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THE UNIVERSITY OF MICHIGAN

VOL. 23, No. 8, p. 105–169 (2 pls., 10 text-figs.) FEBRUARY 22, 1971

EVOLUTION OF THE FERN FAMILY OSMUNDACEAE BASED ON ANATOMICAL STUDIES

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ABSTRACT—The fern family Osmundaceae has only 16 living species, but nearly 100 fossil species have been named on the basis of various detached organs. Most important of these are 29 species based on petrified axes which provide a partial but substantial record of the family from the Late Permian to the present. These axes and some of the Recent species have been important in the formulation of concepts of stelar evolution and in our understanding of the evolutionary relationships of living ferns, but an intensive investigation of the evolution of the species of the Osmundaceae has never been made. Thus, the purpose of the present work is to investigate the phylogenetic interrelationships of the species of the family as interpreted from anatomical and morphological characters of their stems, leaf-bases, and roots.

Types or representative materials of 14 Recent and 21 fossil species were examined for variable characters. Information about nine additional species of petrified axes came from descriptions in the literature. These species were then analyzed by the ground plan method of multiple character correlation in three samples: (1) analysis of 43 species based on six characters, (2) analysis of 31 species based on 13 characters, and (3) analysis of 14 Recent species based on 18 characters. By this means the species were arranged according to lines of specialization, and when these lines are considered with respect to geologic time, nine groups of phylogenetically related species are resolved. Five of the groups are represented by the present-day genera and subgenera and their fossil members. Three groups are subdivisions of *Osmundacaulis,* and the remaining group includes the extinct protostelic forms.

The results show large gaps between these groups. This indicates that the fossil record of the family contains only a small number of those species that existed in the past. It is evident, however, that the modern species evolved from protostelic ancestors by intrastelar origin of a pith and subsequent (or concurrent) dissection of the xylem cylinder by leaf-gaps. The living species and most of the fossil forms are products of slight modifications of the dictyoxylic-siphonostele plan of organization. However, two of the groups of species became highly specialized in the Mesozoic but died out near the close of that era. The Recent genera *Todea* and *Leptopteris* are as distinct from one another as each is from the subgenera *Osmunda, Osmundastrum,* or *Plenasium,* but their fossil records are not sufficient to indicate their origin. *Osmunda, Osmundastrum,* and *Plenasium* were distinct lines of evolution in the Paleocene, and *Osmunda* and *Plenasium* are represented by foliage remains in the Cretaceous. No definite source for *Osmunda* and *Osmundastrum* can be determined, but *Plenasium* shares a number of characters with *Osmundacaulis atherstonei* and *O. natalensis,* both of which are from the Lower Cretaceous, and they may have evolved from forms similar to these species.

The Osmundaceae probably arose during Early Permian or Pennsylvanian time from forms similar to *Grammatopteris baldaufi* or *G. rigolloti,* but neither of these species can be considered a precursor of the family. Further, no ancestors of other fern taxa can be found among the known Osmundaceae.

Taxonomically, the protostelic forms are treated in the subfamily Thamnopteroideae with the remaining species forming the subfamily Osmundoideae.

CONTENTS

INTRODUCTION

THE OSMUNDACEAE is a primitive family of ferns that is assigned by most authorities to the Filicales. The family is important because it is intermediate between the Eusporangiatae and Leptosporangiatae in many respects and because it has the most extensive fossil record of any fern family (Arnold, 1964). Only sixteen living species are generally recognized, but nearly one hundred fossil forms have been named (Jongmans & Dijkstra, 1962). About fifty of the fossil species are based on compressed foliage, about twenty species are represented only by isolated spores and sporangia, and thirty species are represented by petrified stems. The last show that the Osmundaceae was a distinct line of evolution by Late Permian time, though sporangia that may be osmundaceous occur in the Coal Measures of Great Britain, France, and Asia Minor (Seward, 1910).

While the Osmundaceae is most often included in the Filicales, it has many features in common with the Eusporangiatae, and other characters that are intermediate between comparable eusporangiate and leptosporangiate conditions. Furthermore, several attributes are completely unique to the Osmundaceae and suggest long isolation of the family (table 1).

This peculiar mixing of characters and the great antiquity of the family has led to speculation that certain groups of "higher ferns" may have evolved from the Osmundaceae rather than from other ancient ferns. Besides the Osmundaceae, only the Marattiales, Gleicheniaceae, Schizaeaceae, and the Coenopteridales occur in the Late Paleozoic, and the Coenopteridales apparently did not survive into the Mesozoic. The Gleicheniaceae and Schizaeaceae are known in the Paleozoic only by sporangia and some questionable foliage remains (Arnold, 1964). Early marattiaceous ferns already show the specialized synangia that are characteristic of many of the Recent species, and the polycyclic stele of the Psaroniaceae suggests that members of this group were too specialized to have served as a probable source of other fern taxa. Thus, the Paleozoic Osmundaceae, which have a very simple protostelic organization, seem likely as a possible ancestral stock for certain other fern groups.

Clarification of the phylogenetic relationships within the Osmundaceae is basic to understanding the role of the family with regard to the possible derivation of other fern groups from it, and this treatment is an attempt to place the structurally preserved remains of the Osmundaceae in phylogenetic series with the present-day species. While relationships are interpreted mostly from comparative characters of rhizome anatomy, information from osmundaceous foliage, spores, and sporangia is used as additional source of evidence where available.

ACKNOWLEDGMENTS

This work represents a portion of a dissertation submitted to The University of Michigan in partial fulfillment of the requirements of the Ph.D. degree in Botany. The Department of

Botany and the Botanical Gardens of The University of Michigan are gratefully acknowledged for the financial support, supplies, and facilities they provided during the investigation. In addition, officials of the British Museum (Nat. Hist.), London, and the Department of Botany, University of Glasgow, Scotland, allowed me to examine fossil material in their collections. Dr. W. H. Hewitson, College of the Pacific, Stockton, California, contributed a large collection of rhizomes of Recent species remaining from his investigation (1962), and numerous other people supplied material of living species (table 2).

My special thanks are extended to the members of my doctoral committee for many constructive suggestions regarding my work. Throughout the study Dr. C. A. Arnold has been a reliable source of aid and encouragement and I also wish to thank Dr. W. H. Wagner for allowing me to draw upon his knowledge of living ferns and for help in applying multiple character correlation. I am deeply indebted to my wife Susan for the many sacrifices she made to facilitate my work.

CLASSIFICATION

The living species of the Osmundaceae are placed in three genera: *Leptopteris,* with six species; *Osmunda,* with nine species; and *Todea,* which is monotypic. *Leptopteris* was originally treated as a subgenus of *Todea,* but Presl (1845) separated the two. Although some workers favor the original grouping (Seward &

TABLE 1—COMPARISON OF LIVING OSMUNDACEAE AND OTHER RECENT FERN FAMILIES

Osmundaceous Character	Other Taxa Having Character
1) Massive photosynthetic thallus with thick midrib (Bower, 1926).	Marattiaceae and primitive leptosporangiate ferns.
2) Gametangia superficial (Bower, 1926).	Leptosporangiatae.
3) Archegonia borne in two parallel rows, one to either side of the midrib (Atkinson & Stokey, 1964, p. 66).	None
4) Archegonia with six tiers of neck cells (Sporne, 1962, p. 144).	Intermediate between eusporangiate and leptosporangiate situations.
5) Large number of spermatocytes produced per antheridium (Bower, 1926).	Intermediate between eusporangiate and leptosporangiate situations.
6) Spores chlorophyllous.	Various Grammitidaceae and Hymenophyllaceae (also *Equisetum*).
7) Spores trilete.	Various fern taxa, primitive and otherwise.
8) Dehiscence of antheridium by forcible ejection of cap cell (Atkinson & Stokey, 1964).	Primitive Leptosporangiatae.
9) Spore germination bipolar (Atkinson & Stokey, 1964).	None.
10) Number of spores per sporangium 128–512 (Bower, 1926).	Intermediate between eusporangiate and leptosporangiate situations.
11) Embryo prone (Bower, 1926).	Leptosporangiatae.
12) Quadrants of embryo situated with respect to thallus but not to archegonium (Bower, 1926).	Intermediate between eusporangiate and leptosporangiate situations.
13) Embryo persisting in globular stage (Bower, 1926).	Eusporangiatae.
14) Shoot apex, foot, root, and leaf not referable to distinct portions of embryo (Bower, 1926).	Eusporangiatae.
15) Persistence of endodermis into mature parts of sporophyte, rather than disappearance after juvenile stage (Bower, 1926).	Leptosporangiatae.
16) Stipular expansions on petiole base (Bower, 1926).	Eusporangiatae, Plagiogyriaceae (also *Matteuccia pensylvanica*).
17) Transverse commissure on stipule in *Leptopteris* and *Todea* (Bower, 1926).	Eusporangiatae (also Cycadaceae).
18) Indefinite segmentation of leaf-blade from single row of marginal initials (Bower, 1926).	Marattiaceae.
19) Root initials varying between:	
a) tetrahedral, and	Leptosporangiatae.
b) four, truncated prismatic cells, (Bower, 1926).	Marattiaceae.
20) Sporogenous cells:	
a) cubical, or	Eusporangiatae.
b) tetrahedral (Bower, 1926).	Leptosporangiatae.
21) Sporangium not always referable to single initial (Bower, 1926).	Intermediate between eusporangiate and leptosporangiate situations.

Ford, 1903; Tansley, 1907), Presl's classification is preferred here. *Leptopteris* has filmy fronds, while the lamina of *Todea barbara* is coriaceous. Sporangia are borne on the abaxial surface of typical vegetative fronds in both genera. *Osmunda* differs in this respect, the sporangia being attached to specialized pinnae that lack a lamina. The degree of fertile and sterile frond dimorphism varies from complete —the entire fertile frond consisting of specialized pinnae—to incomplete—the fertile frond bearing mainly typical vegetative pinnae with a few fertile pinnae inserted in apical, medial, or basal position on the rachis. *Osmunda* is traditionally divided into the subgenera *Osmunda, Osmundastrum,* and *Plenasium,* on the basis of frond morphology. Species of the subgenus *Osmunda* have bipinnate fronds while the fronds are once-pinnate in *Plenasium* and *Osmundastrum.* Pinnules in *Osmundastrum* are pinnatifid while the margins of *Plenasium* pinnules are entire to coarsely serrate. There are also differences in venation (Hewitson, 1962). Recent evidence from the fossil record indicates that the subgenera of *Osmunda* have been separate lines of specialization since the Paleocene (Miller, 1967).

Fossil forms have always been assigned to Recent taxa where possible, but because of lack of knowledge of the structure of many of the living species, most of the petrified remains of the Osmundaceae were originally assigned to form genera. Recent work has permitted the transfer of a number of fossil species to living genera (Hewitson, 1962; Chandler, 1965; Miller, 1967), but most of the petrified organs belonging to the family remain in form genera. *Osmundacaulis,* a *nomen novum* replacing *Osmundites* Unger, which is invalid (Miller, 1967), includes rhizomes or trunks or their parts which bear structural resemblance to the present-day species but which cannot be referred to any of the Recent genera. Certain ancient species differ significantly from the more recent forms in hav-

Table 2—Source of Materials of Recent Species

Rhizomes:		
Leptopteris fraseri	M. Tindale	Sydney, N.S.W.
L. hymenophylloides	G. Baylis	Dunedin, New Zealand
	C. Quinn	Auckland, New Zealand
L. superba	G. Baylis	Dunedin, New Zealand
	C. Quinn	Auckland, New Zealand
L. wilkesiana	J. Parham	Suva, Fiji
Osmunda regalis	C. Miller	Florida and Michigan, U.S.A.
O. japonica	T. Chung	Seoul, Korea
	S. Kokawa	Osaka, Japan
O. lancea	S. Kokawa	Osaka, Japan
O. claytoniana	C. Miller	Michigan, U.S.A.
O. cinnamomea	C. Miller	Florida and Michigan, U.S.A.
O. banksiaefolia	K. Iwatsuki	Kyoto, Japan
O. javanica	N. Seneviratne	Gurutalawa, Ceylon
Todea barbara	M. Tindale	Sydney, N.S.W.

Spores (my number in parentheses):

Osmunda regalis, Indiana, Gates #61 (1-17-63-2)
Osmunda regalis, Texas, Thorp in 1929, (1-17-63-3)
Osmunda regalis, Michigan, Ehlers #45 (1-8-63-8)
Osmunda regalis, Brazil, Mexia #5169 (1-8-63-6)
Osmunda lancea, Japan, Copeland #1318 (1-17-63-1)
Osmunda claytoniana, location unknown, Koelz #1987 (1-8-63-2)
Osmunda claytoniana, Phunkia, India, Flemming #87 (1-8-63-7)
Osmunda claytoniana, Michigan, Voss #6895, (1-15-63-4)
Osmunda claytoniana, Wisconsin, Copeland #1315 (1-15-63-3)
Osmunda claytoniana, Virginia, Tidestrom #4584 (1-15-63-2)
Osmunda claytoniana, Quebec, Canada, Storer #268 (1-15-63-1)
Osmunda cinnamomea, Florida, McFarlin #3313 (1-17-63-6)
Osmunda cinnamomea, Indiana, Gates #1058 (1-17-63-5)
Osmunda cinnamomea, Michigan, Davis in 1891 (1-8-63-1)
Osmunda cinnamomea, Michigan, Voss #8431 (1-17-63-4)
Osmunda banksiaefolia, Luzon, Philippines, Copeland #12298 (1-17-63-8)
Osmunda banksiaefolia, Luzon, Philippines, Copeland #22472 (1-17-63-1)
Osmunda javanica, Kwangtung, China, Tsang #21186 (1-8-63-3)
Osmunda vachellii, Canton, China (introduced), McClure #18580 (1-8-63-5)

TABLE 3—ASSOCIATION OF *Osmundacaulis* WITH *Cladophlebis*

Osmundacaulis	*Cladophlebis*	*Horizon*	*Location*
O. kolbei[1]	*C. denticulata*	Lower Cretaceous	South Africa
O. kolbei	*C. browniana*	Lower Cretaceous	South Africa
O. patagonica[2]	*C. patagonica*	Upper Jurassic	Argentina
O. dunlopi[3]	*C. denticulata*	Jurassic	New Zealand
O. gibbiana[3]	*C. denticulata*	Jurassic	New Zealand
O. herbstii[4]	*Cladophlebis* sp.	Upper Triassic	Argentina

1) Kidston & Gwynne-Vaughan, 1910.
2) Archangelsky & de la Sota, 1962.
3) Kidston & Gwynne-Vaughan, 1907.
4) Archangelsky & de la Sota, 1963.

ing a protostele, and these species have been placed in *Bathypteris, Chasmatopteris, Iegosigopteris, Petcheropteris, Thamnopteris,* and *Zalesskya.* In addition, one Permian species, which is known only by its leaf-bases, is classified in the genus *Anomorrhoea. Itopsidema* includes one siphonostelic species from the Triassic, but its relationship to the Osmundaceae is questionable.

In addition to these taxa based on petrified axes and leaf-bases, over forty species represented only by foliage have been referred to *Osmunda* (table 4). *Todites* includes fronds from Mesozoic sediments that are similar to those of *Todea* and bear osmundaceous sporangia. Furthermore, some species of *Cladophlebis* probably also belong to the Osmundaceae. This genus includes sterile foliage from the Mesozoic; and certain species frequently occur in association with *Osmundacaulis* of that time (table 3), but no organic connection between them has been found.

Fossil spores and sporangia that are more or less similar to those of the living species have been referred to the Recent genera or to numerous form genera.

HISTORY OF INVESTIGATION

Early investigations of the anatomy of the Osmundaceae dealt with the arrangement, ontogeny and phylogeny of the pith and vascular tissues, but little attention was given to structural features useful in distinguishing between the species. The first author to deal with the anatomy of osmundaceous stems was DeBary (1884) who envisoned a series of sympodial "fibro-vascular" strands arranged in a ring around the pith as in the conifers, each strand branching to form leaf-traces but otherwise running independently through the stem. Van Tieghem & Douliot (1886) described the osmundaceous stele as a "medullated monostele," one in which the pith formed ontogenetically by "expansion" of a single, central, "fibrovascular" strand. In 1895, Zenetti demonstrated the reticulate nature of the xylem cylinder in *Osmunda regalis* and speculated upon the evolution of such a stele from a "medullated monostele" by dissection of the xylem cylinder by leaf-gaps. Jeffrey (1899) took exception to Van Tieghem & Douliot's (1886) postulated ontogenetic intrastelar origin of the pith and later (1902) extended his opinion to phylogenetic origin as well. He believed that the "medullated monostele" of Van Tieghem was derived from an amphiphloic siphonostele by degeneration of the internal phloem and endodermis. Accordingly, Jeffrey (1902) postulated the evolution of the living Osmundaceae from a dictyostelic form, such as *Osmundacaulis skidegatensis,* and interpreted *Osmunda cinnamomea,* which has an internal endodermis, as representing an intermediate stage. Faull's (1901) study of *Osmunda regalis, O. claytoniana, O. cinnamomea, Leptopteris superba,* and *Todea barbara,* and his (1910) investigation of young sporophytes of *Osmunda cinnamomea* brought forth evidence supporting Jeffrey's concept and supplemented it by noting the occurrence of internal phloem near the branching region of certain plants of *O. cinnamomea.* Seward & Ford (1903), who examined stems of *Leptopteris hymenophylloides, L. superba,* and *Todea barbara,* thought that these species were primitive among the living forms and that the stele of *Osmunda cinnamomea* represented a specialization of an ectophloic condition. Material of their species displayed somewhat confluent xylem strands suggestive of Recent origin from an ancestor having an ectophloic siphonostele with the xylem cylinder uninterrupted by leaf-gaps.

At this time structural details of only three fossil stems of the Osmundaceae were known. These were *Osmunda dowkeri, O. iliaensis* [=*Osmundites schemnicensis* (Pettko) Unger], and *Osmundacaulis skidegatensis.* The first two are similar to the living species and occur in the Eocene and Miocene-Pliocene respectively; but *O. skidegatensis,* a dictyostelic form from the Lower Cretaceous, offered overwhelming support for the "extrastelar" school of thought.

Between 1907 and 1914, Kidston & Gwynne-Vaughan published a series of five memoirs on petrified osmundaceous axes, naming two new species and reinvestigating several other previously described forms whose internal structure, and thus their relationship to the Osmundaceae, was unknown. Five of these were from the Upper Permian of Russia. The Russian forms are the most ancient and the least specialized known in the family; and when they are considered with the other species treated by Kidston & Gwynne-Vaughan, they offer strong evidence for the derivation of the present-day species from protostelic ancestors by intrastelar origin of the pith and subsequent dissection of the xylem cylinder of an ectophloic siphonostele by leaf-gaps, a view that is widely accepted today (Posthumus, 1924b; Bower, 1926).

Lack of adequate information about the comparative anatomy of the Recent species has hindered investigation of the relationships between the fossil species and the living ones. Until recently, more was known about the internal structure of the fossil material than the extant species, and comparisons of one with the other were made only in the broadest sense. (Arnold, 1964). While subsequent discoveries of petrified stems have doubled the number of species known to Kidston & Gwynne-Vaughan, the only addition to our knowledge of the living species was the description of the stele of *Osmunda javanica* by Posthumus (1924b).

Hewitson's (1962) survey of thirteen of the Recent species marked the first significant attempt to find characters that would be useful in comparing the extant and extinct forms. He concluded that the arrangement of sclerenchyma tissues in the stipular petiole bases is the most diagnostic feature and that such characters as the number of strands of stem xylem and the number of leaf-traces in the cortex, as viewed in transverse stem sections, are not in themselves diagnostic but are useful as correlative evidence. Hewitson (1962) also noted that the outer cortex in rhizomes of *Osmunda* is constructed entirely of very long, thick-walled fibers while in *Leptopteris* and *Todea* these cells occur only around departing leaf-traces with the bulk of the tissue consisting of relatively short sclereids. Bower (1926) and Chandler (1965) also point out that in *Todea* and *Leptopteris* the margins of the stipular expansions are joined across the adaxial face of the petiole base by a transverse commissure, and this structure is lacking in *Osmunda*. *Todea* differs from *Leptopteris* in having strands of sclerenchyma scattered in the inner cortex of the petiole base, while such strands are absent in *Leptopteris*. Within the genus *Osmunda*, species of the subgenus *Plenasium* differ from those of the subgenera *Osmunda* and *Osmundastrum* in having leaf-traces that are deeply curved at their point of separation from the stele and have two distinct groups of protoxylem elements at this location. In species of the two latter subgenera the xylem of the leaf-trace diverges from the stem xylem as an oblong strand with a single protoxylem group. *Osmunda* and *Osmundastrum* are most easily distinguished from each other on the basis of the pattern formed by thick-walled fibers in the outer cortex of the petiole base. In the subgenus *Osmunda* at some level in the stipular region these cells are organized in two lateral clusters while in *Osmundastrum* two lateral clusters and one abaxial mass occur at all levels of section. Furthermore, *Osmunda cinnamomea* typically has an internal endodermis which is lacking in all Recent species of the subgenus *Osmunda*.

These comparative characters and others to be mentioned later have enabled investigators to distinguish between the living genera of the Osmundaceae, and in 1965 Chandler transferred *Osmundacaulis* (*Osmundites*) *dowkeri* to *Osmunda*. Since then seven other species of petrified rhizomes have been assigned to *Osmunda, Osmundastrum,* and *Plenasium* showing that these subgenera existed as independent lines of evolution as early as the Paleocene (Miller, 1967).

MATERIALS AND METHODS

Type material of 22 of the 32 previously described species of petrified stems and (or) petiole bases were re-examined during the course of this investigation. Whenever the original or later preparations were not available, special preparations were made for me by curators of the various collections. The 13 species in the Kidston Collection were examined in the Department of Botany, The University of Glasgow, Scotland, while six other species were studied in the British Museum (Nat. Hist.), London, England. The remaining species were studied from specimens and preparations in the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan, or from loans made to the Museum.

Materials of 14 of the 16 Recent species were obtained for reference and comparison with the fossils. Much of this was generously contributed by Hewitson at the completion of his (1962) investigation. These specimens were already embedded in celloidin. Additional material (table 2) was acquired by personal collection of the three North American species and from foreign collectors. Living plants were maintained in the greenhouses of The University of Michigan Botanical Gardens until they could be prepared for sectioning.

Axes of the living plants were treated according to the method of Hewitson (1962). Petiole bases were removed from the stems, and they and the stems were cut into sections 0.5–1.0 cm long. The pieces were then softened for two weeks in a 1:1 solution of 48% hydrofluoric acid and 98% ethyl alcohol, washed in tap water for 24 hours, dehydrated in an ethyl alcohol series, and embedded in celloidin (Method 2 of Johansen, 1940). Sections were cut on a sliding microtome at 20 to 40 microns depending on the friability of the material. They were stained in 1% aqueous solution of Safranin "O" and 0.5% Fast Green in absolute alcohol and mounted in Canada Balsam.

Spores of certain Recent species (table 2) were obtained from specimens in The University of Michigan Herbarium, and voucher labels were attached to the herbarium sheets of the specimens used. The sporangia were washed in running water, softened and wetted in 5% KOH for two minutes at 90°C, and strained through a wire screen to separate spores from sporangia. The spores were then acetolyzed for three minutes at 90°C, mounted unstained in glycerine jelly, and the cover slips sealed with diaphane. A slide of each specimen has been placed in the Palynological Collection of the Department of Botany, The University of Michigan.

ANATOMY AND MORPHOLOGY

Structurally, the Osmundaceae is a highly variable group. The majority of the species have a parenchymatous pith, but at least four have a column of tracheids occupying the center of the stele. Most species have external phloem only, but one has internal as well as external phloem. Likewise, the endodermis in many species is external to the stele; but several species have external and internal endodermal layers, and in at least four species these cylinders connect through leaf-gaps. The cortex of osmundaceous stems generally consists of an inner parenchymatous layer and an outer sclerotic layer, but one species has a homogeneous cortex. Petiole bases of most species have pronounced stipular expansions, but they are lacking in one species. No tissue has the same construction in all members of the family; every tissue has undergone some evolutionary change.

Stem

Stele. — **Tissue construction.** Protostelic species, all of which are extinct, have stems that contain a central column of relatively short tracheids surrounded by a cylinder of longer tracheids that are more typical of fern metaxylem. Since the central column is well differentiated from the outer cylinder, and since the central xylem shows evidence of evolutionary change toward pith tissue, it is treated here descriptively as a tissue distinct from the outer cylinder metaxylem.

The cells of the central metaxylem tissue are large-diameter tracheids whose walls bear elliptical or oval pits. In *Zalesskya gracilis* the tracheids are ten or more times longer than broad (pl. 2, fig. 10). Several vertical series of elliptical pits occur on each wall; but the files are not in strict vertical alignment, so the arrangement is termed "irregular scalariform." In contrast, the central xylem tracheids of *Thamnopteris* and *Zalesskya diploxylon* are two to five times as long as broad (pl. 2, fig. 9), their pits are oval, and the arrangement of pits results in a "reticulate" pattern.

It is of particular interest that in *Thamnopteris kidstoni* parenchyma cells occur singly or in clusters near the periphery of the central xylem tissue (Zalessky, 1924). They are the same size and shape as the tracheids but lack pits. The association of these cells with the short central xylem tracheids is important evidence of the intrastelar origin of a pith in the Osmundaceae.

Central xylem is preserved completely to the center of the stem in only four species. In other cases a zone of decay occurs in this tissue; and while typical central xylem tracheids border the vacant zone, other cell types may have occurred within. The fact that the central region

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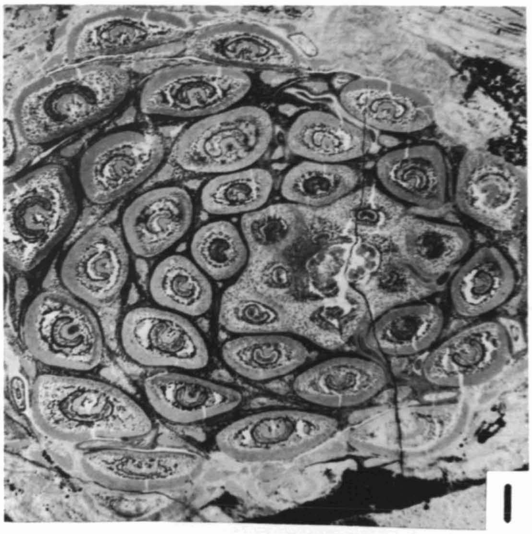
EXPLANATION OF PLATE 1

FIGS. *1, 2*—*Osmunda pluma* Miller. *1,* transverse section of rhizome, × 4½, holotype, UMMP 52157. *2,* transverse section of stele, × 24, holotype, UMMP 52157.

3, 4—*Osmunda precinnamomea* Miller. *3,* transverse section of rhizome, × 5 1/10, holotype, UMMP 52159. *4,* transverse section of stele, × 30, holotype, UMMP 52159.

5, 6—*Osmunda arnoldii* Miller. *5,* transverse section of rhizome, × 4½, holotype, UMMP 52161. *6,* transverse section of stele, × 20, holotype, UMMP 52161.



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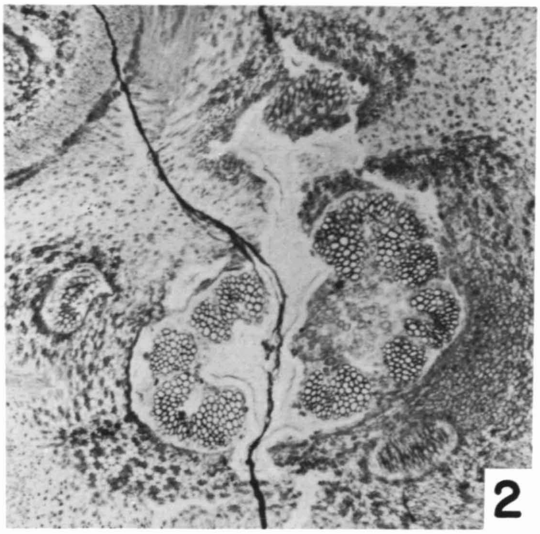

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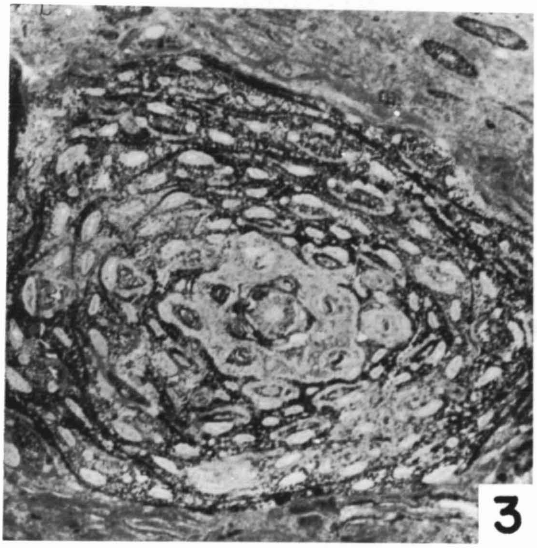

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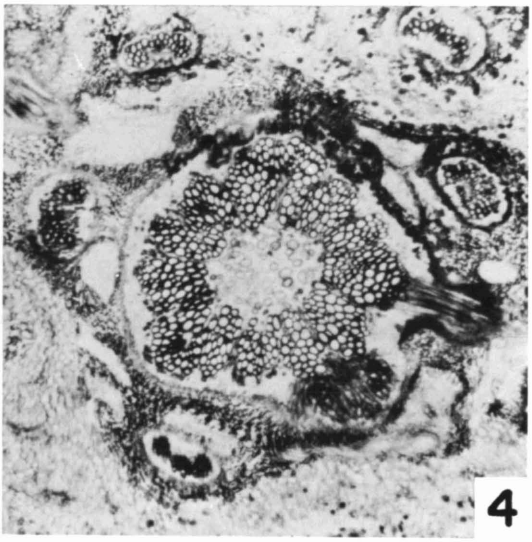

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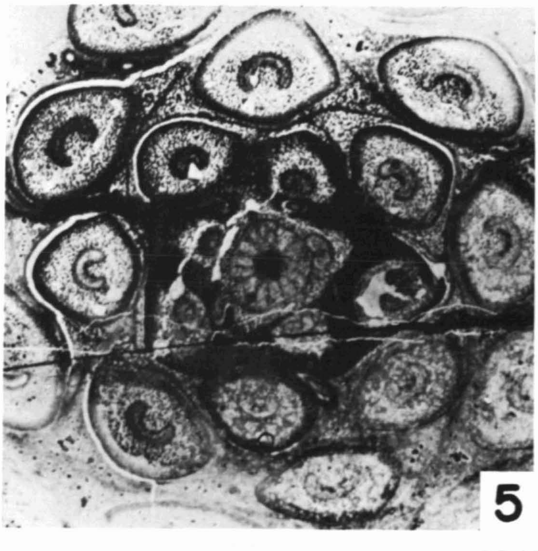

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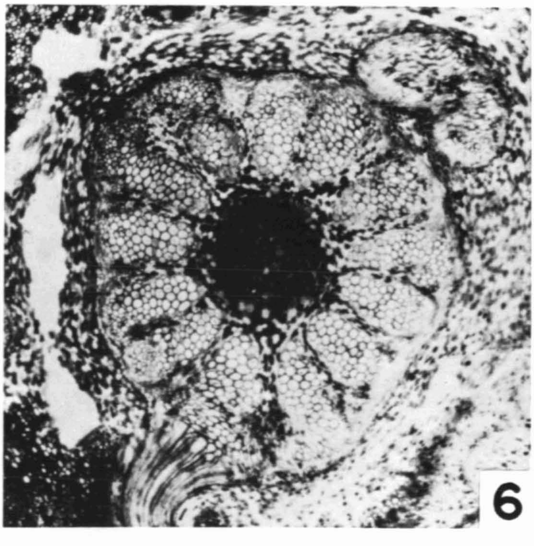

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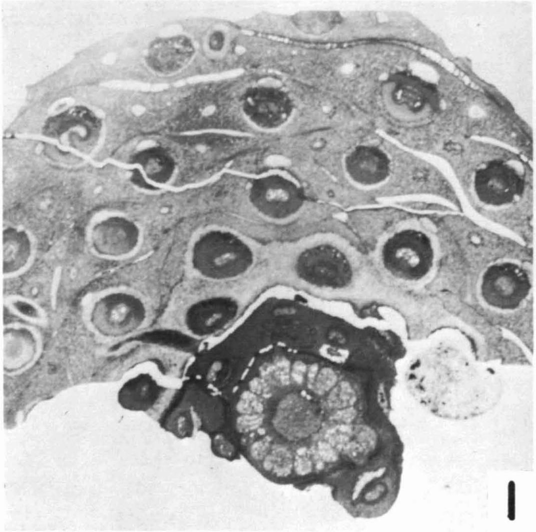
PLATE 1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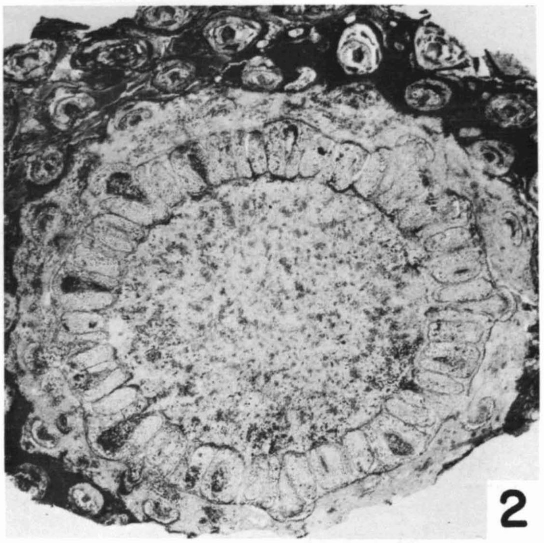
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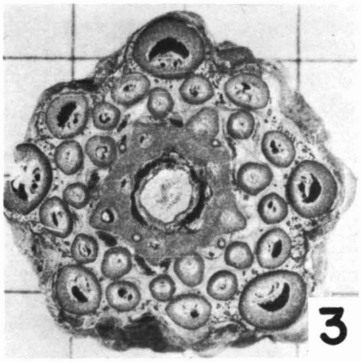
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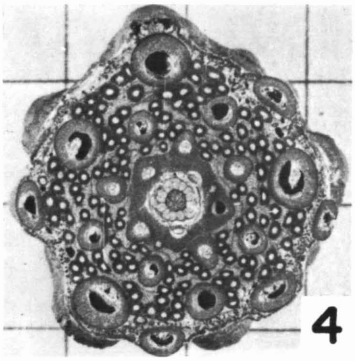
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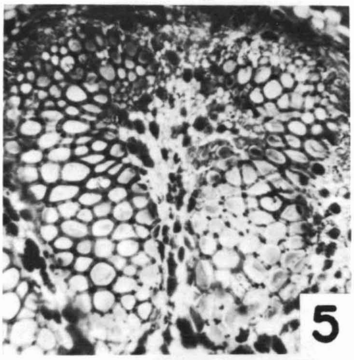
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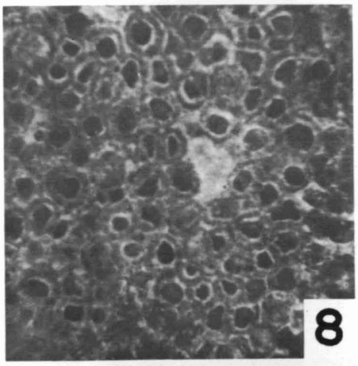
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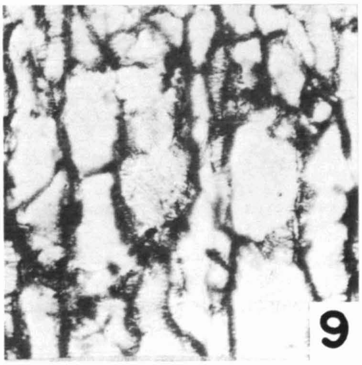
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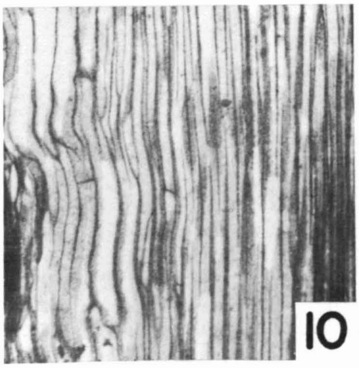
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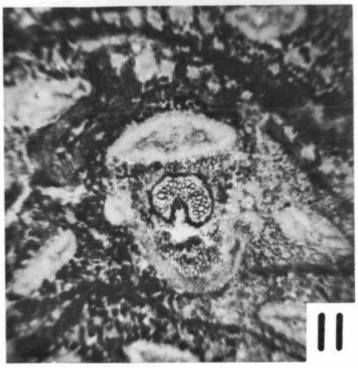
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PLATE 2

had decayed may indicate a structural difference.

