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# *Osmunda shimokawaensis* sp. nov. and *Osmunda cinnamomea* L. based on permineralized rhizomes from the Middle Miocene of Shimokawa, Hokkaido, Japan

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**Abstract.** This paper describes two species of the leptosporangiate fern genus *Osmunda* Linnaeus (Osmundaceae) based on permineralized rhizomes from late Middle Miocene sediments in the Mosanru Formation, Shimokawa Group, in Shimokawa, north-central Hokkaido, Japan. *Osmunda shimokawaensis* sp. nov. has an ectophloic dictyoxyllic siphonostele radiating numerous leaf traces in spiral order, and stipulate leaf bases characteristic of the Osmundaceae. Mode of leaf-trace departure and sclerenchyma distribution at the leaf base strengthen its affinity with *Osmunda* (*Osmunda*). This species is important in being the first record of the subgenus from Asia based on permineralized rhizomes. One rhizome is attributable to the extant species *Osmunda cinnamomea* L. of subgenus *Osmundastrum* Presl. *Osmunda shimokawaensis* and *O. cinnamomea* provide new evidence for better understanding the evolution and phytogeography of the genus *Osmunda*.

**Key words:** fern, Japan, Miocene, *Osmunda cinnamomea*, *Osmunda shimokawaensis*, rhizome

## Introduction

Among extant leptosporangiate fern families, the Osmundaceae as well as the Gleicheniaceae are agreed to have oldest fossil records that can be traced back to the Permian (Seward and Ford, 1903; Gwynne-Vaughan, 1911; Miller, 1967, 1971; Yao and Taylor, 1988; Tidwell and Ash, 1994; Serbet and Rothwell, 1999; Skog, 2001). The antiquity of the Osmundaceae is also supported by molecular phylogenetic analysis (Hasebe *et al.*, 1994; Yatabe *et al.*, 1999). Most fossil records of the family are based on permineralized rhizomes, that allow for comparative anatomical studies, identification, and taxonomic comparison (Jeffrey, 1899; Faull, 1901; Gwynne-Vaughan, 1911; Hewitson, 1962; Miller, 1967, 1971, 1982; Rothwell, 1996; Serbet and Rothwell, 1999). Hewitson (1962) and Miller (1967) showed that rhizome anatomy provides diagnostic characters, which help identify and infer affinities of permineralized rhizomes.

Fossil records show that osmundaceous ferns have been widespread and diverse in the past (Miller, 1967, 1971;

Tidwell and Ash, 1994; Serbet and Rothwell, 1999). There are at least 150 extinct osmundaceous species known to date worldwide (Taylor and Taylor, 1993), of which more than 50 are anatomically preserved rhizomes. Tidwell and Ash (1994) classify the permineralized rhizomes into 14 genera. Among permineralized rhizome species, those younger in age than *Osmunda cinnamomea* from the Late Cretaceous of Alberta, Canada (Serbet and Rothwell, 1999) are generally attributable to extant genera or to a certain living species.

Modern species of the Osmundaceae are classified into three genera: *Osmunda* L., *Todea* Willdenow and *Leptopteris* Presl, which contain eight, one, and six species, respectively (Kramer, 1990). In the genus *Osmunda*, recognition of three subgenera; *Osmunda*, *Osmundastrum* and *Plenasium* Presl is widely accepted on the basis of comparative morphology, although there has been delimitation disagreement in relation to the affinity of a morphologically intermediate species *O. claytoniana* L. (e.g., Miller, 1967, 1971; Kramer, 1990). Recent molecular sequencing study, however, attributes *Osmunda claytoniana*

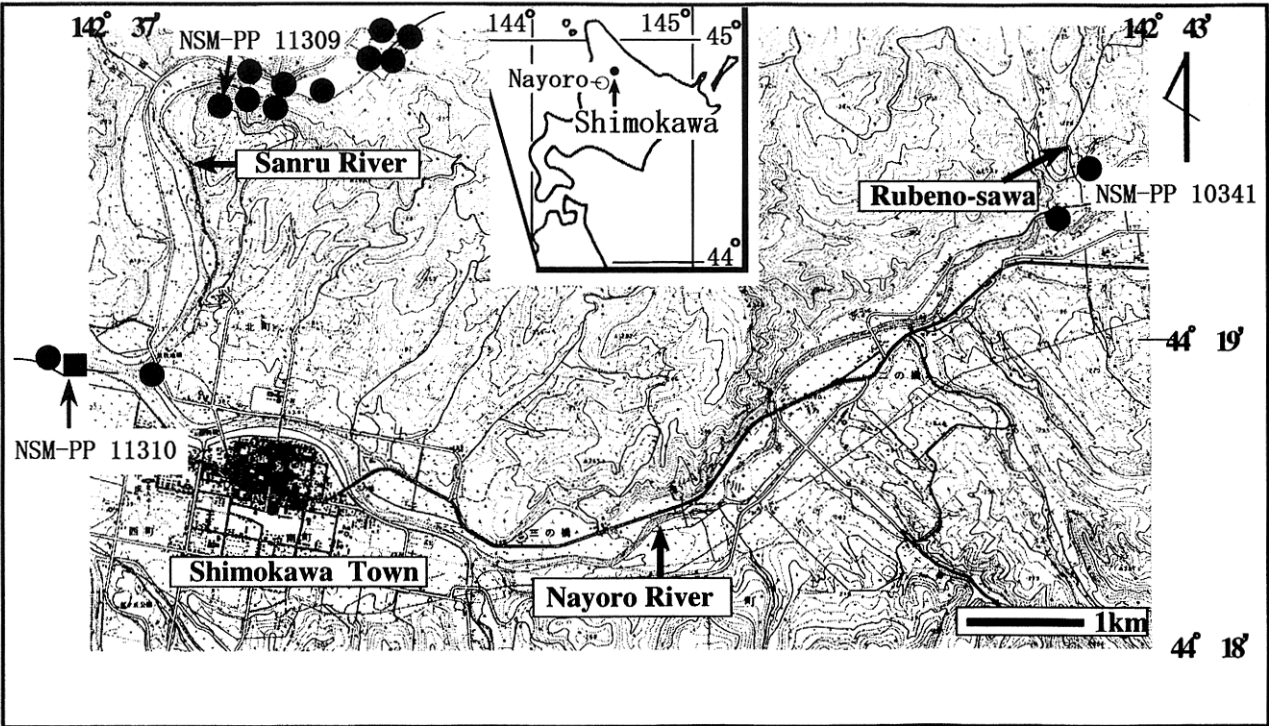


Figure 1. Collection localities of rhizomes of *Osmunda shimokawaensis* sp. nov. (●) and *Osmunda cinnamomea* (■). Topographic map adapted from 1:25,000 “Shimokawa”, Geological Survey, Ministry of Construction of Japan.

