

Midori Matsumoto\*, Arata Momohara\*\*, Takeshi Asakawa  
Ohsawa\*\*\* and Yukio Shoya\*\*\*\* : Permineralized *Decodon*  
(Lythraceae) Seeds from the Middle Miocene of Hokkaido,  
Japan with Reference to the Biogeographic  
History of the Genus

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北海道の中部中新統産のデコドン属 (ミソハギ科)

珪化種子化石とその植物地理

**Abstract** Anatomically well-preserved permineralized seeds of a new species, *Decodon mosanruensis* sp. nov. (Lythraceae), were obtained from the late Middle Miocene Shimokawa Group, Shimokawa, central Hokkaido, Japan. Based on the seed shape and three well-developed integumentary zones, the fossil seeds were compared with fossil and extant taxa and were found to most closely resemble those of the only extant species, *Decodon verticillatus*, which is restricted to the subtropical and temperate regions of eastern North America. A cladistic analysis using seven seed characters of the fossil and living representatives of *Decodon* indicate that *D. mosanruensis* is most closely related to the extant *D. verticillatus*. The occurrence of *D. mosanruensis* in lacustrine sediments, together with *Glyptostrobus*, *Alnus*, *Osmunda*, and plants commonly growing in mesic habitats, provides compelling evidence that this species grew in wetlands associated with a lake and represents part of a fairly autochthonous flora. Based on the distribution patterns of fossil representatives of the genus, it appears that *Decodon* migrated from western North America into Europe via the more southern North Atlantic Thulian route sometime prior to late Eocene. By Oligocene, the genus had become widely distributed throughout eastern Siberia. It appears that *D. mosanruensis* probably evolved from the North American population and migrated into northern Japan through Beringian Corridor sometime prior to the Miocene.

**Key Words** : Biogeography, *Decodon mosanruensis*, Hokkaido, Late Middle Miocene, Permineralized seed

**要 旨** 北海道中部下川町の下川層群(中部中新統上部)から産出した珪化種子化石の内部構造を観察した。この珪化種子は、よく発達した3層の珠皮を持つことから、現在北米東部に1種類だけが分布するデコドン属(ミソハギ科)に同定され、新種 *Decodon mosanruensis* として記載された。他のデコドン属の化石種子や現生種の種子とともに、7つの形質を使って系統解析を行った結果、現生種の *Decodon verticillatus* に最も近縁であることがわかった。湖沼堆積物でスイショウ属、ハンノキ属、ゼンマイ属といった水湿地の植物とともに化石が産出することから、*D. mosanruensis* は湖の縁辺の湿地に生育していたと考えられる。化石記録から見てみると、北大西洋のチュリアンルートを通してデコドン属は始新世後期までに北米西部からヨーロッパへと分布が移動し、漸新世から中新世にかけて東シベリアまで分布が広がった。*D. mosanruensis* は北米西部の種から分化してベーリング陸橋を通じて北日本に分布を拡大してきたと考えられる。