Kidston & Gwynne-Vaughan (1908) believed that the central metaxylem tracheids were specialized for water storage as compared with the longer tracheids of the outer metaxylem that were adapted for conduction. Numerous pits on the cell walls of the central metaxylem tracheids would prevent any significant water retention within these cells. On the other hand, their shorter length would place more cross walls within a given distance than in the case of longer tracheids, so the central xylem elements may be more reasonably viewed as less efficient water conductors than the tracheids of the outer metaxylem. Nonetheless, there is no evidence that the central tracheids served any storage function.

The pith is most often constructed of parenchyma cells that are isodiametric or up to three times longer than broad. The cell walls are usually thin and bear numerous fields of simple pits. While the cells are arranged in approximately lengthwise rows, enough cells occur between the rows to indicate a strong tendency for derivatives of the initials to divide laterally as well as longitudinally. In some species, particularly *Osmunda javanica,* lateral division was minimal. In this case axial rows are regular, and certain cells have transverse end walls while in others they are more oblique. The pattern formed by these cells in longitudinal section is suggestive of their ontogenetic derivation by transverse septation of a fusiform initial (Hewitson, 1962).

Sclerenchyma occurs in the pith of many species. Most often, the sclereids are stone cells that form in the normal ontogenetic sequence by gradual increase in wall thickness of parenchyma cells some distance behind the growing point (pl. 2, fig. 8). The pith of such stems is entirely parenchymatous near the shoot apex, entirely sclerotic several centimeters behind it, and has a transition region of parenchyma and stone cells in between.

In some stems, certain cells of the pith are thick-walled, while others remain thin-walled. Both cell types have the same size and shape, and there do not seem to be more thick-walled cells in sections farther from the shoot apex. In *Osmundacaulis skidegatensis* such thick-walled cells are concentrated opposite leaf-gaps but some are scattered singly or in clusters throughout the pith (pl. 2, fig. 2). The clusters near the leaf-gaps and incipient leaf-traces follow the traces out through the stem and form a small cluster of sclerotic cells in the concavity (text-fig. 1D). Similar cells occur in *O. kolbei.*

Fibers may also occur in the pith of certain species. In *Osmunda cinnamomea* they are common in stems having a dissected siphonostele, and appear to connect upward through the leaf-gap with the cluster of similar cells that is axillary to each leaf-trace in the inner cortex. A similar situation occurs in *Osmundacaulis natalensis* and possibly in *O. atherstonei.*

The pith of certain species may also contain tracheids. Hewitson (1962) found them occasionally in *Osmunda javanica* and was able to trace them in serial sections to nearby xylem strands. In *Osmundacaulis kolbei* there are enough tracheids in the pith to warrant describing the tissue as a "mixed pith." The tracheids are of the *Thamnopteris*-type and are probably a primitive condition that has persisted in the genome of this species. Anomalous

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EXPLANATION OF PLATE 2

FIG. *1*—*Osmunda cinnamomea* L. Transverse secton of fossil rhizome, × 5½, paratype, UMMP 52163.

2—*Osmundacaulis skidegatensis* (Penhallow) Miller. Transverse section of axis, × 2½, "peel" of holotype, UMMP 52164.

3, 4—*Leptopteris wilkesiana* (Brack.) Christ. *3,* transverse section of trunk near apex showing few roots in mantle, × $1\frac{7}{10}$. *4,* transverse section of trunk near base showing numerous vertically running roots in mantle, × $1\frac{9}{10}$.

5—*Osmunda arnoldii* Miller. Transverse section of xylem strands showing "*Plenasium*-type" leaf-trace formation, × 48, holotype, UMMP 52161.

6–8—*Osmunda pluma* Miller. *6,* transverse section of petiole base showing arch of thick-walled fibers in sclerenchyma ring, × 20, holotype, UMMP 52157. *7,* transverse section of petiole base just above stipular region showing two lateral masses of thick-walled fibers in sclerenchyma ring, × $20\frac{7}{10}$, paratype, UMMP 52158. *8,* transverse section of pith showing thick-walled sclereids, × 60, paratype, UMMP 52158.

9—*Thamnopteris schlechtendalii* (Eichwald) Brongniart. Longitudinal section of central xylem showing short tracheids (from Kidston & Gwynne-Vaughan, 1909, pl. III, fig. 11), × 62½.

10—*Zalesskya gracilis* (Eichwald) Kidston & Gwynne-Vaughan. Longitudinal section of central xylem showing long tracheids (from Kidston & Gwynne-Vaughan, 1908, pl. II, fig. 4), × $23\frac{3}{10}$.

11—*Osmunda precinnamomea* Miller. Transverse section of petiole base showing three patches of thick-walled fibers in sclerenchyma ring, × 20, holotype, UMMP 52159.

tracheids have been reported in the pith of *Osmunda regalis* (Gwynne-Vaughan, 1914), and they have been induced experimentally in *O. regalis* and *Todea barbara* (Wardlaw, 1946).

Tracheids of the outer metaxylem cylinder are long, thick-walled cells that are polygonal in transverse outline. They are narrower (30–150 microns) than tracheids of the central metaxylem and are generally more than twenty times longer than broad. The tracheids have one to six, but most often, two or three, vertical series of scalariform pits on each wall, and the vertical alignment of each series is regular. The pits themselves are elongated transversely to the long axis of the cell and those of a given vertical series may be opposite or subopposite to, or alternate with, those of the adjacent vertical series.

The outer metaxylem cylinder typically consists of tracheids alone, with no mixing of parenchyma cells (pl. 1, figs. 2, 4, 6). The cylinder may be from five to fifty-five cells thick in the radial dimension depending on the species and degree of maturity.

Those elements most frequently referred to as protoxylem in osmundaceous stems are in reality early-formed metaxylem tracheids because they have one vertical series of scalariform pits on each wall and are not conspicuously stretched. True protoxylem tracheids, those with annular or helical wall thickenings, can be located in Recent material near the shoot apex, but in more mature parts of the stem these cells become obliterated by growth of the cells around them. The early formed metaxylem elements develop immediately around the protoxylem elements and serve as a guide to the location of these cells where they are not visible.

Clusters of protoxylem elements occur in the xylem cylinder only below points of leaf-trace departure and have no protoxylem lacuna in association. These clusters may be mesarch or endarch depending on the species and the manner of leaf-trace formation. Frequently, an island of parenchyma cells of the xylem sheath occurs adaxial to a given protoxylem cluster just below the point of leaf-trace departure, and this situation is not to be confused with the occurrence of parenchyma mixed with the tracheids in the xylem of some ferns.

The xylem sheath consists of thin-walled cells that are about 15 microns in diameter and about 75 microns in length. These cells occur in intimate association with metaxylem tracheids forming a narrow cylinder around the metaxylem in protostelic stems and around each xylem strand in dictyoxylic stems. The tissue may be up to six cells thick, but in dictyoxylic stems the sheath generally becomes thinner toward the adaxial side of each xylem strand and may be represented by a few scattered cells.

Phloem consists of three tissues, the metaphloem, the "porose layer" or "quergestrecken Zellen," and the protophloem. These tissues consist of sieve cells alone that are typically thin-walled with sieve areas on all surfaces. Protein granules occur against the wall near sieve areas in extant species (Janczewski, 1880); and because they appear as bright dots in transmitted light at high magnification, they are often described as "globules brillant."

Sieve cells of the metaphloem are long cells with rounded ends that overlap the tips of cells above and below. The metaphloem of protostelic stems forms a continuous cylinder several cells thick around the xylem sheath. In dictyoxylic stems, however, sieve cells of the metaphloem are concentrated in wedges opposite xylic gaps and extend inward for a short distance between adjacent xylem strands. The clusters are connected laterally around the xylem cylinder by a thin layer of sieve cells to form a continuous cylinder. Sieve cells may also occur adaxial to xylem strands in certain species, as near branching regions of certain stems of *Osmunda cinnamomea,* and in *Osmundacaulis skidegatensis* the internal metaphloem forms a continuous cylinder that connects with the outer metaphloem layer through leaf-gaps.

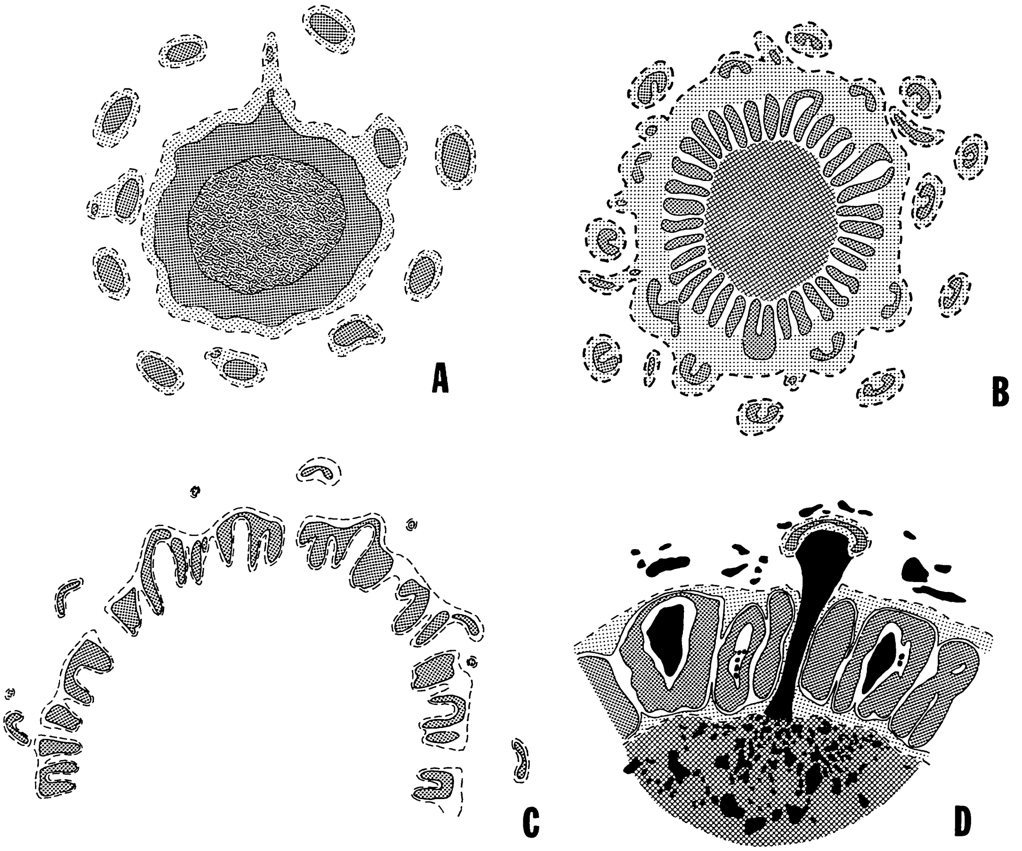
Cells of the protophloem occur just inside the pericycle at the periphery of the stele. They are small cells whose longitudinal axes have no definite orientation with respect to that of the stem. They are visible in sections made near the shoot apex but are frequently crushed in more mature parts of the stem. Protophloem is always external to the xylem cylinder and does not occur with internal phloem in amphiphloic or dictyostelic stems.

Between the protophloem and metaphloem occurs a narrow layer of cells that combine characters of the two. These cells have been called the "porose layer" (Seward & Ford, 1903) and "quergestrecken Zellen" (Zenetti, 1895). These sieve cells are larger than those of the protophloem, but like them they lack definite vertical orientation. They are more resistant to crushing than cells of the protophloem, but less resistant than sieve cells of the metaphloem. Proper classification of this tissue is the subject of some controversy (Seward & Ford, 1903; Hewitson, 1962). Distinction between protophloem and metaphloem is based on whether or not certain elements mature before or after shoot elongation has occurred (Esau, 1953); and in osmundaceous stems, where seasonal growth in length is small, some cells probably mature during shoot elongation. Thus, I prefer to consider this tissue as "transitional phloem," that is ontogenetically intermediate between protophloem and metaphloem. The pericycle in osmundaceous stems is a narrow layer of cells at the periphery of the stele just inside the outer endodermis. These cells are similar in morphology and arrangement to sieve cells of the protophloem but lack sieve areas on their walls. Most often the pericycle is crushed in mature parts of the stem and appears, with the protophloem and transitional phloem, as a cylinder of tabular cells between the endodermis and the metaphloem. The endodermis in most species is a continuous cylinder one or two cells thick around the stele. The cells are oval in transverse section and are several times longer than broad. The Casparian strip, typical of endodermal cells, is not conspicuous, and most often the tissue is recognized by the darkly staining contents of its cells. In certain cases the contents do not stain, and the tissue then is extremely difficult to distinguish; but generally, the cells are smaller than those of the cortex and more resistant to crushing than those of the pericycle.

Certain stems, *Osmunda cinnamomea* and *Osmundacaulis natalensis* for example, have an endodermal layer between the pith and inner xylem sheath; and in other stems an internal cylinder connects with the external cylinder through leaf-gaps.

Tissue arrangement. Protostelic stems of the Osmundaceae consist of concentric cylinders of tissue, which are central metaxylem, outer metaxylem, xylem sheath, phloem, pericycle, and endodermis (text-fig. 1A). Protoxylem is generally mesarch in projections at the periphery of the outer metaxylem cylinder, and the number of these bulges in a given transverse section of the axis varies from species to species.

Of the twelve Permian species, only *Bathypteris rhomboidea, Petcheropteris splendida,* and



TEXT-FIG. *1*—Stelar types. A, Protostele, *Thamnopteris schlechtendalii,* × 2, (after Kidston & Gwynne-Vaughan, 1909). B, Ectophloic-dictyoxylic siphonostele, *Osmunda dowkeri,* × 4½. C, Dissected siphonostele, *Osmundacaulis carnieri,* × 1¼, (after Kidston & Gwynne-Vaughan, 1914). D, Dictyostele, *Osmundacaulis skidegatensis,* × 7½.

Thamnopteris gwynne-vaughani contain a solid column of central metaxylem. *T. kidstoni* has some parenchyma in the central metaxylem, but the column consists predominantly of tracheids, and the stele is essentially a protostele. A small cavity occurs in the central xylem of *T. schlechtendalii,* but Kidston & Gwynne-Vaughan (1909) reported that the crushed tracheids bordering the cavity would be sufficient to fill it if returned to their original size. This species is probably protostelic also. The cavities in other species are larger, however, and may have contained cells other than tracheids.

Chasmatopteris principalis is of particular interest in that the metaxylem cylinder is conspicuously indented opposite certain leaf-traces (text-fig. 10C). Zalessky (1931a) reported that none of these rudimentary leaf-gaps actually pierced the metaxylem cylinder, but many of the fissures extend more than halfway through it. This species has a large cavity in the central xylem region with the latter tissue represented only in places by a layer of specialized tracheids two or three cells thick. This species is generally regarded as protostelic, but it may have been siphonostelic.

The ectophloic-dictyoxylic siphonostele is essentially an ectophloic siphonostele in which only the xylem cylinder is interrupted by leaf-gaps (text-fig. 1B; pl. 1, figs. 2, 4, 6). Stelar tissues outside the xylem cylinder develop immediately around each leaf-trace to maintain their continuity. Central metaxylem tissue, as such, does not occur in species having this type of stele. All or most of the tracheids are replaced by pith parenchyma or sclerenchyma, but the "mixed pith" of *Osmundacaulis kolbei* represents a persistence of a more primitive state. The anomalous and the induced "mixed pith" of *Osmunda regalis* (Gwynne-Vaughan, 1914) and *Todea barbara* (Wardlaw, 1946) indicates that even these extant species are still capable of producing tracheids in the pith if suitably stimulated.

The most important variable character in this type of stele is the number of xylem strands visible in a given transverse section of the stem. This feature is dependent upon the state of maturity, the mature size, and the nature of the leaf-gaps.

Examination of Recent material shows that the sporeling stage of probably all species has a protostele (Faull, 1901, 1910; Leclerc du Sablon, 1890; Seward & Ford, 1903). As the sporeling matures, the axis grows in length and diameter, and the xylem cylinder becomes interrupted by leaf-gaps. Thus, the number of xylem strands visible in a given transverse section depends to a great extent on the state of development.

In mature axes growth of the shoot is mainly elongation, with little change in stem diameter. Thus, the number of xylem strands in a transverse section of a mature part of a rhizome is limited to a specific range of variation inherent in each species. Furthermore, dichotomous branching of mature axes reduces the number of xylem strands and increases the variation. Thus, the number of xylem strands occurring in a transverse section of an axis has some limited importance, and the use of this feature as a diagnostic character should be restricted to cases in which there is knowledge of the range of variation for a species.

As might be expected, species whose xylem cylinders are large in diameter tend to have more xylem strands than species whose xylem cylinders are smaller. The differences are not in direct proportion, however, since the number of xylem strands is also dependent on the height and breadth of the leaf-gaps characteristic of a given species. Short, narrow leaf-gaps tend to dissect a xylem cylinder into more strands than leaf-gaps that are broad and high acting in a comparable cylinder.

In two species, *Osmundacaulis braziliensis* and *O. carnieri,* an internal endodermis connects with an external endodermis through the leaf-gaps (text-fig. 1C). Both of these species are based upon poorly preserved fossils, and the arrangement of their phloem tissues is unknown. All vascular tissues between the inner and outer endodermal cylinders must be interrupted by the leaf-gaps, so the term "dissected siphonostele" best describes this condition (compare with dictyostele below).

Branching regions of certain stems of *Osmunda cinnamomea* contain dissected siphonosteles which may be ectophloic or amphiphloic (Faull, 1901, 1910; Hewitson, 1962). This type, however, is not typical of the species.

The term dictyostele is applied in the sense of Esau (1953) to stems in which an internal cylinder of phloem connects with an external cylinder of phloem through leaf-gaps. The connection results in a series of xylem strands each of which appears in transverse section to be completely surrounded by phloem. The position of the endodermis is not a criterion and is thus irrelevant to the definition. Among the Osmundaceae, only the stele of *Osmundacaulis skidegatensis* qualifies for the dictyostele designation (text-fig. 1D; pl. 2, fig. 2).

Cortex.—The cortex of osmundaceous ferns is generally as thick as or thicker than the diameter of the stele it surrounds. In all but one species, the cortical region is differentiated into an inner parenchymatous cylinder and an outer sclerotic cylinder. Both cortical cylinders vary in thickness in a given transverse section because they include leaf-traces which increase in size toward the periphery of the stem. Furthermore, the relative thickness of the two cortices varies from species to species.

Inner cortex. The inner cortex consists mostly of parenchyma cells that are about 50 microns in diameter and 80 microns in length. The cell walls are thin (1–2 microns) and pitting, if visible, is simple. The parenchyma cells are oval in transverse outline and form a loose tissue with conspicuous intercellular spaces.

In *Osmunda cinnamomea, O. precinnamomea,* and *Todea barbara* conspicuous clusters of thick-walled fibers occur immediately adaxial to leaf-traces in the inner cortex. These fibers are very long cells, and their ends taper to fine points. Further, the walls of these fibers are so thick (10–15 microns) that the lumina are nearly occluded. The clusters are three or four cells thick in radial dimension and equal in transverse width to the leaf-trace with which they are associated. Except in dissected siphonosteles of *Osmunda cinnamomea,* where certain individual fibers may project downward through leaf-gaps, the cluster of fibers does not penetrate the stele. These thick-walled fibers merge upward with relatively thin-walled fibers of the outer cortex and are replaced by them.

Thick-walled schlereids are scattered singly or in clusters in the inner cortex of *Osmundacaulis kolbei* and *O. skidegatensis* (text-fig. 1D; pl. 2, fig. 2). These cells are similar to the parenchyma cells of the inner cortex and pith but have thick walls (4–5 microns). They are also similar to the sclereids that occur in the pith of these species.

Outer cortex. The outer cortex of most species consists of long fibers whose ends taper to fine points. These cells are about 40 microns at their greatest diameter, and they are oval in transverse section. However, because tips of these cells project between fibers above and below, the outer cortex is a dense tissue without conspicuous intercellular spaces. The walls of the fibers are 5–8 microns thick and bear simple pits that appear as diagonal ovals or ellipses.

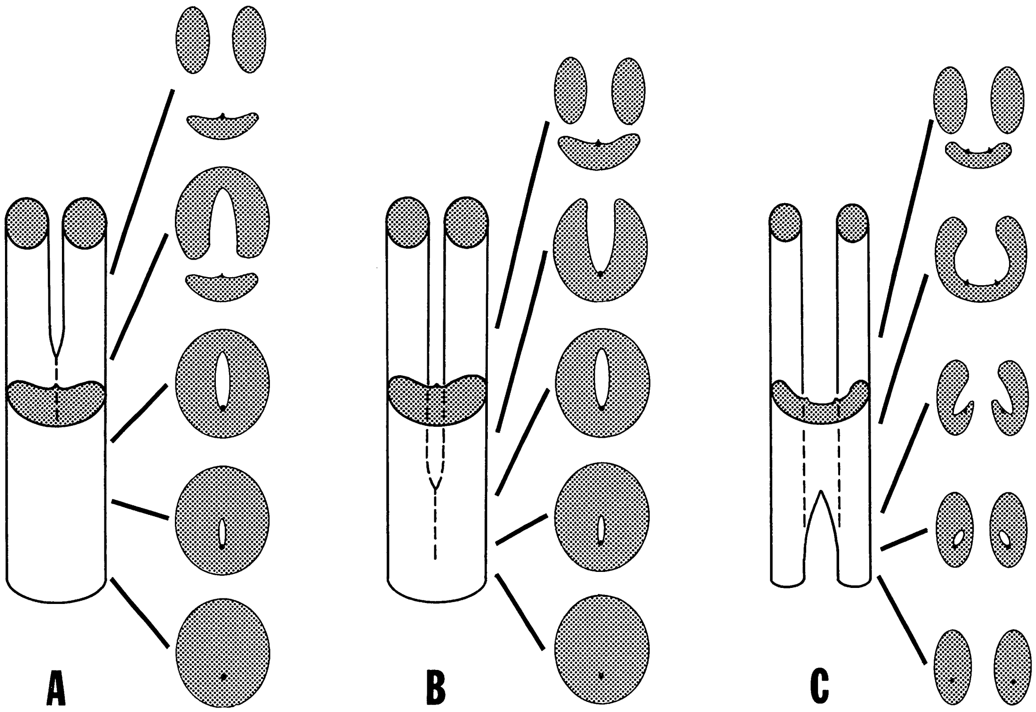
Hewitson (1962) reported the presence of short fibers with relatively thin walls in the outer cortex of *Leptopteris* and *Todea.* The long fibers form a cylinder around each leaf-trace, and the shorter sclereids fill in the interstices. Further, the outer cortex *Thamnopteris schlechtendalii* consists entirely of sclereids that are only four or five times longer than broad and have blunt tips (Kidston & Gwynne-Vaughan, 1909). In all other fossils examined during the course of my investigation, the outer cortex appeared to be wholly fibrous, but preservation of several species was poor and many longitudinal sections were slightly oblique, making the determination of the actual length of cortical cells difficult. The structure of the outer cortex is a character that requires additional investigation.

Homogeneous cortex. The cortex of *Osmundacaulis braziliensis* is described as homogeneous (Andrews, 1950), but the apparent uniformity of the tissue may be an artifact of preservation. The specimen is poorly preserved, and cells of the cortex cannot be distinguished. A somewhat similar situation occurs in *O. carnieri,* which is in a comparable state of preservation. This specimen appears to have inner and outer cortical cylinders, but the boundary between them, which is sharply defined in other species, cannot be located (Kidston & Gwynne-Vaughan, 1914).

Leaf-trace.—**Formation of the xylem strand.** The mesarch, submesarch, and endarch types of leaf-trace xylem occur in the Osmundaceae. Then there is in addition the *Plenasium* type which is a modification of the endarch type. Each of these is briefly discussed in turn.

A leaf-trace xylem strand that is elliptical in transverse section and bears a mesarch cluster of protoxylem elements occurs in most of the protostelic or supposedly protostelic species (text-fig. 1A). Formation of such a strand is first noted by the appearance of a cluster of protoxylem elements in mesarch position within a slight projection of the periphery of the metaxylem cylinder. This bulge increases in size upward, and finally breaks away from the stem xylem as an elliptical strand with the protoxylem tracheids at its center. Most often, there is one protoxylem group per metaxylem strand, but certain leaf-traces of *Thamnopteris schlechtendalii* have two. No indentation suggestive of a leaf-gap occurs in the stem xylem opposite the mesarch type of leaf-trace.

Leaf-traces in which the protoxylem is submesarch, i.e., the protoxylem is within a metaxylem strand but is distinctly to the adaxial side of it, occur in *Chasmatopteris principalis,* a supposedly protostelic species, and in *Osmundacaulis kolbei,* a dictyoxylic form. The leaf-trace xylem diverges from a continuous cylinder of metaxylem in the former species and from an individual strand in the latter species. As would be observed in a hypotheti-



TEXT-FIG. 2—Types of leaf-gap formation. Diagrammatic sectional and face views of xylem strands. A, "Delayed" gap. B, "Immediate" gap. C, *Plenasium*-type gap.

cal series of transverse sections from base to apex, the first indication of a leaf-trace is the appearance of a mesarch cluster of protoxylem elements in the metaxylem. Just above, cells of the xylem sheath appear adaxial to the protoxylem replacing metaxylem tracheids, and more of these cells occur upward forming a cluster which extends toward the center of the stem. There are fewer metaxylem tracheids between the cluster of xylem sheath cells and the protoxylem group than between the latter and the periphery of the metaxylem cylinder or strand; and, as the cluster of xylem sheath cells enlarges, the protoxylem and metaxylem abaxial to it projects outward. More apically, the projection breaks away to become the submesarch xylem strand of the leaf-trace.

In *Chasmatopteris principalis* xylem sheath cells do not replace all metaxylem tracheids adaxial to the leaf-trace, and a fissure is thus formed in the outer metaxylem cylinder which extends about halfway through it (text-fig. 10C). Certain leaf-traces of *Osmundacaulis kolbei* leave similar fissures or incomplete leaf-gaps behind them, but replacement of tracheids by cells of the xylem sheath continues, and a complete gap is formed somewhat above the point of departure of the leaf-trace (text-fig. 2A). This situation was termed a "delayed gap" by Kidston & Gwynne-Vaughan (1910). In other leaf-traces of this species, replacement of all adaxial tracheids occurs before divergence of the leaf-trace xylem, so formation of the leaf-gap is "immediate" when the leaf-trace xylem separates from the stem xylem.

In most species the xylem of the leaf-trace bears a single endarch protoxylem group as it separates from the stem xylem (text-fig. 2B). This type of leaf-trace, because of the nature of its formation, occurs only in dictyoxylic species. A mesarch cluster of protoxylem elements appears in a metaxylem strand. Slightly upward, metaxylem tracheids immediately adaxial to the protoxylem are replaced by cells of the xylem sheath. Substitution continues upward forming a cluster of these cells, which generally connects with the pith prior to the separation of the leaf-trace xylem. The result is the formation of a U-shaped metaxylem strand with the protoxylem in medial, endarch position on the concave surface of the strand. The curved part of the U then breaks away, leaving an "immediate" leaf-gap behind it.

In certain stems and commonly in branching regions of dictyoxylic steles, not all metaxylem tracheids adaxial to the protoxylem group are replaced at the time of separation of the leaf-trace xylem (text-fig. 2A). Prior to divergence, the metaxylem strand has the shape of an O; and after separation of the leaf-trace xylem, the strand is U-shaped with the concavity directed outward. Often replacement continues with the eventual formation of a "delayed" leaf-gap, but in branching regions replacement may cease without a leaf-gap being formed. Generally, the latter condition is confined to certain xylem strands in the branching region with normal or "delayed" gaps forming in others.

The *Plenasium*-type of leaf-trace xylem formation is a modification of the endarch type and accommodates leaf-gaps that are high and wide (text-fig. 2C). Divergence of the leaf-trace is from two adjacent metaxylem strands. A mesarch protoxylem cluster forms in each strand; and concurrently, a cluster of xylem sheath cells replaces metaxylem tracheids adaxial to the protoxylem group and slightly to one side of it toward the adjacent metaxylem strand. Upward, the xylem sheath cluster extends obliquely toward the pith and breaks out of each metaxylem strand on the side next to the adjacent strand. A transverse section at this level shows the two metaxylem strands as crosiers which face toward each other (pl. 1, fig. 6; pl. 2, fig. 5) with the protoxylem cluster on the concave surface of the "hook" portion of each crosier. More apically, the curved tips of the two strands connect across the leaf-gap forming a single strand that is broadly U-shaped in transverse section. A short distance above, the curved portion of the U breaks away becoming the xylem of the leaf-trace. The latter already has a pronounced curvature at the point of its separation and bears two protoxylems.

Some *Plenasium*-type leaf-traces lack the symmetry of formation described above. The steps of formation are the same, but one of the two contributing strands is always in a slightly more advanced state of formation than the other.

Changes in the leaf-trace in its course through the stem. Regardless of its mode of origin, the xylem of the leaf-trace becomes surrounded by xylem sheath, phloem, pericycle, endodermis, inner cortex, and outer cortex as it passes through each of these respective stem tissues; and each addition increases the size of the leaf-trace. Other changes are ramification of the protoxylem, increase in curvature of the vascular tissues, and the change from concentric arrangement of xylem and phloem to bicollateral. The changes described below are for a mesarch leaf-trace, but all types of leaf-traces undergo the same series of modifications beginning with the stage that the leaf-trace xylem is in as it separates from the stem xylem.