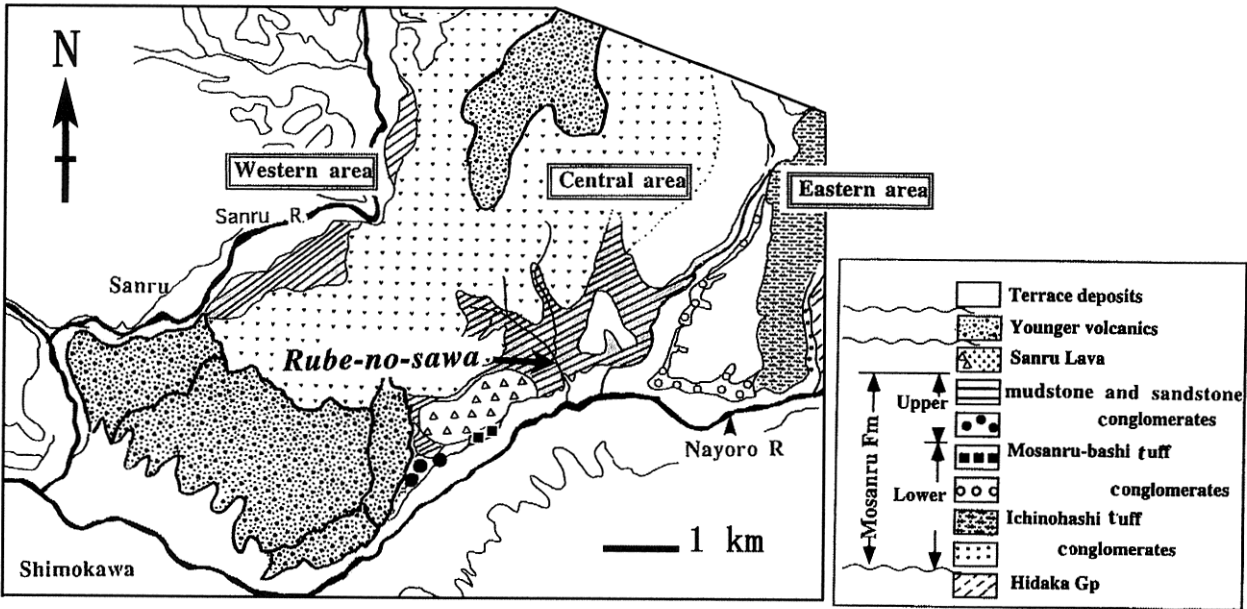


Figure 2. Geologic map of Shimokawa region.

Age	Stratigraphy			Lithology	Member	Thickness
Quaternary				Terrace deposits		
Pliocene				Volcanic rocks		
Late Miocene		Younger volcanics		Andesite		
		Sanru Lava		Rhyolite		200-300 m
Middle Miocene	Shimokawa Group	Mosanru Formation	Upper part	Mudstone Sandstone Conglomerates		50-100 m
				Tuffaceous mudstone Pumice tuff	Mosanru-bashi tuff	30 m
			Lower part	Mudstone Sandstone Conglomerates		90 m
				Pumice tuff Welded tuff	Ichinohashi tuff	60 m
				Conglomerates		10 m
Pre-Tertiary		Hidaka Group		Sandstone, Mudstone		

Figure 3. Stratigraphic sequence of the Shimokawa Group.

to subgenus *Osmunda*, rather than to *Osmundastrum*, which eventually contains only *O. cinnamomea* (Yatabe *et al.*, 1999).

The fossil evidence of modern Osmundaceae can be traced from the Triassic foliage *Osmunda claytoniites* Phipps *et al.* from Antarctica, which resembles extant *O. claytoniana* in having a semi-dimorphic fertile frond (Phipps *et al.*, 1998). Meanwhile, Yatabe *et al.* (1999) inferred that *Osmunda cinnamomea*, which is similar to *O. claytoniana* in sterile frond morphology but has a completely dimorphic fertile frond, is the most basally positioned species based on *rbcL* analysis. These authors consider *O. claytoniites* to be also comparable to *O. cinnamomea* because the fertile frond dimorphism varies much in extant species and is not a diagnostic character.

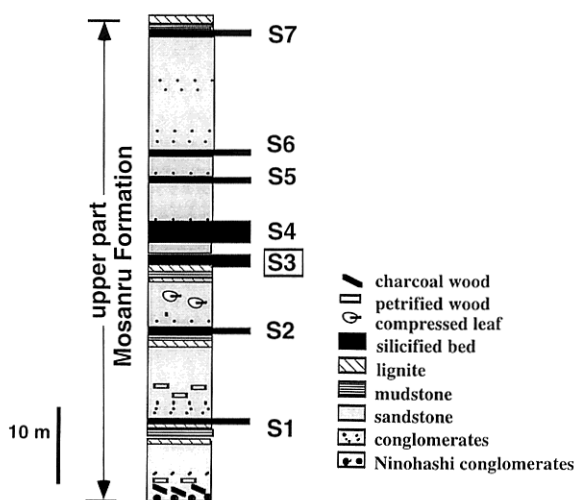
Yatabe *et al.* (1999) also estimated the time of subsequent divergence within the family by combining *rbcL* average molecular substitution rate and fossil records. According to their analysis and estimation, the basal *Osmunda cinnamomea* group first diversified into a *Todea-Leptopteris* clade and another clade that includes all other species of *Osmunda*, eventually subgenera *Osmunda* and *Plenasium* (*sensu* Miller, 1967). Molecular estimation by Yatabe *et al.* (1999) suggests that major specific diversification within subgenera *Osmunda* and *Plenasium* has occurred within the last 150 Myrs (Million years). This result conforms closely with evidence from the fossil record (Miller, 1971).

Since a major diversification within the genus *Osmunda* has occurred during post-Cretaceous time, Tertiary rhizomes are indispensable for tracing the evolutionary history

of the genus. Previously described Tertiary rhizomes are, however, all from North America and Europe, and none has been reported from Asia and Japan, where abundant osmundaceous foliage has been found at many Tertiary localities (Oishi and Huzioka, 1943; Matsuo, 1953; Tanai, 1970). This paper describes two species of Miocene silicified *Osmunda* rhizomes, the first from Japan.

