

Distribution of Osmundaceae

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Abstract The distributions of Osmundaceae are synthesized based on phylogenetic relationships. The distribution patterns may reflect the long evolutionary and geographic history of the family. They are divided into worldwide (in *Osmunda* subgenus *Osmunda*), eastern Asian–eastern North American (in *Osmundastrum* and *Osmunda* subgenus *Claytosmunda*), Southern Hemispheric (in *Leptopteris* and *Todea*), and Asian (in *Osmunda* subgenus *Plenasium*). *Osmunda regalis* is worldwide while the closely related *O. japonica* is eastern Asian, and both occur in the Himalayas. The eastern Asian–eastern North American pattern is seen in each of the remotely related *Osmundastrum cinnamomeum* and *Osmunda claytoniana*. The Southern Hemispheric pattern is shared by the sister genera *Leptopteris* and *Todea*, but it does not necessarily support a hypothesis for the Southern Hemispheric origin of the whole family.

Key words: Distribution, Osmundaceae, *Leptopteris*, *Osmunda*, *Osmundastrum*, *Plenasium*, *Todea*.

Introduction

Osmundaceae are a family of monilophytes that is intermediate between eusporangiate and leptosporangiate ferns, or basal in the leptosporangiate ferns, in having massive sporangia developed from one or two initials. The osmundaceous ferns appeared in the Permian or possibly in the Carboniferous, and diversified and thrived in the Mesozoic (Tidwell and Ash, 1994; Collinson, 1996; Skog, 2001). Compared to the Cretaceous or later origin of most of the higher ferns or “polypods” s. l. following the diversification of angiosperms (Schneider *et al.*, 2004), the primitive Osmundaceae are estimated by a molecular analysis to have arisen ~323 million years ago (mya), as long ago as in the Mississippian–Pennsylvanian of the Carboniferous (Pryer *et al.*, 2004). Yatabe *et al.* (1999) estimated that the family’s deepest divergence time of *Osmundastrum cinnamomeum* from the rest was 294 mya or the Late Pennsylvanian, and the divergence time of a clade of *Leptopteris* and *Todea* from *Osmunda* including *O. claytoniana* (subgenus *Claytosmunda*) was 210 or 206 mya, or the Late

Triassic (Yatabe *et al.*, 1999; Pryer *et al.*, 2004). The estimated divergence time of *Osmunda* s. s. and *Plenasium* (*Osmunda* subg. *Plenasium*) is 150 mya or the Late Jurassic (Yatabe *et al.*, 1999). Therefore, the distributions of the genera and subgenera were probably strongly influenced by the geological and climatic changes of the past 300 million years.

The family is small, comprising three extant genera (four according to recent analyses) and 15–38 species (Kramer in Kubitzki, 1990; 21 species in Hewitson, 1962). It is distributed worldwide in all major continents except for Antarctica. This paper examines its distribution ranges and patterns by synthesizing data from local floras and examining herbarium specimens. The distribution ranges of the family or part of it were illustrated by Polunin (1960) and Bovrov (1967). The distributional information will be useful to understand the phylogeny, biogeography, and evolution of the Osmundaceae.

Materials

Distribution data were obtained from examina-

tion of specimens at National Museum of Nature and Science Herbarium (TNS) and University of Tokyo Herbarium (TI), and published data in local floras and fossil data (Miller, 1967, 1971, 1982; Collinson, 2001).

Distribution of Genera

Comparison of the distributions of the genera and subgenera of Osmundaceae and classifications deducible from recent molecular phylogenetic analyses, shows that they are divided into four patterns, i. e., worldwide, eastern Asian–eastern North American, Southern Hemispheric, and Asian.