In mesarch leaf-traces cells of the xylem sheath begin to replace tracheids adaxial to the protoxylem soon after the strand diverges from the stem xylem. The strand eventually becomes endarch and the protoxylem bifurcates. As the distance between the leaf-trace and the stele increases, the xylem of the leaf-trace elongates tangentially and begins to curve adaxially. Concurrently, layers of metaphloem and transitional phloem on each lateral side of the leaf-trace diminish in thickness and eventually disappear, changing the xylem-phloem arrangement from concentric to bicollateral. Additional ramification of the protoxylem occurs with the tissue spreading over the concave surface of the xylem strand. The xylem of the leaf-trace eventually attains a C-shape and the surrounding vascular tissues conform to this.

The degree of leaf-trace curvature at a given location in the stem varies from species to species, yet is relatively constant within a species. In some species the leaf-trace already has a pronounced curvature as it leaves the stele; in other cases, the leaf-trace separates from the stele as an oblong or reniform strand and remains so until it enters the petiole base. There are many intermediate situations between these two extremes.

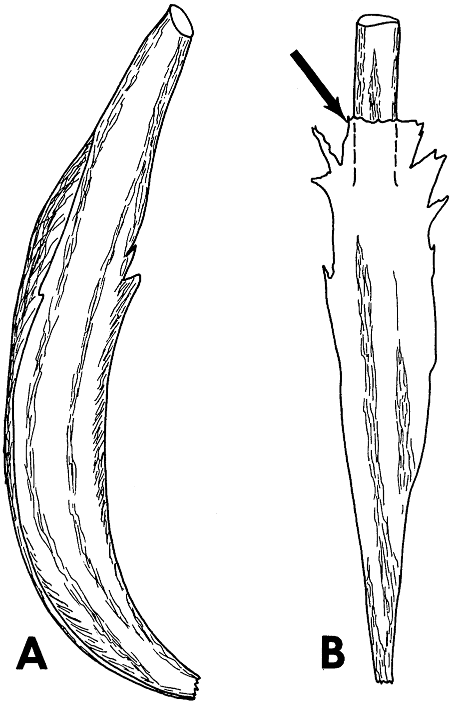
Ramification of the leaf-trace protoxylem is correlated with the increase in curvature of the leaf-trace, and the location of the leaf-trace in the stem or petiole base when its protoxylem initially bifurcates serves as an index to the degree of curvature and relationships of other leaf-trace tissues.

Shape of the leaf-trace. The leaf-trace, as it occurs in the stems of most species, is C-shaped in transverse sections of the axis; although in some species it appears to be V- or Y-shaped. Such shapes are the result of a greater than average angle of leaf-trace divergence. The leaf-trace is C-shaped in sections transverse to it, but in transverse sections of the stem it is cut very obliquely and appears V- or Y-shaped.

Number of leaf-traces in a cortical cross-section. Hewitson (1962) used the number of leaf-traces in a given transverse section of the cortex as a character in differentiating between the extant taxa; but because of overlapping limits of variation, the character is not diagnostic and can only be used as a guide to relationships in conjunction with other characters. The number of leaf-traces in a given cortical cross-section varies from over 100 in species of *Zalesskya* to less than ten in certain species of the subgenus *Plenasium*. This number depends on the size of the leaf-trace relative to the stem, the breadth of the cortex, the angle of leaf-trace divergence, and the number of internodes traversed before the leaf-trace reaches the petiole.

Petiole base

As a leaf-trace approaches the periphery of the stem, a distinct bulge is formed in the outer part of the outer cortex. This bulge increases in size and separates from the stem becoming the petiole base. Tissues arising in the stem pass into it as an oval unit consisting of the vascular strand, a surrounding cylinder of cells that are continuous downward with those of the inner cortex of the stem, and a similar cylinder of fibers continuous with those of the outer cortex. Parenchyma tissue extends for a short distance to each side of the unit tangential to the stem, forming short stipular expansions. These expansions increase in size upward proportionally more than do the other tissues of the petiole base so that a distinctly winged stipular region is produced at the base of the petiole (text-figs. 3, 4). Apically, the wings diminish in size, and the vascular strand, inner cortex, and outer cortex of the petiole base extend upward as the rachis of the frond (pl. 1, figs. 1, 3, 5).



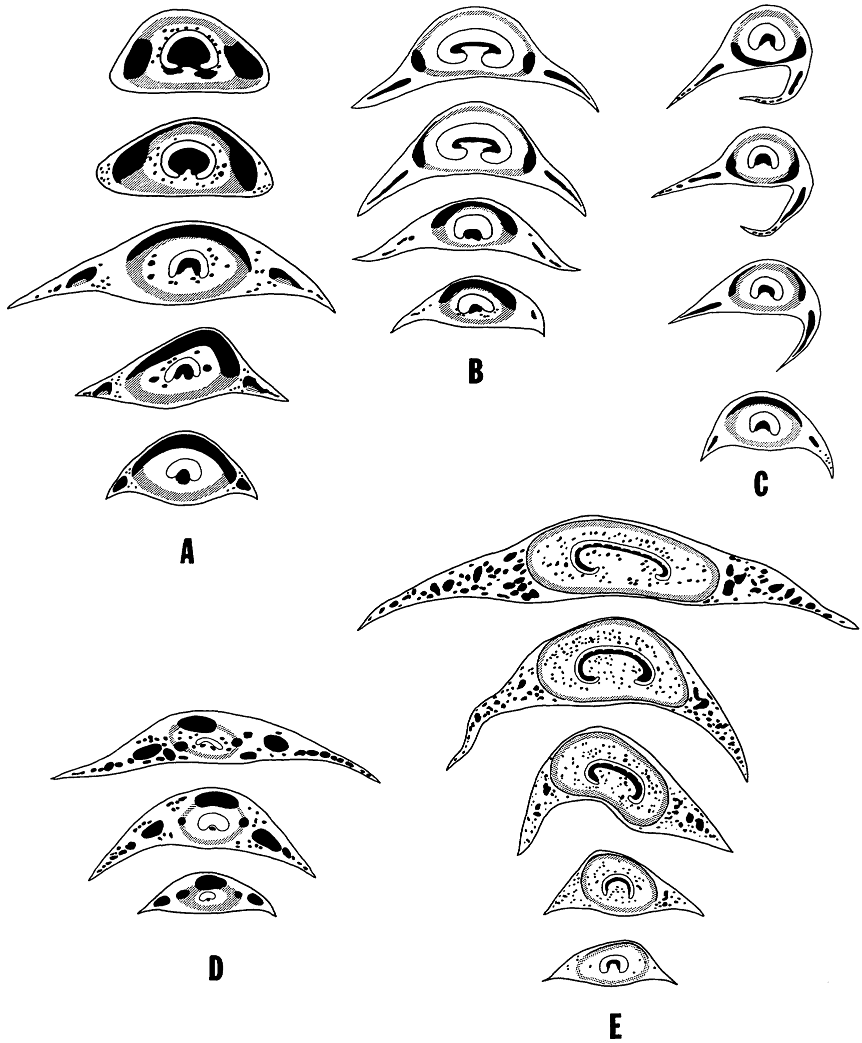
TEXT-FIG. *3*—Illustrations of stipular petiole bases. A, *Osmunda claytoniana,* × 1½. B, *Leptopteris superba,* × 1½, with the transverse commissure indicated by the arrow.

Sclerenchyma tissues, mostly fibers whose walls are so thick that the cell lumina are nearly filled (pl. 2, figs. 6, 7, 11) occur in the stipular expansions and in the cortices of the petiole base forming various patterns which are generally most complex where the stipular wings are the widest (text-fig. 3). These patterns vary from species to species and are very constant within a species if compared at equivalent levels of the stipular region. Thus, the arrangement of sclerenchyma tissues in stipular petiole bases is a useful comparative character.

In some species "fiddleheads" that develop late in the growing season abort and fail to form fronds. The stipular regions of these crosiers ("cataphylls" of Steeves & Wetmore, 1953) form a series of protective scales around the shoot apex during climatic periods adverse to continued growth. Such aborted petiole bases may be recognized in transverse sections of axes by poor development of their xylem; only the protoxylem and a few nearby metaxylem tracheids become thick-walled. These aborted leaves occur in many fossil species, the oldest being *Osmundacaulis herbstii,* from the Upper Triassic of Argentina (Archangelsky & de la Sota, 1962).

Transverse commissure.—A transverse commissure is a membranous tissue that extends from the apical extremity of the stipular expansions and connects the two lateral (as opposed to abaxial and adaxial) sides of the stipule across the adaxial surface of the rachis just above the stipular region of the petiole base (text-fig. 3B). This structure occurs in the Cycadales, Ophioglossales, Marattiales, and in species of *Leptopteris* and in *Todea barbara* in the Osmundaceae (Bower, 1926). It is lacking in all species of *Osmunda.* Transverse commissures have not been recognized in petrified axes of the Osmundaceae probably because they have not been preserved. The tissue would be visible only at the extreme periphery of the mantle of petiole bases, and in most specimens this region was eroded away prior to petrifaction.

Trichomes and spines.—Actual spines emerge from the surface of the petiole base only in *Bathypteris rhomboidea.* These structures are multicellular and contain a strand of fibers



TEXT-FIG. 4—Transverse sections of stipular expansions at various levels. A, *Osmunda pluma,* × 4½. B, *Osmunda claytoniana,* × 4½. C, *Osmunda regalis,* × 4½. D, *Osmunda precinnamomea,* × 4½. E, *Osmunda arnoldii,* × 4½. Thin-walled fibers, gray; thick-walled fibers, black.

that connects downward with fibers of the sclerenchyma ring of the petiole base.

Trichomes occur on petiole bases of living species and exude a mucilaginous substance that acts to lubricate growth movements of the petiole bases around the shoot apex (Gardiner & Tokutaro, 1887). Similar trichomes occur in fossil species (Arnold, 1952), but their presence or absence depends on the proximity of a given petiole base to the shoot apex. The trichomes, which consist of delicate, thin-walled cells, expand and burst as the petiole base grows, not persisting after maturity.

Sclerenchyma tissues. — **Stipular expansions.** Thick-walled fibers may form small clusters which are scattered throughout the stipular region or concentrated near the sclerenchyma ring, larger clusters which are scattered or in line, elongate strips which extend from the continuous ring nearly to the lateral margins of the stipular expansion, or various combinations of these conditions (text-fig. 4). Relatively thin-walled fibers often occur within elongate strips or large masses of thick-walled fibers but make up only a small part of them (text-fig. 4A). The pattern of sclerenchyma tissues in the stipular expansions is best expressed where the expansions are most extended.

Inner cortex. Thick-walled fibers form small clusters which are scattered in the inner cortex of the petiole base of many species. Their density varies, and in some ancient species the fibers form a solid sheath around the vascular strand.

Fibers also occur in the inner cortex in the concavity of the vascular strand. In most species these fibers form one group at the base of the stipular region. This mass extends upward as a solid band of fibers which lines the concave side of the vascular strand in some species. In others the band is very narrow and appears to be broken into many small groups in transverse section, but the groups are usually connected by one or two cells. The single basal mass may also bifurcate with each branch lying against a recurved tip of the vascular strand.

Thick-walled fibers in the sclerenchyma ring. The sclerenchyma ring or outer cortex of the petiole base of many species consists entirely of thin-walled fibers that are continuous below with those of the outer cortex of the stem. In certain species, however, thick-walled fibers occur in the continuous ring forming patterns which can be used as additional evidence of relationships. In *Osmunda cinnamomea* and *O. precinnamomea* three masses of thick-walled fibers develop in the sclerenchyma ring as it diverges from the stem (pl. 1, fig. 3; pl. 2, figs. 1, 11). One mass occurs on the abaxial side of the ring while an additional mass occurs on each lateral side of the ring. These masses extend without change throughout the length of the stipular region (text-fig. 4D).

In *Todea, Leptopteris,* and the subgenus *Plenasium* of *Osmunda* a thin arch of thick-walled fibers develops at the periphery of the sclerenchyma ring on its abaxial side as it diverges from the stem. Slightly upward, the band of thick-walled fibers extends completely around the ring to form its outer layer (text-fig. 4E).

Variation of the ring in species of the subgenus *Osmunda* presents an interesting series. In *O. pluma* and *O. oregonensis* a thick arch of thick-walled fibers occupies the abaxial semicircle of the sclerenchyma ring throughout the length of the stipular region. Just above the stipular region, however, this mass divides to form two lateral clusters which are first connected across the abaxial face of the ring and later become separate (text-fig. 4A; pl. 2, figs. 6, 7). A similar arch occurs in the sclerenchyma ring of *O. claytoniana,* but division of the mass occurs in the lower one-third of the stipular region, and the two lateral masses extend upward the remaining length of the stipular region (text-fig. 4B). In *O. regalis, O. japonica,* and *O. lancea* the same sequence occurs, but the two lateral masses, once formed, diminish in size almost immediately to form a very narrow band in the adaxial semicircle of the sclerenchyma ring. This narrow band, which is one or two fibers thick, extends upward the remaining length of the stipular region (text-fig. 4C).

Root

One or two roots originate from each leaf-trace near its place of attachment to the stem xylem. In some cases roots diverge below the point where the xylem of the leaf-trace becomes free from the stem xylem, and in other cases departure occurs from leaf-traces in the inner cortex. However, in regions where the pericycle is fully matured, no roots arise (Hewitson, 1962).

The xylem of the root is a diarch strand having an elliptical shape in transverse section. It is surrounded by xylem sheath, phloem, pericycle, endodermis, and a cortex that is differentiated into an inner parenchymatous and an outer sclerotic layer. Roots generally grow out through the cortex of the stem and the mantle of petiole bases surrounding it. They often penetrate the stipular expansions but rarely enter the sclerenchyma ring around the vascular strand. Roots branch frequently within the mantle and outside of it to form a dense mat which is the "osmundine" of horticulture.

Most often the root diverges from the lateral edge of the leaf-trace. In certain cases, however, departure is from the medial, abaxial surface. This condition occurs in certain protostelic species and also in *Osmundacaulis braziliensis* and *O. carnieri.* Observation of this condition is a matter of chance if only one or two transverse sections of a species are available; and it may be more widespread in fossils than is indicated.

Living species of the subgenera *Osmunda* and *Plenasium* have two roots (sometimes one) diverging from each leaf-trace while the remaining Recent species have only one (sometimes two) roots per leaf-trace. In species having usually two roots per leaf-trace, both do not always come off at the same level, and serial sections of the axis are required for verification of the condition. Thus, the character cannot be adequately studied from much of the previously described fossil material where serial preparations are not available.

Stem branching

Branching is dichotomous, yielding two axes of about equal diameter. Where one is much larger than the other, it bifurcates again (Faull, 1901). Forking is accomplished by an elongation of stem tissues along the transverse plane followed by constriction of the tissues perpendicular to the direction of flattening and splitting and rounding of the two branches. Often, there is a decrease in radial thickness of the xylem cylinder to as few as five tracheids. Furthermore, in species whose normal leaf-gap formation is "immediate," gaps tend to become "delayed" or may fail to form entirely. Thus, xylem strands tend to have greater confluency in a branching region of the axis than in an unbranched portion. In addition leaf-traces fail to develop between the two stems where they are close to one another, but normal leaf-trace formation resumes when the distance between branches increases.

Branching regions of some plants of *Osmunda cinnamomea* are atypical for this species. Anomalous xylem cylinders or complete vascular strands may develop in the pith of the branching region (Hewitson, 1962). Furthermore, the stele may become a dissected ectophloic or amphiphloic siphonostele with the connection of the internal endodermis and external endodermis through leaf-gaps and with the formation of internal phloem. On the other hand, many plants of this species show normal branching.

Growth habit

Most of the extant species and many fossil species have rhizomatous axes, but one extant species and numerous fossils exhibit the columnar arborescent habit. These types of growth can be recognized in transverse sections of the axes by the angle at which most of the roots in the cortex and mantle are cut. Roots of rhizomatous axes grow more or less directly out from their place of origin in the stem to the mantle, and are cut longitudinally or obliquely. In arborescent axes, on the other hand, the roots grow out from their place of origin near the shoot apex through the cortex and down through the petiole bases, and more of them are thus cut transversely than obliquely (pl. 2, figs. 3, 4).

SYSTEMATIC DESCRIPTIONS BASED ON STEM, ROOT, AND LEAF BASE CHARACTERS

Described in this section are the present-day species and those structurally-preserved fossil stems and (or) petiole bases that are sufficiently well known to permit reasonably accurate comparison. Such fossils as stem casts, compressed foliage, isolated spores and sporangia, which cannot be compared with the petrified organs, are briefly discussed in a later section. Diagnoses of the species included in the systematic descriptions are based mainly on the anatomy and morphology of stems, roots, and petiole bases. The important features of each species are italicized.

Order Filicales
Family Osmundaceae

Ferns with radially symmetric arborescent to rhizomatous stems, surrounded by more or less closely adhering petiole bases; stele consisting of a protostele, an ectophloic siphonostele, an ectophloic dictyoxylic siphonostele, a dissected ectophloic or amphiphloic siphonostele, or a dictyostele; secondary xylem absent; leaf-traces near point of attachment to stele mesarch or endarch with one or two protoxylems; cortex consisting of an outer sclerotic layer and an inner fleshy cylinder or rarely a single layer of thin-walled cells; leaves given off in a tight spiral; petiole bases mostly stipular, containing an adaxially curved vascular strand; roots with diarch xylem strand, arising from leaf-traces in some cases before latter are free from the stem xylem.

Type Genus.—Osmunda L.

Key to the subdivisions based on anatomical characters

No key that treats both the living and the fossil Osmundaceae has been presented in the literature before. With inclusion of its fossil members, the family is a relatively large one; and since past treatments have been devoted mostly to descriptions of new species, information on features useful in distinguishing between the genera is not readily available.

Constructing a key that embraces fossil and living taxa presents a problem that requires some explanation. Traditional keys offer the reader a series of opposing choices based on differing conditions in similar or at least comparable organs. In fossil material comparable organs are not always available because of imperfect preservation. Descriptions of several of the fossil species are based on single specimens of a particular organ. The stems, for example, of *Anomorrhoea fischeri, Osmundacaulis kidstoni,* and *Osmunda nathorstii* are completely unknown as are the petiole bases of all three species of the genus *Zalesskya* and two species of *Osmundacaulis*. The only way such taxa can be handled in a key is to make assumptions regarding the structure of the missing organs. This problem also arises in applying numerical methods of comparison in a later section, and the solution is the same. Assumed features for each species are listed in parentheses with the binomial in text-figures 6 and 7. These assumptions are made only where necessary and are founded upon characters that are known for a given species, its geologic age, and the construction of similar species.

A. Xylem cylinder of stem interrupted opposite leaf-traces; central region of stele consisting dominantly of parenchyma or sclerenchyma; leaf-trace endarch or rarely subendarch at its base .... B (Subfamily Osmundoideae)

A′. Xylem cylinder of stem not interrupted opposite leaf-traces; central region of stele consisting dominantly of tracheids; leaf-trace mesarch or subendarch at its base .... I (Subfamily Thamnopteroideae)

  B. Leaf-traces where separating from stem xylem, bearing two clusters of protoxylem elements and having strong adaxial curvature at point of divergence C

  B′. Leaf-traces where separating from stem xylem, bearing one cluster of protoxylem elements and having shallow adaxial curvature or an oblong shape at point of divergence .... E

C. Xylem cylinder of stem less than 30 tracheids in radial thickness .... *Osmunda,* Subgenus *Plenasium*

C′. Xylem cylinder of stem more than 30 tracheids in radial thickness .... D

  D. Stems less than 7 cm in diameter; leaf-traces in cortex having a C-shaped transverse outline .... *Osmundacaulis skidegatensis* group

  D′. Stems 10 cm or more in diameter; leaf-traces in outer part of outer cortex having a V-shaped transverse outline .... *Osmundacaulis braziliensis* group

E. Outer cortex of stem constructed entirely of long thick-walled fibers; transverse commissure on petiole base absent .... F

E′. Outer cortex of stem with long thick-walled fibers only around leaf-traces, bulk of tissue made up of short sclereids; transverse commissure on petiole base present .... H

  F. Outer cortex of petiole base containing conspicuous masses of thick-walled fibers .... G

  F′. Outer cortex of petiole base lacking conspicuous masses of thick-walled fibers .... *Osmundaucaulis herbstii* group

G. Inner cortex of stem with strand of thick-walled fibers axillary to each leaf-trace; outer cortex of petiole base containing one abaxial and two lateral masses of thick-walled fibers .... *Osmunda,* Subgenus *Osmundastrum*

G′. Inner cortex of stem lacking a strand of thick-walled fibers axillary to each leaf-trace; outer cortex of petiole base containing an abaxial arch or two lateral masses of thick-walled fibers .... *Osmunda,* Subgenus *Osmunda* (see also *Osmundacaulis kidstoni*)

  H. Inner cortex of petiole base containing many small strands of thick-walled fibers; sclerenchyma in concavity of vascular strand of petiole base poorly developed or absent; inner cortex of stem containing a strand of thick-walled fibers axillary to each leaf-trace .... *Todea*

  H′. Inner cortex of petiole base lacking small strands of thick-walled fibers; sclerenchyma in concavity of vascular strand of petiole base well developed; inner cortex of stem lacking a strand of fibers axillary to each leaf-trace .... *Leptopteris*

I. Petiole bases lacking stipular expansions, bearing multicellular spines each containing a strand of thick-walled fibers .... *Bathypteris*

I′. Petiole bases with stipular expansions, multicellular spines absent .... J

  J. Inner cortex of petiole base containing a narrow cylinder of thick-walled parenchyma cells or fibers parallel to the outer cortex .... *Anomorrhoea*

  J′. Inner cortex of petiole base lacking a narrow cylinder of thick-walled cells parallel to the outer cortex .... K

K. Outer cylinder of stem metaxylem conspicuously constricted (indented both from the inside and the outside) opposite each departing leaf-trace .... *Chasmatopteris*

K′. Outer cylinder of stem metaxylem not conspicuously constricted opposite each departing leaf-trace L
  L. Outer cortex of stem thicker than the inner cortex .... M
  L′. Outer cortex of stem as thick as or thinner than the inner cortex .... N
M. Leaf-traces numbering 70 or more in a cross section of the cortex .... *Zalesskya*
M′. Leaf-traces numbering less than 70 in a cross section of the cortex .... *Petcheropteris*
  N. Tracheids of the central metaxylem of the stem about 3–5 times longer than broad .... *Thamnopteris*
  N′. Tracheids of the central metaxylem of the stem about 10–15 times longer than broad .... *Iegosigopteris*

Subfamily OSMUNDOIDEAE

Stele an *ectophloic dictyoxylic siphonostele,* a dissected ectophloic or amphiphloic siphonostele, or a dictyostele; pith consisting of parenchyma and (or) sclerenchyma, occasionally with some tracheids.

Type genus.—Osmunda L.

Other genera.—Leptopteris Presl, *Todea* Willdenow, and *Osmundacaulis* Miller (form genus).

Genus OSMUNDA L.

Stems short upright to rhizomatous; *stele an ectophloic-dictyoxylic siphonostele* (rarely a dissected ectophloic- or amphiphloic-dictyoxylic siphonostele); xylem cylinder about 15 (5–25) tracheids thick; leaf-gaps immediate, narrow or wide; inner cortex consisting entirely of parenchyma, or mainly parenchymatous but with a cluster of thick-walled fibers adaxial to each leaf-trace; *outer cortex homogeneous, fibrous,* broader than the inner cortex; leaf-trace oblong or adaxially curved, containing two endarch protoxylems or one which bifurcates as the leaf-trace passes through the cortex or enters the petiole base; petiole base stipular, *transverse commissure absent;* vascular strand of petiole base C-shaped, containing in its concavity a mass of thick-walled fibers in lower part of stipular region which extends upward as a narrow band lining the concavity or bifurcates with each branch lying against a recurved tip of the vascular strand; inner cortex of petiole base consisting entirely of parenchyma or containing scattered strands of thick-walled fibers; sclerenchyma ring of petiole base heterogeneous; stipular expansion of petiole base containing strands of thick-walled fibers of various shapes and sizes; roots arising singly or in pairs from leaf-traces sometimes before latter separate from stem xylem.

Generitype.—Osmunda regalis L.

Subgenera. — Osmunda, Osmundastrum, Plenasium.

Subgenus OSMUNDA

Stele an ectophloic dictyoxylic siphonostele; endodermis external only; inner cortex homogeneous; *leaf-trace oblong or with slight adaxial curvature, each bearing one mesarch protoxylem (rarely two) which bifurcates as leaf-trace passes through inner cortex or inner part of outer cortex;* sclerenchyma ring of petiole base with *abaxial arch of thick-walled fibers in lower part of stipular region bifurcating upward to produce two lateral masses which may or may not extend around ring to form narrow adaxial band;* inner cortex of petiole base consisting entirely of parenchyma or containing scattered strands of thick-walled fibers; stipular expansions containing an elongate strip or an oblong mass of thick-walled fibers and small strands of thick-walled fibers; *roots arising in pairs* (sometimes singly) from leaf-traces occasionally before latter become free from stem xylem.

Type.—Osmunda regalis L.

OSMUNDA REGALIS L.

Spec. Plant. 2, p. 1065; 1753.

Stem 5.5–7.5 mm in diameter; stele 2.5–2.75 mm in diameter; pith 1.0–1.5 mm in diameter, *consisting of parenchyma and sclerenchyma;* xylem cylinder about 1.0 mm thick, with 4–11 strands; leaf-trace protoxylem bifurcating as latter passes through inner cortex (rarely lower); inner cortex 0.3–1.0 mm thick, including *2–3 leaf-traces* in transverse section; outer cortex 0.6–2.0 mm thick, including *5–11 leaf-traces* in transverse section; single mass of thick-walled fibers in concavity of petiolar bundle at basal part of stipular region, *bifurcating above to form two masses,* one lying against each incurved tip of the vascular strand; *abaxial arch of thick-walled fibers in sclerenchyma ring of petiole base bifurcating in lower one-third of stipular region, two lateral masses extending around ring in lower one-half of stipular region and extending upward as a* *narrow, inconspicuous band in the adaxial part of the ring;* inner cortex of petiole base with *about 12 clusters of thick-walled fibers;* stipular expansions containing *an elongate strip* of thick-walled fibers and *several small clusters* of fibers between the strip and the tip of the lateral margin of the expansion.

Occurrence.—Recent. Cosmopolitan in the Northern Hemisphere, and extending into the Southern Hemisphere in South America and Africa.

Basis of description.—Literature accounts of Faull (1901), and Hewitson (1962) and my examination of plants of the species (table 2).

Discussion.—While Hewitson's (1962) material of this species was from diverse localities, most of the plants that have been examined anatomically have been *O. regalis var. spectabilis.* Polunin (*in:* Hewitson, 1962) recognizes six geographic varieties of this species, so the above description may not be representative of the whole.

OSMUNDA JAPONICA Thunberg

Fl. Jap., p. 330; 1784.

Stem 5.0–9.0 mm in diameter; stele 2.0–2.75 mm in diameter; pith about 0.75 mm in diameter, *consisting entirely of parenchyma;* xylem cylinder about 1.0 mm thick, consisting of *4–11 strands;* leaf-trace protoxylem bifurcating as it passes through inner cortex; inner cortex 0.5–1.0 mm thick, including *2–4 leaf-traces* in transverse section; outer cortex 1.5–2.5 mm thick, including *5–11 leaf-traces;* single mass of thick-walled fibers in concavity of petiolar strand at basal part of stipular region, *bifurcating above to form two masses,* one lying against each incurved tip of the vascular strand; *abaxial arch of thick-walled fibers in sclerenchyma ring of petiole base bifurcating in lower one-third of stipular region, two lateral masses extending around ring in lower one-half of stipular region and extending upward as a narrow, inconspicuous band in the adaxial part of the ring;* inner cortex of petiole base consisting entirely of parenchyma; stipular expansions containing *an elongate strip* of thick-walled fibers, several small clusters of thick-walled fibers between the strip and the lateral margin of the expansion, and *numerous small clusters of thick-walled fibers near the sclerenchyma ring.*

Occurrence.—Recent. Japan, Formosa, and China.

Basis of description.—Literature account of Hewitson (1962) and my examination of plants of this species (table 2).

Discussion.—There are few differences of a fundamental nature between *O. regalis* and this species, and an investigation of a large sample of each may reveal that they are conspecific, with *O. japonica* distinct only at the subspecies or varietal level. Hewitson (1962) states that this species is most often incompletely dimorphic; but the majority of my Korean specimens, which have been growing for two years in a greenhouse, are completely dimorphic. This character requires further study.

OSMUNDA LANCEA Thunberg

Fl. Jap., p. 330; 1784.

Stem 4.5–9.0 mm in diameter; stele 0.75–2.75 mm in diameter; pith 0.25–1.75 mm in diameter, *consisting entirely of parenchyma;* xylem cylinder 0.5–1.0 mm thick, consisting of *6–8 strands;* leaf-trace protoxylem bifurcating as latter *passes through outer cortex;* inner cortex 0.25–1.75 mm thick, including *1–5 leaf-traces* in transverse section; outer cortex 0.25–4.0 mm thick, including *11–15 leaf-traces* in transverse section; single mass of thick-walled fibers in concavity of petiolar bundle at basal part of stipular region extending upward as a *narrow band lining the concavity; abaxial arch of thick-walled fibers in sclerenchyma ring of petiole base bifurcating in lower one-third of stipular region, two lateral masses extending around ring in lower one-half of stipular region and extending upward as a narrow inconspicuous band in the adaxial part of the ring;* inner cortex of petiole base consisting entirely of parenchyma; stipular expansions containing *an oblong mass* of thick-walled fibers and *numerous small strands* of thick-walled fibers, some between the oblong mass and the lateral margin of the expansion and some near the sclerenchyma ring.

Occurrence.—Recent. Japan, China.

Basis of description.—Literature account of Hewitson (1962) and my examination of plants of this species (table 2).

OSMUNDA ILIAENSIS Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 159; 1967.

Osmundites schemnicensis (Pettko) Unger, Denksch. d. math. Naturwiss., Classe d. K. Akad. d. Wissensch., Bd. iv, p. 1, pl. i; 1854. Kidston & Gwynne-Vaughan, Fossil Osmundaceae, Trans. Roy. Soc. Edinburgh 47, p. 461; 1910. Hirmer, Handbuch der Paläobotanik, p. 603; 1927. Scott, Studies in Fossil Botany, pt. I, p. 279; 1909.

Asterochlaena schemnicensis Pettko, Haidinger's Naturwissenschaftliche Abhandl., Bd. iii, Theirl. i., p. 163, pl. xx; 1849.

Stem 11.0 mm in diameter; stele 4.0 mm in diameter; pith about 1.0 mm in diameter, *constructed entirely of parenchyma;* xylem cylinder about 1.0 mm thick, consisting of *17–18 strands;* leaf-trace protoxylem bifurcating as it *enters outer cortex;* inner cortex 0.5–0.7 mm thick, including *2–5 leaf-traces* in transverse section; outer cortex 1.0–3.5 mm thick; including *13–15 leaf traces* in 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 at inner edge of mantle near stem and at the periphery of the mantle, presumably continuous between,* probably bifurcating above stipular region to form two lateral masses; 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 lateral margin of the expansion but mostly concentrated near the sclerenchyma ring.*

Holotype.—Present location unknown.

Occurrence.—At or near the contact of the Miocene and Pliocene. Ilia, near Schemnitz, Hungary.

Basis of description.—Literature accounts of Unger (1854) and Kidston & Gwynne-Vaughan (1910) and my examination of preparations of specimens collected at the type locality in the Kidston Collection, Department of Botany, University of Glasgow, Glasgow, Scotland.

Discussion.—While I have not examined the holotype of this species, Kidston & Gwynne-Vaughan's (1910) material fully agrees with Unger's (1854) figures and description; and I am certain that the material I saw belongs to this species.

OSMUNDA CLAYTONIANA L.

Sp. Pl. 2, p. 1066; 1753.

Stem 6.0–9.0 mm in diameter; stele 2.0–3.5 mm in diameter; pith 0.75–1.5 mm in diameter, *consisting entirely of parenchyma;* xylem cylinder about 1.0 mm thick, *consisting of 7–16 strands;* leaf-trace protoxylem bifurcating as latter *enters petiole base;* inner cortex 0.5–1.75 mm thick, including *4–7 leaf-traces* in transverse section; outer cortex 1.0–3.5 mm thick, including *11–13 leaf-traces* in transverse section; single mass of fibers in concavity of petiolar bundle extending upward as *a narrow band lining concavity; sclerenchyma ring with abaxial arch of thick-walled fibers in lower one-third of stipular region, bifurcating in lower one-half of stipular region to form two lateral masses which extend upward the remaining length of the stipular region;* inner cortex of petiole base containing *numerous small strands of thick-walled fibers scattered near vascular strand;* stipular expansions containing an *elongate strip* of thick-walled fibers occurring between the strip and the tip of the expansion.

Occurrence.—Recent. Eastern North America, N. Japan, and Himalayas. Possibly also the Miocene of Idaho (Brown, 1937).

OSMUNDA NATHORSTII Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 160; 1967.

Osmundites spetsbergensis (Nathorst) Kidston & Gwynne-Vaughan, Trans. Roy. Soc. Edinburgh 50, pt. V, no. 16, p. 469, pls. XLI, XLII (*in part*); 1914.

Osmunda spetsbergensis Nathorst, Bull. Geol. Instit. Upsala 10, p. 382 (*in part*); 1910.

