and species of *Leptopteris* are similar in this respect, so the condition is of limited value as a comparative character.

SYSTEMATIC DESCRIPTION

Genus: *Osmunda* Linneaus

Subgenus: *Plenasium* Presl

Osmunda arnoldii sp. nov., C. N. Miller

(Figs. 6–7; Pl. IV, Figs. 1–4)

Diagnosis.—Petrified rhizomes about 6.0 cm. in diameter, consisting of a stem about 10 mm. in diameter surrounded by a mantle of closely adhering petiole bases; xylem cylinder of stem about 2.5 mm. in diameter, 1.0 mm. thick, and consisting of 8–12 strands as observed in transverse section; leaf-gaps high and wide, formed immediately opposite each departing leaf-trace; cortex consisting of a thin inner parenchymatous zone and a thick outer fibrous zone, together including 5–7 departing leaf-traces in a given transverse section; leaf-trace endarch, separating from the stem xylem with two protoxylems and with a pronounced curvature; petiole base stipular, containing numerous masses of sclerenchyma scattered throughout, and an elongate strip of fibers lining the concavity of the vascular strand; roots with diarch xylem strand, separating from leaf-traces as latter diverge from stem xylem.

Locality and Horizon.—Morton County, North Dakota; Paleocene Fort Union Formation.

Holotype and Paratypes.—UMMP 52161 and 52162 respectively.

Introduction.—This new addition to the fossil Osmundaceae is based on five specimens which came from the Fort Union (Paleocene) locality in central North Dakota that was described in detail earlier. The stem of *Osmunda arnoldii* (Pl. V, Fig. 1) is about 10 mm. in diameter; and while none of the specimens shows bifurcation of the axis, two rhizomes in one of the rocks are suspiciously close to one another. The stele (Pl. V, Fig. 2) of the new species is an ectophloic-dictyoxylic siphonostele and is about 3.0 mm. in diameter. The xylem cylinder is dissected into 8–12 separate strands by leaf-gaps which form immediately opposite the point of divergence of each leaf-trace. The stem cortex consists of a narrow inner layer of parenchyma and a thick outer layer of fibers which together include five to seven leaf-traces in a given transverse section. The xylem of each leaf-trace separates from the stem xylem in the characteristic *Plenasium* manner (Hewitson, 1962) bearing two protoxylems and having a pronounced adaxial curvature. The petiole base of this species is winged and contains a vascular strand that is C-shaped in transverse section with its margins curved inward. Small strands of sclerenchyma are scattered throughout the petiole base, and an elongate strip of fibers lines the concavity of the vascular strand. In all respects, this Paleocene species bears a striking similarity to living species of *Plenasium* and is considered to be more or less directly ancestral to these Recent forms.

Stem.—The pith of *Osmunda arnoldii* is about 1.5 mm. in diameter and consists of parenchyma cells that are 80–120 microns in diameter and 13–210 microns in length. In most specimens the walls of these cells are thin (1–2 microns thick), but in one stem the cell walls are about 5 microns thick. No doubt there is a tendency in this species for the walls of the pith cells to become thicker some distance behind the shoot apex as in *O. pluma* but not to the extent of becoming stone cells as in that species. Furthermore, large diameter parenchyma cells normally occur near the center of the pith while smaller diameter cells occupy a more peripheral position. In one section a tracheid occurs within the pith. However, there are only two parenchyma cells between it and the nearest xylem strand. Hewitson (1962) reported similar "misplaced" tracheids in the pith of *O. javanica.* The pith parenchyma in *O. arnoldii* occurs in irregular axial rows, and the cells have mainly transverse, but some oblique, end walls. Those parenchyma cells adjacent to the xylem are about 30 microns in diameter and form the inner part of an inconspicuous sheath around the xylem. The sheath is only one or two cell layers thick between the pith and the xylem but extends through xylic gaps and forms a layer two to three cells thick between the xylem and phloem.

The xylem cylinder is 2.5 mm. in diameter and 1.0 mm. thick. It consists of 8–12 strands of tracheids as observed in cross-section. Each strand, where it is not just below a leaf-gap, is 10–15 cells thick in radial dimension. The metaxylem tracheids are about 80 microns in diameter and have one to three, but mostly two, vertical series of scalariform pits on each wall. Protoxylem tracheids, in comparison, are 10–30 microns in diameter. Some of them have helical wall thickenings but most have a single vertical series of scalariform pits on each wall. These elements occur within the strands of metaxylem tracheids only below departing leaf-trace.

Beyond the outer part of the xylem sheath are cells of the phloem, porose layer, and pericycle. Of these only sieve cells of the metaphloem can be identified, the remaining tissues being represented by one or more layers of crushed cells. Sieve cells are about 50 microns in diameter and are concentrated in wedges opposite xylic gaps. The groups of sieve cells project for a short distance between adjacent xylem strands and are connected with one another by one or two layers of cells outside the xylem cylinder.

The endodermis completely surrounds the zone of crushed cells. It consists of small cells which are slightly elongated in the tangential dimension. Casparian strips are not visible as such, but the tissue is distinctly darker than tissue to either side of it (Pl. IV, Fig. 2). No endodermis occurs between the pith and the xylem.

Both the inner and outer layers of cortex are irregular in breadth because they include departing leaf-traces. The inner cortex is 1–2 mm. thick and is made up of parenchyma cells with cell walls that are about one micron thick. The cells are 45–70 microns in diameter and 80–120 microns in length. They are oval in transverse section and have conspicuous intercellular spaces between them. This tissue may contain up to two leaf-traces in a given cross-section. The outer cortex, on the other hand, is 1–4 mm. thick and consists of fibers. These cells are long and have ends that taper to a fine point. The fibers have a maximum diameter that averages 40 microns, and their cell walls are 5–8 microns thick. These elements are polygonal in transverse outline and make up a dense tissue without conspicuous intercellular spaces. Four to seven leaf-traces appear in the outer cortex in a given cross-section.