#### Occurrence and age of fossils

Many osmundaceous rhizomes have been collected in riverbeds of the Rubeno-sawa, the Sanru River, and downstream as far as to the Nayoro River near Shimokawa, Hokkaido, Japan (Figure 1). The specimens are isolated or embedded rhizomes in black chalcedonic-quartz rocks that are washed out from the original sediments (Matsumoto, 2000). In the collection area are distributed the late Middle Miocene Mosanru Formation of the Shimokawa Group (Figures 2–4). The Shimokawa Group unconformably covers the pre-Tertiary Hidaka Group and is unconformably overlain by younger volcanics and Quaternary sediments (Sako and Osanai, 1955; Sako *et al.*, 1960; Suzuki and Matsui, 1975; Yamaguchi and Watanabe, 1990; Oka, 1994; Matsumoto, 2000; Figures 2, 3). The Mosanru Formation is divided into lower and upper sedimentary facies (Figures 2, 3). The upper part is composed mainly of volcanic sedimentary rocks, most of which show seven cyclic accumulations, intercalating seven silicified seams (S1–S7) on top of each sequence (Figure 4). Although the original source rocks are uncertain, all specimens are probably derived from seam S3 as has been inferred for previously described



**Figure 4.** Columnar section of the upper part of the Mosanru Formation. S1-S7: silicified beds (thickness exaggerated).

silicified plant remains from the same formation (Matsumoto *et al.*, 1994, 1995; Matsumoto *et al.*, 1997a; Matsumoto *et al.*, 1997b; Matsumoto, 2000).

Although we have no explicit age for the S3 seam, the age of the Mosanru Formation is inferred from several datings of volcanic rocks obtained from Shimokawa and adjacent regions. By radiometric dating, the lower part of the Shimokawa Group is assigned a date ranging between 11 and 13 Myrs, while the Sanru Lava is assigned one ranging between 10 and 12 Myrs (Koshimizu and Kim, 1986, 1987; Watanabe and Yamaguchi, 1988; Watanabe *et al.*, 1991). These radiometric data suggest that the Mosanru Formation was deposited during the late Middle Miocene (ca. 12 Myrs), and that the silicified seams are not younger than 10 Myrs.

### Materials and methods

Fourteen permineralized rhizomes have been collected by Isekichi Nakauchi from Shimokawa Town, Kamikawa District, Hokkaido, and one specimen by Takeshi A. Ohsawa of Chiba University. Two specimens (NSM-PP 10341 from the Rube-no-sawa, NSM-PP-11309 from the Sanru River) were donated by Nakauchi for anatomical study. NSM-PP 10341 is the largest specimen, 11 × 16 × 21 cm in dimensions, and contains two rhizomes A and B. NSM-PP 11310 is an isolated rhizome collected from the Nayoro River (Figure 1).

All the specimens are silicified to various degrees; most were applicable to the modified cellulose acetate peel method using 25–45% hydrofluoric acid as an etching reagent (Joy *et al.*, 1956; Basinger, 1981). The peels were

mounted on microscope slides in xylene-soluble Canada balsam for microscopic examination and photography.

### Systematic paleontology

#### Order Filicales

Family Osmundaceae Diels, 1898

Genus *Osmunda* Linnaeus, 1753

Subgenus *Osmunda* Linnaeus, 1753

*Osmunda shimokawaensis* sp. nov.

Figures 5–8

**Diagnosis.**—Fern rhizomes, attaining 20 cm long or more, 4–7 cm in diameter distally, tapering proximally, consisting of stem 2.0–2.5 cm in diameter and a mantle of closely adhering stipular petiole bases; stem ectophloic dictyoxyletic siphonostele. Stelar cylinder 5.0–7.0 mm in diameter; xylem plate 0.8–1.0 mm thick, consisting of 14–18 cauline xylem bundles separated by leaf gaps formed opposite to each departing leaf trace as observed in transverse section. Pith 2.0–3.0 mm in diameter, parenchymatous; stem inner cortex 0.3–1.6 mm thick, including 6–8 leaf traces in a given transverse section; outer cortex 0.8–1.5 mm thick, including 12–18 leaf traces in a given transverse section. Leaf trace protoxylem single at base of trace, bifurcating as leaf trace passes through inner cortex or sometimes through outer cortex. Petiole in transverse section 6.0–7.0 mm high, up to 22 mm wide at widest stipular region. Outer sclerenchyma ring of petiole heterogeneous with a thin crescent shape strip of thick-walled fibers limited to adaxial side of stipular region. Fibers in adaxial concavity of vascular bundle form small mass at petiole base, expanding laterally along inner contour of petiolar strand forming a pair of thin strips at each inner side of vascular bundle in distal part of petiole. Stipular expansion containing single, laterally elongated mass of sclerenchyma throughout its length; sclerenchyma mass heterogeneous with a thin strip of thick-walled fibers on abaxial margin. Some small clusters of thick-walled fibers in stipular wing tip.