キーワード：珪化種子、生物地理、中期中新世後期、デコドン・モサンルエンシス、北海道

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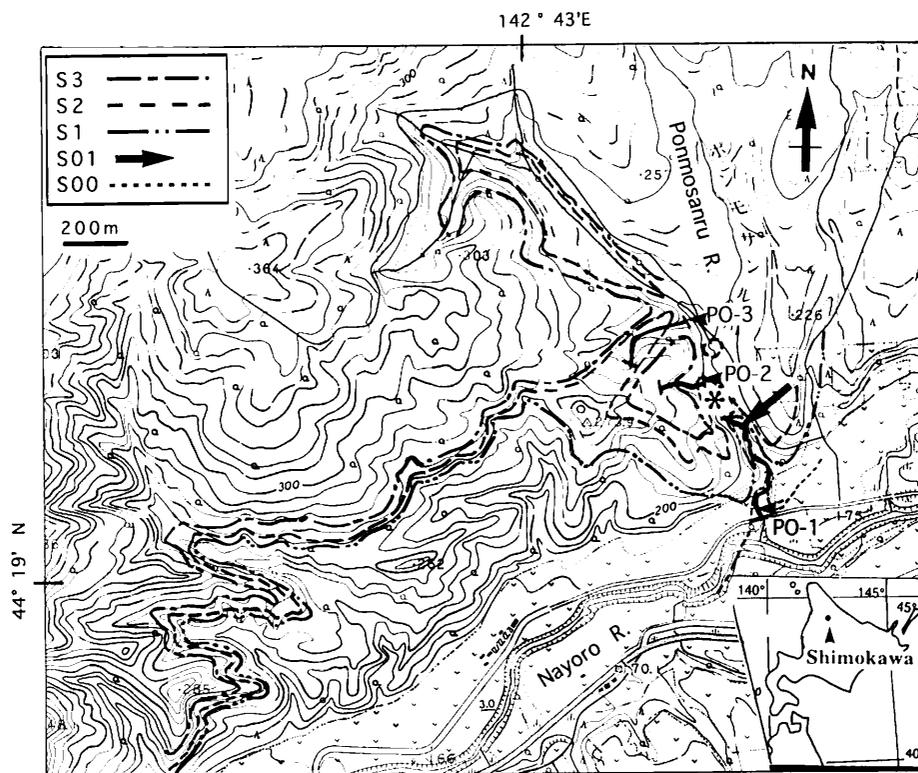
### Introduction

Permineralized fossil plants previously described from the late Middle Miocene Shimokawa Group deposits in Shimokawa Town, central Hokkaido, Japan include leaves of *Picea* Dietrich (Matsumoto *et al.*, 1994) and *Tsuga* (Endlicher) Carrière (Matsumoto *et al.*, 1995), and fertile and vegetative organs of *Glyptostrobus* Endlicher (Matsumoto *et al.*, 1997). In addition to these conifers silicified stems, seeds, flowers, leaves and wood of a number of undescribed angiosperm taxa have been collected.

The genus *Decodon* is monotypic, consists of *D. verticillatus* (L.) Ell., and is distributed from Ontario to central Florida, U.S.A. in eastern North America (Britton & Brown, 1970 ; Manchester, 1994). It occurs as a submerged aquatic plant in swamps and rivers where climate is subtropical and temperate. In contrast to the narrow range of distribution seen today, fossil *Decodon* was widely distributed through-

out the northern hemisphere during the Tertiary (Tiffney, 1981).

Fossil remains of *Decodon* have been recovered from Middle Eocene to Pliocene deposits throughout Eurasia and western North America (Sahni, 1943; Chandler, 1960, 1963 ; Dorofeev, 1963, 1968, 1969, 1972, 1977 ; Graham & Graham, 1971 ; Eyde, 1972 ; Wolfe & Tanai, 1980 ; Tiffney, 1981 ; Cevallos-Ferriz & Stockey, 1988 ; Manchester, 1994). However, in almost every case these reports are based on compression fossils, and details of their anatomy are unknown. The only anatomical preserved fossils are those of *Decodon allenbyensis* Cevallos-Ferriz et Stockey (1988) from the Middle Eocene Princeton chert of southern British Columbia, Canada (Cevallos-Ferriz & Stockey, 1988). The *Decodon* fossils from Hokkaido are significant, for they are the first anatomically preserved angiosperm seeds described from the Tertiary of Japan and provide additional data on the



**Fig. 1** The study site in Shimokawa Town. Broken lines and arrow showing the distribution of silicified mudstones and solid lines showing the locations of columnar sections PO-1, PO-2 and PO-3 shown in Fig. 2. Asterisk showing Itoge-no-taki (locality PO-1) where the plant megafossils were collected. Map modified from the Shimokawa topographical map published by Geographical Survey Institute, Ministry of Construction of Japan.

evolution and biogeographic history of the genus.