Worldwide pattern

The genus *Osmunda* has usually been treated to comprise three subgenera (Hewitson, 1962; Kramer in Kubitzki, 1990). However, Yatabe *et al.*'s (1999) molecular phylogenetic analysis revealed that the genus is paraphyletic because *Leptopteris* and *Todea* are nested in the genus (Fig. 1). The subgenera have sometimes been recognized as genera (Tagawa, 1941, 1959; Zhang, 2006). Neither subgenus- nor genus-rank classification is congruent with the molecular evidence. Yatabe *et al.* (1999) showed that *Osmunda* subgenus *Osmundastrum*, which is tradition-

ally bispecific, is also paraphyletic. In conclusion, *Osmunda* is divided into four clades, *Osmundastrum cinnamomeum*, *O.* (subgenus *Claytosmunda*) *claytoniana* (which has been assigned to subgenus *Osmundastrum*), subgenus *Osmunda*, and subgenus *Plenasium*, in addition to a clade of *Leptopteris* and *Todea* (Yatabe *et al.*, 1999, 2005). The six clades may be classified at the genus rank. The clades have characteristic distribution patterns, among which the worldwide distribution pattern is seen in subgenus *Osmunda*.

Subgenus *Osmunda* comprises three or more species. *Osmunda regalis* is distributed in Europe east to Middle East (var. *regalis*), northern Africa (whole plants have been assigned as var. *plumieri*), tropical and southern Africa, along with Madagascar and adjacent islands (var. *abyssinica*, var. *capensis*, var. *oblongifolia*, var. *transvaalensis*), southern Asia (*O. huegeliana*), and North America (var. *spectabilis*) through South America (var. *palustris*) (Fig. 2). It also occurs in the Azores and Vermuda in the Atlantic, and in Laos, which is the most eastern in Asia (Fig. 3A). Lao *O. regalis* was collected for the first time by T. Tuyama (*Tuyama L57063*, TI; but identified as *O. japonica*) in 1957, and recollected by M. Kato *et al.* in 2007. The species has been divided into several regional taxa, as shown

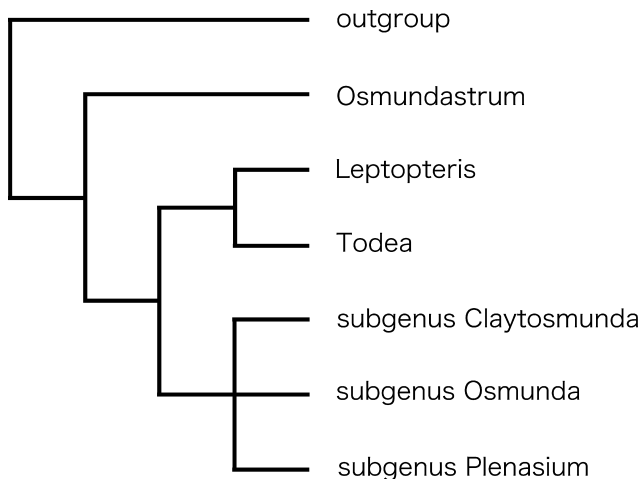


Fig. 1. Phylogenetic tree of Osmundaceae, simplified from Yatabe *et al.* (1999). *Osmundastrum* and *Osmunda* subgenus *Claytosmunda* are monotypic while the other taxa are multispecific.