Leaf-trace.—The xylem of the leaf-trace in *O. arnoldii* separates from two adjacent strands of stem xylem (Fig. 6). At its point of divergence it bears two groups of protoxylem and has a pronounced adaxial curvature. Each of the two strands that are involved in the formation of the leaf-trace xylem are originally oval in transverse outline and consist entirely of metaxylem tracheids. Some distance below the point of divergence of the leaf-trace, however, each strand becomes mesarch with the appearance of a cluster of protoxylem elements within the group of metaxylem tracheids. A group of parenchyma cells like those of the xylem sheath forms immediately adaxial to the protoxylem. These parenchyma cells increase in number upward replacing metaxylem tracheids adaxial to the protoxylem and somewhat toward the adjacent strand of stem xylem, and eventually they contact cells of the xylem sheath. At this point each of the two xylem strands are endarch and have a crosier or query shape in transverse outline with the protoxylem on the "hook" part of the strand. The tips of the adjacent strands connect forming a single xylem strand that is U-shaped in cross-section. The curved part of the strand then diverges to form the xylem of the leaf-trace and carries with it the protoxylem of each of the two strands of stem xylem originally involved.

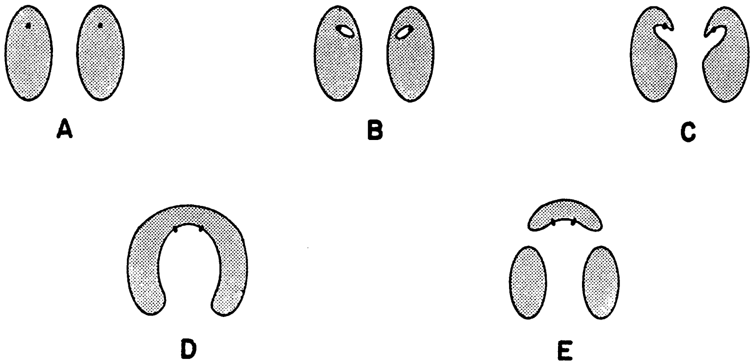

FIG. 6. *Osmunda arnoldi* sp. nov., transverse sections of xylem strands through a leaf gap showing leaf-trace formation, the letters A to E indicate an acropetal series.

Because of these changes, the xylem of the leaf-trace has a pronounced curvature from its inception. Its radial dimension is limited to two or three tracheids at its mid-region, while the ends of the strand are about six tracheids thick. Departing leaf-traces make an angle of 5–8° with the longitudinal axis of the stem. As it passes through the phloem, porose layer, pericycle, endodermis, inner cortex, and outer cortex, the leaf-trace becomes surrounded by a layer of each of these respective tissues. Furthermore, each tissue fills in immediately behind the leaf-trace to maintain its continuity.

Petiole base.—Near its point of attachment to the stem the petiole base consists of a C-shaped vascular strand whose xylem bears about six adaxial protoxylems, a surrounding cylinder of parenchyma cells that are continuous downward with those of the inner cortex of the stem, and a narrow ring of fibers of the outer cortex of the stem. A tissue of thin-walled parenchyma cells extends laterally to each side of the sclerenchyma ring forming short stipular expansions. At this level, the petiole base is about 10 mm. from "wing-tip" to "wing-tip" and 2.5 mm. at its greatest radial thickness. The ring of fibers is about 0.25 mm. thick and has outside dimensions of 2 mm. by 5 mm. as measured radial and tangential to the stem respectively. Fibers whose walls are so thick that the lumina are nearly occluded form a few small clusters in the inner cortex and in each stipular expansion. Furthermore, a narrow band of thick-walled fibers line the concavity of the vascular strand (Pl. IV, Fig. 4). The sclerenchyma ring has a narrow arch of thick-walled fibers on its abaxial side. The arch only one or two cells thick, and in sections more distant from the stem these thick-walled cells completely encircle the ring forming an inconspicuous layer that is one or two cells thick (Fig. 7).

The petiole base enlarges upward. The tips of the vascular strand recurve slightly, and the band of fibers in its concavity of the strand conform to its shape. The xylem strand becomes thinner, and the protoxylem clusters project from its adaxial surface giving the concave side of the vascular strand an irregular outline. The band of fibers is thinner opposite the protoxylems than it is between them; and in some petiole bases the irregularity is sufficiently pronounced to break the band of fibers into separate patches, but most often the tissue remains continuous along its adaxial face. Additional small clusters of thick-walled fibers appear in the petiole base, and many of those in the stipular expansions coalesce to form larger, irregular masses. Where the stipular expansions of a petiole base are compressed, the larger masses of fibers appear in linear series; but their placement is random in unaltered wings (Fig. 7).

Petiole bases at the periphery of the mantle are about 30 mm. by 5 mm. Their sclerenchyma rings are about 0.5 mm. thick and have outside dimensions of 10 mm. by 5 mm. The vascular strand contains as many as twelve adaxial protoxylems. The number of masses of thick-walled fibers increases slightly, but those in the inner cortex of the petiole base do not form large masses as do those in the stipular expansions (Pl. IV, Fig. 4; Fig. 5).

Roots.—One root-trace generally diverges from each leaf-trace as the latter separates from the stem xylem. In most cases, the leaf-trace is still connected to the stem xylem when the root-trace separates from it; but one instance of root-trace divergence from a leaf-trace in the inner cortex was observed. Hewitson (1962) mentions that normally two roots diverge from each leaf-trace in living species of *Plenasium* but that they do so at different levels and serial sections are required to see them both. While serial petrologic sections were prepared from one of the rhizomes of *O. arnoldii,* they were not in close sequence; so it is possible that more than one root-trace diverges from each leaf-trace in this species. The roots of *O. arnoldii* have an elliptical xylem strand with a protoxylem at each end. The xylem is surrounded by phloem, several layers of flattened cells which probably represent the protoxylem, porose layer and pericycle, an endodermis, and a cortex. The cortical region consists of an inner zone of thin-walled cells, that is quite variable in thickness, and an outer zone of thick-walled cells, that is usually one to four cells thick.