Stem not preserved; *vascular strand of innermost petiole bases containing single protoxylem;* mass of fibers in concavity of petiolar strand in lower part of stipular region *bifurcating upward to form two masses,* one against each recurved tip of the vascular strand; inner cortex of petiole base with *small strands of thick-walled fibers; sclerenchyma ring of some petiole bases containing two lateral masses of thick-walled fibers;* stipular expansions containing *an elongate strip of thick-walled fibers.*

Holotype.—Present location unknown. Topotypes are in the Geology Annex, British Museum (Natural History), London, England.

Occurrence.—Uppermost Tertiary. Nordenskiöldsberg and Van-Mijensberg, Spitzbergen.

Basis of description.—Literature accounts of Nathorst (1910) and Kidston & Gwynne-Vaughan (1914) and my examination of preparation of topotypes in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

OSMUNDA OREGONENSIS (Arnold) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 157; 1967.

Osmundites oregonensis Arnold, Pap. Michigan Acad. Sci., Arts & Letters, 30, p. 5; 1945. Arnold, Palaeontographica XCII(B), p. 63; 1952.

Stem about 10 mm in diameter; stele about 3.0 mm in diameter; pith about 0.5 mm in diameter, structure unknown; xylem cylinder about 0.5–1.0 mm thick, consisting of *16–20 strands;* leaf-trace protoxylem bifurcating as latter passes *through inner cortex;* inner cortex 0.5–1.0 mm thick, containing *0–2 leaf-traces* in transverse section; outer cortex 2.0–4.5 mm thick, containing about *15 leaf-traces* in transverse section; single mass of thick-walled fibers in concavity of petiolar bundle *extending upward as band lining concavity; abaxial arch of thick-walled fibers in sclerenchyma ring occur-*

ring 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 between the strip and the tip of the expansion.*

Holotype and paratypes.—Museum of Paleontology, University of Michigan.

Basis of description.—Literature accounts of Arnold (1945, 1952) and my examination of the holotype and paratypes.

Discussion.—This species is very similar to and probably evolved more or less directly from *Osmunda pluma.* The tissues of the holotype are badly disorganized.

OSMUNDA PLUMA Miller

Pl. 1, figs. 1, 2; pl. 2, figs. 6–8

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 150; 1967.

Stem 5.0–7.0 mm in diameter; stele 1.5–3.0 mm in diameter; pith 0.5–1.0 mm in diameter; xylem cylinder about 0.75 mm thick; consisting *of 7–12 strands;* leaf-trace protoxylem bifurcating as latter *passes through inner cortex;* inner cortex 0.5–1.0 mm thick, including *1–3 leaf-traces* in transverse section; outer cortex 0.5–2.0 mm thick, including *6–10 leaf-traces* in transverse section; single mass of thick-walled fibers in concavity of petiolar bundle *extending upward as a band lining the concavity; abaxial arch of thick-walled fibers of sclerenchyma ring occurring throughout the 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 numerous small clusters of thick-walled fibers, some between the strip and the lateral margin of the expansion but most concentrated near the sclerenchyma ring.*

Holotype and paratypes.—Museum of Paleontology, University of Michigan.

Occurrence.—Paleocene, Fort Union Formation. Morton County, North Dakota.

Basis of description.—Investigation of the holotype, paratypes, and topotypes.

Discussion.—*Osmunda pluma* differs from *O. oregonensis* mainly in its smaller size and its arrangement of sclerenchyma tissues in the stipular expansions.

Subgenus OSMUNDASTRUM

Stems short—upright to rhizomatous; stele an ectophloic-dictyoxylic siphonostele (rarely a dissected ectophloic- or amphiphloic-dictyoxylic siphonostele); endodermis external only or external and internal; xylem cylinder about 15 tracheids thick; leaf-gaps immediate, narrow or wide; inner cortex mainly of parenchyma but containing a cluster of thick-walled fibers adaxial to each leaf-trace; leaf-trace oblong, *containing one endarch protoxylem which bifurcates as leaf-trace enters petiole base;* mass of thick-walled fibers in concavity of petiolar bundle *extending downward only to base of stipular region, not into stem;* sclerenchyma ring of petiole base heterogeneous, *containing one abaxial and two lateral masses of thick-walled fibers throughout;* stipular expansions of petiole base containing an oblong mass of thick-walled fibers; roots arising singly (sometimes in pairs) from leaf-traces occasionally before latter free from stem xylem.

Type.—*Osmunda cinnamomea* L.

OSMUNDA CINNAMOMEA L.

Pl. 2, fig. 1

Spec. Plant. 2, p. 1066; 1753.

Stem 4.0–8.0 mm in diameter; stele 1.75–3.0 mm in diameter, an ectophloic-dictyoxylic siphonostele or a dissected ectophloic or amphiphloic siphonostele; pith 0.5–1.25 mm in diameter, *consisting of parenchyma and sclerenchyma;* xylem cylinder about 1.0 mm thick, consisting of *7–22 strands; endodermis external and internal, occasionally connecting through certain leaf-gaps;* inner cortex 0.5–1.0 mm thick, including *4–12 leaf-traces* in transverse section; outer cortex 0.75–2.0 mm thick, including *7–15 leaf-traces* in transverse section; mass of fibers in concavity of petiole base *bifurcating upward to form two masses, one against each incurved tip of the vascular strand; inner cortex of petiole base consisting entirely of parenchyma;* stipular expansions containing an oblong mass of thick-walled fibers and several small masses scattered throughout.

Occurrence.—Miocene-Pliocene, near Yakima, Washington (Miller, 1967) to Recent. Eastern North America, Japan, Northern Europe, Mexico.

Basis of description.—Literature accounts of Faull (1901, 1910) and Hewitson (1962) and my investigation of living plants (table 2) and fossils (Miller, 1967) of this species.

OSMUNDA PRECINNAMOMEA Miller

Pl. 1, figs. 3, 4; pl. 2, fig. 11

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 171; 1967.

Stem 6.0 mm in diameter; stele about 1.5 mm in diameter, and *ectophloic-dictyoxylic siphonostele;* pith about 0.5 mm in diameter, *consisting of parenchyma;* xylem cylinder 0.5

mm thick, consisting of *3–7 strands; endodermis external only;* inner cortex 0.25–0.75 mm thick, including *4–5 leaf-traces* in transverse section; outer cortex 0.75–1.5 mm thick, including *6–8 leaf-traces* in transverse section; mass of fibers in concavity of petiolar bundle *bifurcating upward to form two masses, one against each incurved tip of the vascular strand;* inner cortex of petiole base *containing small strands of thick-walled fibers scattered throughout;* stipular expansions containing an oblong mass of thick-walled fibers and several small masses scattered throughout.

Holotype and paratypes.—Museum of Paleontology, University of Michigan.

Occurrence.—Paleocene, Fort Union Formation. Morton County, North Dakota.

Basis of description.—Investigation of the holotype and paratypes.

Discussion.—This species differs from *Osmunda cinnamomea* in lacking an internal endodermis and in having sclerenchyma in the inner cortex of the petiole base. In all other respects it is similar to the living form and is considered ancestral to it (Miller, 1967).

Subgenus Plenasium

Stele an ectophloic-dictyoxylic siphonostele; endodermis external only; inner cortex homogeneous; leaf-trace adaxially curved, containing *two endarch protoxylems* near point of attachment to stem; mass of thick-walled fibers in concavity of petiolar bundle extending downward into stem in some species, extending upward as a narrow band lining concavity; *abaxial arch of thick-walled fibers in sclerenchyma ring thin near attachment to stem extending to surround ring as a narrow band in lower one-third of stipular region; inner cortex of petiole base containing scattered strands of thick-walled fibers; stipular expansions of petiole base containing scattered masses of thick-walled fibers of irregular shapes and various sizes;* roots arising in pairs (sometimes singly) from each leaf-trace occasionally before latter is free from stem xylem.

Type.—*Osmunda banksiaefolia* (Presl) Kuhn.

Osmunda banksiaefolia (Presl) Kuhn

Ann. Lugd. Bat., p. 276; 1869.
Plenasium banksiaefolium Presl, Tent. Pterid., p. 110; 1836.

Stems 10–14 mm in diameter; stele 2.5 mm in diameter; pith 0.75 mm in diameter, *consisting entirely of parenchyma;* xylem cylinder 0.15–1.0 mm thick, consisting of *4–9 strands;* inner cortex 0.25–1.0 mm thick, including *0–1 leaf-traces* in transverse section; outer cortex 1.5–5.0 mm thick; including *4–8 leaf-traces* in transverse section; mass of thick-walled fibers in concavity of petiolar bundle *extending downward into* stem; stipular expansions of petiole base *containing 8–12 medium-size masses of thick-walled fibers and numerous small masses scattered throughout.*

Occurrence.—Recent. Japan, China, Formosa, Philippines.

Basis of description.—Literature account of Hewitson (1962) and my examination of plants of this species (table 2).

Osmunda bromeliaefolia (Presl) Copeland

Philp. Jour. Sci. Bot., p. 2; 1907.
Plenasium bromeliaefolium Presl, Tent. Pterid., p. 110; 1836.

Stems 6.5–7.0 mm in diameter; stele about 1.5 mm in diameter; pith 0.25–0.5 mm in diameter, *consisting entirely of parenchyma;* xylem cylinder 0.5–0.75 mm thick, *consisting of 3–12 strands;* inner cortex 0.25–1.0 mm thick, including *0–1 leaf-traces* in transverse section; outer cortex 1.0–3.0 mm thick, including *4–8 leaf-traces* in transverse section; mass of thick-walled fibers in concavity of petiolar bundle *extending downward into stem;* stipular expansions of petiole base *containing one irregularly-shaped dominant mass and several smaller masses of thick-walled fibers, the smaller masses occurring between the dominant mass and the tip of the expansion.*

Occurrence. — Possibly Miocene (Endo, 1961) to Recent. Japan, China, Formosa, Philippines.

Basis of description.—Literature account of Hewitson (1962) and my examination of plants of this species (table 2).

Osmunda javanica (Presl) Blume

Enum., p. 252; 1828.
Plenasium javanicum Presl, Abhandl., p. 5; 1848.

Stem 6–12 mm in diameter; stele 1.5–2.5 mm in diameter; pith 0.25–0.75 mm in diameter, *consisting of either parenchyma or sclerenchyma or both;* xylem cylinder 0.5–1.0 mm thick, consisting of *3–11 strands;* inner cortex 0.25–0.75 mm thick, including *0–1 leaf-traces* in transverse section; outer cortex 0.25–4.0 mm thick, including *3–6 leaf-traces* in transverse section; mass of thick-walled fibers in concavity of petiolar strand *extending downward only to base of petiole, not into stem;* stipular expansion *containing one irregularly-shaped dominant mass and several smaller masses of thick-walled fibers scattered throughout.*

Occurrence.—Recent. Philippines and S. E. Asia.

Basis of description.—Literature accounts of Posthumus (1924b) and Hewitson (1962) and my examination of plants of this species (table 2).

OSMUNDA VACHELLII (Presl) Hooker

Ic. Plant., p. 15; 1837.
Plenasium vachellii Presl, Abhandl., p. 5; 1848.

Stem about 10 mm in diameter; stele about 2.5 mm in diameter; pith about 1.0 mm in diameter, *consisting of either parenchyma or sclerenchyma or both;* xylem cylinder about 1.0 mm thick, consisting of about *9 strands;* inner cortex 0.25–0.5 mm thick, including *0–1 leaf-traces* in transverse section; outer cortex 1.0–4.0 mm thick, including about *7 leaf-traces* in transverse section; mass of thick-walled fibers in concavity of petiolar strand *presumably extending downward only to base of stipular region, not into stem;* stipular expansions of petiole base *containing scattered small masses of thick-walled fibers throughout.*

Occurrence.—Recent. Philippines and S. E. Asia.

Basis of description.—Literature account of Hewitson (1962).

OSMUNDA ARNOLDII Miller

Pl. 1, figs. 5, 6; pl. 2, fig. 5

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 181; 1967.

Stem 8–10 mm in diameter; stele about 3.0 mm in diameter; pith 1.5 mm in diameter, *consisting of either parenchyma or sclerenchyma or both;* xylem cylinder 1.0 mm thick, consisting of *8–12 strands;* inner cortex 1.0–2.0 mm thick, including *0–2 leaf-traces* in transverse section; outer cortex 1.0–4.0 mm thick, including *4–7 leaf-traces* in transverse section; mass of thick-walled fibers in concavity of petiolar strand *extending downward into stem;* stipular expansions of petiole base *containing many irregularly-shaped masses of thick-walled fibers of various sizes scattered throughout.*

Holotype and paratypes.—Museum of Paleontology, University of Michigan.

Occurrence.—Paleocene, Fort Union Formation. Morton County, North Dakota.

Basis of description.—Investigation of the holotype, paratypes, and two topotypes (Miller, 1967).

Discussion.—In this species are combined the sclerotic pith of *O. vachellii* and the occurrence of thick-walled fibers in the concavity of the leaf-traces as in *O. banksiaefolia.* In other respects, particularly the arrangement of sclerenchyma in the stipular expansions, *O. arnoldii* is very similar to these extant species. The fossil represents a general type from which the two Recent species evolved almost unchanged (Miller, 1967).

OSMUNDA DOWKERI (Carruthers) Chandler

Bull. British Mus. (Nat. Hist.) Geology, London 10(6) p. 139–161; 1965.
Osmundites dowkeri Carruthers, Quart. Jour. Geol. Soc. London xxvi, p. 349; pl. xxiv, figs. 1–3; pl. xxv, figs. 1–4; 1870.
Osmundites chandleri Arnold, Palaeontographica XCII, Abt. B, p. 68–72, text-figs. 3, 4, 5b; pls. VII, VIII; 1952.

Stem 9.0–15.0 mm in diameter; stele 4.0–6.0 mm in diameter; pith about 1.5 mm in diameter, *consisting of either parenchyma or sclerenchyma or both;* xylem cylinder *0.7–1.25 mm (15–25 tracheids)* thick, consisting of *20–33 strands;* inner cortex 1.0–3.0 mm thick, including *2–7 leaf-traces* in transverse section; outer cortex 2.5–4.0 mm thick, including *8–14 leaf-traces* in transverse section; mass of thick-walled fibers in concavity of petiolar strand *extending downward into stem;* stipular expansions of petiole base *containing 6–8 irregularly-shaped masses of thick-walled fibers and several small masses scattered throughout.*

Holotype.—Paleobotanical Collection, British Museum (Natural History), London, England.

Occurrence.—Lower Eocene; Herne Bay, Isle of Wight, England. Upper Eocene, Clarno Formation; Jefferson County, Oregon. Four other specimens are known from Utah, from South Dakota, from the Oregon coast, and from near Muddy Creek, Oregon (Miller, 1967). The latter specimen is in the Hancock Collection, Oregon Museum of Science and Industry, Portland, Oregon. The ages of these four specimens are unknown.

Basis of description.—Literature accounts of Kidston & Gwynne-Vaughan (1910), Arnold (1952), and Chandler (1965), and my examination of the above mentioned specimens.

Discussion.—This species differs in too many respects from *O. arnoldii* and the Recent species of this subgenus to be considered a derivative of the former or a progenitor of the latter. More likely, it represents an extinct branch of the *Plenasium* line of evolution that arose from forms that predate *Osmunda arnoldii* (Miller, 1967).

Genus TODEA Willdenow

Stems short, upright, *branching frequently in older plants to form, with surrounding mantle of petiole bases and roots, mound-shaped false trunks up to 3 m in diameter; stele an* *ectophloic-dictyoxylic siphonostele;* xylem cylinder about 15 tracheids thick; endodermis external only; leaf-gaps immediate, narrow; *inner cortex consisting mainly of parenchyma but with a strand of thick-walled fibers axillary to each leaf-trace; outer cortex consisting of fibers immediately around each leaf-trace with short sclereids filling in the interstices;* leaf-trace oblong in cross section, *containing one endarch protoxylem which bifurcates as the leaf-trace passes through the outer cortex and enters the base of the petiole;* petiole base stipular with *transverse commissure,* vascular strand C-shaped with narrow band of sclerenchyma lining its concavity; sclerenchyma ring of petiole base about as thick as vascular strand, *containing an abaxial arch of thick-walled fibers in lower part of stipular region which extends upward to surround ring as a thin band;* inner cortex of petiole base and stipular expansion *containing numerous small strands of thick-walled fibers scattered throughout; roots arising singly* (sometimes in pairs) from leaf-traces as latter separate from stem xylem.

Generitype.—Todea barbara (L.) Moore.

TODEA BARBARA (L.) Moore

Index Filicum, p. 119; 1857.

Stem 7.0–20.0 mm in diameter; stele 1.5–5.0 mm in diameter; pith 0.75–3.0 mm in diameter, *consisting of parenchyma or sclerenchyma or both;* xylem cylinder 0.5–1.0 mm thick, *consisting of 2–11 strands;* inner cortex 0.25–2.0 mm thick, including *2–5 leaf-traces* in transverse section; outer cortex 1.25–5.0 mm thick, including *3–8 leaf-traces* in transverse section.

Occurrence. — Recent. Eastern Australia, Tasmania, and South Africa.

Basis of description.—Literature accounts of Faull (1901), Seward & Ford (1903), and Hewitson (1962) and my examination of plants of this species (table 2).

Discussion.—Bifurcation of the leaf-trace protoxylem commonly occurs as the leaf-trace passes through the inner cortex in small plants of this species but in the outer cortex or petiole base in larger plants. The latter situation was considered to be the typical condition for comparative purposes.

Genus LEPTOPTERIS Presl

Stems arborescent to rhizomatous; *stele an ectophloic dictyoxylic siphonostele;* xylem cylinder about 15 tracheids thick; endodermis external only; leaf-gaps immediate, narrow; cortex with a thin inner cylinder and a thick outer cylinder; inner cortex consisting of parenchyma; *outer cortex consisting of fibers immediately around each leaf-trace with short sclereids filling in the interstices;* leaf-trace oblong in cross section, containing *one endarch protoxylem which bifurcates as leaf-trace passes through outer cortex or enters petiole base;* petiole base stipular *with transverse commissure,* vascular strand C-shaped with narrow band of sclerenchyma lining its concavity; sclerenchyma ring of petiole base with narrow, abaxial arch of thick-walled fibers in lower part of stipular region, extending upward to surround ring as a thin, inconspicuous band; *inner cortex of petiole base lacking sclerenchyma;* stipular expansions containing sclerenchyma in various patterns; *roots arising singly* (sometimes in pairs) from each leaf-trace, in some cases before latter is free from stem xylem.

Generitype.—Leptopteris fraseri (H. & G.) Presl.

LEPTOPTERIS FRASERI (H. & G.) Presl

Suppl. Tent. Pterid., p. 71; 1845.

Stems short, upright to rhizomatous, 4.5–10.0 mm in diameter; stele about 3.0 mm in diameter; pith about 1.0 mm in diameter; xylem cylinder 0.5–1.0 mm thick, *consisting of 2–12 strands;* inner cortex 0.25–1.0 mm thick, including *0–2 leaf-traces* in transverse section; outer cortex 2.0–3.0 mm thick, including *6–9 leaf-traces* in transverse section; *stipular expansions of petiole base containing numerous, small strands of thick-walled fibers scattered throughout.*

Occurrence.—Recent. Eastern Australia.

Basis of description.—Literature account of Hewitson (1962) and my examination of plants of this species (table 2).

LEPTOPTERIS HYMENOPHYLLOIDES (A. Rich.) Presl

Suppl. Tent. Pterid., p. 71; 1845.

Stems short, upright to rhizomatous, 5.0–6.5 mm in diameter; stele 1.5–2.0 mm in diameter; pith about 0.5 mm in diameter; xylem cylinder about 0.5 mm thick, *consisting of 5–12 strands;* inner cortex 0.25–0.5 mm thick, including *0–2 leaf-traces* in transverse section; outer cortex 1.0–2.5 mm thick, including *6–10 leaf-traces* in transverse section; *stipular expansions of petiole base containing one dominant irregularly-shaped mass of thick-walled fibers and three or four smaller scattered masses.*

Occurrence.—Recent. New Zealand.

Basis of description.—Literature accounts of Seward & Ford (1903) and Hewitson (1962) and my examination of plants of this species (table 2).

Discussion. — Past descriptions and the present one are based on relatively immature stems. The internal endodermis reported by Seward & Ford (1903) in one of their specimens must be regarded as an anomaly since it did not occur in Hewitson's material (1962) or mine.

LEPTOPTERIS SUPERBA (Col.) Presl

Abh. böhm Ges. V, 5, p. 326; 1848.

Stems short upright to rhizomatous, 5.0–10.0 mm in diameter; stele 1.75–3.0 mm in diameter; pith 0.5–1.0 mm in diameter; xylem cylinder 0.5–1.0 mm thick, *consisting of 3–11 strands;* inner cortex 0.25–1.5 mm thick, including *2–8 leaf-traces* in tranverse section; outer cortex 1.0–3.5 mm thick, including *6–20 leaf-traces* in transverse section; *stipular expansions of petiole base containing one large, irregularly-shaped mass and numerous small, scattered masses of thick-walled fibers.*

Occurrence.—Recent. New Zealand.

Basis of description.—Literature accounts of Faull (1901), Seward & Ford (1903), and Hewitson (1962) and my examination of plants of this species (table 2).

Discussion.—As with *Leptopteris superba,* all descriptions of this species are based on relatively immature stems.

LEPTOPTERIS WILKESIANA (Brack.) Christ

Pl. 2, figs. 3, 4

Farnkr., p. 334; 1897.

Stems arborescent, about 1–3 m (but up to 10 m) tall, 7.0–14.5 mm in diameter; stele 3.5–5.0 mm in diameter; pith 1.25–2.5 mm in diameter; xylem cylinder 0.75–1.0 mm thick, consisting of *9–17 strands;* inner cortex 0.25–0.75 mm thick, including *1–6 leaf-traces* in transverse section; outer cortex 1.25–4.5 mm thick, including *6–14 leaf-traces* in transverse section; *stipular expansions of petiole base containing one large, irregularly-shaped mass of thick-walled fibers and about 12 scattered masses of medium size.*

Occurrence. — Recent. Fiji, Samoa, New Caledonia, New Hebrides, and possibly New Guinea.

Basis of description.—My examination of plants of this species (table 2).

Discussion.—The above description is the first information to be published about the internal structure of trunks of *L. wilkesiana.* Because this species is the only living member of the family to display the arborescent habit, additional information is desirable. The material at my disposal consisted of three dried trunks each about five feet long. Making preparations suitable for study under the compound microscope was not possible due to the hardness and impenetrability of the specimens. The above information is based on reflected light examinations of pieces that were cut from the trunks with a fine-toothed saw, sanded smooth, and polished with furniture wax. A large sample of fresh or fixed material should be studied microscopically to establish limits of variation of the important features.

Genus OSMUNDACAULIS Miller

Structurally preserved rhizomes, roots, and (or) leaf-bases of plants resembling species of *Leptopteris, Osmunda,* and *Todea,* but which cannot be assigned to any 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) Miller.

Discussion.—*Osmundacaulis* (Miller, 1967, p. 146) was proposed as a new name for *Osmundites* Unger (1854) because the latter is preoccupied by *Osmundites* Jaeger (1827), and because Unger's generitype *Osmundites schemnicensis* belongs to *Osmunda* and was transferred to that genus under the new name *O. iliaensis* (Miller, 1967). Jaeger (1827) based his definition of *Osmundites* on misidentified cycadophyte fronds.

The species of *Osmundacaulis* are arranged below in groups believed to be phylogenetic groups, which are not given taxonomic designations.

OSMUNDACAULIS HERBSTII Group

Stems arborescent to rhizomatous; xylem cylinder about 15 tracheids thick; leaf-trace separating from xylem cylinder with *one protoxylem;* inner and outer cortical cylinders *well differentiated.*

OSMUNDACAULIS HERBSTII (Archangelsky & de la Sota) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites herbstii Archangelsky & de la Sota, Ameghiniana 3(5), p. 135–140, figs. 1–3; 1963.

Stem probably rhizomatous, about 9.0 mm in diameter, surrounded by a mantle of petiole bases and roots; *stele an ectophloic-dictyoxylic siphonostele,* about 4.0 mm in diameter; pith cavity about 2.0 mm in diameter, cells not preserved; xylem cylinder 0.5–1.5 mm thick, consisting of *18 strands; leaf-gaps narrow, immediate;* xylem sheath, phloem, pericycle, and endodermis not preserved; phloem, pericycle, and endodermis probably external; inner cortex 0.7–1.5 mm thick, homogeneous, consisting of parenchyma; outer cortex sclerotic, exact composition unknown; number of leaf-traces in transverse section of cortex unknown; protoxylem of leaf-trace not preserved, probably single endarch and bifurcating as leaf-trace enters petiole base; petiole bases stipular, cataphylls present, sclerenchyma in concavity of petiolar bundle absent or not preserved; *inner cortex of petiole base containing numerous, small, scattered strands of thick-walled fibers;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions containing *3–5 rounded masses of thick-walled fibers in rough, linear series with those nearer the sclerenchyma ring larger;* roots probably arising singly or in pairs from leaf-traces.

Holotype.—Paleobotanical Collection, Museum of La Plata, Argentina.

Occurrence.—Upper Triassic, El Tranquilo Formation. Santa Cruz, Argentina.

Basis of description.—Literature account of and personal communication with Archangelsky & de la Sota (1963).

Discussion.—It should be noted that this species is the oldest osmundaceous stem to bear cataphylls.

OSMUNDACAULIS SAHNII
(Vishnu-Mittre) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites sahnii Vishnu-Mittre, The Palaeobotanist 4, p. 113–119, pls. I, II, text-figs. 1–13; 1955.

Stem probably rhizomatous, 10–26 mm in diameter, surrounded by a mantle of petiole bases and roots; *stele an ectophloic-dictyoxylic siphonostele,* about 7.0 mm in diameter; pith about 4.0 mm in diameter, *consisting of parenchyma;* xylem cylinder about 1.0 mm thick, consisting of *50–70 strands; leaf-gaps narrow, mostly immediate with some delayed;* inner cortex about 1.0 mm thick, probably parenchymatous, cells not preserved; outer cortex 4.0–6.0 mm thick, sclerotic, exact composition unknown; number of leaf-traces in transverse section of cortex unknown; protoxylem of leaf-trace *single, endarch, and bifurcating as leaf-trace enters petiole base;* petiole base stipular, cataphylls absent; sclerenchyma in concavity of petiolar bundle *absent; inner cortex of petiole base containing numerous, small scattered strands of thick-walled fibers;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions containing *one rounded mass of thick-walled fibers of medium size and numerous, small strands which are scattered throughout;* roots generally arising in pairs (occasionally singly) from leaf-traces.

Holotype.—Museum of the Birbal Sahni Institute of Paleobotany, Lucknow, India.

Occurrence.—Jurassic. Bindrabum, India.

Basis of description.—Literature account of and personal communication with Vishnu-Mittre (1955).

OSMUNDACAULIS DUNLOPI
(Kidston and Gwynne-Vaughan) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites dunlopi Kidston & Gwynne-Vaughan, Trans. Roy. Soc. Edinburgh 45, pt. I, no. 27, p. 759–763, pl. I, figs. 1–3; pl. II, figs. 4–9, 12, 13; pl. III, figs. 14–16; 1907.

Osmundites aucklandicus Marshall, Trans. & Proc. New Zealand Institute 56, p. 210–213; 1924.

Stem *rhizomatous,* 15–19 mm in diameter, surrounded by a mantle of petiole bases and roots; *stele an ectophloic-dictyoxylic siphonostele,* 4.0–7.0 mm in diameter; pith 2.0–6.0 mm in diameter, *consisting of parenchyma;* xylem cylinder about 0.5 mm thick, *consisting of 20–50 strands; leaf-gaps very narrow, some immediate, some delayed, some incomplete;* phloem and endodermis external only; inner cortex 0.5–2.0 mm thick, parenchymatous; outer cortex about 6.0 mm thick, sclerotic, exact composition unknown; *number of leaf-traces in transverse section of cortex 70–79; protoxylem of leaf-trace single, endarch, bifurcating as leaf-trace passes through outer part of outer cortex;* petiole bases stipular, cataphylls absent, sclerenchyma in concavity of petiolar strand *a single mass in lower part of stipular region bifurcating above to form two masses,* one against each incurved tip of the vascular strand; inner cortex of petiole base containing *numerous, small scattered strands of thick-walled fibers;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions containing *numerous small masses of thick-walled fibers scattered throughout with those nearer the sclerenchyma ring slightly larger;* roots arising singly or in pairs from leaf-traces.

Holotype.—Geology Annex, British Museum (Natural History), London, England.

Occurrence.—Jurassic. Near Gore, Otago District, New Zealand.

Basis of description.—Literature accounts of Kidston & Gwynne-Vaughan (1907), Sinnott (1914), Marshall (1924), and Edwards (1933), and my examination of slides of the holotype, specimen V7060 and slides 2654 and

2655 of the British Museum (Natural History), London.

Discussion.—Marshall's (1924) specimen is the lower portion of the piece he gave to Sinnott (1914) for description (Edwards, 1933). The near absence of leaf-gaps in the type specimen is not typical for the species. In all instances leaf-gaps are very narrow but they are generally present with most of them being incompletely formed. Leaf-gaps are more distinct in other specimens of this species.

OSMUNDACAULIS GIBBIANA (Kidston & Gwynne-Vaughan) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites gibbiana Kidston & Gwynne-Vaughan, Trans. Roy. Soc. Edinburgh 45, pt. I, no. 27, p. 763–768, pl. III, figs. 17–19; pl. IV, fig. 20; 1907.

Stem *rhizomatous,* 15–17 mm in diameter, surrounded by a mantle of petiole bases and roots; stele *an ectophloic-dictyoxylic siphonostele,* about 3.5 mm in diameter; pith cavity about 1.5 mm in diameter, cells not preserved; xylem cylinder about 0.5 mm thick, consisting of about 20 *strands; leaf-gaps narrow, immediate;* xylem sheath and pericycle not preserved; phloem and endodermis external; inner cortex 0.5–1.0 mm thick, sclerotic, exact composition unknown, *number of leaf-traces in transverse section of cortex about 70–75; protoxylem of leaf-trace single, endarch, bifurcating as leaf-trace passes into petiole base;* petiole base stipular, cataphylls absent; sclerenchyma in concavity of petiolar strand *a single mass in lower part of stipular region, bifurcating upward to form two masses,* one against each incurved tip of the vascular strand; inner cortex of petiole base containing *numerous, small clusters of thick-walled fibers scattered throughout;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions containing *about 12 large masses of thick-walled fibers arranged in linear series with those nearer the sclerenchyma ring larger, and with those nearest the ring possibly in contact with it;* roots arising singly or in pairs from leaf-traces.

Holotype.—Geology Annex, British Museum (Natural History), London, England. Preparations of the holotype are preserved in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

Occurrence.—Jurassic. Near Gore, Otago District, New Zealand.

Basis of description.—Literature account of Kidston & Gwynne-Vaughan (1907) and my examination of slides of the holotype.

OSMUNDACAULIS PATAGONICA (Archangelsky & de la Sota) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites patagonica Archangelsky & de la Sota, Ameghiniana II(9), p. 153–163, pls. I–IV, text-figs. 1, 2; 1962.

Stem *rhizomatous,* about 15 mm in diameter, surrounded by a mantle of petiole bases and roots; stele probably an ectophloic-dictyoxylic siphonostele, about 7.0 mm in diameter; pith cavity about 4.0 mm in diameter, cells not preserved; xylem cylinder 1.0-1.5 mm thick, consisting of *28–34 strands;* xylem sheath preserved only in places; phloem, pericycle, and endodermis not preserved, probably external; inner cortex 0.5–1.0 mm thick, cells not preserved, probably parenchymatous; outer cortex 2.0–3.0 mm thick (outer limit not distinct), consisting of fibers; *number of leaf-traces in transverse section of cortex about 40; protoxylem of leaf-trace single, endarch, bifurcating as leaf-trace passes through outer part of outer cortex;* petiole base stipular, cataphylls present; sclerenchyma in concavity of petiolar bundle *a single mass in lower part of stipular region, bifurcating above to form two masses,* one against each incurved tip of the vascular strand; inner cortex of petiole base containing *numerous, small scattered strands of thick-walled fibers;* sclerenchyma ring of petiole base homogeneous; stipular expansions containing about *ten large clusters of thick-walled fibers arranged in irregular-linear series and several small scattered clusters;* roots arising singly or in pairs from leaf-traces.

Holotype.—Paleobotanical Collection, Museum of La Plata, Argentina.

Occurrence.—Upper lower Jurassic. Santa Cruz, Argentina.

Basis of description.—Literature account of and personal communication with Archangelsky & de la Sota (1963), and my examination of "peels" of the holotype.

OSMUNDACAULIS KOLBEI (Seward) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites kolbei Seward, Geol. Mag., N.S., decade V, IV, p. 482, pl. xx, figs. 2–4; pl. xxi, figs. 5a–d; 1907.