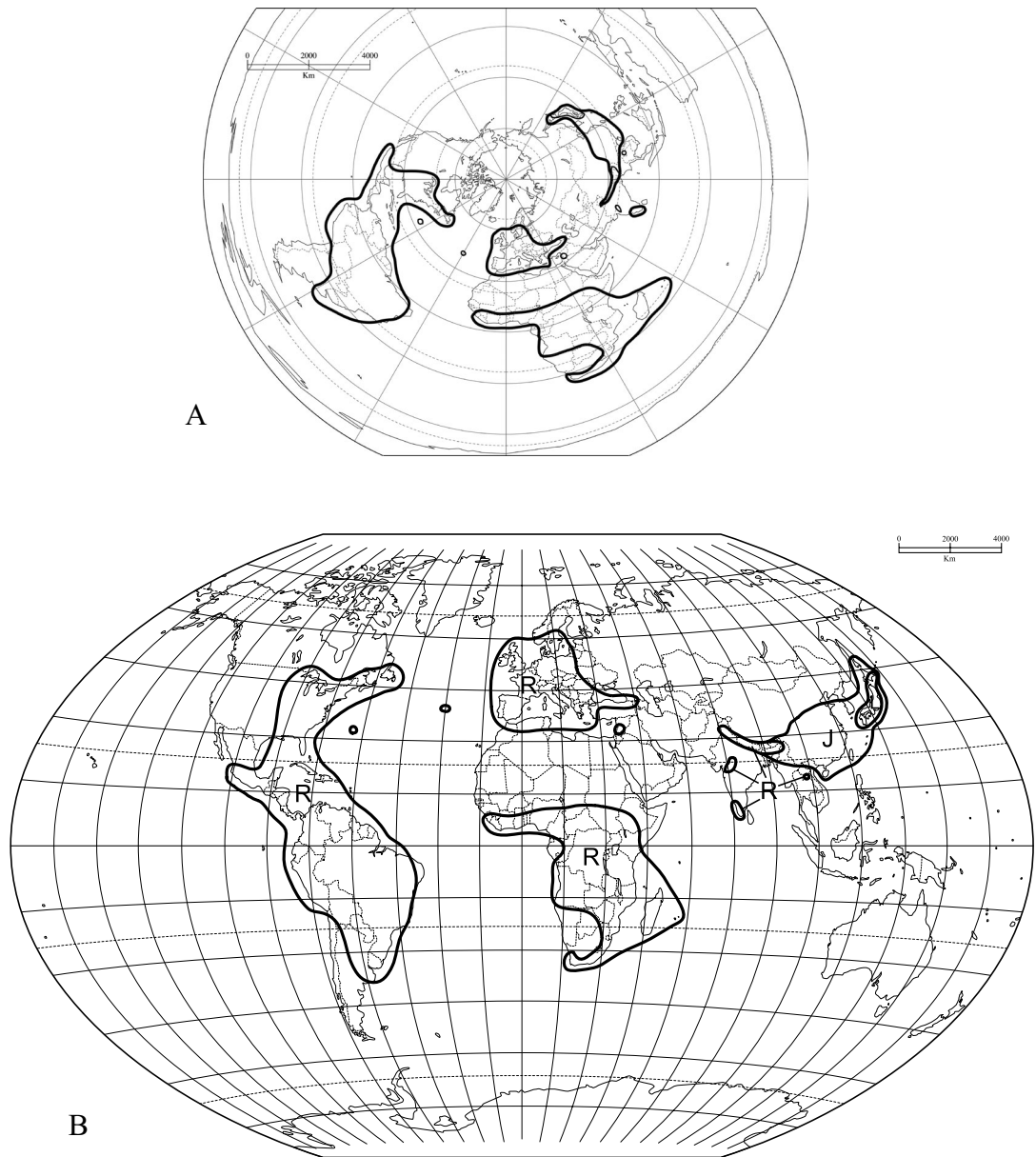


Fig. 2. Worldwide distribution ranges of *Osmunda* subgenus *Osmunda*. A. Arctic polar view. B. Equatorial view. J, *O. japonica*; L, *O. lancea*; R, *O. regalis*.

above in parentheses following the regions (Polunin, 1960; Bovrov, 1967). *Osmunda japonica* (Fig. 3B) is distributed in eastern Asia, ranging west to the Himalayas and south to northern Vietnam in southeastern Asia. It is generally allopatric to *O. regalis*, although the two are sympatric in the Himalayas and peripatric in the

northern parts (N Vietnam and Laos) of southeastern Asia. *Osmunda lancea*, an ecologically and morphologically specialized rheophyte, is endemic to Japan (Fig. 3C) (Imaichi and Kato, 1992). It should be noted that Franchet and Savatier (1877) recorded *O. regalis* with citation of a specimen (*Savatier 1608*, duplicate TI), besides



Fig. 3. Three species of *Osmunda* subgenus *Osmunda*. A. *Osmunda regalis* in Laos. B, C. *O. japonica* (B) and *O. lancea* (C) cultivated in Tsukuba Botanical Garden.