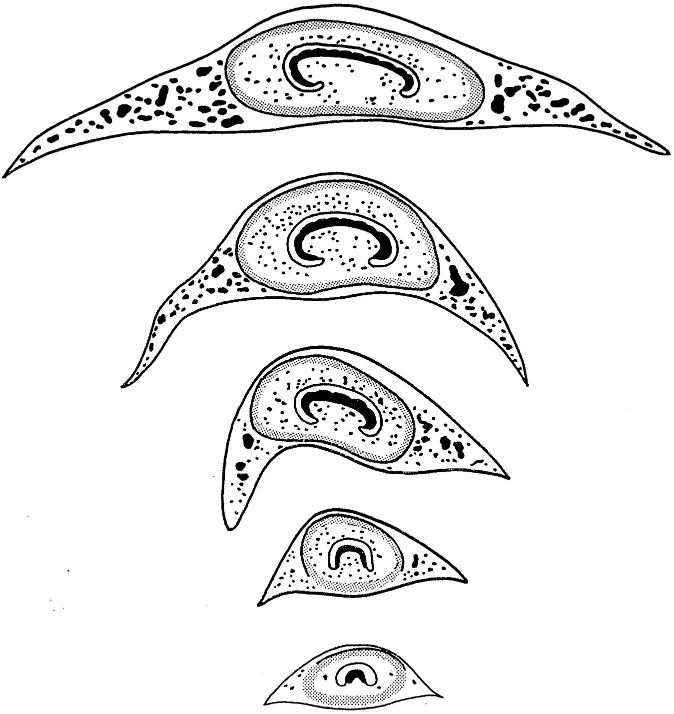

FIG. 7. *Osmunda arnoldii* sp. nov., transverse section of stipular petiole base at five levels showing sclerenchyma arrangement; thin-walled fibers, gray; thick-walled fibers, black.

In transverse sections of the stem, roots are cut longitudinally and obliquely as they pass out through the cortex and petiole bases. Roots occasionally grow through stipular expansions, but none were observed to penetrate the sclerenchyma ring. At the outer part of the mantle some branching of roots occurs, but there is apparently no ramification further inward.

Discussion.—The characteristic manner of leaf-trace formation, the strong curvature of the leaf-traces as they separate from the stem xylem, and the peculiar arrangement of sclerenchyma tissues in the petiole bases are features which lead to the classification of *O. arnoldii* in the subgenus *Plenasium* of the genus *Osmunda.* Stem characters of the new species, such as the number of xylem strands and the number of leaf-traces in each of the cortical zones as observed in transverse section, compare favorably with similar determinations in the present-day species of this subgenus. In fact, the similarity of the fossil to the living forms is so close that without the additional characters in the petiole base, it would be difficult to distinguish between them.

O. arnoldii differs from the living members of *Plenasium* mainly in regard to the sclerenchyma in the stipular expansion (Table 4). All species of the subgenus have scattered strands of sclerenchyma in the wings, but in *O. arnoldii* these masses are larger and more numerous than in any of the living species. Some additional differences may also be noted. The fossil differs from *O. banksiaefolia* and *O. bromeliaefolia* in its tendency to form a sclerotic pith. Furthermore, in these two living species the mass of fibers in the concavity of the petiolar strand extends downward with the leaf-trace into the stem, but in *O. arnoldii* these fibers reach only to the base of the petiole. Both *O. javanica* and *O. bromeliaefolia* have a large cluster of fibers in the concavity of the petiolar strand rather than a narrow band of tissue as in *O. arnoldii.* Thus, there is good reason to consider *O. arnoldii* a distinct species, but one that is very similar to and more or less directly ancestral to the living forms.

Osmunda dowkeri (Carruthers) Chandler
1965, pp. 139–161.

Osmundites dowkeri Carruthers. 1870, p. 349, Pl. xxiv, Figs. 1–3; Pl. xxv, Figs. 1–4.

Osmundites chandleri Arnold. 1952, p. 68–72; Text-figs. 3, 4, and 5b; Pls. VII–VIII.

Discussion.—This species of petrified rhizome was first described by Carruthers (1870) from material of Early Eocene age that was collected at Herne Bay, United Kingdom. In 1965 Chandler published an account describing a new rhizome of this species that came from the same location as the holotype. The new material shows that a typical leaf-trace bears two protoxylems at its point of divergence from the stem xylem; and because of this feature, the occurrence of strands of stem xylem have a crosier-shape in cross section, and the scattered arrangement of petiolar sclerenchyma, Chandler (1965) transferred this species from *Osmundites* to the subgenus *Plenasium* of *Osmunda.* It should be noted that this was the first species of petrified rhizomes to be assigned to *Osmunda* even though the genus is represented in the fossil record by thirty-odd species of compressed foliage which range in age from Early Cretaceous to Pleistocene (Jongmans, 1961, Fossilium Catalogus).

Arnold (1952) noted a similarity between *Osmunda dowkeri* and *Osmundites chandleri,* a species of petrified rhizomes that he described from the Upper Eocene Clarno Formation in Oregon. However, he considered the two species to be distinct from one another because of their great geographic separation (Arnold, 1952). Chandler (1965) also mentions the possible identity of these two forms but declined to merge the Oregon form with the British species because of the higher number of xylem strands in the stem of the former (34 as compared to 20–28 in the British fossils), and because none of these strands in *Osmundites chandleri* has a distinct crosier shape in cross-section. Another difference between the two forms is the manner of leaf-trace formation. Leaf-traces in *Osmundites chandleri* diverge from the stem xylem bearing two protoxylem strands and having a pronounced curvature, but they generally arise from only one strand of stem xylem (Arnold, 1952, Text–fig. 3). Having seen preparations of the holotypes of both species and sections of Chandler's new material, however, I feel that all these specimens belong to the same species and have placed *Osmundites chandleri* in synonymy with *Osmunda dowkeri* (Carruthers) Chandler.

The major differences between the British and American specimens of this species can all be reasonably explained. While the living species of *Plenasium* are restricted in their geographic ranges to southeast Asia, it is possible that extinct species enjoyed a more widespread distribution. Many parts of the Northern Hemisphere had a climate in the Eocene similar to that presently occurring in southeast Asia and these northern regions could have supported populations of extinct species of *Plenasium* that had ecological requirements similar to the living species. Furthermore, *O. regalis, O. claytoniana,* and *O. cinnamomea* each have present geographic ranges that far exceeds the separation of the British and America fossils of *O. dowkeri.* Thus, the distance between collecting localities of the British and American fossils alone does not justify their separation as distinct species.

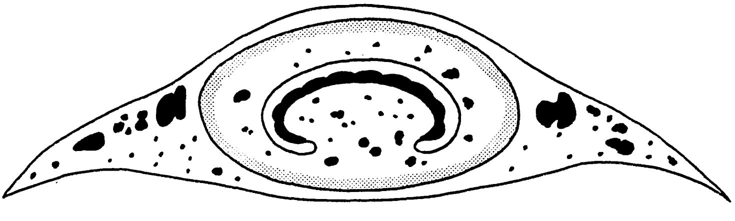

FIG. 8. *Osmunda dowkeri* (Carruthers) Chandler, transverse section of stipular petiole base showing sclerenchyma arrangement; thin-walled fibers, gray; thick-walled fibers, black.