### Geology of the study area

The study area is located near the town of Shimokawa, about 15 km east of Nayoro City, Kamikawa District, central Hokkaido, Japan (Fig. 1). Geology of the area has been studied by Sako & Osanai (1955), Sako *et al.* (1960), Suzuki & Matsui (1975) and Yamaguchi *et al.* (1990).

Sediments of the Shimokawa Group rest unconformably on the pre-Tertiary Hidaka Group and are unconformably overlain by Pliocene and Quaternary sedimentary or volcanic deposits. The Shimokawa Group covers an area approximately 600 km<sup>2</sup>, and reaches a thickness of 500–600 m. In the eastern part of Shimokawa Town where the fossiliferous *Decodon* bearing beds occur, the Shimokawa Group is divided into three units: the basal volcanics, the Mosanru Formation, and the upper volcanics, in the ascending order. The basal volcanics are about 60 m thick and consist of welded tuffs and pyroclastic flows. The Mosanru Formation consists of about 200 m of interbedded conglomerate, sandstone, tuffaceous mudstone, and volcanic fall and flow deposits. The geographic extent of the Mosanru Formation corresponds roughly to a low-gravity area Bouguer anomaly (Yamaguchi *et al.*, 1990) and indicates that the mudstone represents lacustrine deposits in a lake (Matsumoto *et al.*, 1997). The tuffaceous mudstone is regionally silicified, hydrothermal altered, and contains well-preserved permineralized fossil plants. The uppermost 300 m of rock is rhyolitic and belongs to the upper volcanics. A similar stratigraphic succession occurs in the southern and western parts of Shimokawa Town (Sako & Osanai, 1955; Sako *et al.*, 1960; Suzuki & Matsui, 1975).

Radiometric ages based on fission track and K-Ar analyses of the basal volcanics provide an age range of 11 and 13 Ma, while those of upper volcanics range from 10 and 12 Ma (Matsumoto *et al.*, 1997). These data indicate that the Mosanru Formation was deposited during the late Middle Miocene.

### Occurrence and taphonomy of plant fossils

Five silicified mudstone layers (S00, S01, S1, S2 and S3) and two agate mudstone layers (A1 and A2) are

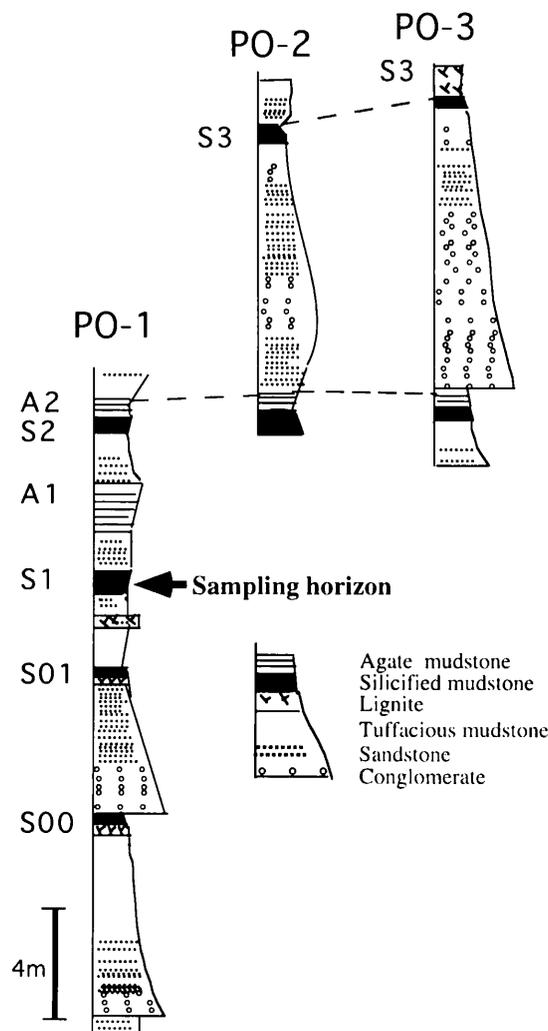


Fig. 2 Columnar sections of the lacustrine deposits in the Mosanru Formation showing the horizon where the plant fossils were collected S00–S3: silicified tuffaceous mudstone layers. A1 and A2: agatized mudstone layers.