O. japonica (as variety), from around Yokosuka, Japan in their *Enumeratio Plantarum*. It may be *O. regalis* or subdimorphic *O. japonica* (see below). Further search is necessary to reveal the exact distribution ranges of the species.

Osmunda regalis and *O. japonica* have been

treated as a single species, but at the varietal rank, or as separate species (e.g. Christensen, 1906; Polunin, 1960; Bovrov, 1978; Iwatsuki, 1995). The two differ mainly in leaf dimorphism: *O. regalis* has subdimorphic leaves with the fertile distal half and the sterile proximal half, and

O. japonica has completely dimorphic leaves with separate fertile and sterile leaves. However, late-growing leaves of *O. japonica* are occasionally subdimorphic so that there is little stable distinction between the two. *Osmunda regalis* happens to show dimorphism. Available molecular data, though insufficient, may show that the two species are hardly different (Yatabe *et al.*, 1999), implying a recent separation. Their historical biogeography may differ from that of *Osmundastrum* and *Osmunda* subgenus *Claytosmunda* with partly similar distribution patterns (see below). Furthermore, the rheophilous *O. lancea* endemic to Japan does not differ from *O. japonica* at the molecular level (Yatabe *et al.*, 1999), suggesting the recent ecological speciation of the rheophyte. It might be likely that the ancestral species of *Osmunda* diversified into regional species or entities such as *O. japonica* and *O. regalis* var. *regalis*. Further analysis will unravel the evolution and speciation of the *O. regalis* complex.

East Asian–eastern North American pattern

Osmundastrum and *Osmunda* subgenus *Claytosmunda* show the disjunct distribution pattern (Fig. 1). They are characterized by having bipinnatifid leaves with oblong, adnate pinnules, by which they have been recognized as a taxonomic group (Hewitson, 1962). Both *Osmundastrum cinnamomeum* and *Osmunda* (subgenus *Claytosmunda*) *claytoniana* prefer damp grounds and occasionally grow sympatric. However, they are distinct in leaf dimorphism: the leaves are subdimorphic with contracted fertile pinnae borne in the middle in *Osmunda claytoniana*, while completely dimorphic with separate fertile and sterile leaves in *Osmundastrum cinnamomeum*. *Osmunda claytoniana* is distributed in eastern Asia and eastern North America (Fig. 4), typically representing the eastern Asian–eastern North American pattern of ferns (Li, 1954; Kato and Iwatsuki, 1983). *Osmundastrum cinnamomeum* also shows such a pattern, but it extends south to Central and South Americas (Fig. 5). It may be likely that the formerly continuous Northern Hemispheric distribution range was separated into the two distant

ranges, associated with extinction in intervening regions (e.g. western North America and far-northeastern Asia) due to climate change, particularly cooling (see also fossil data below and Fig. 6).

The eastern Asian–eastern North American populations of each of the two species have sometimes been segregated at the infraspecific rank: Asian *Osmundastrum cinnamomeum* was named as var. *fokienensis* or var. *asiatica* (Ching, 1959; Tagawa, 1959) and Asian *Osmunda claytoniana* was segregated as var. *vestita* (Wall.) Milde (Tagawa, 1941). Using molecular data, Yatabe *et al.* (1999) estimated that the divergence time is 35 mya (Eocene) and 25 mya (Oligocene) in *Osmundastrum cinnamomeum* and *Osmunda claytoniana*, respectively. In these epochs, eastern Asia and North America were dominated by more or less continuous, warm/cool and cool/cold temperate vegetations (Willis and McElwain, 2002). As fossils of *Osmundastrum cinnamomeum* are recorded from the upper Middle Miocene of Hokkaido and Miocene–Pliocene of Washington in northwestern USA (Miller, 1967; Yatabe *et al.*, 1999), where extant plants do not occur, it is likely that extinction during the Neogene caused the disjunct distribution pattern independently in the two species. Similar disjunct biogeographies are reviewed for a variety of seed plants by Donoghue *et al.* (2001), Tiffney and Manchester (2001), and Wen (2001).