Stem *probably arborescent,* about 36 mm in diameter, surrounded by a mantle of petiole bases and roots; stele probably *an ectophloic-dictyoxylic siphonostele,* about 19.0 mm in diameter; pith cavity about 15 mm in diameter, *containing short tracheids, thick-walled cells and vacant spaces which probably held parenchyma;* xylem cylinder about 1.0 mm thick, consisting of *about 55 strands; leaf-gaps narrow, mostly immediate, some delayed;* xylem sheath, phloem, pericycle, and endodermis not preserved; inner cortex about 2.0 mm thick, *containing parenchyma and thick-walled sclereids scattered singly or in clusters;* outer cortex about 4.0–5.0 mm thick, consisting of fibers; *number of leaf-traces in transverse section of cortex about 75; protoxylem of leaf-trace single, submesarch in some, endarch in others, bifurcating as leaf-trace passes through outer part of outer cortex;* petiole base stipular, cataphylls absent; sclerenchyma in concavity of petiolar bundle absent or not preserved; *inner cortex of petiole base entirely parenchymatous;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions containing *two or three small, rounded strands of thick-walled fibers;* roots arising singly or in pairs from leaf-traces.

Holotype.—Preparations of the holotype are preserved in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

Occurrence.—Lower Cretaceous, Uitenhagen Series, Wealden. Herbertsdale, Cape Colony, South Africa.

Basis of description.—Literature account of Kidston & Gwynne-Vaughan (1910) and my examination of preparations of the holotype in the Kidston Collection.

OSMUNDACAULIS KIDSTONI (Stopes) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites kidstoni Stopes, Ann. Bot. 35, p. 55–61, pls. 1, 2; 1921.

Stem completely decayed, probably rhizomatous; petiole bases stipular, cataphylls absent; sclerenchyma in concavity of petiolar bundle absent or not preserved in lower part of stipular region, *two masses above,* one against each recurved tip of the vascular strand; inner cortex of petiole base *consisting entirely of parenchyma;* sclerenchyma ring of petiole base with *thin, abaxial arch of thick-walled fibers in upper two-thirds of stipular region, absent or decayed below; stipular expansions containing one large mass of thick-walled fibers and about 6 small masses scattered throughout.*

Holotype.—Geology Annex, British Museum (Natural History), London, England.

Occurrence.—Probably Cretaceous. Wollumbilla Creek, Queensland, Australia.

Basis of description.—Literature accounts of Stopes (1921), Posthumus (1924a), and Edwards (1933), and my examination of preparations of the holotype.

Discussion.—Stopes (1921) described the stele of what she thought was the "primitive" osmundaceous form as postulated by Kidston & Gwynne-Vaughan (1908, 1910), but the stele was later found to be a foreign axis of unknown affinity that had grown into the stem region of the fern (Posthumus, 1924a). The species has been largely ignored since, other than Edward's (1933) suggestion that *Osmundacaulis kidstoni* and *O. dunlopi* were conspecific. However, the abaxial arch of thick-walled fibers in the petiole base of this species is a valuable character which does not occur in *O. dunlopi* nor in any other *Osmundacaulis.* It does occur in four of the five Recent genera and the fossil representatives and suggests *O. kidstoni* as a possible precursor of these taxa.

OSMUNDACAULIS BRAZILIENSIS Group

Stem arborescent; xylem cylinder about 50 tracheids thick; leaf-trace probably separating from the xylem cylinder with two protoxylems; inner and outer cortical cylinders poorly differentiated or undifferentiated.

OSMUNDACAULIS BRAZILIENSIS (Andrews) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites braziliensis Andrews, Bull. Torrey Bot. Club 77, p. 29–34; 1950.

Stem *arborescent, 80–90 mm in diameter,* surrounded by a mantle of adventitious roots; stele about 50 mm in diameter; stele type uncertain, a dissected ectophloic or amphiphloic siphonostele; pith cavity about 30 mm in diameter, cells not preserved; *xylem cylinder 5–6 mm (50–60 tracheids) thick,* consisting of *22 strands; leaf-gaps wide, immediate;* xylem sheath, phloem, and pericycle not preserved; *endodermis external and internal, connecting through leaf-gaps;* cortex about 50 mm thick, *apparently not divided into inner fleshy and outer sclerotic cylinders;* number of leaf-traces in transverse section of the cortex *about 22;* protoxylem of leaf-trace not preserved, *probably two endarch strands;* leaf-traces in cortex *C-, V-, and Y-shaped, some with islands of parenchyma at tips and (or) in medial position;* roots arising singly or in pairs from leaf-traces; petiole bases not preserved.

Holotype.—United States National Museum.

Occurrence.—Horizon uncertain, between the Permian and the Jurassic. Rio Pardo, Brazil.

Basis of description.—Literature account of Andrews (1950).

Discussion.—This specimen was labeled as coming from the Permian, but Andrews (1950) suggested a Mesozoic age for it because of its advanced stelar structure.

OSMUNDACAULIS CARNIERI (Schuster) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites carnieri Schuster, Berichte den Deutsch. Bot. Gesellsch. xxix, p. 534, pls. xx, xxi, text-figs. 1, 2; 1911.

Stem *arborescent, 90 mm in diameter,* surrounded by a mantle of adventitious roots; stele 35 mm in diameter; stele type uncertain, a dissected ectophloic or amphiphloic siphonostele; pith about 30 mm in diameter, cells not preserved; xylem cylinder *about 4.0 mm (55 tracheids) thick,* consisting of *35 strands; leaf-gaps wide, immediate;* xylem sheath, phloem, and pericycle not preserved; *endodermis external and internal, connecting through leaf-gaps;* cortex about 30 mm thick, *differentiated into inner fleshy and outer sclerotic cylinders but without definite line of demarcation between the two;* number of leaf-traces in transverse section of the cortex *about 35;* protoxylem of leaf-trace not preserved, *probably two endarch strands;* leaf-traces in cortex *shallowly curved to C-shaped, without islands of parenchyma;* petiole bases not preserved; roots arising singly or in pairs from *lateral edges and abaxial side of leaf-traces.*

Holotype.—Preparations of the holotype are in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

Occurrence.—Horizon uncertain, between the Jurassic and the Tertiary. South Paraguay.

Basis of description.—Literature account of Kidston & Gwynne-Vaughan (1914) and my examination of preparations of the holotype in the Kidston Collection.

OSMUNDACAULIS SKIDEGATENSIS Group

Stem *arborescent;* xylem cylinder *about 50 tracheids thick;* leaf-trace separating from xylem cylinder with *two protoxylems; inner and outer cortical cylinders well differentiated.*

OSMUNDACAULIS SKIDEGATENSIS (Penhallow) Miller

Pl. 2, fig. 2

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.

Osmundites skidegatensis Penhallow, Trans. Roy. Soc. Canada, ser. 2, viii, p. 3, pls. i–iv, figs. 1–8; p. 32, pls. vii–xi; 1902.

Stem *arborescent,* 25–30 mm in diameter, surrounded by a mantle of petiole bases and roots; stele 17–23 mm in diameter, a *dictyostele;* pith 13–15 mm in diameter, *consisting of parenchyma and thick-walled stone cells* (occasionally containing one or more roots of unknown affinity); xylem cylinder *2.0 mm (27–43 tracheids) thick,* consisting of *32–39 strands;* leaf-gaps *mostly immediate, some delayed;* xylem sheath surrounding each xylem strand; *phloem internal and external, connecting through leaf-gaps;* pericycle external only; *endodermis internal and external, connecting through leaf-gaps;* inner cortex 1.5–3.5 mm thick, mainly parenchymatous *but containing thick-walled stone cells like those of the pith scattered singly or in clusters;* outer cortex 1.0–4.0 mm thick, consisting of fibers; number of leaf-traces in transverse section of cortex *25–45;* protoxylem of leaf-trace *two endarch strands;* petiole base stipular, cataphylls absent, only lower part of stipular region included in specimen; *sclerenchyma in concavity of petiolar bundle a single mass which connects downward with similar cells of the pith;* inner cortex of petiole base containing *several large, circular masses of thick-walled cells;* sclerenchyma ring of petiole base *homogeneous;* stipular expansions of petiole base *containing thick-walled cells scattered singly and in one or two large groups;* roots arising singly or in pairs from leaf-traces.

Holotype.—Geological Survey of Canada, Ottawa, Ontario, Canada. Preparations of the holotype are in the Kidston Collection, Department of Botany, University of Glasgow, Scotland, and in the Museum of Paleontology, The University of Michigan, UMMP 52164.

Occurrence. — Lower Cretaceous. Queen Charlotte Islands, British Columbia, Canada.

Basis of description.—Literature account of Penhallow (1902), Kidston & Gwynne-Vaughan (1907), and my examination of preparations of the holotype.

Discussion.—Kidston & Gwynne-Vaughan (1907, pl. IV, figs. 22, 23) show the presence of about seven xylem strands with adjoining phloem within the pith of the section they received from Penhallow. Personal communication between these investigators brought out the fact that sections 5.0 mm to either side do not show the misplaced strands (Penhallow, 1902, fig. 2). Further, no such strands occur in the preparations in the museum of The University of Michigan. These strands must, therefore, be regarded as anomalous and not typical of the species. While three small vascular strands do occur in the central pith of The University of Michigan preparations, they are most likely those of roots that invaded the central cylinder.

OSMUNDACAULIS ATHERSTONEI (Schelpe) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.
Osmundites atherstonei Schelpe, Ann. & Mag. Nat. Hist. (12) 9, p. 330–332; 1956.

Stem *arborescent,* about 17 mm in diameter, surrounded by a mantle of petiole bases and roots; stele 11.5–13.0 mm in diameter; stelar type unknown, probably an ectophloic-dictyoxylic siphonostele; pith 3.0–5.0 mm in diameter, cells not preserved; *xylem cylinder 3.5–6.0 mm (about 50 tracheids) thick,* consisting of *24 strands; leaf-gaps immediate;* xylem sheath, phloem, pericycle, endodermis, and inner cortex not preserved; outer cortex about 3.0 mm thick, sclerotic, exact composition unknown; number of leaf-traces in transverse section of cortex *about 25;* protoxylem of leaf-trace not preserved, *probably two endarch strands;* petiole bases stipular, cataphylls absent; sclerenchyma in concavity of petiolar bundle *a single mass extending downward into xylem cylinder;* inner cortex of petiole base not preserved; sclerenchyma ring of petiole base apparently homogeneous; stipular expansions apparently lacking sclerenchyma; roots arising singly or in pairs from each leaf-trace.

Holotype.—Part in British Museum (Natural History), London, England, and part in Dept. of Botany, The University of Cape Town, South Africa.

Occurrence.—Lower Cretaceous, Cape Province, South Africa.

Basis of description.—Literature account of Schelpe (1956) and my examination of part of the holotype in the British Museum.

OSMUNDACAULIS NATALENSIS (Schelpe) Miller

Contrib. Mus. Paleo. Univ. Michigan XXI, p. 146; 1967.
Osmundites natalensis Schelpe, Ann. & Mag. Nat. History (12) 8, p. 654–656, figs. 1–5; 1955.

Stem *arborescent,* about 19 mm in diameter, surrounded by a mantle of petiole bases and roots; stele 14.0–16.0 mm in diameter; stelar type uncertain, probably an ectophloic-dictyoxylic siphonostele; pith 9.0 mm in diameter, cells not preserved; *xylem cylinder 2.5–4.0 mm (53 tracheids) thick,* consisting of *25 strands, leaf-gaps immediate;* xylem sheath, phloem, pericycle not preserved; *endodermis external and internal,* preserved only in places; inner cortex 1.0–1.6 mm thick, cells not preserved; outer cortex 1.0–1.4 mm thick, sclerotic, exact composition unknown; number of leaf-traces in transverse section of cortex *about 30;* protoxylem of leaf-trace not preserved, *probably two endarch strands;* petiole bases stipular, cataphylls absent, *sclerenchyma* in concavity of *petiolar bundle a single mass, extending downward into xylem cylinder;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions apparently lacking sclerenchyma; roots arising singly or in pairs from each leaf-trace.

Holotype.—Part in British Museum (Natural History), London, England, and part in the Dept. of Botany, The University of Cape Town, South Africa.

Occurrence.—Lower Cretaceous. Cape Province, South Africa.

Basis of description.—Literature account of Schelpe (1955) and my examination of part of the holotype in the British Museum.

Subfamily THAMNOPTEROIDEAE

Stele a *protostele or an ectophloic siphonostele,* xylem cylinder *not interrupted by leaf-gaps.*

Type genus.—*Thamnopteris* Brongniart.

Other genera. — *Anomorrhoea* Eichwald, *Bathypteris* Eichwald, *Chasmatopteris* Zalessky, *Iegosigopteris* Zalessky, *Petcheropteris* Zalessky, and *Zalesskya* Kidston & Gwynne-Vaughan.

Genus ANOMORRHOEA Eichwald

Stele, inner cortex, most of outer cortex unknown; protoxylem of leaf-trace bifurcating *as leaf-trace passes through outer cortex;* petiole bases stipular, containing a C-shaped vascular strand; sclerenchyma in concavity of petiolar bundle apparently lacking; inner cortex of petiole base parenchymatous, *containing cylinder of tissue parallel to sclerenchyma ring which may become sclerotic upward;* sclerenchyma ring apparently homogeneous; stipular expansions apparently without sclerenchyma.

Generitype. — *Anomorrhoea fischeri* Eichwald.

ANOMORRHOEA FISCHERI Eichwald

Lethaea Rossica I, p. 102; 1860.

Trunk about 60 mm across at the widest part; stele, inner cortex, and most of outer cortex missing.

Holotype.—Present location unknown, possibly the Geology Annex, British Museum (Natural History), London, England. Preparations of the holotype are preserved in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

Occurrence.—Upper Permian, "Gres cuivreux" strata. Kloutschewsk, Bjelebei district, Orenburg, USSR.

Basis of description.—Literature account of Kidston & Gwynne-Vaughan (1909) and Zalessky (1927) and my examination of preparations of the holotype.

Discussion.—So little is known about this axis that it could be assigned to *Thamnopteris, Zalesskya, Chasmatopteris, Iegosigopteris,* or *Petcheropteris* with as much justification as its present treatment in its own genus. Until the investigation of better preserved material allows a more accurate placement, the classification of the fossil is probably best left as it is.

Genus BATHYPTERIS Eichwald

Stem arborescent, surrounded by a mantle of petiole bases and roots; stele a *protostele;* xylem column *differentiated into central and outer regions; petiole bases lacking stipular expansions, loosely arranged around stem;* vascular strand of petiole base C-shaped; *multicellular spines* occurring on surface of petiole bases.

Generitype.—*Bathypteris rhomboidea* (Kutorga) Eichwald.

BATHYPTERIS RHOMBOIDEA (Kutorga) Eichwald

Lethaea Rossica I, p. 96, pl. iv, figs. 1, 2; 1860.
Tubicaulis rhomboidalis Kutorga (pars), Verhandl. d. miner. Gesell. zu St. Petersburg, pl. i, fig. 6; 1844.

Stem about 95 mm in diameter; stele about 6.5 mm in diameter; central xylem consisting of *large tracheids with scalariform wall thickenings,* relative length of cells unknown; inner cortex parenchymatous, thickness unknown; outer cortex sclerotic, thickness unknown; protoxylem of leaf-trace *a single, possibly endarch, strand,* point of bifurcation unknown; number of leaf-traces in transverse section of cortex unknown; *vascular strand of petiole base surrounded by sclerotic cells which diminish upward to form a narrow band around the strand;* sclerenchyma ring of petiole base homogeneous, *sclerotic cells of ring passing out to spines.*

Holotype.—Present location unknown, possibly the Geology Annex, British Museum (Natural History), London, England. Preparations of the holotype are preserved in the Kidston Collection, Department of Botany, University of Glasgow, Scotland. The specimen described by Zalessky (1924) is preserved in the University of Kazan, Kazan, USSR.

Occurrence. — Upper Permian. Bjelebei, Orenburg, USSR (Zalessky's (1924) specimen came from the Ural Mts.).

Basis of description.—Literature accounts of Kidston & Gwynne-Vaughan (1909) and Zalessky (1924, 1927) and my examination of preparations of the holotype in the Kidston Collection.

Discussion.—The unknown features mentioned above might be revealed if Zalessky's (1924) specimen were to be re-examined.

Genus CHASMATOPTERIS Zalessky

Stem arborescent, surrounded by a mantle of petiole bases and roots; stele presumably a protostele, possibly an ectophloic siphonostele; *xylem differentiated into central and outer regions;* outer xylem *conspicuously indented above point of contact with leaf-traces;* leaf-traces *with single mesarch protoxylem;* cortex well differentiated into inner fleshy and outer sclerotic cylinders, number of leaf-traces in cortex *about 35;* petiole base stipular, containing a C-shaped vascular strand; roots *arising directly from stele.*

Generitype. — *Chasmatopteris principalis* Zalessky.

CHASMATOPTERIS PRINCIPALIS Zalessky

Bull. Acad. Sci. de l'U.R.S.S., ser. 7, Cl. Sci. Math. Nat. V, p. 715–720; 1931a.

Trunk 200–300 mm in diameter; stem about 50 mm in diameter; stele 16 mm in diameter, with cavity at center about 11 mm in diameter; inner xylem ring about 1.0 mm thick, consisting of large diameter tracheids of unknown length (probably 1–3 times longer than broad); outer xylem ring about 1.5 mm thick with *5–8 mesarch protoxylems in rounded projections at periphery;* inner cortex 9.5 mm thick, parenchymatous; outer cortex 10.5 mm thick, sclerotic, exact composition unknown; number of leaf-traces in transverse section of cortex *about 35;* protoxylem of leaf-trace *a single endarch strand, bifurcating as leaf-trace passes through inner cortex; inner cortex of petiole base containing scattered masses of thick-walled cells;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions *containing about ten scattered masses of thick-walled cells;* roots *arising directly from stele, relation to incipient leaf-traces unknown.*

Holotype.—Museum of Natural History, Orenburg, USSR.

Occurrence.—Upper Permian, "ouraliene" zone. Geographic location not precisely known, USSR.

Basis of description.—Literature account of Zalessky (1931a).

Genus IEGOSIGOPTERIS Zalessky

Stem probably arborescent, surrounded by a mantle of petiole bases and roots; stele a protostele; xylem differentiated into central and outer regions, *border between layers indistinct;* petiole bases stipular; vascular strand of petiole base C-shaped; sclerenchyma ring of petiole base *rhomboidal in transverse outline.*

Generitype.—Iegosigopteris javorskii Zalessky.

IEGOSIGOPTERIS JAVORSKII Zalessky

Bull. de l'Acad. des Sci. de l'U.R.S.S., VII Serie, Cl. d. Sci., Math., et Nat. 5, p. 747–752, pls. I–III; 1935.

Trunk 45–60 mm in diameter; stem about 35 mm in diameter; stele 3.5 mm in diameter; central xylem consisting of large diameter tracheids *15 times longer than broad,* with scalariform wall thickenings; inner cortex about 4.0 mm thick, probably parenchymatous; outer cortex 4.0–6.0 mm thick, sclerotic; number of leaf-traces in transverse section of cortex *about 50;* protoxylem of leaf-trace *a single, mesarch strand, bifurcating as leaf-trace passes through inner cortex;* sclerenchyma ring of petiole base *rhomboidal in transverse outline;* sclerenchyma in inner cortex of petiole base and in stipular expansions apparently lacking; *roots arising from stele or from leaf-traces.*

Syntypes.—Zalessky's (1935) description of this species is based on three specimens no one of which is designated as the holotype. The disposition of these specimens is not given in Zalessky's report.

Occurrence.—Upper Permian. Kusnetz basin near the Iegosikha River, USSR.

Basis of description.—Literature account of Zalessky (1935).

Discussion.—The relatively long tracheids in the interior of the xylem cylinder of this species are similar to those of *Zalesskya gracilis* (pl. 2, fig. 10), but other features of *Iegosigopteris* are more characteristic of *Thamnopteris,* a fact which Zalessky (1935) recognized. He placed the fossils in a separate genus, however, because of the rhomboidal transverse outline of the sclerenchyma ring of the petiole base, a feature also occurring in *Thamnopteris* to a lesser extent (Kidston & Gwynne-Vaughan, 1909, pl. I, fig. 1).

Genus PETCHEROPTERIS Zalessky

Stem arborescent, surrounded by a mantle of petiole bases and roots; stele *a protostele; xylem differentiated into central and outer regions;* cortex well differentiated into inner fleshy and outer sclerotic cylinders; number of leaf-traces in transverse section of cortex unknown; petiole base stipular, containing a C-shaped vascular strand; roots arising directly on stele or from leaf-traces.

Generitype.—Petcheropteris splendida Zalessky.

PETCHEROPTERIS SPLENDIDA Zalessky

Bull. Acad. Sci. de l'U.R.S.S., ser. 7, Cl. Sci. Math. Nat. V, p. 705–710; 1931b.

Trunk 165 mm by 145 mm thick; stem 31–56 mm in diameter; stele about 7.5 mm in diameter; central xylem consisting of large diameter tracheids, relative length unknown; outer xylem ring 2.0–2.5 mm thick *with 7–10 mesarch protoxylems* in rounded projections at periphery; inner cortex 4.0 mm thick, parenchymatous; outer cortex 10–23 mm thick, sclerotic, exact composition unknown; protoxylem of leaf-trace *a single mesarch strand, becoming endarch as leaf-trace passes through inner cortex,* point of bifurcation unknown, probably as leaf-trace passes through inner cortex; inner cortex of petiole base apparently lacking sclerenchyma; sclerenchyma ring of petiole base apparently homogeneous; stipular expansions *containing 1–5 clusters of thick-walled cells in each wing.*

Holotype.—Location unknown, original description based on a stem in the private collection of M-elle T. Dobroliubova.

Occurrence. — Upper Permian. Petchora River near mouth of the Yd-jid-chor stream, USSR.

Basis of description.—Literature account of Zalessky (1931b).

Discussion.—Zalessky (1931b) founded the genus and the species mainly on the sinuous pattern of the sclerenchyma rings. However, their shapes are due to compression prior to preservation. This species probably belongs to *Thamnopteris.*

Genus THAMNOPTERIS Brongniart

Stem arborescent, surrounded by a mantle of petiole bases and roots; stele *a protostele,* possibly a siphonostele; xylem differentiated into central and outer regions; cortex well differentiated into inner fleshy and outer sclerotic cylinders; leaf-trace *containing one* (rarely two) *mesarch protoxylem which becomes endarch and bifurcates as leaf-trace passes through inner cortex;* petiole base stipular, containing a C-shaped vascular strand; *number of leaf-traces in transverse section of cortex 30–70;* roots arising directly on stele or from leaf-traces.

Generitype. — Thamnopteris schlechtendalii (Eichwald) Brongniart.

THAMNOPTERIS SCHLECHTENDALII (Eichwald) Brongniart

Pl. 2, fig. 9

Tableaux des genres des veget. foss., p. 35–36; 1849.
Anomopteris schlechtendalii Eichwald, Urwelt Russlands II, p. 180, pl. IV, figs. 3–5; 1842.

Trunk about 120 mm in diameter; stem about 50 mm in diameter; stele 13 mm in diameter; central xylem consisting of large diameter tracheids that are *about 1–3 times longer than broad;* small cavity at center of central xylem region; outer xylem ring 2.0 mm thick with *3–5 protoxylems* in rounded projections at periphery; inner cortex 5.0–9.5 mm thick, parenchymatous; outer cortex 5.0–11.0 mm thick, *consisting of short sclereids that are about 4–5 times longer than broad and have blunt ends; number of leaf-traces in transverse section of cortex 34–36;* inner cortex of petiole base with *a narrow band of thick-walled cells around vascular strand against the endodermis;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions containing *about 3 clusters of thick-walled cells;* roots arising *directly from stele or from lateral edges or adaxial side of leaf-trace.*

Holotype.—Museum of the Institute of Mines, Leningrad, USSR.

Occurrence.—Upper Permian, "gres cuivreux" zone. Kamskowatkinsk, Wjatka, USSR. The specimen figured by Eichwald (1860) and Kidston & Gwynne-Vaughan (1909) came from Bjelebei, Orenburg, USSR.

Basis of description.—Literature account of Kidston & Gwynne-Vaughan (1909) and my examination of their preparations in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

THAMNOPTERIS GWYNNE-VAUGHANI Zalessky

Jour. Linnaean Soc. London XLVI, p. 354–356, pl. 33, figs. 1–5; 1924.

Trunk about 70 mm in diameter; stem about 50 mm in diameter; stele 11.0 mm in diameter; central xylem consisting of large diameter tracheids that are *about 1–3 times longer than broad;* central xylem solid to the center; outer xylem ring about 1.0 mm thick with *about 7 protoxylems* in rounded projections at the periphery; inner cortex 9 mm thick, parenchymatous; outer cortex 10 mm thick, *consisting of thick-walled prosenchymatous cells; number of leaf-traces in transverse section of cortex about 70;* inner cortex of petiole base with *sclerenchyma in clusters near vascular strand;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions *apparently without sclerenchyma;* roots arising *from lateral edges or abaxial side of leaf-traces.*

Holotype.—Location unknown.

Occurrence.—Upper Permian. River Kozva, basin of Petchora River, USSR.

Basis of description.—Literature accounts of Zalessky (1924, 1927).

THAMNOPTERIS KIDSTONI Zalessky

Jour. Linnaean Soc. London XLVI, p. 348–354, pl. 32, pl. 34, figs. 6, 7; 1924.

Trunk about 60 mm in diameter; stem about 30+ mm in diameter; stele 11.5 mm in diameter; central xylem *consisting for the most part of large diameter tracheids that are 1–3 times longer than broad, but containing zone of parenchyma cells mixed with tracheids about 2 mm from periphery of column;* outer xylem ring 2.0 mm thick with *5–10 protoxylems* in projections at periphery; inner cortex 6.0 mm thick, parenchymatous; outer cortex poorly preserved, at least 2.5 mm thick, *consisting of thick-walled prosenchymatous cells; number of leaf-traces in transverse section of cortex about 30;* inner cortex of petiole base *with thick-walled cells forming band in concavity of vascular strand;* sclerenchyma ring of petiole base apparently homogeneous; stipular expansions *containing a single cluster of thick-walled cells;* roots arising singly or in pairs *from lateral edges or abaxial side of leaf-trace.*

Holotype.—Location unknown, specimen was in possession of Zalessky's son, George, at time of description.

Occurrence.—Upper Permian. Probably the mine Kirmensky, Ural Mts., USSR.

Basis of description.—Literature accounts of Zalessky (1924, 1927).

Genus ZALESSKYA Kidston & Gwynne-Vaughan

Stems arborescent to short upright; stele a protostele or an ectophloic siphonostele; *xylem differentiated into central and outer regions;* cortex well differentiated into inner fleshy, and outer sclerotic cylinders; leaf-traces containing *one mesarch protoxylem which becomes endarch and bifurcates as leaf-trace passes through inner cortex; number of leaf-traces in transverse section of cortex 100–150;* roots arising singly or in pairs from lateral edges of leaf-traces; petiole bases unknown.

Generitype.—*Zalesskya gracilis* (Eichwald) Kidston & Gwynne-Vaughan.

ZALESSKYA GRACILIS (Eichwald) Kidston & Gwynne-Vaughan

Pl. 2, fig. 10

Trans. Roy. Soc. Edinburgh 46, pt. II, no. 9, p. 220–226, pl. I; pl. II, figs. 4, 5, 8; pl. III; 1908.

Chelepteris gracilis Eichwald, Lethaea Rossica I, p. 98, pl. III, figs. 4, 5 (non fig. 6); 1860.

Stem about 56 mm in diameter, partly decorticated; stele 13 mm in diameter; central xylem column about 8 mm in diameter, consisting of large diameter tracheids that are *about ten times longer than broad,* central xylem containing vacant cavity 5.6 mm in diameter at center; outer xylem ring 2.0 mm thick, with *20–25 protoxylems* in prominences at periphery; inner cortex 20 mm thick, parenchymatous; outer cortex preserved only in places, consisting of fibers; *number of leaf-traces in transverse section of cortex 130+, probably about 150.*

Holotype.—Museum of the Institute of Mines, Leningrad, USSR.

Occurrence.—Upper Permian. Mine Kluczersky, Bjelebei, Orenburg, USSR.

Basis of description.—Literature accounts of Kidston & Gwynne-Vaughan (1908) and Zalessky (1927) and my examination of preparations of the holotype in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

ZALESSKYA DIPLOXYLON
Kidston & Gwynne-Vaughan

Trans. Roy. Soc. Edinburgh 46, pt. II, no. 9, p. 226–229, pl. IV; 1908.

Stem 35 mm in diameter, partly decorticated; stele 7.0 mm in diameter; central xylem column consisting of large diameter tracheids that are *about 1–3 times longer than broad;* central xylem containing vacant cavity 1.4 mm in diameter at center; outer xylem ring about 1.5 mm thick, with *about 3 protoxylems* in prominences at the periphery; inner cortex 15 mm thick, parenchymatous; outer cortex not preserved; *number of leaf-traces in transverse section of cortex 58+, probably well over 100.*

Holotype.—Museum of the Institute of Mines, Leningrad, USSR.

Occurrence.—Upper Permian. Mine Kluczersky, Bjelebei, Orenburg, USSR.

Basis of description.—Literature accounts of Kidston & Gwynne-Vaughan (1908) and Zalessky (1927) and my examination of preparations of the holotype in the Kidston Collection, Department of Botany, University of Glasgow, Scotland.

ZALESSKYA URALICA Zalessky

Jour. Linnaean Soc. London 46, p. 356–357, pl. 34, figs. 1–3; 1924.

Stem about 25 mm in diameter, partly decorticated; stele 11.0 mm in diameter; central xylem column about 6 mm in diameter, consisting of large diameter tracheids of unknown length, containing vacant cavity about 3 mm in diameter at center; outer xylem ring about 1 mm thick, with *about 20 protoxylems* in prominences at periphery; inner cortex about 13 mm thick, parenchymatous; outer cortex preserved only to a thickness of 6 mm, sclerotic, exact composition unknown; *number of leaf-traces in transverse section of cortex over 100.*

Holotype.—Location unknown; specimen belonged to an artist named Denisov-Ouralsky, who gave Zalessky one transverse section for description.

Occurrence.—Upper Permian. Ural Mts., USSR.

Basis of description.—Literature accounts of Zalessky (1924, 1927).

INCERTAE SEDIS

ITOPSIDEMA VANCLEAVEI Daugherty

Amer. Jour. Bot. 47(9), p. 771–777; 1960.

Daugherty's diagnosis (1960, p. 775): "Stems arborescent, covered by rather well-spaced, persistent, apterous leaf-bases, basal portion clothed in adventitious roots. Transverse section of petiole containing a single large fungiform, amphiphloic, endarch vascular bundle; gland-tipped, multicelled spines attached to surface of the stem and base of the petioles, spines and petioles embedded in delicate multicelled trichomes each consisting of a single row of elongated cells; leaf-traces in inner cortex oblong to crescent-shaped, in outer cortex hippocrepiform; roots adventitious, arising from abaxial side of leaf-traces, the cortex consisting of thin-walled or sclerotic cells, the xylem diarch; stem containing ectophloic, mesarch, siphonostele without leaf-gaps, metaxylem of multiseriate, scalariform pitted tracheids, xylem parenchyma present but may, or may not, accompany protoxylem; pith consisting of parenchyma cells showing variation in size and shape, and with reticulate pitted tracheids present but rare in central portion."

Occurrence.—Upper Triassic, Chinle Formation. Arizona.

Discussion.—This axis has no characteristics that positively indicate affinity with the Osmundaceae, and several of its features are not typical of this family. While leaf-traces of this fern are adaxially curved in the cortex, the vascular strand of the petiole base is mushroom-shaped with tips that curve outward rather than inward as in the Osmundaceae. A mixing of parenchyma cells with the xylem tracheids in *Itopsidema* is another non-osmundaceous feature. While some of these cells may be associated with protoxylem strands running out to leaf-traces, the parenchyma is too abundant and too scattered to allow this interpretation for all such cells. This admixture of parenchyma must be considered a regular feature of the xylem of this stem and, as such, would be unique in the Osmundaceae. The homogeneous cortex of *Itopsidema* is another suspicious character. All species of the Osmundaceae except *Osmundacaulis braziliensis* have parenchymatous inner and sclerotic outer cylinders, and the apparent homogeneity of the cortex in *O. braziliensis* may be an artifact of preservation. Thus, this feature of *Itopsidema* is atypical of the Osmundaceae. Moreover, conspicuous mucilage ducts occur in the cortex and petiole bases of this fern axis, but no other member of the Osmundaceae has them. Other features, such as the lack of stipular expansions and the occurrence of multicellular spines on the stem and leaf-bases, do occur in the Osmundaceae, but only rarely.

Thus, *Itopsidema vancleavei* should be regarded as a non-osmundaceous fern. Its true affinities are unknown. Mucilage ducts are a feature of the Marattiaceae, but the stele of these ferns is highly specialized, and stipular expansions occur on their petiole bases. The unspecialized ectophloic siphonostele and the very specialized petiolar bundle of *Itopsidema* are unparalleled among the better known Recent or extinct ferns. *Itopsidema* may well represent an extinct line of evolution, and it is placed in the Osmundaceae *incertae sedis* until a more accurate classification can be made.

TAXONOMIC CONSIDERATIONS

Division of the Osmundaceae into the subfamilies Osmundoideae and Thamnopteroideae is a natural or phylogenetic classification based on the assumed evolution of the former group from the latter. While stelar morphology is important in distinguishing between the subfamilies, the entire spectrum of variation included within each group must be given primary consideration. More specifically, the Thamnopteroideae should not be viewed as a group in which all species are protostelic nor should the Osmundoideae be treated as a category restricted to siphonostelic forms that have leaf-gaps. Atypical forms occur in both subfamilies; and since the Osmundoideae evolved from the Thamnopteroideae, species displaying intermediate structure must have existed in the past. Classification of such forms cannot be made arbitrarily on whether or not they have a protostele, but intermediates should be assigned to the group to which they bear the greatest overall resemblance.