The difference in the number of strands of stem xylem in the various specimens is not significant enough to separate the materials into two species. Chandler (1965) mentions that her rhizome was probably a young one having only 20 strands of stem xylem. The holotype shows 28 strands and the Oregon fossil 30–34. The sample of this species is too small to allow accurate interpretation of the range of variation of this character, but if any of the fossils should be segregated on this basis it should be Chandler's new rhizome since it has only 20 strands.

The manner of leaf-trace formation in the Oregon material is the most significant of the differences between it and the British fossils. Leaf-traces of the former generally diverge from a single strand of stem xylem as in the subgenus *Osmunda* but nonetheless have two protoxylems and a pronounced adaxial curvature as is typical of *Plenasium* (Arnold, 1952, Text-fig. 3; Chandler, 1965). While the divergence of the leaf-trace from a single xylem strand is atypical of *Plenasium,* it does occur in certain of the living members of this subgenus (Hewitson, 1962, p. 79–80, Figs. 22–25). A number of the xylem strands in the Oregon rhizomes are somewhat crosier-shaped in transverse section. However, because of their great number and nearness to one another, the precise manner of leaf-trace formation cannot be determined in each case. It is difficult to determine in the preparations available whether all leaf-traces are derived by the atypical sequence, or if some might be formed through the more common series of changes. Since the British and American materials are similar in all other respects, I do not feel that these differences in leaf-trace formation constitute grounds for maintaining two separate species.

Three other specimens of *Osmunda dowkeri* are in the University of Michigan Museum—one is a beach boulder found along the Oregon coast, another is from Utah, and the third is from the Black Hills of South Dakota. While the ages of these fossils are unknown, they indicate that this species was more widespread than was previously known. Furthermore, the rhizome contained in the beach boulder from Oregon shows two ramifications of a branch. The actual branching region, unfortunately, was not included in the specimen. The Black Hills specimen also shows additional variation in the species, for its xylem cylinder is about twenty-five tracheids in radial thickness, while those of other specimens are about fifteen tracheids deep. The branched rhizome shows leaf-trace formation as in Arnold's material of *O. dowkeri,* while the South Dakota and Utah fossils have the typical method of leaf-trace formation. Rather than basing new species on each of these departures from the holotype, it is better to include these specimens in the same species until the variation is better understood.

Phylogeny of the subgenus *Plenasium*

Plenasium presently includes four living members and two species of petrified rhizomes of Early Tertiary age. In addition, two forms of compressed foliage. *Osmunda arctica* Heer and *O. delawarensis* Berry, give evidence of the subgenus during the Late Cretaceous.

Osmunda arnoldii, from the Paleocene of North Dakota, closely resembles the living species being differentiated from them mainly in the arrangement of its petiolar sclerenchyma. On the other hand, *O. dowkeri,* from the Eocene of Great Britain and western North America, differs from the Paleocene and Recent species in a number of respects. Its xylem cylinder is thicker and is dissected into more strands, and more leaf-traces can be observed in a cross-section of its cortex than in the other species (Table IV). Because of these differences and because of the relatively short time span between the known occurrences of these species, it is difficult to envision the direct evolution of *O. dowkeri* from *O. arnoldii.* It is even more unlikely that *O. dowkeri* arose from *O. arnoldii* gaining these previously mentioned modifications only to lose them in giving rise to the present-day species. Thus, while the chronological occurrence of the species suggests that they form a single line of evolution, morphological evidence indicates that the living species arose with few changes from *O. arnoldii* and *O. dowkeri* represents a divergent branch of the *Plenasium* line that did not persist to the present.

Even though *Osmunda dowkeri* is younger than *O. arnoldii,* it is probably a more primitive species. The very features which distinguish it from other members of the subgenus (thick xylem cylinder, many strands of stem xylem, many leaf-traces in the cortices) occur in species of the *Osmundicaulis skidegatensis* group, all of which are Early Cretaceous in age. These species also have a type of leaf-trace formation similar to that in *Plenasium.* Many of these extinct species have highly specialized steles, so it would be presumptive in the absence of intermediate forms to postulate the origin of *Plenasium* from this complex through *Osmunda dowkeri.* However, these Mesozoic rhizomes do indicate that the features which characterize *O. dowkeri* are probably held over from an earlier ancestor rather than being derived from *O. arnoldii.*

Although the foliage species *O. arctica* and *O. delawarensis* are important in marking the earliest recorded occurrence of *Plenasium,* two Tertiary species also contribute to our understanding of *Plenasium* phylogeny. *Osmunda lignitum* (Giebel) is known from Eocene, Oligocene, and Miocene sediments throughout the world, and its abundance indicates that *Plena-*

sium reached its zenith at this time. Chandler (1965) comments on the possibility that *Osmunda lignitum* may have been the foliage of *O. dowkeri,* but present evidence for such a connection is limited to the association of these two species. Another species, *O. bromeliaefolioides,* Matsuo, from the Miocene of Japan, was considered by Endo (1965) to be so like the foliage of the living *O. bromeliaefolia* that he transferred the fossil material to this species. Thus, it is quite possible that one or more of the living forms may be of relatively ancient origin, and the similarity of *O. arnoldii* and the living members of the subgenus also supports this idea.

In summary, it is evident that the living species of *Plenasium* evolved from *Osmunda arnoldii* or forms very similar to this one and that they together constitute the main line of evolution within the subgenus. *Osmunda dowkeri,* on the other hand, represents a divergent line which did not persist to the present. These lines probably converge on a common precursor in the Cretaceous. Foliage remains indicate that *Plenasium* reached its peak of geographic distribution during the Middle Tertiary, and certain of the living species may have originated at this time.

PHYLOGENY OF THE GENUS *Osmunda*

The Recent species of *Osmunda* are products of three lines of specialization, each of which is represented by one of the three subgenera. These phylogenetic lines have been distinct since the Paleocene and probably were differentiated as long ago as Early Cretaceous (Fig. 9).