Southern Hemispheric pattern

Leptopteris with ca. five species is distributed in New Zealand, eastern Australia, the southern Pacific, New Guinea, and the Moluccas (Seram Island; Kato, 1989) (Fig. 5). This fern is characterized by the thin, finely dissected leaves with superficial sori. *Todea* of two species has thick, bipinnate, monomorphic leaves with similarly superficial sori. It is disjunct in Australasia and Africa (Fig. 4). *Todea barbara* occurs in New Zealand, eastern and southeastern Australia, and disjunctly in southern Africa, while *T. papuana* Hennipm. occurs in Papua New Guinea. As suggested by comparative morphology (Hewitson,

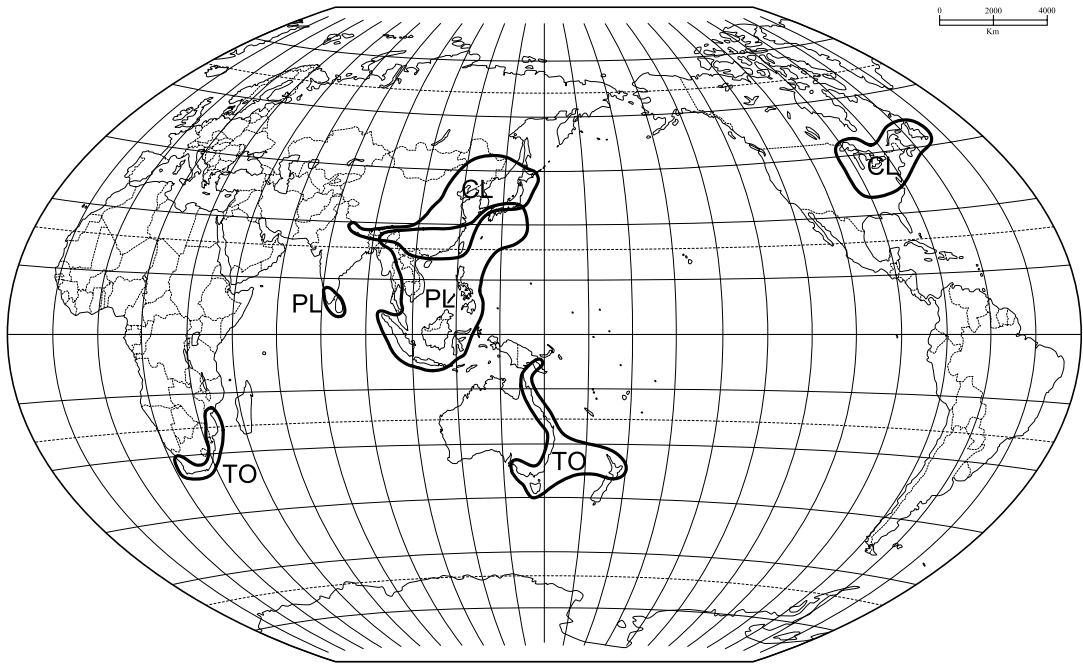


Fig. 4. Distribution ranges of *Osmunda* (subgenus *Claytonmunda*) *claytoniana* (CL), *Osmunda* subgenus *Plenasium* (PL), and *Todea* (TO).