Tagawa's (1941) separation of the Recent species into the subfamilies Osmundoideae *(Osmunda)* and Todoideae *(Todea* and *Leptopteris)* is based primarily on the dimorphic fronds of the former as compared with the isomorphic foliage of the latter. As such the majority of the fossil species assigned to the family cannot be classified in one or the other of the subfamilies because their foliage is unknown. While there is some phylogenetic basis for Tagawa's division, it is of minor consequence compared to the evolution of the "modern" osmundaceous stele from protostelic ancestors. Thus, separation of the Osmundaceae into the subfamilies Thamnopteroideae and Osmundoideae serves the dual purpose of accommodating all important fossil and living species and recognizing the most important phylogenetic development that has occurred during the evolution of the family.

While most authorities (Bower, 1926; Copeland, 1947; Hewitson, 1962) recognize only three Recent genera, certain investigators (Tagawa, 1941; Bobrov, 1967) separate the subgenera *Osmundastrum* and *Plenasium* from *Osmunda* and treat them as genera. Copeland admitted that there is good reason on the basis of differences in frond morphology to raise these taxa to genera but preferred the traditional treatment because having so many genera with so few species would be confusing. The three subgenera of *Osmunda* have been distinct lines of specialization since the Paleocene (Miller, 1967), and treating them as genera would reflect this long separation. Furthermore, the numerical analysis of the living species presented later in this work (text-fig. 8) shows that *Leptopteris, Todea,* and the three subgenera of *Osmunda* are more or less equally distinct from one another, and treating *Plenasium* and *Osmundastrum* as genera would lead to greater consistency in the taxonomy of the family. However, the characters selected for comparison in this analysis were mostly features of the rhizomes and leaf-bases with only a few from the foliage. So although it is recommended that the three subgenera be raised to genera, such an action should be based on a thorough investigation of the living species, including foliage and fructifications.

OTHER OSMUNDACEOUS FOSSILS

Rhizomes and trunks

Several species of rhizomes and trunks that may be osmundaceous are on record in the literature, but they could not be included in the analyses or systematic descriptions because little is known about their structure. However, they have been classified in taxa of the Osmundaceae, and are therefore of general interest.

Bathypteris lesangeana Schimper, *B. strongylopeltis* Schimper, *Thamnopteris vogesiaca*

Blanckenhorn, and *Zalesskya fistulosa* (Eichwald) Zalessky are treated in the literature as though they are casts with only external features preserved (Schimper, 1869; Blanckenhorn, 1886; Zalessky, 1927). Attempts to section these axes have not been reported; so what these fossils may hold is unknown. The protostelic Osmundaceae described by Kidston & Gwynne-Vaughan (1908, 1909) were first mistaken for casts and later discovered to contain important structural detail. Thus, the aforementioned species may possibly have preserved tissues and certainly warrant reinvestigation.

Description of *Thamnopteris kazanensis* Zalessky is limited to four photographs (Zalessky, 1927, pl. 24, figs. 1–4). The material is poorly preserved, but sufficient detail can be observed from the figures to confirm assignment of this species to the Osmundaceae and to *Thamnopteris*. A large cavity occupies the center of what was presumably a protostele, and the vascular tissues that were petrified are badly disorganized. Leaf-traces are probably mesarch near their point of attachment to the stele. They become endarch and attain pronounced adaxial curvature in the inner cortex. The petiole bases are stipular and contain a C-shaped vascular strand and a sclerenchyma ring. The xylem of the root is diarch. The small number of leaf-traces in the cortex and their relatively large size indicate alliance of the axis with *Thamnopteris*.

A cast of an osmundaceous rhizome or trunk from the Upper Triassic of Virginia is described by Bock (1960) as *Osmundites winterpockensis*. The surface of the material shows imprints of about 25 leaf-bases. Each has a C-shaped vascular strand that is surrounded by a raised circle which no doubt represents the remains of the sclerenchyma ring. Stipular expansions are not visible, but the wide spaces between each of the scars suggests their presence in the living condition. The structure described by Bock as an "interior accessory vascular bundle" in the concavity of each petiole trace no doubt represents a strand of sclerenchyma which occupies this position in most species of the family.

Compressed rhizomes are rare, but Harris (1961) reports such a fossil from the Yorkshire Jurassic which he referred to *Todites princeps* because of the close association of the axis with fertile fronds of this species. Harris (1961) also mentions another compressed rhizome from the Lower Lias (Lower Jurassic) of West Germany. Few characters can be distinguished in Harris' specimen, but the stipular expansions sheathing the stem are visible.

Kidston & Gwynne-Vaughan (1910, 1914) mention four other species of petrified axes that have not been fully investigated. One is from the Lena River in Siberia and is included in the Paleontological Collection of the University of Göttingen. A second axis is registered in the British Museum as *Asterochlaena cottai* but it is a poorly preserved *Osmundacaulis*. Two other stems have been referred to *Osmundites sp.* due to their poor preservation. One is from the (?) Tertiary near Rockhampton, Queensland, while the other is from the Triassic-Jurassic of New Zealand and had been originally referred to *Psaronius*. These specimens should now be considered species of *Osmundacaulis*.

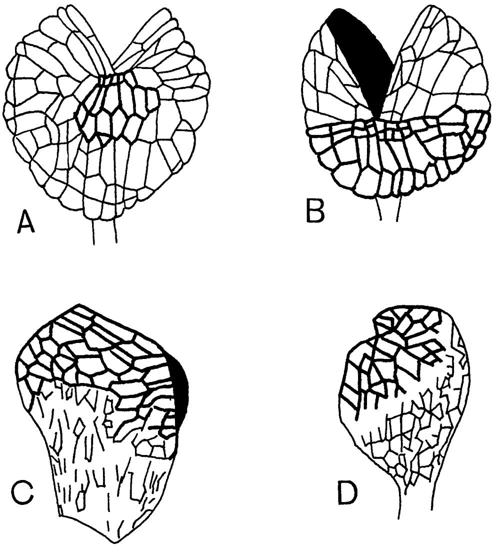
Three petrified stems that were originally treated in the Osmundaceae instead belong to the Lepidophyta. *Protoösmundites wilsoni,* a decorticated axis described by Andrews & Baxter (1948) from the Pennsylvanian of Iowa, has an ectophloic siphonostele in which the xylem is exarch and forms an uninterrupted ring around the pith. Numerous terete leaf-traces that have mesarch xylem are arranged spirally in the parenchymatous cortex, but the outer layer of this tissue is missing. Additional stems from the Pennsylvanian of Illinois that were investigated by Evers (1951) have lepidodendroid leaf bases and fimbrils between the transverse wall thickenings of the scalariform tracheids. The species was therefore transferred to *Lepidodendron* (Evers, 1951).

Chinlea campii and *Osmundites walkeri* are stems from the Upper Triassic of Arizona that Daugherty (1941) described as members of the Osmundaceae. Recent work (Miller, 1968) indicates that the two species represent different ontogenetic stages of the same type of stem, and *Osmundites walkeri* is placed in synonymy with *Chinlea campii. Chinlea* represents robust seasonal or ephemeral stems of an herbaceous lepidophyte that is somewhat more similar to *Nathorstiana* and *Pleuromeia* than to *Lepidodendron*.

The original material of both *Chinlea* and *Lepidodendron wilsoni* was decorticated so that the sheath of stipular petiole bases and the broad zone of sclerotic outer cortex, which are distinctive features in osmundaceous stems, were lacking. The erroneous assignment of these stems is indicative of the degree of difficulty in interpreting relationships on the basis of the stele, inner cortex and the leaf-traces that are included in the latter tissue. However, both *Chinlea* and *Lepidodendron wilsoni* lack adventitious roots and adaxially curved leaf-traces which osmundaceous ferns have.

Fructifications

Osmundaceous sporangia are sufficiently distinctive in their structure to be distinguished from those of other extant fern families, but they are so nearly uniform within the family that they cannot be used to differentiate taxa of lower rank. Sporangia of the living species are spherical to reniform, 330 to 660 microns in diameter, and have a multicellular stalk. Dehiscence is along an apical suture, and a group of thick-walled cells placed laterally on the body functions as a rudimentary annulus. The annulus in sporangia of *Leptopteris* touches the stalk or is one cell removed from it (text-fig. 5B), but in *Todea* several cells separate the annulus and stalk (text-fig. 5A). The annulus in sporangia of *Osmunda* is intermediate between these two extreme positions. However, overlapping limits of variation do not permit accurate identification of sporangia with taxa below the family level (Hewitson, 1962).



TEXT-FIG. 5—Sporangia. A, *Todea barbara,* × 50. B, *Leptopteris fraseri,* × 7½. C, *Osmundopsis sturi,* × 45. D, *Todites williamsonii,* × 45. A and B after Hewitson (1962), C and D after Harris (1961).

Sporangia of *Todites* from the Yorkshire Jurassic (Harris, 1961) differ significantly from those of the extant species (text-fig. 5D). The line of dehiscence is lateral, extending slightly over the top of the sporangium, and the annulus is nearly apical. The structure is somewhat similar to that of the extant Schizaeaceae, but these fossil sporangia contain spores that are osmundaceous.

Several fructifications from Paleozoic sediments suggest the osmundaceous condition; but departures from the structure characteristic in the Recent species of the Osmundaceae (and other fern families) are more pronounced, and many sporangia cannot be confidently assigned to Recent taxa. *Todeopsis primaeva* Renault, which occurs in the Culm (Lower Carboniferous) of France, is pyriform and has a plate of large cells comparable with the annulus of the extant Osmundaceae (Seward, 1910). *Pteridotheca butterworthi* Scott also has a group of large cells in lateral position, but its shape and manner of attachment suggest a mixing of marattiaceous and osmundaceous characters. This sporangium comes from the Coal Measures of Great Britain (Scott, 1909). *Sarcopteris bertrandi* B. R. is another sporangium that may be osmundaceous. It was apparently attached to *Pecopteris* foliage, but its age and geographical location are unknown. *Kidstonia heracleensis* Zeiller mixes characters of the Osmundaceae with those of the Schizaeaceae. It was described from the Coal Measures of Heraclea in Asia Minor and has an elongate shape as in the Schizaeaceae and a plate of large cells in lateral position as in the Osmundaceae (Zeiller, 1899). *Sturiella* Weiss, from the Permian of France, bears some similarity to sporangia of the Osmundaceae, but Zeiller did not think the similarity close enough to refer the organ to this family (*in:* Seward, 1910).

Thus, there is some evidence for the existence of ferns with osmundaceous affinities in the Carboniferous; but because of the generalized structure of many of these sporangia of that time, none of the sporangia can be confidently assigned to the Osmundaceae.

Isolated spores

Identification of the genera of the Osmundaceae by spore morphology is not possible. Characters generally used to distinguish fern spores are shape, size, nature of the contact scar, and spore wall ornamentation. Spores of the present-day Osmundaceae, however, are all spherical to subtriangular and are marked with a triradiate scar which occupies most of one hemisphere. Their diameter ranges from 40–70 microns; and while average size differs between species, ranges overlap making it impossible to identify unknowns on this basis. Echinae, clavae, baculae, and gemmae ornament the sporine wall in all species, but the degree of coalescence of elements varies between species from complete independence to complete joining of elements to form irregular scabrae and (or) rugulae. Palynologists working with Pleistocene material from North America have used this character to distinguish between spores of

Osmunda cinnamomea (elements independent), *O. claytoniana* (elements partly independent, partly fused), and *O. regalis* (elements completely coalesced). Yet, this character becomes invalid with the addition of other species of *Osmunda* as possible unknowns, for the various conditions occur in both of these subgenera. Spores of *Todea* and *Leptopteris* tend to have independent elements, but not all species of the latter genus have been examined.

Similarly, it is not possible to use spores to mark the first occurrence of the family in the geologic record. While the osmundaceous spore is relatively characteristic when compared with spores of other living ferns, many other vascular cryptogams of the Paleozoic produced spherical spores with a trilete mark; and the ancient Osmundaceae did not necessarily have spores with wall ornamentation like that of the Recent species.

Thus, spore morphology may be used to some extent as a character in analyzing relationships of species within an extant genus or in identifying osmundaceous ferns in the Pleistocene where the species composition can be predicted, but interpretation of broader problems must rest on other lines of evidence.

Foliage

Fronds of the present-day Osmundaceae have generalized form and venation that are duplicated in other fern taxa. Thus, assignment of fossil foliage to the family cannot be accurately made unless the foliage is nearly identical to that of the Recent species or is associated with or in connection with organs of definite osmundaceous affinity. Foliage that has been referred to the family is discussed below in this respect.

Fertile foliage.—**Dimorphic pinnae.** The occurrence of specialized, fertile axes that lack a lamina in Tertiary sediments where the three subgenera of *Osmunda* are already in evidence is not surprising, but reports of such organs in older sediments deserve attention. Heer (1874) illustrates a small, unbranched fragment of a fertile pinnule that occurred in association with *Osmunda oebergiana* in the Upper Cretaceous of Greenland (1874, pl. 26, fig. 9d) and a similar fragment in association with *O. petiolata,* from the Lower Cretaceous of Greenland (1874, pl. 3, fig. 2c, 2d). Both *O. oebergiana* and *O. petiolata* have pinnules that are similar in form and venation to those of *O. regalis* and *O. japonica,* but in *O. petiolata* each pinnule is attached to the rachis by a distinct stalk. The association provides evidence that the subgenus *Osmunda* was distinct in the Cretaceous and that the dimorphic habit it presently displays had evolved by that time.

Species of the form genus *Osmundopsis* Harris indicate that the dimorphic habit had evolved in the Osmundaceae prior to or during the Jurassic. The best known species of this genus is *O. sturi* (Raciborsky) Harris. It is represented in the Yorkshire Jurassic by two specimens (Harris, 1961) and in the Jurassic of Poland by one pinna and possibly a fragment of another (*Osmunda sp.* of Raciborsky, 1890). The pinnae lack a lamina and bear several pinnules, each of which is surrounded by numerous sporangia. Very little is known about *Osmundopsis microcarpa* (Raciborsky) Harris. It is from the Jurassic of Poland and is represented by a pinnule fragment (Raciborsky, 1890). Harris (1961) comments that *O. plectophora* Harris, from the Lias (Lower Jurassic) of Greenland, has broader sporangia with longer stalks than *O. sturi. O. prigorovskii* (Kryshtofovich & Prynada) Harris, from the Triassic of Armenia, could be a *Todites* (Harris, 1961).

The alliance of *Osmundopsis* with the Osmundaceae is definitely established by the morphology of the sporangia (text-fig. 5C). However, Raciborsky's (1890) original reference of his material to *Osmunda* was erroneous, since these organs could have been borne by other, extinct Osmundaceae.

Isomorphic pinnae. Fragments of laminate fronds bearing osmundaceous sporangia occur mainly in Jurassic sediments but range throughout the Mesozoic. They are rare or absent in the Tertiary. Such fronds are generally included in the form genus *Todites* Seward, but most of the species of this genus were first described as sterile fronds of the form genus *Cladophlebis* Brongniart and transferred to *Todites* when their fertile nature was discovered. As a result, there is much confusion over which species belong to which genus. Certain species of *Cladophlebis* are nearly identical in venation and morphology to species of *Todites* but lack sporangia; and Harris (1961), whose classification of the Yorkshire Jurassic material is a definite advance over past treatments, has taken the initiative and grouped some sterile material with the fertile.

Osmunda dicksonioides, O. dicksonioides var. latipennis, and *O. sphenopteroides* are species from the Potomac Formation (Lower Cretaceous) that were referred by Fontaine (1889) to *Osmunda.* The fertile pinnae of these fronds are smaller than the sterile but are still laminate. They would best be included in *To-*

dites because the osmundaceous structure of the sporangia has not been demonstrated.

Sterile foliage.—While the subgenera *Osmunda, Osmundastrum,* and *Plenasium* can only be extended to the Paleocene on the basis of petrified remains, several species of compressed foliage attest to the occurrence of at least *Osmunda* and *Plenasium* in the Mesozoic. Two species of sterile foliage, *Osmunda oebergiana* and *O. petiolata,* from the Upper and Lower Cretaceous of Greenland respectively, have already been mentioned in regard to their association with fertile pinnules. These two species are nearly identical to pinnules of *O. regalis* and *O. japonica,* and five other species of similar pinnules occur in the Cretaceous (table 4). In addition, *O. delawarensis* Berry, from the Upper Cretaceous of the Eastern United States, is referable to the subgenus *Plenasium* (table 4).

Not only is the presence of the subgenus *Osmunda* in the Cretaceous established on the basis of these fossils, but they and others occurring throughout the Tertiary (table 4) form a notable exception to the general belief that foliage is plastic and easily changed by paleoecologic conditions. *Osmunda asuwensis* Matsuo, from the Upper Cretaceous of central Japan, has pinnules that are nearly identical to those of *O. regalis* and *O. japonica.* These fossil pinnules of the subgenus *Osmunda* differ from foliage of the living species only in overall size, length of the petiole, and shape of the pinnule base.

While foliage of *Osmundastrum* is not in evidence below the Miocene (table 4), the subgenus is represented in the Paleocene of North Dakota by *Osmunda precinnamomea,* a species of petrified rhizomes (Miller, 1967). Furthermore, neither *Todea* nor *Leptopteris* are represented by foliage remains although a portion of a frond named *Filicites foeminaeformis* by Sternberg (1823, pl. II, fig. 25) is similar to fronds of *Leptopteris fraseri* and *L. wilkesiana.* The absence of *Todea* and *Leptopteris* may indicate their recent origin, but it can also be explained by their occurrence in montane rain forests of the tropics and subtropics where decay is rapid and good basins of deposition are distant.

Many species of *Cladophlebis* are thought to be osmundaceous (Arnold, 1952). The evidence favoring such a relationship is the occurrence of osmundaceous sporangia on some species (*Todites*), the association of certain species with *Osmundacaulis* (table 3), and the discovery of a C-shaped vascular strand in the petiole of *Cladophlebis australis* (Edwards, 1934). However, *Cladophlebis* is widespread and has been reported in nearly every major deposit of Mesozoic plant compressions. Thus, the apparent association may be interpreted as circumstantial and merely due to the abundance of *Cladophlebis* during the Mesozoic. Furthermore, the C-shaped petiolar strand is by no means unique to the Osmundaceae (Brongniart, 1828, pl. 37). Thus, while a close relationship between *Cladophlebis* and the Osmundaceae is inferred from the available evidence, only those fertile fronds with convincing osmundaceous sporangia can be confidently considered members of the family.

SPECIES RELATIONSHIPS

Phylogenies (i.e., race histories) for the Osmundaceae have been compiled by several authors, but they are either summaries of general evolutionary trends based on one or two characters with certain species mentioned as examples (Kidston & Gwynne-Vaughan, 1910; Bower, 1926; Endo, 1961; Archangelsky & de la Sota, 1962; Emberger, 1965) or historical reviews of the species with comments on certain of the species relationships (Seward & Ford, 1903; Arnold, 1952). These treatments have value in publicizing the major anatomical changes that have occurred in the Osmundaceae and in keeping information about the family up to date, but they fall short of being actual phylogenies because they do not provide accurate information about the interrelationships of all known species.

Placing the structurally preserved fossils and extant species in an accurate phylogeny by inspection of characters alone is impossible. Every tissue in the rhizomes and trunks of these ferns has changed somewhat during the course of evolution of the family; and no investigator can hold all variations in mind long enough to objectively evaluate all possible relationships between the species. For this reason, the phylogeny presented in text-fig. 9 is based on three numerical analyses of the character-states of the species by the "ground plan" method of character correlation. This type of analysis is a method of expressing evolutionary specialization as interpreted from multiple characters. It was originated and developed by Prof. W. H. Wagner, Jr. at The University of Michigan (1961, 1962) and has been used by a number of his students among them Hauke (1963), Mickel (1962), and Evans (1964).

Principles of the analysis

The ground plan method of character analysis consists basically of (a) investigating the

Table 4—Fossil Foliage of the Recent Genera of the Osmundaceae

Mesozoic:

Osmunda asuwensis Matsuo, 1962, Science Reports of the Kanawawa Univ. XIII, no. 1. Late Cretaceous, Japan.

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

Osmunda hollicki Knowlton, 1917, USGS Prof. Pap. 101, p. 246, pl. 30, fig. 6. Cretaceous, Colorado.

Osmunda major Lesquereux, 1883, Rept. U.S. Geol. Surv. Terr. VIII, Cret. and Tert. Fl., p. 212, pl. 18, fig. 5. Upper Cretaceous, Colorado.

Osmunda montanensis Knowlton, 1905, USGS Bull. 257, p. 129, pl. 14, fig. 6. Upper Cretaceous, Montana.

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

Osmunda oebergiana Heer, 1874, Flora foss. arctica, III, 2, Kgl. Sv. Vet. Ak. Handl. XII, 6, p. 98, t. 26, fig. 9, 9b; t. 32, fig. 7a. Upper Cretaceous, Greenland, also U.S.A.

Osmunda delawarensis Berry, 1906, Contributions to the Mesozoic flora of the Atlantic coastal plain — 1. Bull. Torrey Bot. Club XXXIII, pl. 8, fig. 2–4. Upper Cretaceous, Eastern U.S.A.

Cenozoic:

Osmunda affinis Lesquereux, 1878, Tertiary Flora, Hayden's Rept. U.S. Geol. Surv. Terr. VII, p. 60, pl. 4, fig. 1. Miocene, Western U.S.A.

Osmunda bilinica (Ettingshausen) Saporta & Marion, 1874, 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, 3rd. ser., i, p. 332. Paleocene, Alberta.

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

Osmunda regalis var. ? Endo, 1961, Trans. Proc. Palaeont. Soc. Japan, N.S., no. 44, p. 157–160, fig. 2, 3. Eocene, Japan.

Osmunda schemnicensis Stur, 1867, Jahrb. d. K. K. geol. Reichsanst. XVII, p. 136, pl. iii, fig. 1–3. Miocene-Pliocene, Germany.

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

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

Osmunda cf. claytoniana L., Brown, 1937, Additions to some fossil floras of the Western United States, USGS Prof. Pap. 186J, p. 167, pl. 45, fig. 1. Miocene, Idaho.

Osmunda lignitum (Giebel) Stur, 1870, Über zwei neue Farne aus den Sotzka-Schichten von Möttnig in Krain, Jahrb. K. K. Geol. R. A. XX, p. 15. Upper Eocene to Miocene, widespread.

Osmunda bromeliaefolia (Presl) Copeland, Endo, 1961, On the evolution of the Osmundaceae with descriptions of two new species, Trans. Proc. Palaeont. Soc. Japan, N.S., no. 44, p. 157–160. Miocene, Japan.

Incertae sedis:

Osmunda polybotrya (Brongniart) Schimper, 1869, Traite I, p. 679; figured in: Brongniart, A., 1836, Histoire I, p. 390, t. 137, fig. 6. Age and location not given. Fertile pinnule of *Osmunda, Osmundastrum,* or *Plenasium.* Perhaps best referred to *Osmundopsis* Harris.

Species of Uncertain Relationship to Family:

Osmunda arctica Heer, 1883, Flora foss. arctica VII, p. 7, t. 49, fig. 4–7, t. 50, fig. 6-8. Upper Cretaceous, Greenland and Alaska.

Osmunda dicksonioides and *O. dicksonioides var. latipennis* Fontaine, 1889, The Potomac or younger Mesozoic Flora, USGS Monogr. IV, p. 146, *O. dicksonioides:* pl. 41, fig. 5; pl. 58, fig. 9; pl. 59, fig. 1, 4, 8, 9, 11; pl. 60, fig. 2, 4, 5, 9; pl. 61, fig. 1, 2; *O. dicksonioides var. latipennis:* pl. 60, fig. 1, 3; pl. 61, fig. 3. Cretaceous.

Osmunda flexuosa De la Bech, 1824, Trans. Geol. Soc., N.S., I, t. 7, fig. 3. Lias, Great Britain.

Osmunda sepulta (Newberry) Knowlton, 1898, The later extinct floras of North America, USGS Monogr. 35, p. 12, pl. 62, fig. 5, 5a, 6. Upper Cretaceous, Wyoming.

Osmunda sphenopteroides Fontaine, 1889, Potomac or younger Mesozoic Flora, USGS Monogr. 15, p. 145, pl. 25, fig. 13, 13a, 13b. Cretaceous.

Osmunda dubiosa Hollick, 1936, The Tertiary floras of Alaska, USGS Prof. Pap. 182, p. 40, pl. 5, fig. 2.

Osmunda heeri Gaudin, 1856, In: Gaudin & La Harpe, Flore fossile de Lausanne, Bull. Soc. vaudoise des sc. natur., 4 Juill. 1885; figured in: Heer, O., 1868, Flora foss. arctica I, p. 88, t. 1, fig. 6–11, t. 8, fig. 15b.

Osmunda torellii Heer, 1868, Flora foss. arctica I, Miocene flora von Nordgrönland, p. 88, t. 1, fig. 15a, 15b, 15c.

The following species are listed in Fossilium Catalogus (Jongmans & Dijkstra, 1962) but were not included in this investigation:

Osmunda deubensis Hunger
Osmunda eocenica Saporta & Marion
Osmunda kargii Braun
Osmunda leganyii Andreansky
Osmunda novae-caesarae Berry
Osmunda oeningensis A. Braun
Osmunda oppositifolia Baikovskaja

sample and selecting variable characters, (b) determining the primitive, intermediate, and advanced states of each character, (c) assigning numerical values to the character-states, and (d) summarizing the character-states of each species by adding its total number of specialized conditions to form a divergence index. The species are then arranged on a semicircular graph according to their number of mutual character-states.

The evolutionary significance of the analysis depends on the characters selected. A modified Adansonian approach is used in the "ground plan" analysis, since characters that do not vary within the sample have no effect in grouping the taxa and should be excluded to avoid confusion. Dependent characters are also excluded because two directly related characters will reinforce and two inversely related characters will nullify each other, either situation giving a false impression of the degree of actual divergence.

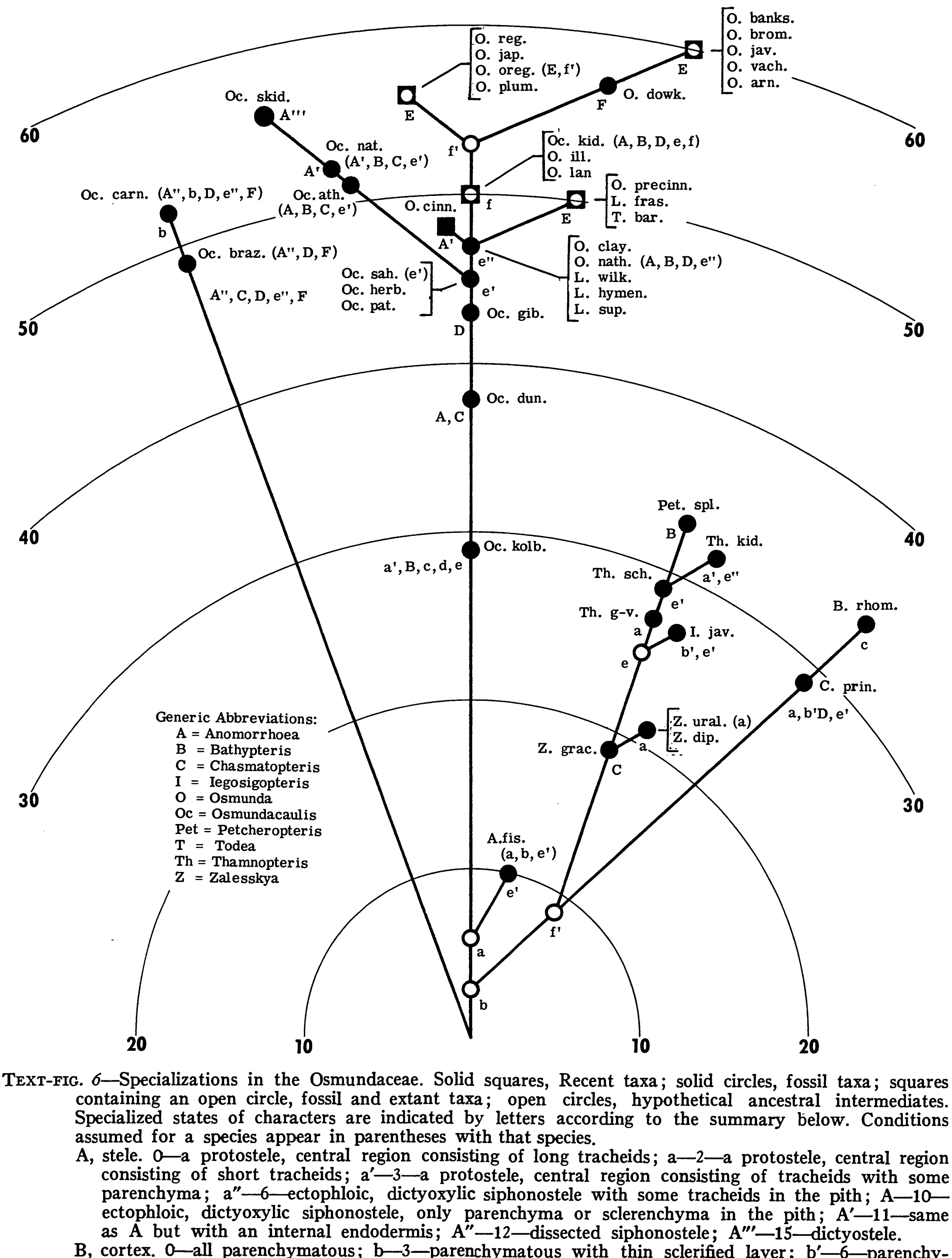
Determination of the primitive, intermediate, and advanced states of each character is critical to the analysis. If possible, all decisions should be confirmed by evidence outside the sample—from the taxonomic group of the next higher order, from closely related taxa, or from evidence in the fossil record. A character-state common to the majority of the species probably occurred in their most immediate ancestor and can often be considered primitive or, at least, generalized. The presence of stipular expansions in osmundaceous ferns, for example, is a general state; but one ancient species lacks them, and their absence in this early form might lead to the hypothesis that stipular expansions are derived in the Osmundaceae. However, evidence from ferns in general confirms the view that stipular expansions represent a primitive state, since they occur mostly in ferns, such as the Marattiales, Ophioglossales and the Plagiogyriaceae, which are believed to be primitive on other evidence (an interesting exception is *Matteuccia pensylvanica* Raymond). Further, character-states that occur rarely in the sample may be either primitive or advanced since organisms evolve by reduction or specialization of their ancestor's characters; and evidence outside the sample must be used for proper interpretation.

Evaluation of the character-states is also important. We have no way of assigning different values to different specializations, so the numerical value assigned to advanced states of the various characters must be the same. The divergence index value of the most primitive state of each character is placed at zero, and intermediate states are given values between zero and that of the advanced condition. Choice of the interval depends on the number of different intermediate states within each character. Where variation is slight and only one or two intermediate situations exist between the primitive and advanced states, the zero to one interval is used with fractions of one representing the intermediate states. Where many intermediate conditions occur within the characters, the variation is more accurately expressed over a larger interval, zero to ten, for example. Certain "ultra-specialized" states (i.e., those that are obviously modifications of an already specialized condition) may be accommodated by a value slightly higher than that given the advanced state, such as 1¼ or 1½ for the zero to one interval and 12 or 15 for the zero to ten interval.

Use of the "ground plan" method, to date, has been restricted to extant plants, and adapting the method to include fossil material requires one modification. The states of characters not preserved in the fossils must be assumed on the basis of those that are. The validity of an assumed state is open to serious question because highly specialized organisms may retain primitive states, and primitive organisms may have a few specialized states. Yet to assume arbitrarily the most primitive state or the most general state consistently throughout the sample for all unknown conditions yields greater inaccuracy for it is often contrary to the characters that are preserved. The assumption of character-states has been kept to a minimum in this work, and those features that have been assumed for a species are listed in parentheses with that binomial (text-figs. 6, 7). In certain cases there is no basis for judgment, particularly where only a few characters are preserved and their states are inconsistent. Such species must be excluded from the sample.

The analyses

Three analyses were conducted. The first analysis included all petrified axes and extant species whose internal structure is known; but because of the great diversity of the sample, the species could only be compared on the basis of six independent characters. While the result reveals the general relationships of the species to one another, it points out only the broader evolutionary trends. For greater accuracy, the thirty species having the "modern form," (designated the *Osmundacaulis kolbei* line) i.e., with stipular expansions, C-shaped leaf-trace, and a dissected xylem cylinder, are compared on the basis of thirteen characters. The group-



Text-fig. 6—Specializations in the Osmundaceae. Solid squares, Recent taxa; solid circles, fossil taxa; squares containing an open circle, fossil and extant taxa; open circles, hypothetical ancestral intermediates. Specialized states of characters are indicated by letters according to the summary below. Conditions assumed for a species appear in parentheses with that species.