Of the three subgenera *Osmunda* has the longest and most extensive fossil record. *Osmunda regalis, O. japonica,* and *O. lancea* are the traditionally-recognized living species; and *O. claytoniana,* which is generally treated in the subgenus *Osmundastrum,* has been included in *Osmunda* because of its structural similarity to the former species. Four species of petrified rhizomes, which range in age from Paleocene to Pliocene, are assigned to this subgenus, and sixteen species of compressed foliage are also classified with *Osmunda.* The latter indicate that this subgenus existed in the Early Cretaceous and has been widespread since that time. The four species of petrified rhizomes indicate that *O. regalis, O. japonica,* and *O. lancea* arose from a line of specialization represented by *O. pluma, O. oregonensis,* and *O. iliaensis,* while *O. claytoniana* developed from a divergent branch of this line through *O. nathorstii.* The steles of these species are very similar, and the interpretation of evolutionary trends is based on differences in the arrangement of petiolar sclerenchyma and in the point of basal branching of the leaf-trace protoxylem. These characters unite the species on their lines of development and suggest that *O. clay-*

TABLE IV

Salient Features of Rhizomes of *Plenasium*

	O. banksiaefolia	*O. bromeliaefolia*	*O. javanica*	*O. vachellii*	*O. dowkeri*	*O. arnoldii*
Age:	Recent	Recent	Recent	Recent	Eocene	Paleocene
Number of strands of stem xylem in a X-section:	4–9*	3–12*	3–11*	9*	20–34	8–12
Number of leaf-traces per X-section of cortex:						
Inner cortex:	0*	0–1*	0–1*	1*	2–7	0–2
Outer cortex:	4*	4–8*	3–6*	7*	2–14	4–7
Pith construction:	par.*	par.*	scl.*	scl.*	scl.	scl.
Angle of leaf-trace divergence:	30°–40°	30°–45°	30°–45°	30°–45°	20°–25°	10°–15°
Thickness of xylem cylinder (number of tracheids):	10–15	10–15	10–15	10–15	10–25	10–15

* Data from Hewitson (1962) confirmed by my investigation.

toniana and *O. nathorstii* arose from some form similar to *O. iliaensis* in the Late Tertiary.

Foliage belonging to the subgenus *Osmunda* is remarkable for its morpohogic uniformity during the last 100 million years. Pinnules from the Cretaceous are nearly identical to those of the living species except for differences in size and minor variations in the venation, which are usually correlated with the latter. This consistency serves as a noteworthy exception to the popular belief that foliage is plastic and easily altered by environmental conditions.

The origin of *Osmunda* is not clear. Species assigned to this subgenus are more similar to petrified rhizomes of the *Osmundacaulis herbstii* group than the other known Mesozoic forms. In fact one species of this group, *Osmundacaulis kidstoni,* shares an important feature with the Early Tertiary *Osmundas.* However, no close relationship between these species and the Cretaceous fossil can be demonstrated because of the absence of the stem in *Osmundacaulis kidstoni.*

The subgenus *Osmundastrum* includes *Osmunda precinnamomea,* from the Paleocene of North Dakota, and *O. cinnamomea,* a Recent species which is also represented by petrified rhizomes from Late Tertiary of Washington. *O. precinnamomea* is similar to its living relative in most respects but differs in having a more complex arrangement of petiolar sclerenchyma and in lacking an internal endodermis. The absence of this tissue in the Paleocene rhizomes indicates that its presence in *O. cinnamomea* represents a specialization of an ectophloic condition rather than a product of the reduction of an amphiphloic arrangement. Since endodermal tissues are not visible in the Washington fossils, it is not possible to determine when the internal endodermis evolved, but its variability in living rhizomes suggests that it is of recent origin. No ancestor of the subgenus *Osmundastrum* can be postulated at this time; but, like members of the subgenus *Osmunda,* species of *Osmundastrum* show a closer relationship to the *Osmundacaulis herbstii* group than to the other two groups of this form genus. *Osmundastrum* must have had a significant history prior to the Paleocene, when it is first in evidence, because the features which characterize the subgenus are well-defined in *O. precinnamomea.* Thus, *Osmundastrum* must have diverged in the Cretaceous and probably in the Early Cretaceous.

Plenasium includes four living species: *Osmunda banksiaefolia, O. bromeliaefolia, O. vachellii,* and *O. javenica.* The subgenus is represented in the fossil record by two species of petrified rhizomes and four species of compressed foliage. Fossil rhizomes of *O. arnoldii,* from the Paleocene of