observed at localities PO-1, PO-2 and PO-3 (Figs. 1, 2). The silicified layers are 0.3–2 m thick and extend laterally over 4.5 km (Fig. 1). The S1 layer consists largely of chalcedonic quartz-replaced mudstone and includes abundant anatomically well-preserved plant remains (Figs. 4A, B). The fossil *Decodon* seeds were collected from this layer which occurs in the middle part of the Mosanru Formation and crops out at Itoge-no-taki, a small waterfall on the Ponmosanru River (also called Rubeno Sawa in Matsumoto *et al.*, 1994, 1995), a tributary of the Nayoro River in the eastern part of Shimokawa Town (PO-1 in Figs. 1–3). In this area the Mosanru Formation consists of mainly

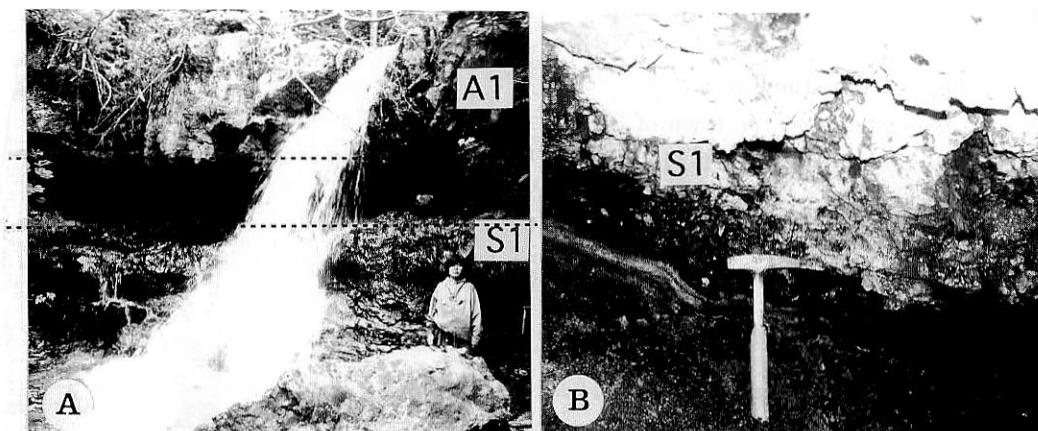


Fig. 3 Study site at PO-1, Itoge-no-taki

A : silicified layers A1 and S1. B : bottom of the silicified mudstone layer S1.