A, stele. 0—a protostele, central region consisting of long tracheids; a—2—a protostele, central region consisting of short tracheids; a′—3—a protostele, central region consisting of tracheids with some parenchyma; a″—6—ectophloic, dictyoxylic siphonostele with some tracheids in the pith; A—10—ectophloic, dictyoxylic siphonostele, only parenchyma or sclerenchyma in the pith; A′—11—same as A but with an internal endodermis; A″—12—dissected siphonostele; A‴—15—dictyostele.

B, cortex. 0—all parenchymatous; b—3—parenchymatous with thin sclerified layer; b′—6—parenchymatous and sclerotic layers about equal in breadth; B—10—sclerified except for thin, parenchymatous layer.

C, petiole bases. 0—closely adhering; C—10—loosely adhering.

D, leaf-traces. 0—basally mesarch; D—10—basally endarch.

E, leaf-traces visible in one cortical cross-section. 0—many (100–150); e—3—(60–100); e′—5—medium (30–60); e″—7—(15–30); E—10—few (5–15).

F, first protoxylem bifurcation in leaf-trace. 0—outer cortex to petiole base; f—3—near boundary of inner and outer cortex; f′—6—in inner cortex; F—10—in stele.

ing of taxa that resulted is considered to be more accurate. For still greater accuracy, a third analysis is given, and the sample is restricted to the living species. Eighteen characters were used, five of them based on aerial parts of the plants that are unknown for the petrified axes. The taxonomic treatment of the family reflects these findings.

Analysis of all species

States of the characters used in this analysis are explained below and correspond to those given in the explanation of text-figure 6.

Characters.—A. **Stele.** A protostele having a central xylem region constructed of long tracheids represents the primitive state while the ectophloic, dicytoxylic siphonostele is treated as the advanced condition. "Ultraspecialized" states in order of increasing advancement are the ectophloic, dictyoxylic siphonostele with an internal endodermis (A′); the dissected siphonostele (A″); and the dictyostele (A‴). Interpretation of this character is based on the general, geologic occurrence of the specimens and on evolutionary trends in other groups of vascular plants.

B. **Cortex.** A cortex made up entirely of thin-walled cells is primitive and the occurrence of sclerenchyma in the cortex is advanced. This interpretation is supported by evidence from ferns in general (Wagner, 1964).

C. **Petiole base.** Closely adhering petiole bases represent a more primitive condition than loosely adhering petiole bases. The latter state occurs rarely in the family, while the former condition is generalized.

D. **Xylem of leaf-trace.** Leaf-traces that have mesarch xylem arrangement at their point of divergence from the stem xylem are treated as being more primitive than those having endarch arrangement at this location. This interpretation is based on the geologic occurrence of the specimens, correlation of the mesarch condition with primitive states of other characters, and evidence from vascular plants in general.

E. **Number of leaf-traces visible in one cortical cross section.** A high number of leaf-traces visible in a transverse section of the cortex represents the primitive state, and a lower number is more specialized. The high number correlates with primitive states of other characters, and the trend agrees with the geologic occurrence of the specimens.

F. **First protoxylem bifurcation in leaf-trace.** Initial branching of the protoxylem strand in the leaf-trace when the latter occurs in the petiole base represents the primitive state of this character, while initial bifurcation closer to the stele or within it is more specialized. The primitive state correlates with primitive conditions in other characters.

Results.—The analysis (text-fig. 6) subdivides the species of the family into three major lines of specialization which are named according to the least specialized member of each line. The *Osmundacaulis braziliensis* line of specialization includes the latter species and *O. carnieri* and is independent from the other two lines. The *Anomorrhoea fischeri* line of specialization includes all of the supposedly protostelic species and is connected for a short distance with the *Osmundacaulis kolbei* line which includes the remaining species.

Limitations.—The accuracy of this analysis is limited by the number of characters it is founded upon. Species of the *Osmundacaulis kolbei* line of specialization are not all resolved to separate points on the diagram. Thus, another analysis of the members of this line of specialization was conducted.

Analysis of the Osmundacaulis kolbei *line*

States of the characters used in this analysis are explained below and correspond to those characters given in the explanation of text-figure 7.

Characters.—A. **Habit.** The arborescent habit is considered to be more primitive than the rhizomatous habit on the basis of the correlation of these two states with the geologic occurrence of the specimens.

B. **Pith.** The so-called "mixed-pith" condition, i.e., a pith constructed of an approximately equal mixture of parenchyma and tracheids, is treated as the primitive state; a pith made up of either parenchyma alone or parenchyma, sclerenchyma, and tracheids is considered to be intermediate; and a pith constructed of parenchyma and sclerenchyma is advanced. Evidence from the geologic occurrence of the specimens and from other groups of lower vascular plants supports this interpretation.

C. **Breadth of xylem cylinder.** Species having a thick xylem cylinder are treated as being more advanced than those having a thin xylem cylinder on the basis of the correlation of these two states with respective specialized and generalized states of other characters.

D. **Position of the phloem.** The ectophloic situation is primitive, the amphiphloic arrangement is intermediate, and the connection of internal and external phloem cylinders through leaf-gaps is advanced. These states correlate with respective primitive and advanced states of other characters within the Osmundaceae and in other ferns.

E. **Position of the endodermis.** A solitary external endodermis represents the primitive condition, independent internal and external endodermal cylinders represent the intermediate state, and connection of internal and external endodermal tissues through leaf-gaps represents the advanced state.

F. **Relative breadth of cortical cylinders.** Cortical cylinders of approximately equal thickness represent a primitive state, while a thick, sclerotic cortex combined with a thin parenchymatous cortex represents an advanced state. Less specialized ferns tend to have less sclerenchyma (Wagner, 1964).

G. **Composition of the inner cortex.** An inner cortex consisting entirely of parenchyma is considered to be more primitive than one including some sclerenchyma. Two equally specialized conditions are recognized: clusters of fibers subtending each leaf-trace in the inner cortex (G), and sclerotic cells scattered in the inner cortex (G^0).

H. **First protoxylem bifurcation in leaf-trace.** (See Character F under Analysis of all species above.)

I. **Number of leaf-traces visible in one cortical cross section.** (See Character E under Analysis of all species above.)

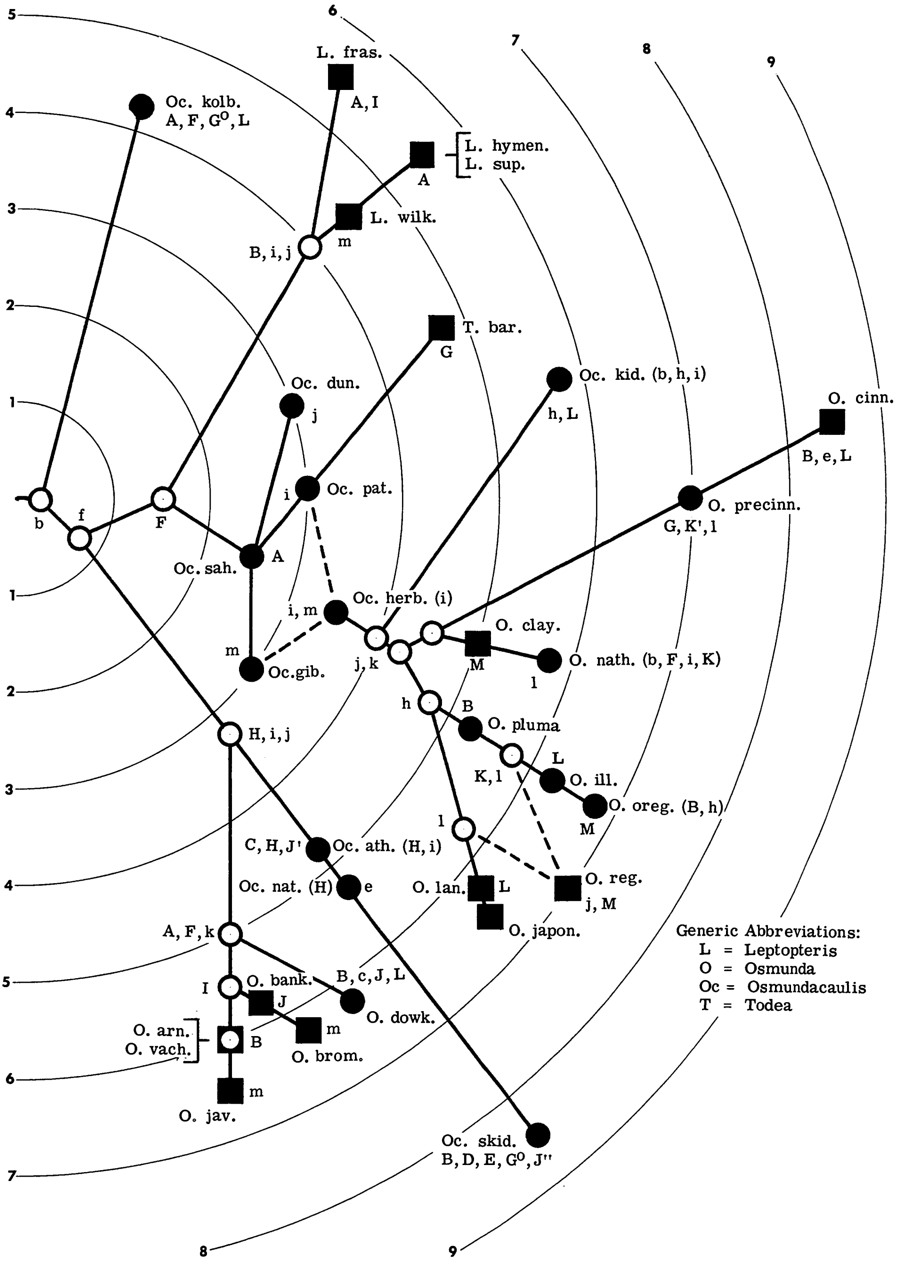
J. **Sclerenchyma in concavity of vascular strand of petiole base.** The following states are recognized in order of increasing specialization: sclerenchyma absent or weakly developed; one mass of sclerenchyma extending the length of the stipular region; one mass occurring in the basal part of the stipular region, dividing into two masses above; one mass occurring in the basal part of the stipular region and forming a narrow band or numerous, apparently separate patches which line the concavity above; and the latter condition, but with the single basal mass extending downward into the stem in the concavity of the leaf-trace. This latter condition is further modified into two "ultraspecialized" states, the single basal mass extending downward with the leaf-trace into the stele (J′), and extending downward into the pith (J″).

K. **Sclerenchyma ring of petiole base.** Homogeneity of the ring is the primitive state, and the following patterns of heterogeneity represent increasingly specialized intermediate conditions: a thin arch of thick-walled fibers occurring in the abaxial semicircle of the ring in the basal part of the stipular region and changing upward to surround the ring; a thick arch of thick-walled fibers occupying the abaxial semicircle of the ring and changing to form two lateral concentrations just above the stipular region; a thick arch of thick-walled fibers occupying the abaxial semicircle of the ring in the lower one-third of the stipular region, dividing to form two lateral concentrations in the lower one-half of the stipular region which extend upward the remaining length of the organ. The advanced state is a thick arch of thick-walled fibers occupying the abaxial semicircle of the ring in the lower one-third of the stipular region, changing to two lateral concentrations in the lower one-half of the stipular region, and extending upward as a thin band of thick-walled fibers at the periphery of the adaxial side of the ring. The occurrence of two lateral and one abaxial clusters of thick-walled fibers in the sclerenchyma rings of some species is considered an "ultraspecialized" state (K′). The various intermediate, specialized, and "ultraspecialized" states are clearly derived conditions since all ancient species have the primitive state.

L. **Sclerenchyma in the inner cortex of the petiole base.** The occurrence of numerous small strands of fibers in the inner cortex of the petiole base represents the primitive state of this character, while the absence of these strands represents the specialized condition. While interpretation of this character is contrary to the general trend of less sclerenchyma in less specialized ferns, it is valid as evidenced by the correlation of these states with respective primitive and advanced states of other characters and with the geologic occurrence of the specimens.

M. **Sclerenchyma in the stipular expansions.** The occurrence of isolated strands of fibers in the stipular expansions is a primitive condition, their partial coalescence to form a dominant mass and several smaller masses is intermediate, and the formation of elongate strips with no isolated strands is the advanced state. This character is analyzed from sections made at the level where the stipular expansions are the most extended and the sclerenchyma pattern in them is the most complex. This trend correlates with the geologic occurrence of the specimens.

Results.—Analysis of the *Osmundacaulis kolbei* line of specialization (text-fig. 7) gives better separation of the species than was accomplished in the analysis of all species. Four major lines of specialization are resolved; and, except for two cases in which species of the same genus or subgenus occur on the same point, the species are effectively distinguished.



TEXT-FIG. 7—Specializations in the *Osmundacaulis kolbei* line. Solid squares represent Recent taxa, solid circles represent fossil taxa, squares containing an open circle represent fossil and Recent taxa, and open circles stand for hypothetical ancestral intermediates. The character letter is given in the lower case the first time the specialized condition appears in an evolutionary line and in the upper case when the fully specialized state of that character appears. The specialized states assumed for a species appear in parentheses with that species.

A, habit. 0—arborescent; 1—rhizomatous.

B, pith. 0—mixed pith; ½—parenchyma or parenchyma, tracheids, and sclerenchyma; 1—parenchyma and sclerenchyma.

C, xylem cylinder. 0—5–15 tracheids deep; ½—20–30 tracheids deep; 1—about 50 tracheids deep.

D, phloem. 0—external only; ½—external and internal; 1—external, internal, and connecting through leaf-gaps.

E, endodermis. 0—external only; ½—external and internal; 1—external, internal, and connecting through leaf-gaps.

F, cortex. 0—inner layer about as thick as outer; 1—inner layer thinner than outer.

Limitations.—The analysis is based on anatomical features of the roots, stems, and petiole bases while the taxonomic classification of Recent species is founded upon characters of aerial parts of the plants such as frond dissection, lamina thickness, and the degree of fertile and sterile frond dimorphism. To confirm the results of the analysis of the *Osmundacaulis kolbei* line of specialization, a third analysis was conducted on the living species alone with characters of the major aerial organs used in conjunction with anatomical features.

Analysis of extant species

States of the characters used in this analysis are explained below and correspond to those given in the explanation of text-figure 8.

Characters.—A. **Composition of the pith.** A parenchymatous pith represents a more primitive condition than a pith containing some sclerenchyma. The latter state is absent in fossil species of the Paleozoic and Mesozoic and is most likely a derived condition.

B. **Position of the endodermis.** An endodermis that is external to the stele represents the primitive state, while external and internal endodermal cylinders in a stele represent the advanced state, as evidenced by the correlation of these states with respective primitive and advanced states of other characters in all species of the family.

C. **Composition of the inner cortex.** An entirely parenchymatous construction is the primitive state of the inner cortex, while the occurrence of clusters of fibers adaxial to each leaf-trace represents the advanced state. A parenchymatous inner cortex is the generalized condition, and it correlates with primitive states of other characters.

D. **Number of leaf-traces visible in one cortical cross-section.** (See under *Analysis of all species* above.)

E. **First protoxylem bifurcation in leaf-trace.** (See under *Analysis of all species* above.)

F. **Number of roots per leaf-trace.** One root per leaf-trace, occasionally two, is considered the primitive state, while two roots per leaf-trace, occasionally one, is treated as the advanced condition. The correlation of the states with fossil material is unknown, since serial sections of petrified axes required for investigation of this character are largely unavailable. The character-states are used here for grouping purposes only.

G. **Sclerenchyma ring of petiole base.** (See under *Analysis of the* Osmundacaulis kolbei *line.*)

H. **Sclerenchyma in concavity of vascular strand of petiole base.** (See under *Analysis of the* Osmundacaulis kolbei *line* above.) "Ultra-specialized" states of this character do not occur in extant species.

I. **Thickness of sclerenchyma ring.** A sclerenchyma ring that is thicker than the vascular strand of the petiole base is treated as the primitive state, while a ring that is as thick as or thinner than the vascular strand represents the advanced state. The evolutionary significance of this character is unknown, and its states are used only for taxonomic grouping purposes.

J. **Sclerenchyma in inner cortex of petiole base.** (See under *Analysis of the* Osmundacaulis kolbei *line.*)

K. **Sclerenchyma in stipular expansions.** (See under *Analysis of the* Osmundacaulis kolbei *line* above.)

L. **Transverse commissure on stipule.** The presence of a commissure is considered primitive, while its absence is advanced. The primitive state is common in the eusporangiate ferns and also occurs in the cycads (Bower, 1926).

M. **Habit.** (See under *Analysis of the* Osmundacaulis kolbei *line.*)

G, inner cortex. 0—parenchyma only; 1—(G^0) parenchyma with scattered stone cells or (G) with nests of fibers adaxial to departing leaf-traces.

H, first protoxylem bifurcation in leaf-trace. 0—in outer cortex to petiole base; ½—inner cortex to inner part of outer cortex; 1—stele.

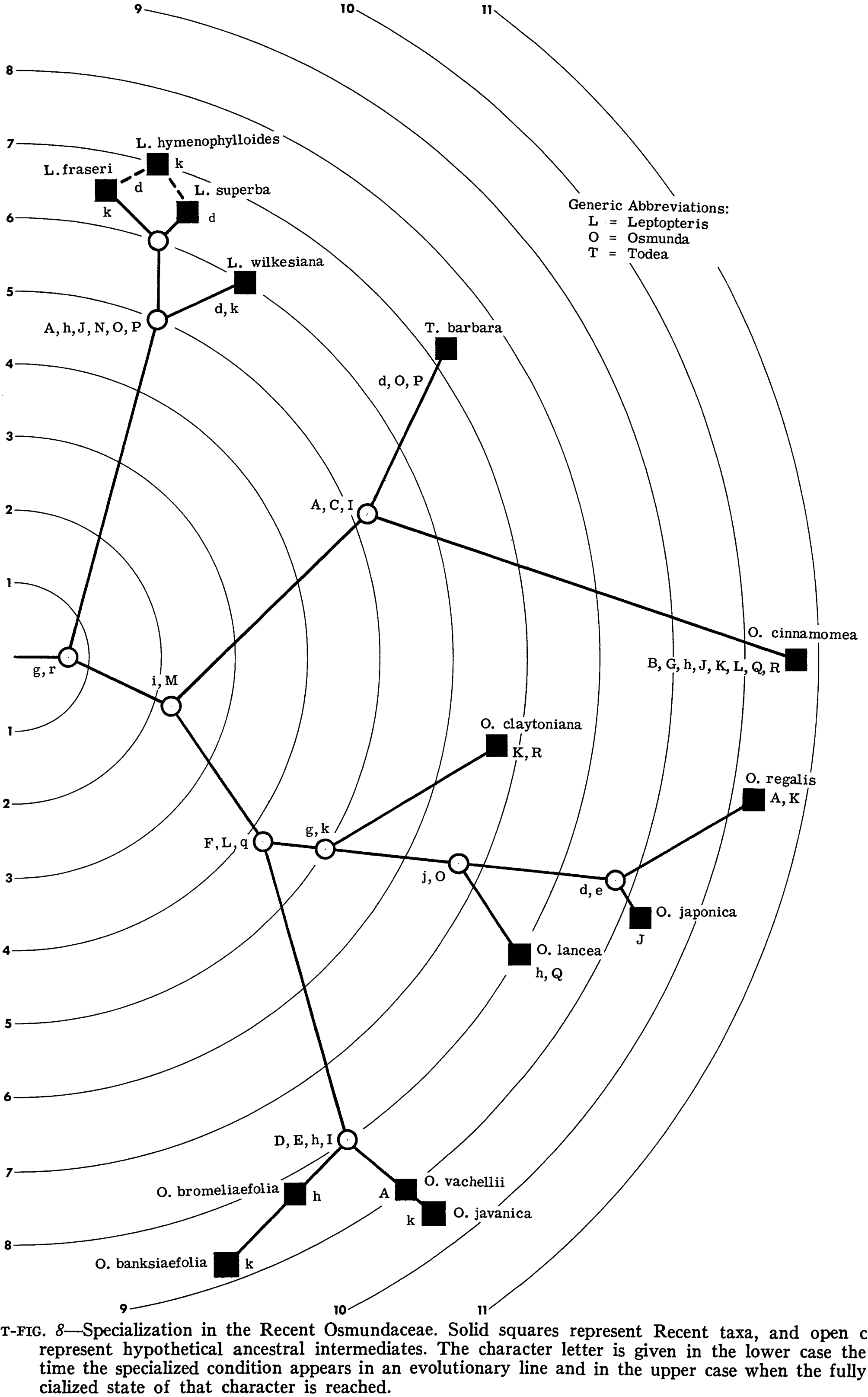
I, number of leaf-traces visible in one cortical cross-section. 0—many (50–100); ½—medium (15–49); 1—few (0–14).

J, sclerenchyma in concavity of vascular strand in petiole base. 0—absent or much reduced; ¼—one mass; ½—one mass basally, bifurcating upward; ¾—one narrow irregular band (may appear as several separate groups); 1—as above but extending downward into stem; 1¼—as above but extending into stele; 1½—as above but extending into pith.

K, sclerenchyma ring of petiole base. 0—homogeneous; ¼—with thin arch of thick-walled fibers in abaxial semicircle in lower region changing upward to surround ring; ½—with thick arch of thick-walled fibers in abaxial semicircle changing upward to two lateral concentrations just above stipular region; ¾—as above but changes occur in lower one-half of stipular region; 1—as above but two lateral masses pass upward into an adaxial arch; 1½—three specialized masses throughout.

L, sclerenchyma in inner cortex of petiole base. 0—abundant; 1—absent.

M, sclerenchyma in stipular expansions. 0—scattered masses; 1—elongate strip.



TEXT-FIG. *8*—Specialization in the Recent Osmundaceae. Solid squares represent Recent taxa, and open circles represent hypothetical ancestral intermediates. The character letter is given in the lower case the first time the specialized condition appears in an evolutionary line and in the upper case when the fully specialized state of that character is reached.

N. **Lamina.** A lamina that is differentiated internally into palisade and spongy mesophyll and bears stomates is generalized in vascular plants, and filmy fronds that are only two to four cells thick and lack such organization are considered derived.

O. **Blade dissection.** The simple pinnate condition is treated here as representing a less specialized state than more complex types of cutting. However, fossil foliage is either similar to that of the living species; or its relationships to stem taxa, which might make possible correlation of characters, is uncertain. Thus, what type of blade dissection is most primitive is unknown, and the character is used only for taxonomic grouping.

P. **Number of spores per sporangium.** Production of a large number of spores per sporangium represents a more primitive condition than production of a smaller number. The large number of spores per sporangium is found in the eusporangiate ferns, and is also inferred from the generally large size of eusporangia in all vascular plant classes.

Q. **Fertile frond dimorphism.** Isomorphism represents the primitive state, incomplete dimorphism (only certain pinnae of a fertile frond modified for sporangia formation) is intermediate, and complete dimorphism is advanced. Dimorphism is generally regarded as a specialized situation in ferns.

R. **Number of xylem strands in a cross section of the stele.** A high number of xylem strands in a given transverse section of the stele represents the primitive condition, while a low number is advanced. This interpretation is based on the generally high numbers of strands occurring in ancient members of the family and the lower numbers common to the more recent species.

Results.—The analysis of the Recent members of the Osmundaceae (text-fig. 8) effectively distinguishes between all species and groups them into their various taxa. The inclusion of *O. claytoniana* in *Osmunda* rather than in *Osmundastrum* where it has been traditionally classified is upheld. This relationship is further supported by *O. x ruggii,* a presumed hybrid between *O. claytoniana* and *O. regalis var. spectabilis* (Tryon, 1940).

Discussion

Even though the fossil record of the Osmundaceae is extensive, it is very incomplete in places with large gaps between groups of related species. Such gaps are illustrated in the ground plan analyses in three ways: the high number of hypothetical intermediate forms (open circles on the diagrams), the long lines connecting certain species to their nearest ally, and the relative positions of species on certain lines of specialization.

Hypothetical intermediate forms are required to connect diverging lines of specialization. Species having the character-states of these intermediates probably occurred in the past, since the species occurring on the two diverging lines must have evolved from a common ancestor having character-states common to the two lines.

Long lines connecting certain species to their

A, pith. 0—parenchyma; 1—parenchyma and sclerenchyma.
B, endodermis. 0—external only; 1—external and internal.
C, inner cortex. 0—parenchyma alone; 1—parenchyma with nests of fibers adaxial to departing leaf-traces.
D, leaf-traces visible in one cortical cross-section. 0—many (14+); ½—medium (8–14); 1—few (0–8).
E, first bifurcation of leaf-trace protoxylem. 0—inner part of outer cortex to petiole base; ½—inner cortex to inner part of outer cortex; 1—stele.
F, roots arising. 0—one per leaf-trace (occasionally two); 1—two per leaf-trace (occasionally one).
G, sclerenchyma ring of petiole base. 0—homogeneous; ¼—thin arch in abaxial semicircle in lower stipular region passing upward to surround ring; ½—thick arch in lower stipular region passing upward to two lateral concentrations; ¾—thick arch in lower stipular region passing upward to two lateral concentrations and then to a thin arch in the adaxial semicircle of ring; 1—three concentrations throughout.
H, sclerenchyma in concavity of vascular strand of petiole base. 0—absent or nearly so; ¼—one mass; ½—one mass below, two above; ¾—one narrow irregular band; 1—one narrow irregular band extending downward into stem.
I, sclerenchyma ring. 0—thick; 1—thin.
J, sclerenchyma in inner cortex of petiole base. 0—abundant; 1—absent.
K, sclerenchyma in stipular expansions. 0—scattered strands; 1—elongate strip.
L, transverse commissure on stipule. 0—present; 1—absent.
M, habit. 0—arborescent; 1—rhizomatous.
N, lamina. 0—thick; 1—filmy.
O, blade. 0—1—pinnate; ½—bipinnate; 1—tripinnate or bipinnate-pinnatifid.
P, number of spores in a sporangium. 0—ca. 512; ½—ca. 256; 1—ca. 128.
Q, sporangia borne on. 0—lamina of vegetative fronds; ½—specialized pinnae of incompletely dimorphic fronds; 1—specialized pinnae of completely dimorphic fronds.
R, xylem strands. 0—many (40+); ½—medium (20–40); 1—few (1–20).

nearest allies represent changes of several character-states. It is unlikely that the species advanced through such evolutionary "spurts." If evolutionary processes operated in the past as they do now, the known species are products of long series of gradual changes; and the intermediate conditions must have been manifested in organisms that are presently unknown.

Several of the lines of specialization involve species that are contemporaneous, while on other lines specialized forms are geologically older than less complex species. The direct evolution of the advanced species from the less specialized forms is chronologically impossible unless reduction of many character-states is postulated. Reduction has, no doubt, played a role in the evolution of certain species, but there are more likely explanations for the juxtaposition of these forms. Certain species may have evolved long before they are actually in evidence, and they could have given rise to the more specialized forms in the meantime. Further, the less specialized forms may be products of slowly-evolving, side branches of the main line of specialization. *Osmundacaulis kolbei, O. dunlopi, O. gibbiana, O. sahnii,* and *O. patagonica* all appear as relatively unspecialized members of their line of specialization in the analysis of all species (text-fig. 6) but they are resolved to side branches when this line is analyzed alone (text-fig. 7). In such cases, intermediate forms are lacking.

Thus, the known petrified remains of the Osmundaceae represent a small sample of the entire family. In some groups of species the sample closely approximates the relationships of the population, while in other groups the sample is not as representative. For this reason, it would be presumptive to construct a species-by-species phylogeny for the family with the evidence currently available, and knowledge of the relationships of the species can be better illustrated by considering the phylogenetic relationships of the species-groups.

PHYLOGENETIC RELATIONSHIPS

Phylogeny of the Osmundaceae

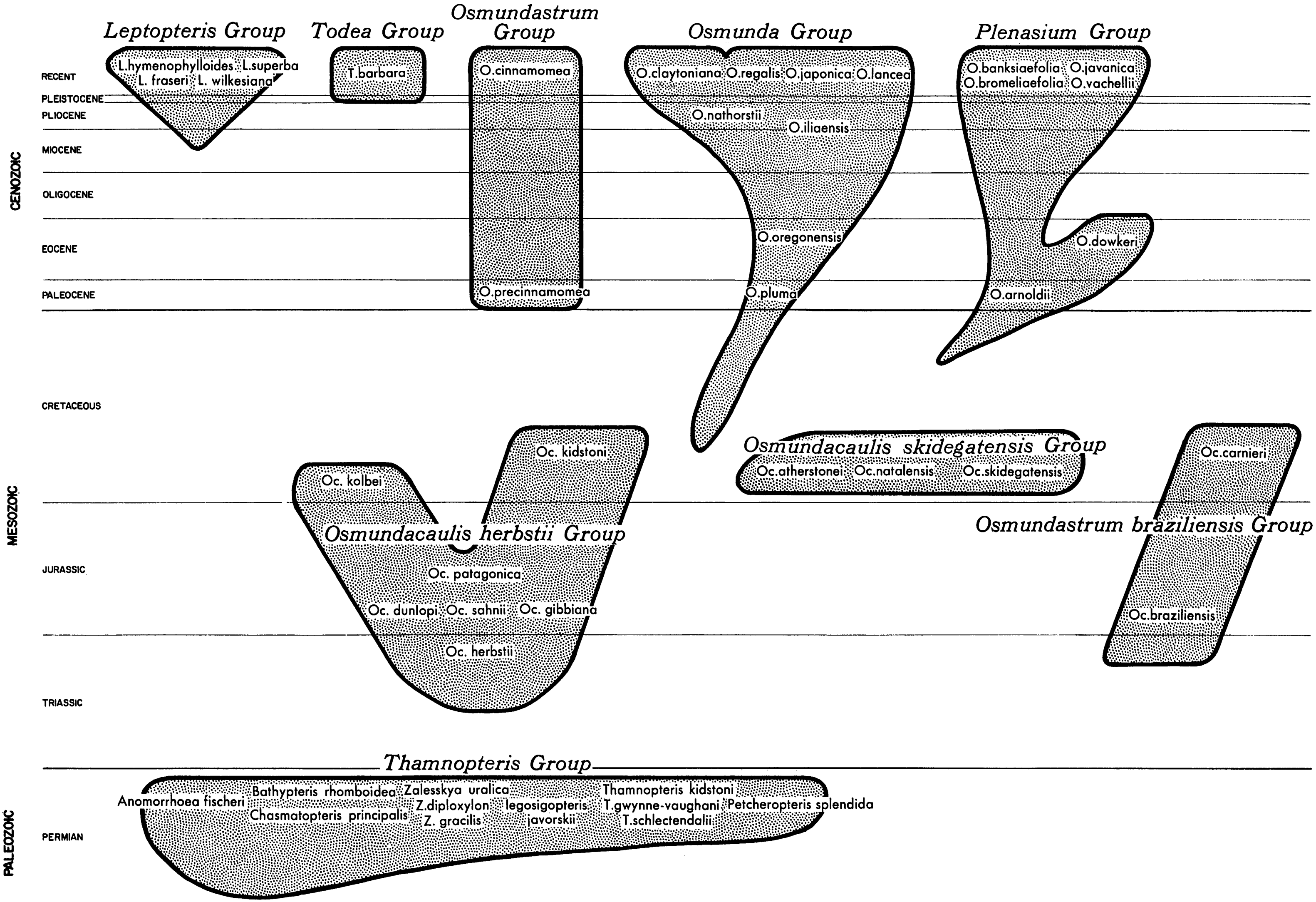
When the arrangement of species by the numerical analyses is plotted against geologic time, nine groups of phylogenetically related species are resolved (text-fig. 9). The purpose of this section is to discuss the interrelationships of these groups as interpreted from the numerical analyses and from evidence derived from osmundaceous fossils not included in the analyses.

Thamnopteris group.—Species of the *Thamnopteris* group represent an extinct branch of the family without known connection to the remaining species. Accordingly, these species are grouped in a separate subfamily, the Thamnopteroideae, with all other species of the Osmundaceae classified in the subfamily Osmundoideae.

The Thamnopteroideae is diversified within itself. Parenchyma occurs in the central xylem of *Thamnopteris kidstoni,* some leaf-traces of *T. schlechtendalii* separate from the stem xylem with two protoxylem groups, rudimentary leaf-gaps dent the xylem cylinder of *Chasmatopteris principalis,* and sclerotic spines emerge from petiole bases of *Bathypteris rhomboidea.* Since all known species of the Thamnopteroideae were more or less contemporaneous in the Late Permian, the existence of older forms must be postulated to allow for the evolution of this diversity.

There are no intermediate forms between the Thamnopteroideae and the *Osmundacaulis herbstii* group, which is closest to this subfamily in time and degree of specialization. Although the stele of *Itopsidema vancleavei* Daugherty, a probable fern from the Upper Triassic of Arizona, is intermediate in structure between the protostele and the ectophloic dictyoxylic siphonostele, *Itopsidema* has no distinctive osmundaceous characters and is treated under *incertae sedis* for lack of a more accurate classification. The two species of the Thamnopteroideae that show definite siphonostelic and dictyoxylic tendencies, *Thamnopteris kidstoni* and *Chasmatopteris principalis* respectively, might be regarded as progenitors of the *Osmundacaulis herbstii* group, but they have extrastelar features that are too specialized to support this ancestral relationship. Only species of *Zalesskya* are unspecialized enough in most of their characters to represent a possible source for the Osmundoideae, and such a course of evolution would necessitate vast changes in the stele. Thus, what is required for ancestry of the *Osmundacaulis herbstii* group is a progenitor that has a stele advanced along the lines of *Thamnopteris kidstoni* and (or) *Chasmatopteris principalis* but with extrastelar characters, especially a high number of leaf-traces in the cortex, as in *Zalesskya.* No such form is known at this time.