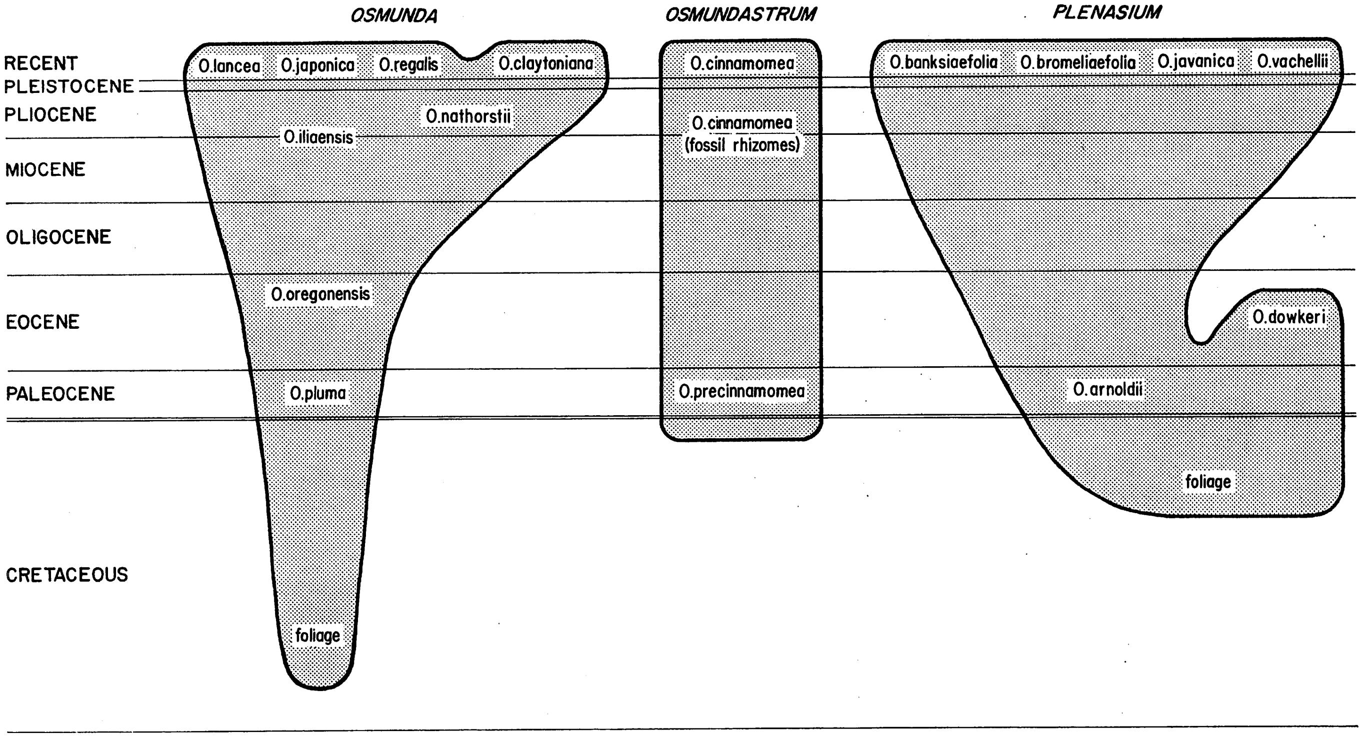

FIG. 9. Phylogeny of the genus *Osmunda*.

North Dakota, differ from those of the living species only in minor respects and indicate that the Recent members of *Plenasium* evolved more or less directly and with few changes from this ancestral form or one similar to it. Rhizomes of *Osmunda dowkeri,* which occur in the Eocene of the United Kingdom and the western United States, are divergent in a number of characters. This species shows affinity with the *Osmundacaulis skidegatensis* group of Mesozoic rhizomes, and some species like those of this group may have been the ancestor of the subgenus. Foliage belonging to *Plenasium* has been reported from the Late Cretaceous and marks the earliest record of the subgenus. A second species of fossil pinnules, *Osmunda lignitum,* occurs widely in Eocene, Oligocene, and Miocene sediments indicating that *Plenasium* probably reached its peak at this time. The close similarity of the Recent species to *O. arnoldii* suggests that certain of the former may have originated early in the Tertiary, and pinnules of *O. bromeliaefolia* have been reported from Miocene sediments. Thus, the living members of *Plenasium* arose early in the Tertiary from *Osmunda arnoldii* or some form very similar to it. *Osmunda dowkeri* represents an extinct branch of the main line of specialization, and the structure of this fossil suggests that the *Osmundacaulis skidegatensis* group may have been the ancestral stock of *Plenasium* giving rise to this subgenus in the Cretaceous.

It is apparent, therefore, that the genus *Osmunda* is an ancient one which extends from the Cretaceous to the present. Furthermore, present evidence suggests that the genus is polyphyletic. Copeland (1947) mentions that there is reason to treat the subgenera as genera because of differences in their fertile and sterile frond morphology, and objection to this has been based mostly on the small number of living species that would be included in each of the genera (*Osmunda* 4, *Osmundastrum* 1, and *Plenasium* 4). However, the number of species is significantly increased with the addition of the known fossil species. Moreover, raising the subgenera to genera reflects that fact that they have been separate lines of evolution for at least the last 70 million years. It is therefore recommended that *Osmunda, Osmundastrum,* and *Plenasium* be treated as genera.

SUMMARY

Recent work on the comparative anatomy of the living Osmundaceae has made it possible to define and distinguish between the three genera of the family and between the three subgenera of *Osmunda* using features contained in rhizomes and their adhering roots and petiole bases. Chandler (1965) has used this new information to transfer *Osmundites dowkeri* to *Osmunda* in the subgenus *Plenasium,* and the new materials described in

this account are also classified with this genus. *Osmunda pluma, O. precinnamomea,* and *O. arnoldii* are petrified rhizomes from the Paleocene of North Dakota which are classified with the subgenera *Osmunda, Osmundastrum* and *Plenasium* respectively. *Osmunda nathorstii,* a new species described from a sheath of petiole bases that was formerly included under *Osmundites spetsbergensis,* is assigned to the subgenus *Osmunda. Osmundites oregonensis,* from the Eocene of Oregon, is transferred to the subgenus *Osmunda;* and *Osmundites schemnicensis,* from the Miocene-Pliocene of Hungary, is also placed with this subgenus under the new name *Osmunda iliaensis.* In addition, *Osmundites chandleri,* from the Eocene of Oregon, is placed in synonymy with *Osmunda dowkeri,* and two petrified rhizomes, from the Late Tertiary of Washington, are identified as *O. cinnamomea.*

Osmundacaulis is a new name for *Osmundites* Unger which is invalid because of prior use by Jaeger (1827) and because the generitype of Unger's *Osmundites* belongs to *Osmunda. Osmundacaulis skidegatensis* is selected as the generitype under the new arrangement, and the species of this form genus are listed and arranged in phylogenetic groups.

Each of the subgenera of *Osmunda* were distinct lines of specialization in the Paleocene, and pinnule compressions belonging to the subgenera *Osmunda* and *Plenasium* have been reported from Lower and Upper Cretaceaus sediments respectively. The living *Osmunda regalis, O. japonica,* and *O. lancea* arose from a phylogenetic line represented by *O. pluma, O. oregonensis,* and *O. iliaensis,* while *O. claytoniana* developed on a divergent branch of this line through *O. nathorstii* from some form similar to *O. iliaensis.* In the subgenus *Osmundastrum* the two known species are so similar that no doubt *Osmunda cinnamomea* arose from *O. precinnamomea* prior to the Pliocene. The four living species of *Plenasium—Osmunda banksiaefolia, O. bromeliaefolia, O. javanica,* and *O. vachellii*—evolved with few changes from the Paleocene *O. arnoldii* or from a form very similar to it. The Eocene *O. dowkeri* represents an extinct branch of the main line of specialization in *Plenasium.*

Although it has not been possible to trace the development of any of the subgenera to specific forms of *Osmundicaulis,* members of *Osmunda* and *Osmundastrum* bear closest resemblance to the *Osmundicaulis herbstii* group while species of *Plenasium* are more similar to the *Osmundicaulis skidegatensis* group. To recognize the probability that *Osmunda* is polyphyletic and that its subgenera have been independent lines of specialization for at least 70 million years, it is recommended that *Osmunda, Osmundastrum,* and *Plenasium* be raised to genera.