1962), the two genera form a monophyletic clade (Fig. 1; Yatabe *et al.*, 1999). Pryer *et al.* (2004) estimated the divergence time of *Leptopteris* and *Todea* to be 206 mya, based on fossil data of *Osmundacaulis*, which is suggested to be a member of the osmundaceous crown group (Tidwell and Ash, 1994; Collinson, 1996; but see Yatabe *et al.*, 1999). In the Late Triassic and Early Jurassic (206–180 mya), the Gondwana was a supercontinent before break and drift (Willis and McElwain, 2002). There are two possibilities of historical biogeographies for *Leptopteris* and *Todea*. One is that, when the genera diverged, they occurred in continuous distribution ranges and retained the similar Southern Hemispheric distribution patterns even after land separation of Australia and New Zealand from Africa. The other is that the distributional similarity is a convergence after different histories.

Fossil data suggested the origin of the family in the Southern Hemisphere followed by migration to the Northern Hemisphere (Tidwell and Ash, 1994; Skog, 2001). However, it is inconsis-

tent with the phylogenetic relationship of the extant *Leptopteris* and *Todea*, which does not suggest that this pattern is an ancestral character state (plesiomorphic).

Asian pattern

Osmunda subgenus *Plenasium* of several species is monophyletic and characterized by the simply pinnate leaves with linear-lanceolate pinnae and remarkably contracted fertile pinnae under the middle of the leaves (Fig. 1; Hewitson, 1962; Yatabe *et al.*, 1999). It is the only member showing the tropical Asian distribution pattern among the genera and subgenera of *Osmundaceae*. It is distributed from temperate Asia (southern Japan) west to eastern Himalaya and south to middle and western Malesia (the Philippines, Malaysia and Indonesia), and also occurs in southern India and Sri Lanka (Fig. 4). This subgenus occupies southeastern Asia, where no other members are distributed. Thus, there is a distributional segregation between the subgenus *Plenasium* and all others, although the subgenus

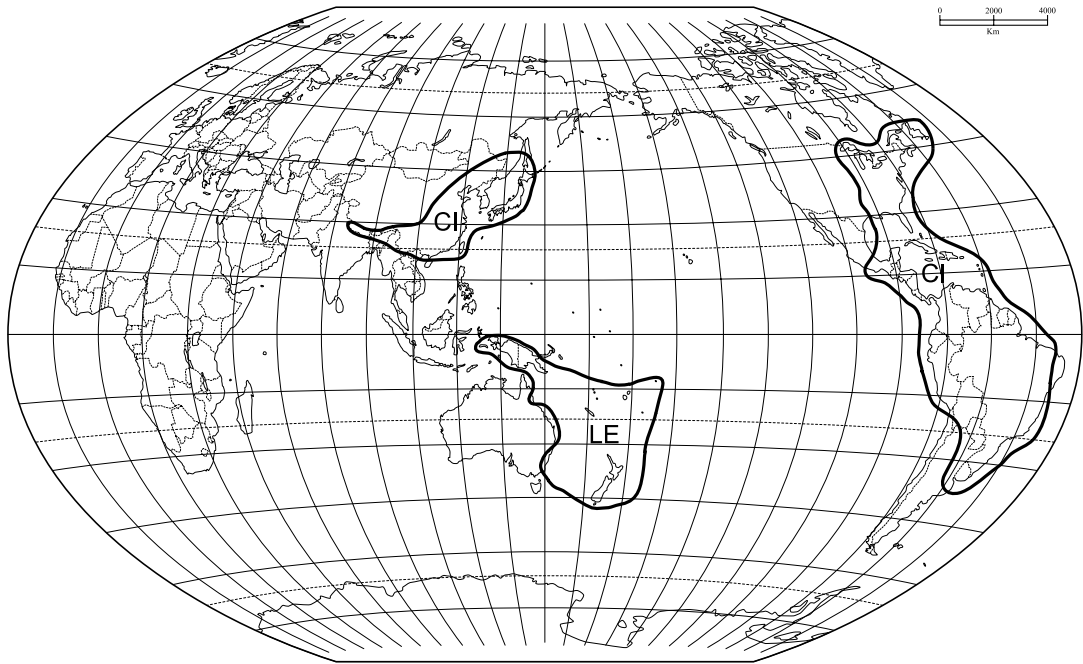


Fig. 5. Distribution ranges of *Osmundastrum cinnamomeum* (CI) and *Leptopteris* (LE).

is phylogenetically close to subgenera *Osmunda* and *Claytosmunda* (Yatabe *et al.*, 1999, 2005).