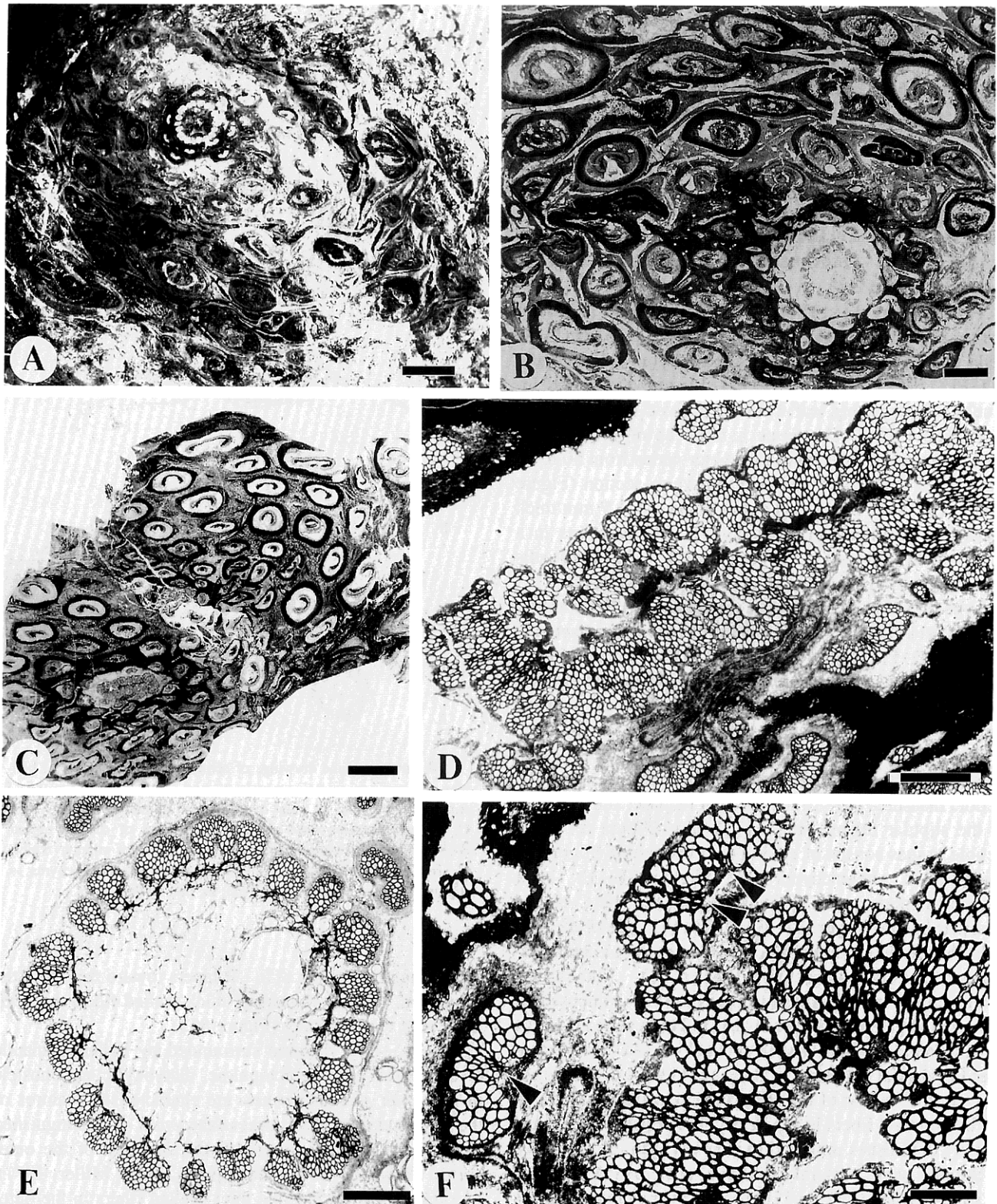
**Types.**—Holotype: Figures 5–8, NSM-PP10341 rhizome A and peels, Paleobotanical Collections, Department of Geology, National Science Museum, Tokyo. Paratypes: NSM-PP10341 rhizome B and NSM-PP11309 rhizome, and their peels, Paleobotanical Collections, Department of Geology, National Science Museum, Tokyo.

**Type locality.**—Shimokawa area, Hokkaido, Japan (Figure 1).

**Occurrence.**—Upper part of the Mosanru Formation, the Shimokawa Group.

**Geologic age.**—Late Middle Miocene.

**Etymology.**—Specific epithet after the fossil locality, Shimokawa Town.



**Figure 5.** *Osmunda shimokawaensis* sp. nov. Surface view (A) and transverse sections (B–F). A. Rhizome and radiating petioles. B, C. Rhizomes radiating numerous leaf traces in spiral order. D–F. Dictyoxylic protostele and departing leaf traces. Arrowheads in F indicate protoxylem. A, B, E = NSM-PP 10341 (B, E, Slide #1); C, D, F = NSM-PP 11309 (Slide #1). Scale bars: A, B = 2 mm; C = 5 mm; D = 300 μm; E = 5 mm; F = 200 μm.



**Description.**—The fossil species has characteristic stipular petiole bases, adaxially concave, C-shaped leaf traces, and an ectophloic-dictyoxylic siphonostele, which is surrounded by an endodermis (Figure 5A–F). Decurrent petiole bases are closely appressed around the stem in a helical order, and form a thick mantle. The rhizome is surrounded by a root mantle. Roots are diarch (Figure 5F, indicated with arrows).

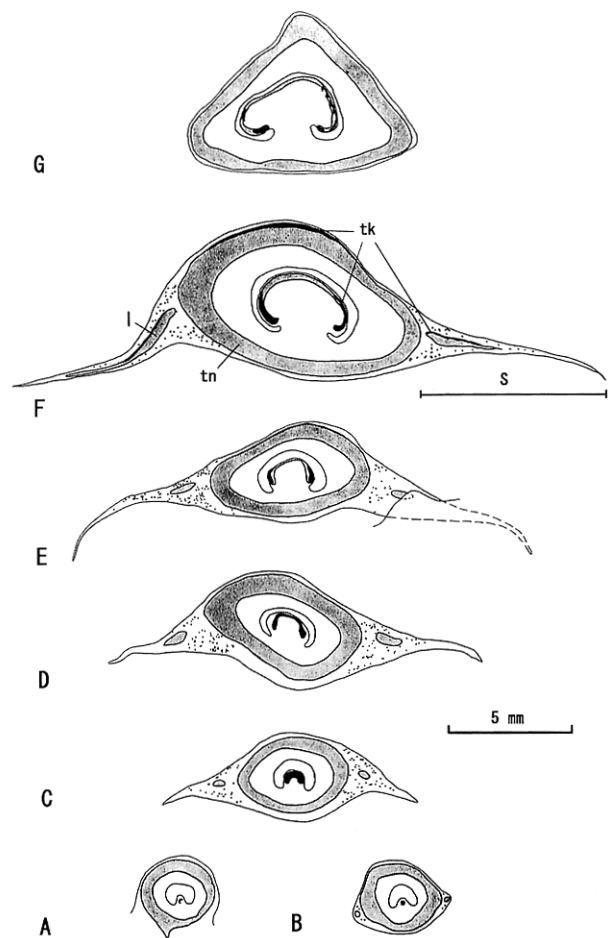
The xylem consists of 14–18 strands of primary xylem tracheids, which are arranged in a circle around the pith (Figure 5D, E). Phloem consists of thin-walled cells, but is not well preserved.

The cortex is differentiated into inner cortex and outer cortex. The inner cortex consists mostly of parenchyma cells and the outer cortex of sclerenchyma cells (Figure 5D–F). The inner cortex is 0.3–1.6 mm thick, and includes 6–8 departing leaf traces in a given transverse section (Figure 5B). The tissue is made up of polygonal or oval parenchyma cells whose diameter varies from 30 to 55  $\mu\text{m}$  with 1–2  $\mu\text{m}$  thick walls in transverse section (Figure 5D). The outer cortex is a dense tissue 0.8–1.5 mm thick consisting of fibers, and includes 12–18 leaf traces in a given transverse section (Figure 5B, C). The fiber cells are 15–75  $\mu\text{m}$  in diameter with walls, 1–3  $\mu\text{m}$  thick.

Type of leaf gap formation is the same as Miller's immediate type (Miller, 1971), featuring the subgenus *Osmunda* (Figure 5D–F). The leaf trace is first embedded in the stem cortical tissue, and subsequently increases the number of protoxylem strands from one to about four as it passes through the inner and outer cortices (Figures 5F, 7A, B).