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EXPLANATION OF PLATE I

PAGE

Osmunda pluma sp. nov. 150

FIG. 1. Transverse section of rhizome, holotype, UMMP 52157, × 6.

FIG. 2. Transverse section of stele, holotype, UMMP 52157, × 20.

FIG. 3. Transverse section of petiole just above stipular region, paratype, UMMP 52158, × 18.

FIG. 4. Transverse section of stipular petiole base in middle of mantle, holotype, UMMP 52157, × 20.

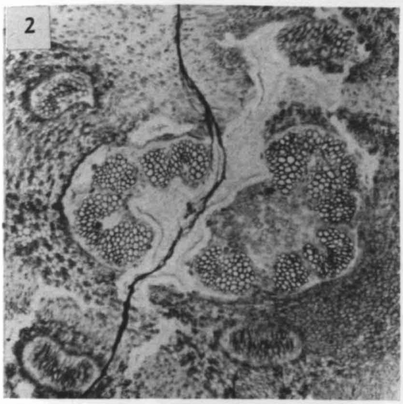
Osmunda oregonensis (Arnold) comb. nov. 157

FIG. 5. Transverse section of mantle of petiole bases near periphery, holotype, UMMP 23389, × 2.

PLATE I

1

2



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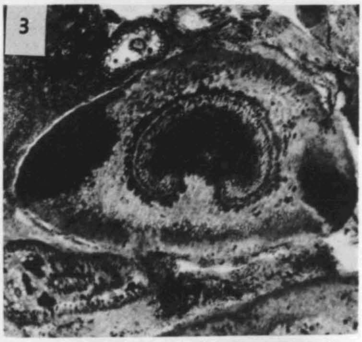

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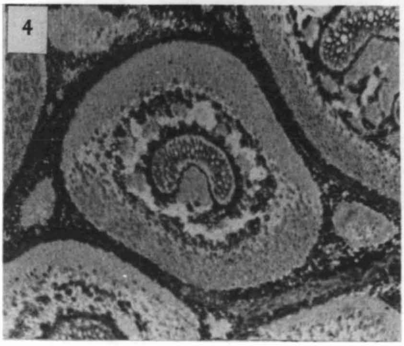

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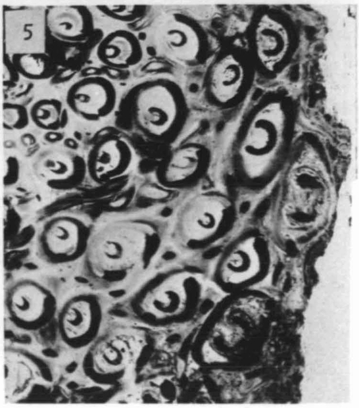

PLATE II

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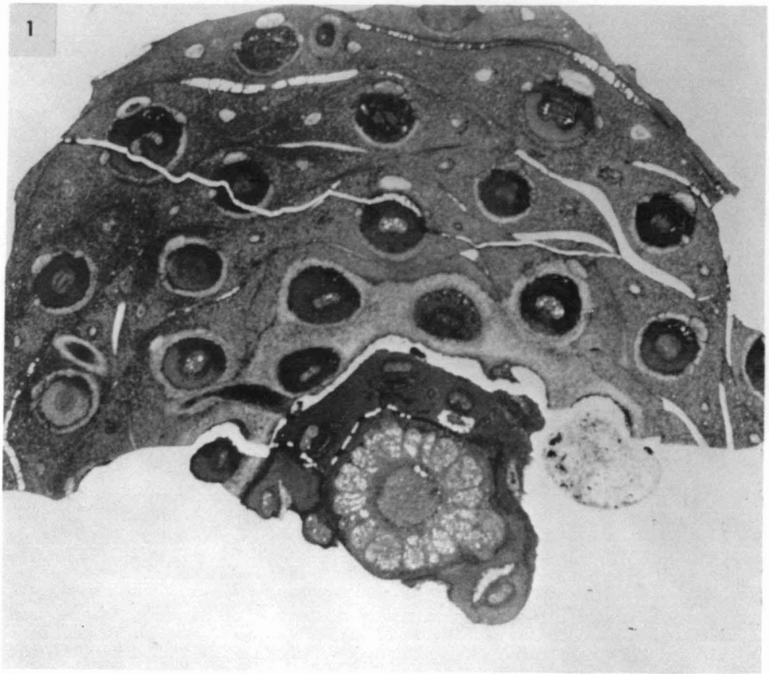

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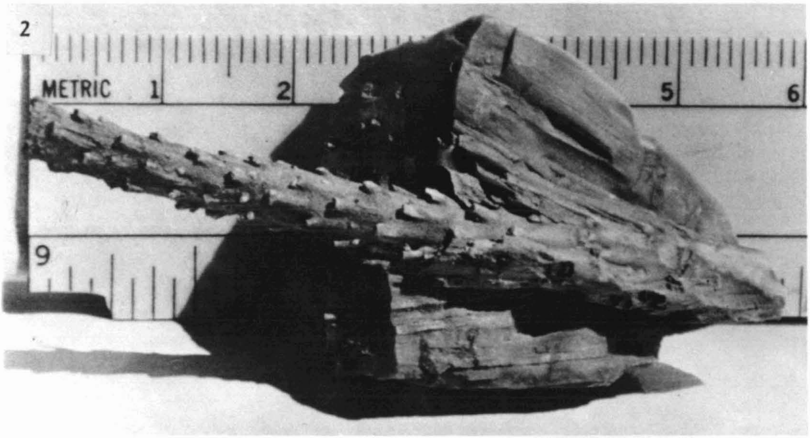

EXPLANATION OF PLATE II

	PAGE
Osmunda cinnamomea, Fossil Rhizomes	168

FIG. 1. Transverse section of rhizome, UMMP 52163, × 7.

FIG. 2. Decorticated specimen, UMMP 52163, × 1.8.