Ancient distributions

The Late Triassic *Osmunda claytoniites* is recorded from Victoria Land of Antarctica (Phipps *et al.*, 1998). Extinct genera from the Triassic to Cretaceous of various localities throughout the world including South America, western Canada, southern Africa and India, e.g. *Osmundacaulis*, formed distinct phylogenetic lineages in the family or had uncertain affinities with the extant members (Boureau [ed.], 1970; Tidwell and Ash, 1994). The distributions of permineralized stem and compressed leaf fossils assigned to *Osmunda* from a long range of the Tertiary and a few from the Cretaceous (Miller, 1967, 1971, 1982) are shown in Fig. 6. They are distributed widely in the Northern Hemisphere. *Osmunda* is characterized as a member of the Paleocene to Eocene circum-Arctic flora (Collinson, 2001; Wang *et al.*, 2006). Many of the *Osmunda* fossils are recorded outside the present range, e. g. in western and northwestern

North America, suggesting the wider distribution range of the genus or related ferns in the Cenozoic (Collinson, 2001). *In situ* osmundaceous spores were recorded since the Late Triassic (van Konijnenburg-van Cittert, 2000), but because the spore morphology does not greatly vary among the genera, it is not useful to determine the distribution of *Osmunda* or close relatives.

Conclusion and Perspective

The molecular phylogeny of extant species and fossil data imply that the four distribution patterns recognizable for the extant Osmundaceae are the result of the distributional and evolutionary changes of the family that happened in a long range of geological times from the Permian. It is noted that *Leptopteris* and *Todea* of the same clade show similar distribution patterns, possibly due to common ancestry. However, available phylogenetic and geographic data of the extant members do not necessarily support the above paleobotanical hypothesis for the Southern Hemispheric origin of the family. *Osmunda regalis* and *O. japonica*, closely related to each other, are gener-