The petiole base increases in size distally due to lateral extension of the stipular wings (Figures 5B, C, 6). The petiole measures 6.0–7.0 mm wide at its base, and is widest at the stipular region, attaining 22 mm (Figure 6). The petiole tissues consist of epidermis, hypodermis (Figure 8), thick-walled sclerenchyma ring (Figure 7B–E), inner parenchymatous cortex (Figure 7A, B), and the C-shaped vascular bundle (Figure 7A–F). The inner side of the vascular bundle is occupied by central parenchyma and a peripheral mass of sclerenchyma (Figure 7B). The cortical sclerenchyma ring is mostly homogeneous, composed of thin-walled parenchyma, but is partly heterogeneous in the stipular region, where a strip of thick-walled fibers occupies the abaxial periphery of the ring (Figures 6, 7C–F, 8A, D). In the middle of the stipular region, the abaxial arch of thick-walled fibers is apparently thin (Figure 6C, D) and distally diminishes until it disappears (Figure 6E, F).

Stipular wing, a lateral expansion of the petiole, consists of parenchymatous ground tissue and sclerenchyma masses of variable size (Figure 8A–C). The sclerenchyma forms a large elongated mass and smaller isolated dots. On the abaxial side of the elongated sclerenchyma is a thin strip of thick-walled fibers, which is only found in the widest

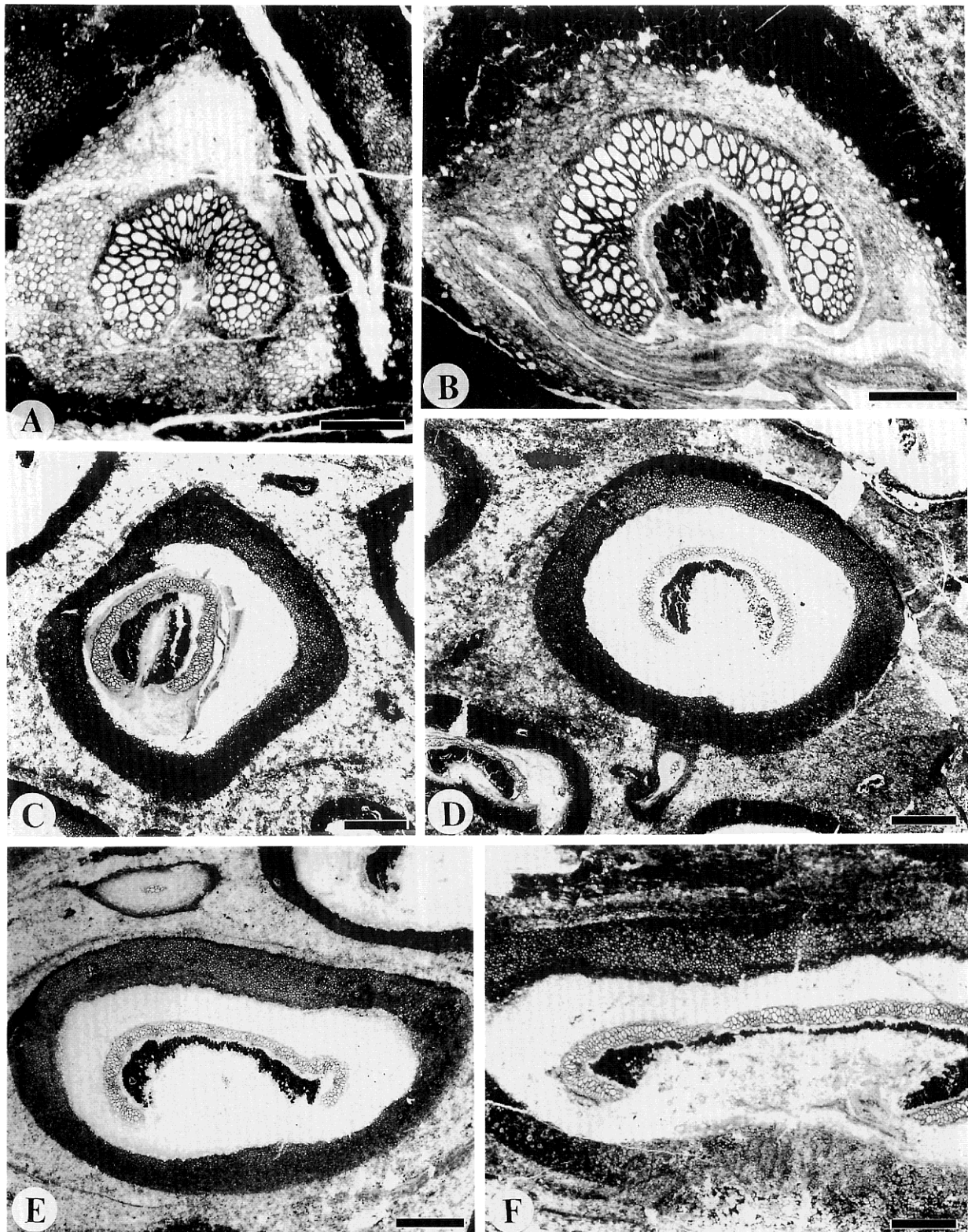


**Figure 6.** Line drawings of serial transverse sections of petioles of *Osmunda shimokawaensis* sp. nov., from base to the top of stipular region. **A.** At point of attachment to stem. **B.** Very base. **C.** Midway between base and middle position of stipular region. **D–F.** Midway between middle and top position of stipular region. **G.** Top of stipular region. **l**, lateral masses of sclerenchyma; **s**, stipular wing; **tk**, thick-walled fibers; **tn**, thin-walled fibers.

stipular region (Figure 8C). It tapers toward the tip of the expansion. Small clusters of thick-walled fibers are scattered near the periphery (Figure 8C).

**Affinity.**—The rhizome surrounded by radiating mantle of leaf bases, and the ectophloic, dictyoxylic siphonostele of *Osmunda shimokawaensis* are characteristic features of the Osmundaceae. *O. shimokawaensis* is distinguished from *Todea* and *Leptopteris* in the structure of the outer cortex (Hewitson, 1962; Hennipman, 1968; Miller, 1971). *O. shimokawaensis* has the thick-walled fibers in the outer cortex. However, *Todea* and *Leptopteris* have relatively thin-walled fibers in the outer cortex.