EXPLANATION OF PLATE III

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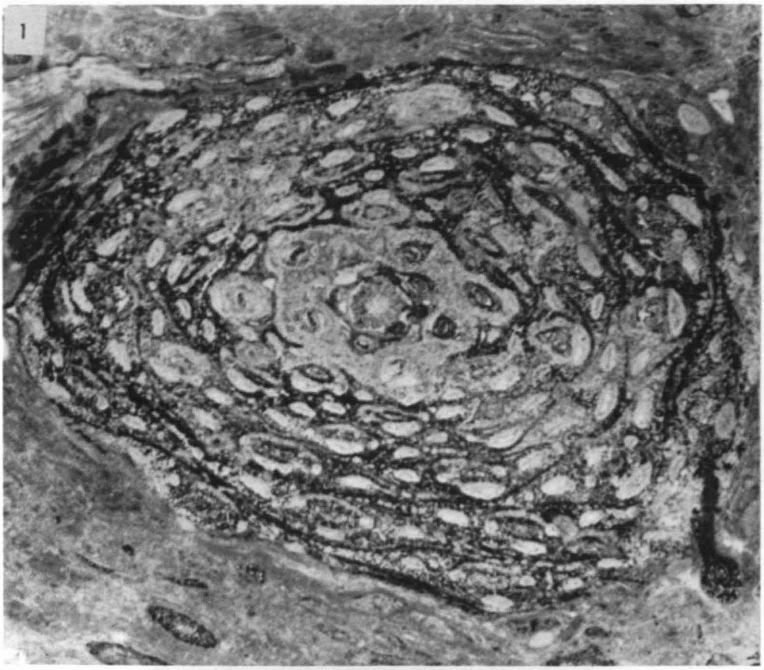
Osmunda precinnamomea sp. nov. 171

FIG. 1. Transverse section of rhizome, holotype, UMMP 52159, × 5.8.

FIG. 2. Transverse section of stele, holotype, UMMP 52159, × 22.

FIG. 3. Transverse section of crosier-shaped xylem strands, holotype, UMMP UMMP 52159, × 20.

PLATE III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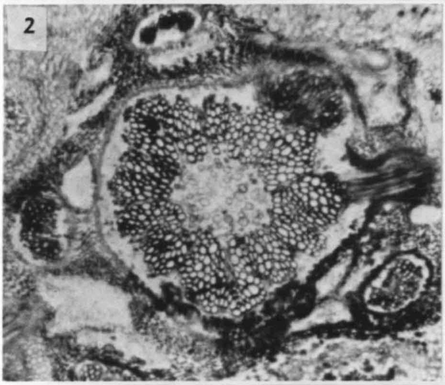
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3

PLATE IV

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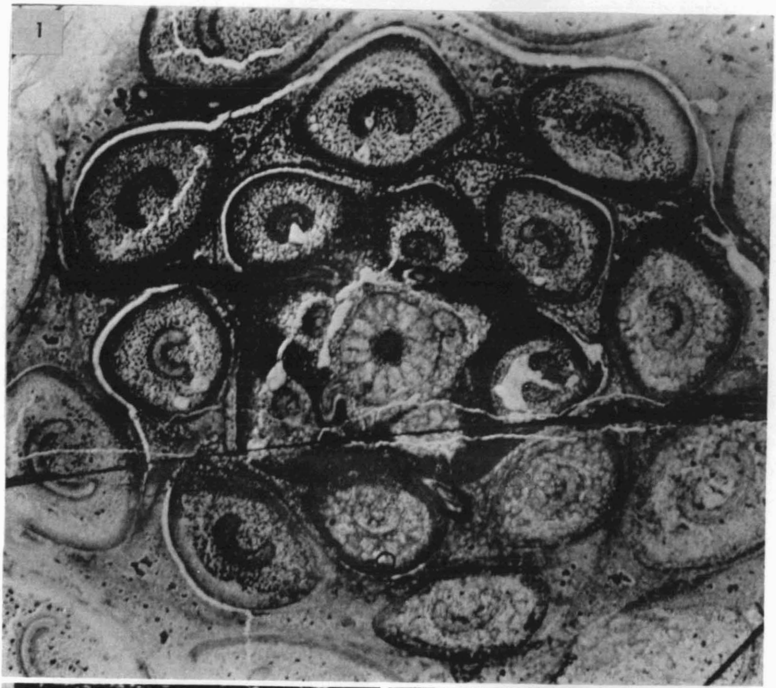

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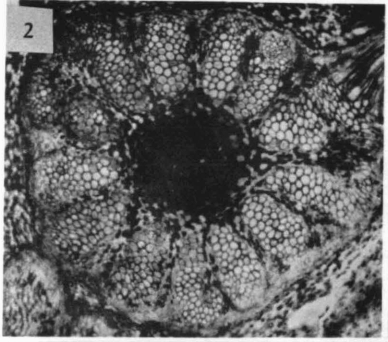

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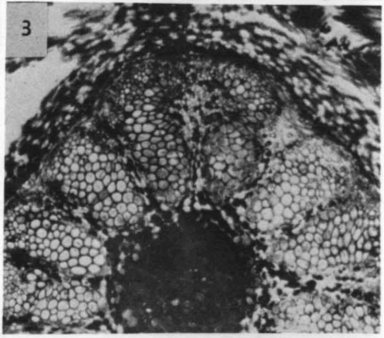

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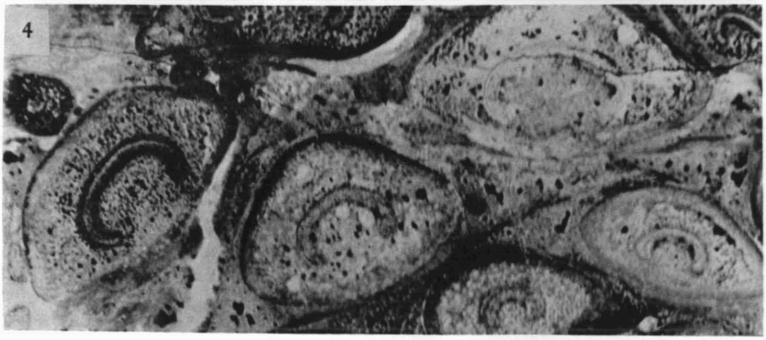

EXPLANATION OF PLATE IV

	PAGE
Osmunda arnoldii sp. nov.	181

FIG. 1. Transverse section of rhizome, holotype, UMMP 52161, × 4.6.

FIG. 2. Transverse section of stele ,holotype, UMMP 52161, × 17.

FIG. 3. Transverse section of crosier-shaped xylem strands, holotype, UMMP 52161, × 20.

FIG. 4. Transverse section of stipular petiole bases near middle of mantle, holotype, UMMP 52161, × 10.