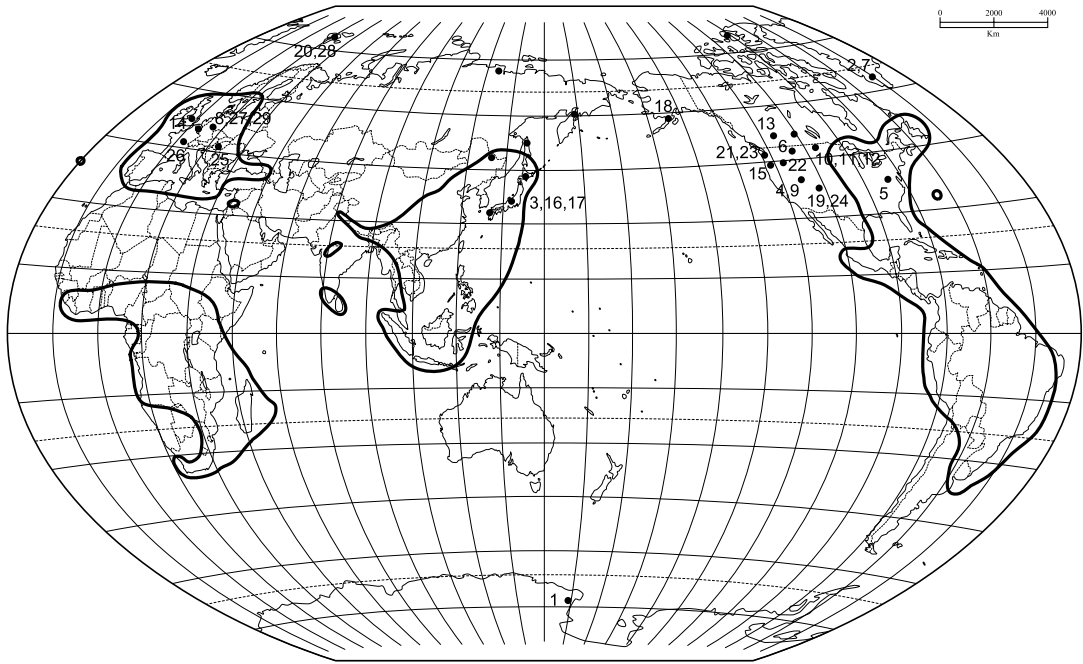


Fig. 6. Places (indicated by solid circles) where fossils assigned to *Osmunda* were collected, based on Miller (1967, 1971, 1982), Phipps *et al.* (1998), Collinson (2001), and Wang *et al.* (2006). Note that their strata are various. Places of fossils 2, 5, 7, 19, 24, and 26 are not exact. Solid lines indicate the distribution ranges of extant *Osmunda*. Figures are in order of earlier to later fossils. Permineralized fossils are marked by asterisks and compressed leaf fossils are unmarked. 1, *O. claytoniites* from Upper Triassic of Victoria Land, Antarctica; 2, *O. petiolata* from Lower Cretaceous of Greenland; 3, *O. asuwensis* from Upper Cretaceous of Japan; 4, *O. major* from Upper Cretaceous of Colorado, USA; 5, *O. delawarensis* from Upper Cretaceous of eastern USA; 6, *O. montanensis* from Upper Cretaceous of Montana, USA; 7, *O. oebergiana* from Upper Cretaceous of Greenland; 8, *O. haldemiana* from Cretaceous of Germany; 9, *O. hollicki* from Cretaceous of Colorado, USA; 10, *O. arnoldii** from Paleocene (65–54.8 mya) of North Dakota, USA; 11, *O. plumosa** from Paleocene of North Dakota, USA; 12, *O. precinnamomea** from Paleocene of North Dakota, USA; 13, *O. macrophylla* from Paleocene of Alberta, Canada; 14, *O. dowkeri** from Eocene (54.8–33.7 mya) of United Kingdom; 15, *O. oregonensis** from Eocene of Oregon, USA; 16, *O. bromeliaefolia* from Eocene of Japan; 17, *O. regalis* from Eocene of Japan; 18, *O. doroschkiana* from Oligocene (33.7–23.8 mya) of Alaska, USA; 19, *O. occidentalis* from Oligocene of western USA; 20, *O. spetsbergensis* from Upper Tertiary (Eocene?) of Spitsbergen; 21, *O. cinnamomea** from Miocene (23.8–5.3 mya) of Washington, USA; 22, *O. cf. claytoniana* from Miocene of Idaho, USA; 23, *O. wehrlii** from Miocene of Washington, USA; 24, *O. affinis* from Miocene of western USA; 25, *O. iliaensis** from Miocene–Pliocene of Hungary; 26, *O. strozzii* from Miocene–Pliocene of Europe; 27, *O. schemnicensis* from Miocene–Pliocene of Germany; 28, *O. nathorsii** from Pliocene (5.3–1.8 mya) of Spitsbergen; 29, *O. bilinica* from Pliocene of Germany.

ally allopatric, although they are sympatric in the Himalayas and peripatric in southeastern Asia. The geographical history and speciation of the species remains uncertain.

Acknowledgments

I thank A. Ebihara and Y. Yatabe-Kakugawa for useful comments to the manuscript, and director, the University of Tokyo Herbarium (TI) for allowing me to examine specimens, and K. Uemura and T. Yamada for providing copies of references. This study was in part supported by a

Grant-in-Aid for Scientific Research from the Japan Society for the Promotion of Science.

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