Among the three subgenera of genus *Osmunda*, *O. shimokawaensis* is attributable to the subgenus *Osmunda*

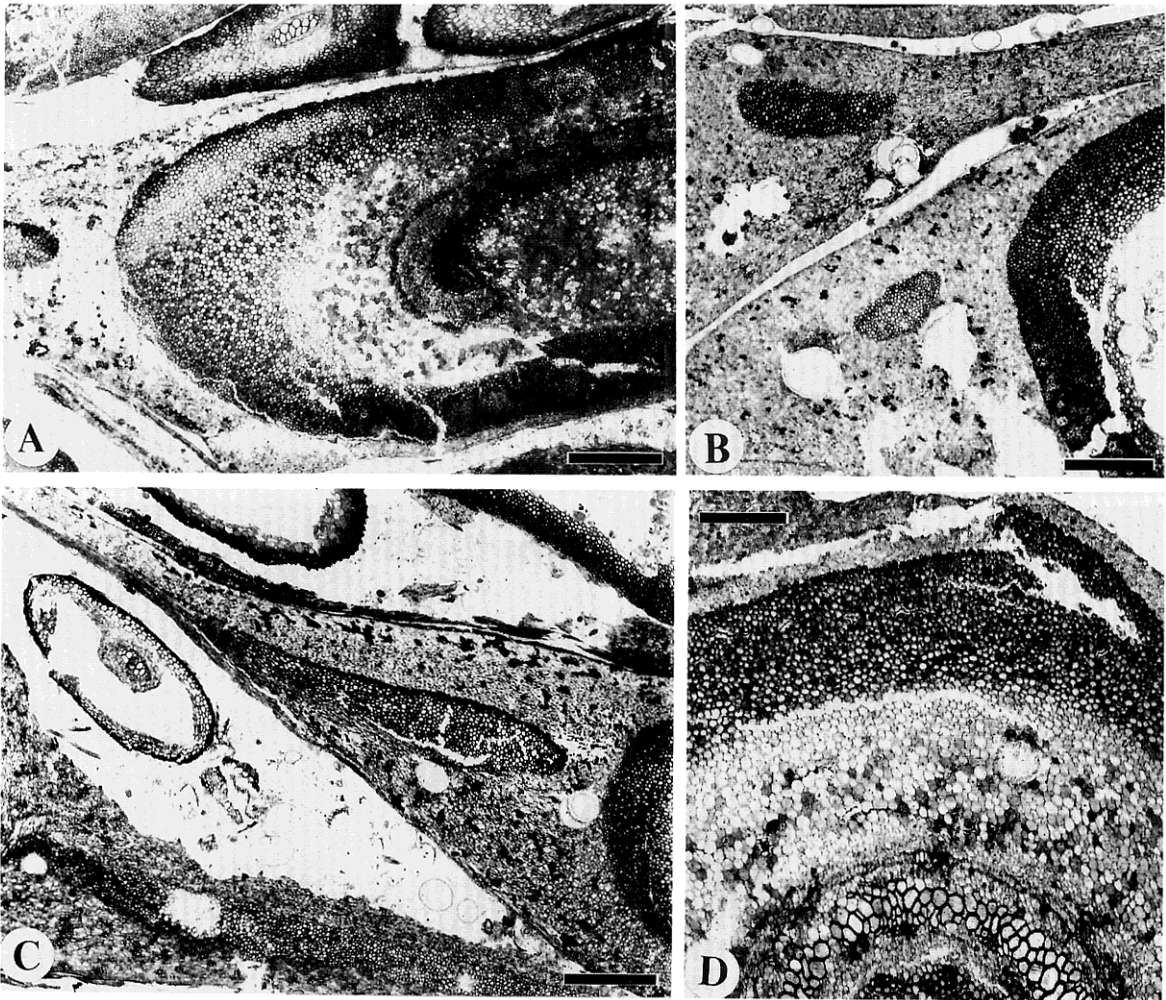


**Figure 7.** Transverse sections of petioles of *Osmunda shimokawaensis* sp. nov., from base to the stipular region (NSM-PP 11309). **A.** Very base, showing two protoxylem masses. **B.** Petiole base more distal to **A.** Note increasing number of divided protoxylem, and central sclerenchyma masses. **C, D.** Midway between base and stipular region. **E, F.** Middle to top of petiole. **A–D,** Slide #1; **E, F,** Slide #2. Scale bars: **A–F** = 2 mm.



**Table 1.** Features of modern and fossil rhizomes of subgenus *Osmunda*. Sources other than

Species	<i>O. claytoniana</i>	<i>O. regalis</i>	<i>O. japonica</i>	<i>O. lancea</i>
Age	Recent	Recent	Recent	Recent
Locality				
No. of stem xylem strands in an X-section	7–16	4–11	4–11	6–9
No. of leaf traces in an X-section of:				
Inner cortex	4–7	2–3	2–4	1–5
Outer cortex	7–15	5–11	5–11	11–15
Point of basal forking of leaf-trace protoxylem	petiole base	inner cortex	inner cortex	inner cortex
Nature of thick-walled fibers in sclerenchyma ring of petiole base at positions indicated below:				
Point of attachment of petiole to stem	abaxial arch	abaxial arch	abaxial arch	abaxial arch
Slightly above point of attachment of petiole to stem	lateral masses	lateral masses	lateral masses	lateral masses
Midway between point of attachment and top of s.r.	lateral masses	adaxial masses	adaxial masses	adaxial masses
Top of s. r.	lateral masses	adaxial masses	adaxial masses	adaxial masses
Just above s. r.	lateral masses	adaxial strip	adaxial strip	adaxial strip



**Figure 8.** Transverse sections of petioles of *Osmunda shimokawaensis* sp. nov., between stipular region and top of petiole (NSM-PP 11309). A–C. Middle to the top of stipular region. C. Sclerenchyma masses in stipular wing. Note adaxial black striation of thick-walled fibers in the largest mass. D. Top of petiole, showing two-zoned cortex and vascular bundle tissues. A, Slide #2; B–D, Slide #3. Scale bars: A–C = 1 mm, D = 500  $\mu$ m.

*O. shimokawaensis* sp. nov.: Hewitson, 1962; Miller, 1967, 1971, 1982. s.r., stipular region.