Osmundacaulis herbstii group.—Evolution of the *Osmundacaulis herbstii* group from its unknown progenitor in the Thamnopteroideae requires derivation of a pith and formation of leaf-gaps in the xylem cylinder. The steps by which these changes most probably occurred are displayed in the known members of the Thamnopteroideae and the *Osmundacaulis herbstii* group and have been summarized by other



TEXT-FIG. 9—Summary of phylogenetic relationships.

authors (Arnold, 1952; Archangelsky & de la Sota, 1962; Posthumus, 1924b). However, both the evolution of the pith and leaf-gaps must be clarified, since the removal of *Itopsidema vancleavei* to *incertae sedis* invalidates arguments that involved this species.

Leaf-gap formation is the result of increased indentation of the xylem cylinder above the point of leaf-trace attachment to the stem xylem. Indentation occurs because cells of the xylem sheath are included between the leaf-trace and the stem xylem and are not immediately replaced by tracheids (Posthumus, 1924b). Rudimentary invaginations are apparent in *Chasmatopteris principalis,* and in several species of the *Osmundacaulis herbstii* group "delayed gaps" are combined with "immediate gaps," all such gaps being very narrow. More recent forms tend to have "immediate gaps" and in some species they are very wide.

Evidence supporting derivation of pith parenchyma from tracheids of the central xylem rather than from the intrusion of cortical tissue is twofold. First, there is a distinct shortening of central xylem tracheids in the Thamnopteroideae that correlates with specialization of other characters. The tendency is most pronounced in *Thamnopteris kidstoni* where small numbers of parenchyma cells are mixed with central xylem tracheids. There is no suggestion of leaf-gaps in this fossil, so these parenchyma cells can only have been derived from tracheids. The subsequent formation of a mixed pith and later a wholly parenchymatous pith can be extrapolated from this known series.

Secondly, extrastelar origin of a pith requires that leaf-gaps not only penetrate the xylem cylinder but also the layers of phloem, pericycle, and endodermis external to it. Such complete gaps must form to allow intrusion of extrastelar tissues, but a few species of the Osmundaceae have such gaps—namely *Osmundacaulis skidegatensis, O. braziliensis, O. carnieri,* and branching regions of certain plants of *Osmunda cinnamomea.* Thus, the *Osmundacaulis herbstii* group most likely evolved from the Thamnopteroideae by intrastelar origin of the pith and subsequent (or concurrent) dissection of the xylem cylinder by leaf-gaps.

Osmundacaulis herbstii, O. dunlopi, O. gibbiana, O. sahnii, and *O. patagonica* form a natural assemblage, but the inclusion of *O. kolbei* and *O. kidstoni* leads to some artificiality. It would appear (text-fig. 7) that *O. dunlopi, O. gibbiana, O. sahnii,* and *O. patagonica* evolved from *O. herbstii* by reduction of single character states, but it is equally possible that these species reflect conditions that existed in forms which predate *O. herbstii* and which gave rise to this species by normal specialization of characters.

Osmundacaulis kolbei presents a puzzling mixture of primitive and advanced character-states at a time when at least one of its contemporaries had achieved dictyostely (*O. skidegatensis*) and others display a strong tendency in this direction. Delayed leaf-gaps, a mixed pith, leaf-traces that are basally subendarch, and first protoxylem bifurcation of the leaf-trace in the petiole base are primitive states in this species, while sclerenchyma in the pith and in the inner cortex are advanced states. Arnold (1964) interpreted the mixed pith as a retention of a primitive state, and the other primitive features must be considered in the same category. This species exists on a definite side branch of the *O. herbstii* group, and of the Osmundaceae, and did not serve as a major source for more specialized forms.

Osmundacaulis kidstoni is included in the *O. herbstii* group for lack of a better place. Only the petiole bases of this fern are known, and they share an important feature with the species of the subgenus *Osmunda*—an arch of thick-walled sclerenchyma in the abaxial semicircle of the sclerenchyma ring. While the remaining sclerenchyma tissues of the petiole base are not directly comparable with the arrangement known in any other species, it is nonetheless possible that *Osmundacaulis kidstoni* may have served as an intermediate in the evolution of the subgenus *Osmunda* from the *Osmundacaulis herbstii* group.

Osmundacaulis braziliensis group.—The two species of this group, *Osmundacaulis braziliensis* and *O. carnieri,* are distinct from all other members of the Osmundaceae (text-fig. 6), and neither of their axes contains features which definitely establish their relationship to this family. Both specimens are poorly preserved; and their exact age is uncertain though they came from some formation of the Mesozoic. They share the following structural features: (a) large size (ca. 10 cm in diameter), (b) dissected siphonostele, (c) thick xylem cylinder (about 55 tracheids in radial dimension), (d) leaf-traces that are C-, V-, and Y-shaped in transverse sections of the cortex, and (e) arborescent habit.

Additional material of these species will be required to gain information for more accurate placement of the group. Present evidence indicates a closer relationship to the *Osmundacaulis skidegatensis* group than to any other. Characters common to the two are the arborescent habit, the thick xylem cylinder, and to a certain extent, the advanced stele.

Osmundacaulis skidegatensis group.—The three species of this group are all Early Cretaceous in age and have such features in common as the arborescent habit, a thick xylem cylinder, leaf-traces that have a strong initial curvature and that probably formed in the *Plenasium* manner, and sclerenchyma that extends into the pith in the concavity of the leaf-trace. *Osmundacaulis atherstonei* and *O. natalensis,* which are from South Africa, are very similar, and the latter has an internal endodermis which is preserved in places. *Osmundacaulis skidegatensis,* which is from Queen Charlotte Island, British Columbia, is the only known dictyostelic member of the Osmundaceae. The concurrence of these species in time, and possibly also their extreme geographic separation, are facts which argue against considering them an evolutionary series in themselves; but it is possible that they represent such a series with *O. atherstonei* and *O. natalensis* reflecting conditions in the more ancient ancestors.

The origin of this group is not clear. The *Osmundacaulis herbstii* group could have been the source, but intermediate forms are unknown. Further, there is no tendency within the *O. herbstii* group toward development of a thick xylem cylinder or *Plenasium*-type leaf-traces. More likely, the *O. skidegatensis* group arose from the same ancestors as the *O. braziliensis* group and together with that group represents a branch of the family that underwent rapid specialization during the Mesozoic.

Plenasium group.—The *Plenasium* group is represented by the four Recent species—*Osmunda banksiaefolia, O. bromeliaefolia, O. javanica,* and *O. vachellii*—and the two extinct species—*O. dowkeri,* from the Eocene of Great Britain and the western United States, and *O. arnoldii,* from the Paleocene of North Dakota.

The xylem cylinder of *O. dowkeri* may be as many as 25 tracheids thick (radial dimension) while it is generally 15 tracheids thick in other species of the subgenus *Plenasium.* Furthermore, in *Osmunda dowkeri* the xylem cylinder is dissected into 22–30 strands, while in *O. arnoldii* and the Recent species there are only 8–10 strands. Members of this group also exhibit minor differences in the arrangement of sclerenchyma in their petiole bases. Thus, the Recent species evolved almost unchanged from *O. arnoldii* or some very similar form, and *O. dowkeri* arose from some unknown species that was less specialized (and probably older) than *O. arnoldii* (text-fig. 7).

The ground plan analysis (text-fig. 7) indicates that the subgenus *Plenasium* evolved from a hypothetical intermediate form on the *Osmundacaulis skidegatensis* line of specialization and that this ancestor was less specialized than any of the known species of that group. The similarity between the two groups is best reflected in the common manner of leaf-trace formation and the resulting occurrence of xylem strands that are predominantly oval-, crosier-, and U-shaped in transverse section. Furthermore, the xylem cylinder of *Osmunda dowkeri* is intermediate in radial thickness between that in the remaining species of the subgenus *Plenasium* and in the *Osmundacaulis skidegatensis* group. Thus, it is likely that this subgenus evolved from either a primitive member of the *Osmundacaulis skidegatensis* group or a precursor to that group.

The subgenus *Plenasium* first occurs in the Early Cretaceous as represented by foliage compressions from the Potomac Formation classified as *Osmunda delawarensis.* The abundance of *O. lignitum* foliage in Oligocene and Miocene sediments (Jongmans & Dijkstra, 1962) suggests that the subgenus *Plenasium* reached its zenith at that time and, since then, has declined with its present distribution limited to Southeast Asia and the Philippines.

Osmunda group.—The subgenus *Osmunda* has been the dominant group of the Osmundaceae throughout the Upper Cretaceous and Tertiary and is presently the most widespread taxon of the family. The group first appears in the Lower Cretaceous, but the pinnules of *Osmunda asuwensis* are so similar to those of the Recent *O. regalis* and *O. japonica* that a significant history prior to this first appearance is suspected.

The petrified axes indicate that this group has evolved through a main line of specialization that terminates in *O. regalis, O. japonica,* and *O. lancea* and a branch from this main line on which *O. claytoniana* developed. Structural differences in the axes are mainly those in the arrangement of sclerenchyma tissues in the petiole base with the major trends indicated by the morphology of the thick-walled fibers of the sclerenchyma ring. In all species of the subgenus an arch of these cells occupies the abaxial semicircle of the ring in the lower part of the stipular region and bifurcates upward to form two lateral clusters. In *O. pluma* and *O. oregonensis,* from the Paleocene and Eocene respectively, bifurcation of the arch occurs just above the stipular region, while in *O. regalis, O. japonica,* and *O. lancea* division of the arch occurs in the lower one-third of the stipular region with the two lateral clusters changing almost immediately to form a narrow, inconspicuous band in the abaxial semicircle of the ring which extends upward the remaining length of the stipular region. *Osmunda iliaensis,* from the Miocene-Pliocene of Rumania, is presumably intermediate in this respect. Actual division of the sclerenchyma arch is not visible in the material due to poor preservation, but petiole bases near the middle of the sheath in transverse sections of the axis contain an arch which probably bifurcates in the upper one-third of the stipular region. *O. claytoniana* is similar to *O. regalis, O. japonica,* and *O. lancea,* but changes are arrested with the formation of two lateral masses of sclerenchyma which extend upward throughout the remainder of the stipular region. All that is known of this condition in *O. nathorstii,* from the Upper Tertiary of Spitzbergen, is that two lateral masses occur in the rings of some petiole bases. The arrangement of other sclerenchyma tissues agrees with the patterns in *O. regalis* and *O. claytoniana,* but the Spitzbergen fossil is considered closer to the latter because the innermost petiole bases of the specimen and *O. claytoniana* have one protoxylem group in the vascular strand. While this series is discussed with respect to one character, others are in agreement with the general trend (Miller, 1967).

Thus, *O. regalis, O. japonica,* and *O. lancea* evolved more or less directly from *O. pluma, O. oregonensis,* and *O. iliaensis,* and *O. claytoniana* developed on a side branch through *O. nathorstii.* The source of this side branch within the main line of specialization is not known. Presumably, the species that gave rise to *O. nathorstii* and *O. claytoniana* was somewhat similar to *O. iliaensis* in having leaf-traces in which the protoxylem bifurcates as the trace passes through the outer cortex. Such a condition would be intermediate between the *O. claytoniana* and the *O. regalis* situations.

The only indication of the source of the subgenus *Osmunda* is the arches of sclerenchyma that occur in petiole bases of *Osmundacaulis kidstoni,* a member of the *O. herbstii* group from the Cretaceous of Australia. The arches in this species, however, are such that it could be ancestral to any of the Tertiary taxa; so this species cannot be considered as anything more than a possible ancestor for the subgenus. The ground plan analysis (text-fig. 7) also points to the *Osmundacaulis herbstii* group as the most likely ancestral source for the subgenus *Osmunda,* but the latter is connected to the former through several hypothetical intermediate forms. Thus, the ancestral relationships of this group are uncertain.

Osmundastrum group.—The subgenus *Osmundastrum* is a natural group of two species: *Osmunda precinnamomea,* from the Paleocene of North Dakota, and *O. cinnamomea,* which extends from the Miocene-Pliocene to the present (Miller, 1967). These two species are nearly identical, but *O. precinnamomea* lacks the internal endodermis that is characteristic of the latter (pl. 1, fig. 4) and has scattered strands of sclerenchyma in the inner cortex of its petiole bases which are absent in the living species (text-fig. 4D). The similarity of these two species in all other respects indicates that *O. precinnamomea* is ancestral to *O. cinnamomea* and shows that the internal endodermis of the latter arose from the ectophloic condition rather than being a remnant of an amphiphloic ancestor as Jeffrey (1917) and Faull (1901, 1910) believed.

The fossils of *O. cinnamomea* from the Miocene-Pliocene near Yakima, Washington, are poorly preserved, and the endodermal tissues are not visible (pl. 2, fig. 1). Thus, it is not possible to fix the date of appearance of the internal endodermis in this species with more precision. The varied occurrence of the internal endodermis in present-day plants indicates that it is of relatively recent origin and has not yet achieved a constant state. Only one of about 200 plants on record lacks an internal endodermis (Faull, 1901; Hewitson, 1962), and in most plants the tissue forms a smooth cylinder between the pith and inner xylem sheath. In some stems it projects slightly into leaf-gaps, and in others the projections are pronounced. Further, in branching regions of certain plants the internal endodermis connects with the external endodermis, and rarely in such stems some internal phloem may develop (Faull, 1901; Hewitson, 1962). Thus, *O. cinnamomea* may be evolving toward dictyostely at the present time.

The origin of the subgenus *Osmundastrum* is not indicated clearly in the ground plan analysis (text-fig. 7), since this line of specialization is connected to a point between the *Osmunda* group and the *Osmundacaulis herbstii* group by a long line involving changes in many characters. The distinct similarity of the Paleocene *Osmunda precinnamomea* to *O. cinnamomea* indicates that the *Osmundastrum* group evolved some time before the Tertiary. While the single abaxial and two lateral clusters of thick-walled fibers in the sclerenchyma ring of *Osmundastrum* suggest relationship to *Osmun-*

da, the three clusters are not parts of an arch. They arise independently as the petiole base separates from the stem. Thus, if *Osmunda* and *Osmundastrum* are allied, the relationship is through some common ancestor that is far removed from either group in time and degree of specialization.

Leptopteris group.—The isolated position of this genus (text-figs. 7, 8) is a result of the close similarity of the species to one another and the lack of fossil remains that might suggest relationship to other groups. The resemblances between these species indicate either slow evolution or recent origin, because they occur in isolated localities in the South Pacific, Australia, and New Zealand where conditions are ideal for diversification even though little variety is apparent.

The only fossil record of *Leptopteris* is some petiole bases that were described as *Osmundites* sp., from questionable Miocene sediments near Toowoomba, Queensland, by Kidston & Gwynne-Vaughan (1914). The Tertiary frond *Filicites foeminaeformis* may represent a species of *Leptopteris,* but the only evidence is its superficial resemblance to foliage of *L. wilkesiana* and *L. fraseri.*

Of the six living species only *L. fraseri, L. hymenophylloides,* and *L. superba* are well known anatomically. Structural details of *L. wilkesiana* are known only from dried stems, and *L. alpina* and *L. moorei* have not been studied anatomically. Yet *Leptopteris* is generically distinct from *Todea;* its resemblance to the latter based on aerial organs is not supported by the majority of the anatomical characters (text-figs. 7, 8).

The origin of this genus is not known. While the ground plan analysis suggests a primitive member of the *Osmundacaulis herbstii* group or some precursor of that group as the source of *Leptopteris* (text-fig. 7), there are no intermediate forms to account for the many differences between them. Further, both the lack of abundant fossil remains and the close similarity of the species could be interpreted to indicate Recent origin. However, it is just as probable that the lack of fossil remains is due to the occurrence of the species in areas of montane topography (various islands of the South Pacific, eastern Australia, New Zealand) which are distant from good basins of deposition.

Todea group.—Much of what has been said for *Leptopteris* also applies to *Todea.* The genus has only one living species and no fossil remains have been found. *T. barbara* occurs in eastern Australia, Tasmania, and South Africa. It is generically distinct within the Osmundaceae, and its closest relative seems to be *Osmundacaulis patagonica,* a species of the *O. herbstii* group from the Upper Jurassic of Argentina (text-fig. 7). However, there are a number of differences between the two and no intermediate forms. The lack of a fossil record for *Todea* is probably due to the same circumstances as in *Leptopteris.* Thus, with the present evidence, it can only be said that *Todea* is generically distinct, and its origin is unknown.

Origin of other fern taxa from the Osmundaceae

Sporangia of the Paleozoic ferns mentioned earlier show a combination of osmundaceous characters with those of the Marattiaceae and Schizaeaceae. This apparent mixing, however, is more likely an illusion resulting from our comparing these sporangia to those of Recent ferns in ignorance of the plants that actually produced them. The latter, for all we know, may have been wholly different.

Sporangia of the Jurassic *Todites* are significantly different from those of the extant Osmundaceae (compare text-fig. 5D with text-figs. 5A, B) and even greater differences may have prevailed in sporangia of the Paleozoic Osmundaceae. Thus, it is difficult to predict precisely what a Paleozoic osmundaceous sporangium, or that of any other extinct fern group (except perhaps the marattiaceous synangium) would look like. While a mixing of characters is observed in these ancient sporangia, our knowledge is insufficient to evaluate the evidence with accuracy.

The Plagiogyriaceae and the Osmundaceae are similar in having radially symmetric rhizomes, short stipular expansions on the petiole bases, and the production of mucilage from immature petiole bases (Bower, 1926). Other features of the Plagiogyriaceae such as the dictyostele with internal sclerenchyma, the parenchymatous cortex, and the sporangium with an oblique annulus, could be derived from characters of the Osmundaceae. However, no ancestor for the Plagiogyriaceae can be found among the known Osmundaceae.

The Cyathaeaceae and Dicksoniaceae are like some of the Thamnopteroideae and the *Osmundacaulis braziliensis* group in their large size and arborescent habit; but there is no confirmatory evidence of a relationship in other characters, and similarity in size and habit are insufficient in themselves to indicate ancestry. Thus, while certain of the organs referred to the Osmundaceae contain characters suggestive of other fern taxa, there is no positive evidence that the Osmundaceae has given rise to other fern groups.

Origin of the Osmundaceae

Prior to discussing possible ancestors of the Osmundaceae, it would be well to describe a truly primitive osmundaceous axis, one that could have given rise to other species. According to the theory of the ground plan analysis, characters that occur in all or most of the known species would appear in their immediate ancestor, and each character would exist in its unspecialized state. Since no known member of the family fills these requirements, the axis described is entirely hypothetical and can be constructed by listing the primitive states of the characters used in the ground plan analysis of all species (text-fig. 6) as supplemented by discussion of these features elsewhere.

The hypothetical osmundaceous ancestor would have a protostele in which the tracheids at the center of the xylem cylinder were similar to or slightly shorter and larger in diameter than those at the periphery. The cortex would be mostly parenchymatous but might contain a thin sclerotic cylinder. Stipular petiole bases would adhere closely around the axis, and their vascular strands would be adaxially concave though not necessarily to the extent of being C-shaped. Furthermore, leaf-traces would be terete, oblong, or elliptical in transverse section and would contain a single mesarch protoxylem. Bifurcation of this protoxylem would occur some distance from the stele, as the leaf-trace approached or entered the petiole base; and many such leaf-traces would be visible in a transverse section of the cortex. Lastly, the axis would be short-upright or arborescent with radial symmetry and would lack secondary xylem.

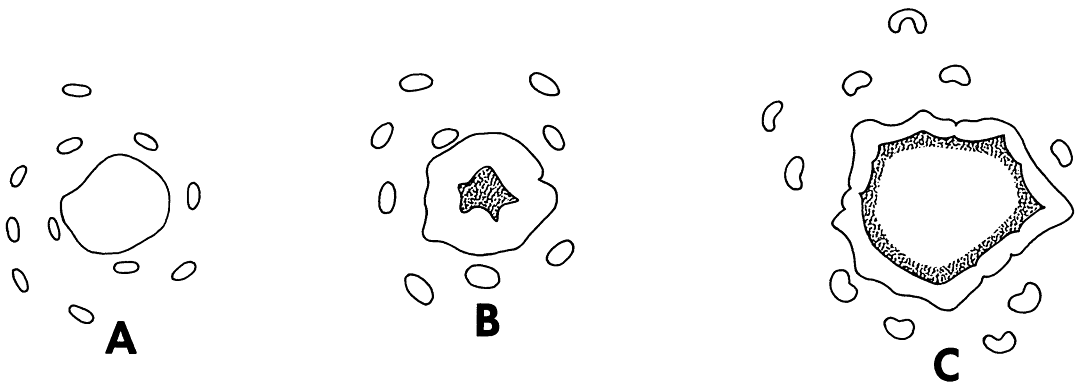
Kidston & Gwynne-Vaughan (1910) pointed out that the Osmundaceae may share a common ancestor with the Zygopterideae. These authors were impressed by the development of pith in the Zygopterideae and in the Osmundaceae. *Zygopteris* (*Diplolabis*) *römeri* is protostelic with its central tracheids shorter and larger in diameter than those at the periphery of the xylem cylinder like those of the Thamnopteroideae; and other zygopterids have a mixed pith as in *Osmundacaulis kolbei* (Kidston & Gwynne-Vaughan, 1910).

Problems arise, however, in deriving the Osmundaceae from known species of the Zygopterideae because their leaf-traces and petiolar strands are specialized along entirely different lines. While the petiole strands of many zygopterids are H-shaped and branch to form complex pinnae systems, Kidston & Gwynne-Vaughan (1910) constructed a convincing argument to demonstrate that the primitive type of leaf-trace in this family is an oblong strand having a mesarch protoxylem at each end similar to that of *Clepsydropsis* and *Dinureon*. They compared this type of leaf-trace to that of *Thamnopteris schlechtendalii* which is oblong and which sometimes separates from the stele bearing two protoxylems. However, this situation is unique in the Thamnopteroideae and, as such, must be viewed as a specialization rather than the primitive condition in this group. Further, *Zygopteris grayi* and *Z. corrugata* have stellate siphonosteles, and secondary xylem develops in *Z. primaria* and *Z. illinoiensis*. It is evident, then, that while the Zygopterideae and the Osmundaceae may show some convergence, the hypothetical primitive form of Kidston & Gwynne-Vaughan is unlike either group.

Of the extinct Paleozoic ferns excluding the Marattiales, species of the Anachoropteridaceae bear the greatest resemblance to any of the living ferns, but their leaf-traces generally curve in the wrong direction (abaxially rather than adaxially). Thus, the majority of these ferns are also specialized along different lines from the Osmundaceae (Eggert, 1964). However, the genus *Grammatopteris* Renault stands out in this family because its leaf-traces do not curve in either direction (text-figs. 10A, B). Further, this genus has a number of characters in common with the Osmundaceae and is recognized as a possible progenitor (Sahni, 1932; Arnold, 1947; Andrews, 1962; Eggert, 1964).

Grammatopteris includes two species. *G. rigolloti* Renault is from the Lower Permian of France, while *G. baldaufi* (Beck) Hirmer is from the Lower Permian of Hilbersdorf, near Karl Marx Stadt, East Germany. Both have small, upright radially symmetric axes, though their size does not indicate arborescence (stem about 15 mm in diameter). The axes contain a protostele in which the tracheids at the center of the xylem column are shorter and wider than those at the periphery. Leaf-traces are small, oblong strands that extend tangentially and enter each petiole base as a straight band that is three to five times longer than broad. Petiole bases are more or less terete and lack stipular expansions but occur in a tight spiral around the stem (Renault, 1896; Sahni, 1932).

G. baldaufi is the better known of the two species due to the efforts of the late Dr. Sahni who located most of the parts of the original specimen. The protostele of this fern has distinct indentations in the xylem column that represent rudimentary leaf-gaps (Arnold, 1947), while the xylem column of *G. rigolloti* is not



TEXT-FIG. *10*—Transverse sections of xylem cylinders and inner leaf-traces. A, *Grammatopteris rigolloti* (after Renault, 1896), × 5. B, *G. baldaufi* (after Sahni, 1932), × 6. C, *Chasmatopteris principalis* (after Zalessky, 1931a), × 2¼. Xylem represented by shading.

indented (Renault, 1896). Furthermore, protoxylem clusters are thought to occur at the periphery of the leaf-trace, on all sides of it, in *G. baldaufi,* but poor preservation of the specimen led to some uncertainty on this point (Sahni, 1932). In *G. rigolloti* leaf-traces supposedly have a cluster of protoxylem immersed at each end (Renault, 1896). Lastly, the cortex of *G. rigolloti* is constructed entirely of "lignified" cells, while in *G. baldaufi* it consists of an inner cylinder of parenchyma, a middle zone of parenchyma and scattered nests of sclerenchyma, and an outer zone that appears in Sahni's photographs (1932, text-fig. 6) to be constructed of sclerenchyma but which he did not describe. Thus, it is apparent that *G. rigolloti* represents a more primitive type than *G. baldaufi.*

The similarity between *Grammatopteris* and the Thamnopteroideae is striking, and it is no wonder that Sahni (1932) considered this genus to be a link between the Zygopterideae and the Osmundaceae. However, *Grammatopteris* differs in a number of important respects from the hypothetical ancestor of the Osmundaceae and cannot be considered a direct ancestor of this family. It is doubtful that the central xylem tracheids of the most immediate ancestor of the Osmundaceae differed much from those at the periphery of the xylem column since central xylem tracheids of *Zalesskya gracilis,* which displays the most primitive state of this character, are about ten times longer than broad. The length of these cells in *Grammatopteris rigolloti* is not known, but in *G. baldaufi* the central xylem tracheids are one to two times as long as broad (Sahni, 1932, text-fig. 5) like those of *Thamnopteris.* Further, invaginations in the stele of *Grammatopteris baldaufi* probably represent a case of development parallel to that in *Chasmatopteris* rather than a condition ancestral to it since leaf-traces of this fern are already specialized along osmundaceous lines. The oblong leaf-traces of *Grammatopteris* compare well with that expected of the ancestor of the Osmundaceae, but the indistinct protoxylem location in *G. baldaufi* and the double protoxylem in *G. rigolloti* represent conditions too specialized to be directly ancestral to the Osmundaceae. The lack of an adaxially curved petiole strand in *Grammatopteris* is another departure from conditions expected of the precursor to the Osmundaceae; yet the fact that these strands do not curve at all indicates that *Grammatopteris* is closer to the Osmundaceae in this respect than any other "coenopterid." The absence of stipular expansions and the sclerotic cortex, particularly of *G. rigolloti,* are other features in which they differ.

Thus, neither of the two species of *Grammatopteris* can be considered the direct ancestor of the Osmundaceae. However, these ferns are closer to the early members of the Osmundaceae than any other ancient fern. Further, the relationship of these taxa has been discussed in a specific sense above, and it is possible that *Grammatopteris baldaufi* and *G. rigolloti* represent a group of much larger proportions than is presently in evidence. If that is the case and if the unknown species are as different from one another as are the two known species, it is entirely possible that one or more of them was involved in the evolution of the Osmundaceae.

Catenopteris simplex Phillips and Andrews, a petrified fern stem described recently (1966) from the Upper Pennsylvanian of Illinois, is closer to the hypothetical ancestor of the Osmundaceae in many respects than are the two species of *Grammatopteris* discussed above. The stem is radially symmetric, about 6.0 mm in diameter, and has a central protostele. Leaf bases lack stipular expansions but contain a shallowly C-shaped petiolar strand that is adaxially concave as in the Osmundaceae. The stele is constructed entirely of tracheids with scalariform wall thickenings that are comparable in size to the outer metaxylem tracheids of osmundaceous ferns. The cortex of *Catenopteris* apparently lacks sclerenchyma but consists of long thin-walled cells. On the other hand, *Catenopteris* displays a number of features that are more advanced than would be expected in an ancestor of the Osmundaceae. The petiole bases lack stipular expansions and are arranged loosely around the stem. There are very few leaf-traces visible in a given cross section of the cortex. Protoxylem groups are not apparent in the stele or leaf-traces of *Catenopteris* but they are very evident in all known Osmundaceae.

Thus, *Catenopteris* must be considered in the same category as *Grammatopteris;* rather than being the actual progenitor, it probably represents a larger group from which the Osmundaceae might have evolved. Because of its less specialized stele and cortex and its C-shaped petiolar bundles, *Catenopteris* seems somewhat closer to the Osmundaceae than is *Grammatopteris.*

Summary of phylogenetic relationships

Despite the occurrence of large gaps between the nine phylogenetic groups of the Osmundaceae, a number of conclusions about the general evolutionary trends in the family can be drawn. It is evident that osmundaceous ferns must have existed prior to the Late Permian, when all known species of the Thamnopteroideae lived, in order to account for the evolution of the diversity observed in this subfamily. Dictyoxylic forms of the Osmundoideae probably also evolved somewhat before they first appear in the Late Triassic. While intermediate forms between these two subfamilies are not in evidence, several stages of the evolution of the Osmundoideae from the Thamnopteroideae by intrastelar origin of pith and formation of leaf-gaps by development of parenchyma axillary to leaf-traces are represented by known forms.

Species of the Osmundoideae are the result of slight modifications of the dictyoxylic plan of organization. Most specializations are extrastelar in nature with only a few changes in the stelar tissues. However, the *Osmundacaulis skidegatensis* and *O. braziliensis* groups developed complex steles during the Mesozoic and became extinct near the close of this era. Connections of these two groups with each other and with the *O. herbstii* group are not clear.

No definite source of the Recent genera and subgenera can be determined. *Todea* is apparently without a fossil record, and *Leptopteris* is represented only by petrified petiole bases from questionable Miocene sediments in Queensland. On the other hand, silicified rhizomes of the three subgenera of *Osmunda* occur in the Paleocene, and the subgenera *Osmunda* and *Plenasium* can be extended into the Early and Late Cretaceous respectively on the basis of foliage compressions. No definite source for *Osmunda* and *Osmundastrum* can be determined, but *Plenasium* shares a number of characters with the *Osmundacaulis skidegatensis* group and may have evolved from forms similar to the known species.

The Osmundaceae probably arose from forms similar to *Grammatopteris baldaufi, G. rigolloti,* and *Catenopteris simplex* although none of these species can be considered the actual progenitor. Furthermore, no ancestor of other fern taxa can be found among the known Osmundaceae.

SUMMARY

1. The purpose of this investigation has been to study the phylogenetic interrelationships of the extinct and living species of the Osmundaceae as revealed by whatever characters are available. These are expressed mostly in the anatomy and morphology of their stems, petiole bases, and roots.
2. The study is based upon: (a) an examination of *Leptopteris wilkesiana* and the 13 Recent species of the family that were investigated by Hewitson (1962), (b) a reinvestigation of type or representative materials of 24 of the 33 previously described species of structurally preserved rhizomes and trunks, and (c) literature descriptions of the remaining species of petrified axes.
3. The phylogenetic significance of other osmundaceous fossils, such as stem casts, foliage compressions, isolated sporangia, and dispersed spores, is evaluated.
4. In all, 29 extinct and 14 Recent species, for which sufficient detail is known, are placed in lines of specialization by the ground plan method of multiple character correlation. When these lines are considered with respect to geologic time, the sample is resolved into nine groups of phylogenetically related species.
5. Gaps occur between these groups indicating that the known fossils represent only a few of those forms that existed in the past.

6. Since the first appearance of the Osmundaceae in the Permian, the group has evolved slowly, and two lines that became highly specialized in the Mesozoic died out near the close of this era.

7. Because of their distinct placement in the ground plan analyses, the Permian species are regarded as representing a subfamily of the Osmundaceae, the Thamnopteroideae, with the Mesozoic, Tertiary, and Recent species forming a second subfamily, the Osmundoideae.

8. *Itopsidema vancleavei* is removed to *incertae sedis,* but sufficient evidence exists within the remaining species to indicate evolution of the Recent forms from protostelic ancestors by intrastelar origin of a pith and subsequent (or concurrent) dissection of the xylem cylinder by leaf-gaps.

9. *Leptopteris* and *Todea* are generically distinct from one another and from *Osmunda,* and neither *Leptopteris* and *Todea* has a sufficient fossil record to suggest their origin.

10. The three subgenera of *Osmunda* were distinct lines of evolution in the Paleocene, and the subgenera *Osmunda* and *Plenasium* are represented by foliage remains in the Cretaceous. No definite source of *Osmunda* or *Osmundastrum* can be determined, but *Osmundacaulis atherstonei* and *O. natalensis,* both from the Cretaceous of South Africa, are similar in some respects to *Plenasium* and may represent the source of this subgenus.

11. The three subgenera of *Osmunda* appear in the numerical analyses to be as distinct from one another as are *Leptopteris* and *Todea.* To achieve consistency within the family and to recognize that *Osmunda, Osmundastrum,* and *Plenasium* have been separate lines of evolution for 70 million years, it is recommended that these taxa be treated as genera.

12. No ancestors of other fern families can be found among the known Osmundaceae.

13. The Osmundaceae probably evolved in the Lower Permian or Pennsylvanian from forms similar to *Grammatopteris baldaufi, G. rigolloti,* and *Catenopteris simplex,* but none of these species can be definitely considered the precursor of the family.

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MANUSCRIPT SUBMITTED DECEMBER 16, 1969.