<i>O. nathorstii</i>	<i>O. iliaensis</i>	<i>Osmunda</i> <i>shimokawaensis</i> sp. nov.			<i>O. wehrii</i>	<i>O. oregonensis</i>	<i>O. pluma</i>
Late Tertiary Spitzbergen not preserved	Mio-Pliocene Hungary 17–18	late Middle Miocene Japan 14–18			Miocene Washington 12–14	Eocene Oregon 16–20	Paleocene North Dakota 7–12
not preserved	2–5	6–8			2–3	0–2	1–3
not preserved	13–15	5–11			10–13	15	6–10
petiole base	outer cortex	inner	sometimes	outer	outer cortex	inner cortex	inner cortex
		cortex					
unknown	abaxial arch	absent			abaxial arch	abaxial arch	abaxial arch
unknown	unknown	absent			abaxial arch	abaxial arch	abaxial arch
lateral masses	unknown	abaxial strip			abaxial arch	abaxial arch	abaxial arch
unknown	abaxial arch	abaxial strip			lateral masses	abaxial arch	abaxial arch
unknown	unknown	almost absent			unknown	lateral masses	lateral masses

because of the immediate type of leaf-trace formation (Hewitson, 1962; Miller, 1971). *O. shimokawaensis* is also distinguishable from *Osmundastrum* and *Plenasium* in the disposition of sclerenchyma in the petiole (Hewitson, 1962). Species of subgenus *Osmunda* have a cortical sclerenchyma ring containing two lateral masses of thick-walled fibers (*O. japonica* Thunb., *O. regalis* L., *O. lancea* Thunb., *O. x ruggii* Tryon) or a distinct abaxial arch of thick-walled fibers (*O. claytoniana*) in a cross section at stipular region. Subgenus *Osmundastrum* has three round masses of thick-walled fibers (one abaxial and two lateral) in the cortical sclerenchyma ring. *Osmunda shimokawaensis*, having a distinct abaxial arch of the thick-walled fibers in the stipular region, is assignable to subgenus *Osmunda*.

Based on a general anatomical comparison of diagnostic characters, *Osmunda shimokawaensis* can be designated as a new species (Table 1). The most distinguishable feature of *O. shimokawaensis* is a thin crescent strip of thick-walled fibers on the abaxial side of the cortical sclerenchyma ring, which occurs only in the stipular region (Figure 6; Table 1). Among fossil and extant species of *Osmunda*, *O. wehrii* Miller from the Miocene of Washington, U.S.A. is most comparable to *O. shimokawaensis* in general structure, especially in having a thin crescent arc of thick-walled fibers on the abaxial side of the cortical sclerenchyma ring in the petiole (Miller, 1982; Table 1). In *Osmunda wehrii*, however, the arc is thicker and found through the length of the petiole.

Subgenus *Osmundastrum* Presl, 1845

*Osmunda cinnamomea* Linnaeus, 1753

Figure 9

*Material*.—NSM-PP 11310, rhizome and peels, Paleo-

botanical Collections, Department of Geology, National Science Museum, Tokyo.

*Locality*.—Shimokawa area, Hokkaido, Japan (Figure 1).

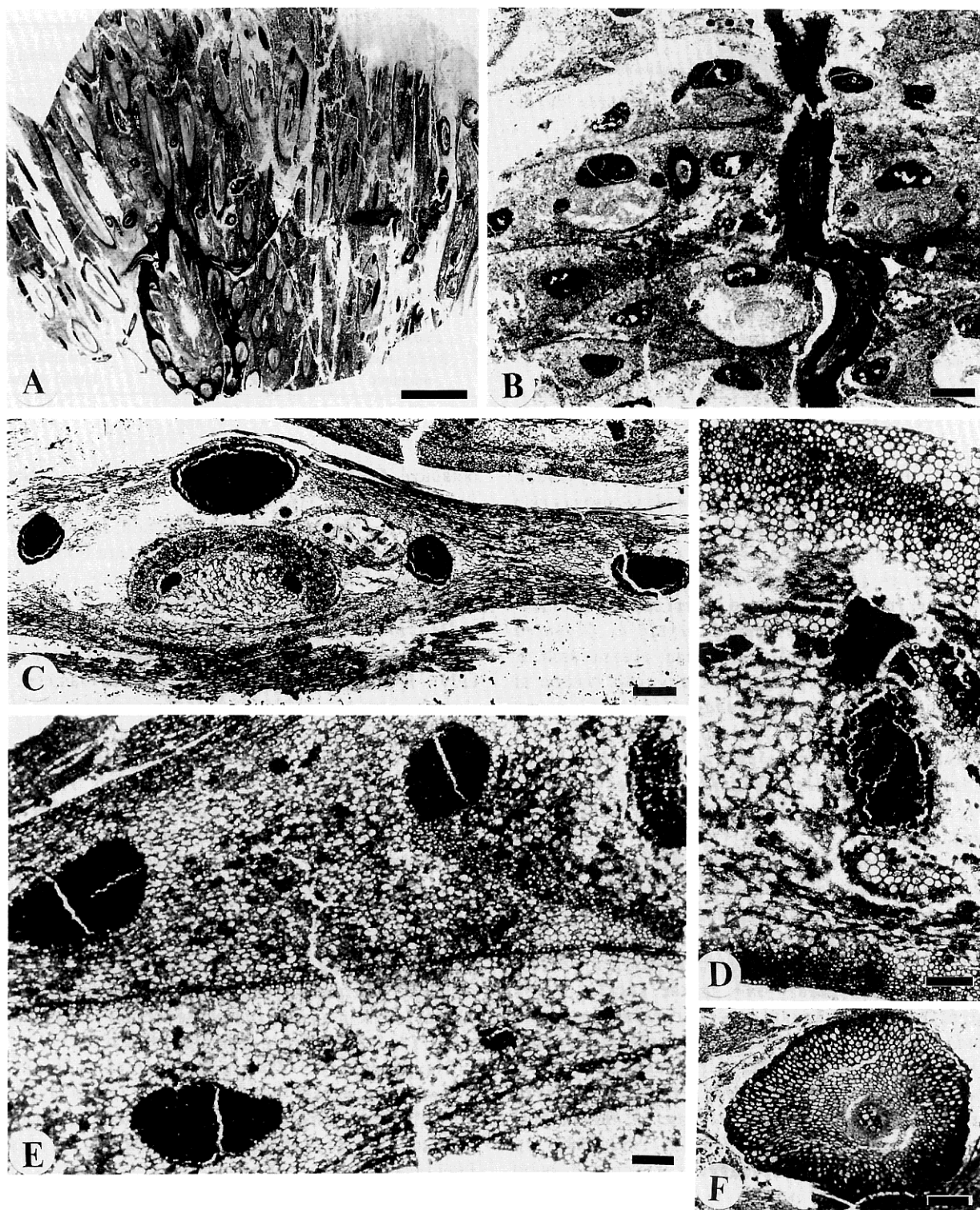
*Occurrence*.—Upper part of the Mosanru Formation, the Shimokawa Group.

*Geologic age*.—Late Middle Miocene.

*Description*.—The fossil rhizome is more than 10 cm long, tapering proximally, and is 5–9 cm in diameter distally. It consists of a stem about 1.5 cm in diameter. The stem has an ectophloic, dictyoxyllic siphonostele with a stelar cylinder about 5.5–7.5 mm in diameter (Figure 9A). The xylem ring is about 1.0 mm thick, consisting of 10–13 primary cauline xylem bundles separated by leaf gaps formed opposite each departing leaf trace. The pith is about 2.0 mm in diameter and composed of poorly preserved parenchyma. The endodermis is poorly preserved, and only confirmed on external side of the vascular bundle. The cortex is composed of inner and outer layers (Figure 9A). In cross section, a leaf trace has one endarch protoxylem at the level of divergence and then bifurcates distally. The inner cortex is 0.5–1.3 mm thick, including 11 leaf traces in a given transverse section. The outer cortex is 1.6–2.2 mm thick, including 10 leaf traces.

The petiole is 4.5–7.5 mm thick and up to 26 mm wide in transverse section at widest stipular region (Figure 9B, C). The sclerenchyma ring of the petiole is heterogeneous, consisting of one abaxial and two lateral, ground masses of thick-walled fibers, and ground thin-walled fibers (Figure 9D, E). This distribution of thick-walled fibers is characteristic of *Osmunda cinnamomea* (Hewitson, 1962; Miller, 1971). One large mass and smaller dots of sclerenchyma are distributed in each stipular wing (Figure 9B, C, E). Roots are diarch (Figure 9F).

*Affinity*.—The fossil is assigned to *Osmunda cinnamomea* based on general anatomical features of the rhizome



**Figure 9.** *Osmunda cinnamomea* (NSM-PP 11310). Transverse sections of rhizome. **A.** Slightly oblique section of rhizome. **B.** Clusters of radiating petioles. **C.** Showing distribution of thick-walled fibers. **D.** Part of vascular bundle and a mass of internal thick-walled fibers. **E.** Showing cluster of thick-walled fibers and dotted sclerenchyma in stipular wing. **F.** Root with diarch xylem. **A.** Slide #1; **B–E,** Slide #2; **F,** Slide #3. Scale bars: **A** = 7 mm; **B** = 600  $\mu$ m; **C** = 150  $\mu$ m; **D, E** = 80  $\mu$ m; **F** = 500  $\mu$ m.

**Table 2.** Features of modern and fossil rhizomes of subgenus *Osmundastrum*. Sources other than present specimen (\*): Hewitson, 1962; Miller, 1967, 1971; Serbet and Rothwell, 1999.

Species	<i>O. cinnamomea</i>	<i>Osmunda cinnamomea</i> *	<i>O. cinnamomea</i>	<i>O. precinnamomea</i>	<i>O. cinnamomea</i>
Age	Recent	late Middle Miocene	Mio-Pliocene	Paleocene	Upper Cretaceous
Locality	Japan	Japan	Washington	North Dakota	Alberta
No. of stem xylem strands in an X-section	7-22	10	12-14	3-7	7-8
No. of leaf traces in an X-section of:					
Inner cortex	4-12	11	6-9	4-5	3-5
Outer cortex	7-15	10	9-12	6-9	6-10
Angle of leaf trace divergence	18-24°	10-18°	10-16°	10-15°	-
Internal endodermis	present-absent	not visible	not visible	absent	absent
Strands of fibers in stipular expansions	few	few	few	many	few
Strands of thick-walled fibers in sclerenchyma ring of petiole	3	3	3	3	3

and petiole base (Table 2). The feature is also conformable with fossil species of *Osmunda cinnamomea* known to date, from the Mio-Pliocene of Washington, U.S.A. (Miller, 1967, 1971), and from the Upper Cretaceous of Alberta, Canada (Rothwell, 1996; Serbet and Rothwell, 1999), and also including Paleocene species previously assigned to *O. precinnamomea* of North Dakota (Miller, 1971; Serbet and Rothwell, 1999).

### Discussion

The two species of fossil rhizomes described here are important for several reasons. They are 1) the first record of permineralized rhizomes of *Osmunda* from the Neogene of Asia, including 2) one new species of the subgenus *Osmunda*, and 3) the first occurrence of *O. cinnamomea* from Asian Miocene strata, which helps trace the biogeographic history of the oldest species of the genus.

Both fossil and molecular data suggest post-Cretaceous major species diversification within the genus *Osmunda*, although *O. cinnamomea* had possibly appeared as early as the Triassic (Miller, 1967, 1971; Tidwell and Ash, 1994; Serbet and Rothwell, 1999; Yatabe *et al.*, 1999). The antiquity of *Osmunda cinnamomea* is supported by continual stratigraphic occurrence of fossils showing similar diagnostic characters (Table 2), including *O. precinnamomea* Miller (Miller, 1967), which Serbet and Rothwell (1999) proposed was a synonym of *O. cinnamomea*. The present fossil rhizome adds a new region, the northern part of Asia, to the distribution of the species in the Miocene, during which time it probably also existed in North America, as revealed by Mio-Pliocene rhizomes from Washington (Miller, 1967). This shows a trans-Pacific distribution of the species at least in the Miocene.

Yatabe *et al.* (1999) detected 7 *rbcL* nucleotide differences between *Osmunda cinnamomea* collected from Japan and United States. Estimated time of divergence between

the two accessions is 35 Myrs, which is Early Oligocene. If the molecular estimate is correct and is combined with fossil evidence, some extant populations of *Osmunda cinnamomea* in Japan and North America could possibly have been isolated from one another since the Early Oligocene or Miocene.

A similar trans-Pacific distributional pattern is supported for the subgenus *Osmunda*, because *O. shimokawaensis* is anatomically very similar to *O. wehrlii* from the Miocene of Washington (Miller, 1982).

The paleoenvironment of the Mosanru Formation has briefly been mentioned by Matsumoto (2000) on the basis of permineralized plant remains previously described from the same formation, such as *Picea*, *Abies*, *Tsuga*, *Glyptostrobus*, *Decodon*, *Alnus*, *Fagus*, and *Ostrya* (Matsumoto *et al.*, 1994, 1995; Matsumoto *et al.*, 1997a; Matsumoto *et al.*, 1997b; Matsumoto, 2000). These assemblages show dominance of temperate conifers mixed with deciduous broadleaves, and the absence of evergreen broadleaves. Some components such as *Glyptostrobus*, *Alnus*, and *Decodon* suggest a local wetland vegetation. Taphonomical studies of the plant-bearing strata also indicate a lacustrine environment (Matsumoto, 2000). The two *Osmunda* species probably grew on wetlands, as does the recent *O. cinnamomea*.

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