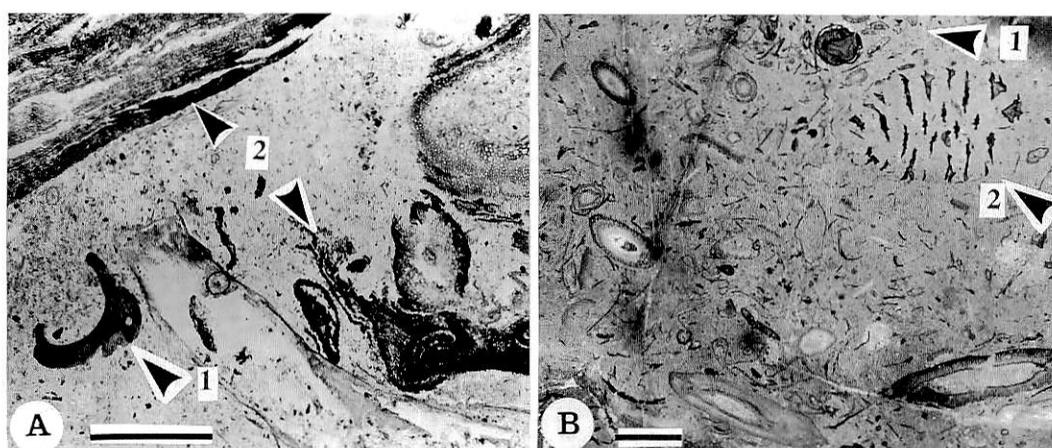


Fig. 4 Thin sections of *Decodon mosanruensis* sp. nov. seeds

A : *D. mosanruensis* (arrow 1) associated with *Osmunda* rhizomes (arrow 2) from the S1 layer (No.940814O). B : *D. mosanruensis* (arrow 1) associated with an *Alnus* cone (arrow 2) from the S1 layer (No.950714F). Scale bars : A=1 mm, B=1 cm.

lacustrine sediments which are often silicified or agatized and includes cycles of upward fining sequences beginning with a conglomerate that is capped with massive tuffaceous mudstone (Fig. 2). Layers S00, S01, S2, and S3 contain many compressed plant fragments, but their anatomical features are not preserved. The agatized mudstone layers, A1 and A2, occur in the upper part of the upward fining sequences and contain only pollen grains and spores. The grain size of these mudstones is very fine, indicating that they were probably deposited as topmost supernatant in slightly deep water.

*Decodon* seeds occur together with the fertile and vegetative remains of *Glyptostrobus rubenosawaensis*

Matsumoto, Ohsawa, Nishida & Nishida, *Osmunda* L. rhizomes, and *Alnus* P. Miller infructescens (Matsumoto *et al.*, 1997; Fig. 4). These fossils show little distortion and no apparent decomposition. Based on the large number of fossils, lack of abrasion, and apparent nature of the *Osmunda* rhizomes, we suggest that this fossil assemblage is relatively autochthonous and represents the flora growing in and around a lake.

Microscopic observations of thin-sectioned rocks show the textures of the well-preserved plant fragments. Numerous quartz network veins surround the plant fragments keeping their structure (Matsumoto *et al.*, 1997). The lack of decomposition and deformation of tissues at the cellular level indicates that

the plant remains were rapidly permineralized in volcanically heated silica-rich water.

### Material and methods

The fossil *Decodon* seeds were obtained from four rock samples (No. 903001, 903005, 94081405, and 950714) that were collected from the S1 layer, locality PO-1 by Mr. Isekichi Nakauchi and the authors from the Ponmosanru River riverbed (Figs. 1-3). The rocks were very fossiliferous, containing more than fifty small dispersed seeds of *Decodon* each. The rocks were cut into slabs about 2 cm thick and were studied using the cellulose acetate peel technique as modified for silicifications using hydrofluoric acid (Joy *et al.*, 1956; Basinge & Rothwell, 1977; Basinger, 1981). The peels were mounted in Canada Balsam for light microscopy.

Seeds of the extant species, *D. verticillatus*, were provided by Dr. B. H. Tiffney which he obtained from herbarium specimens of the L. H. Bailey Herbarium, Cornell University, U.S.A., Dr. Hideaki Ohba, The University Museum, University of Tokyo, Japan, and Dr. Barbara Ertter, Herbarium, University of California, U.S.A. The seeds were air dried, embedded in paraffine, and sectioned with a rotary microtome to 12-20  $\mu\text{m}$ . All specimens are housed in the Laboratory of Paleontology, Department of Earth Sciences, Faculty of Science, Chiba University.

### Systematic treatment

Class : Dicotyledoneae

Order : Myrtales

Family : Lythraceae

Genus : *Decodon* Gmelin, J. F., 1823

Species : *Decodon mosanruensis* Matsumoto,  
Momohara, Ohsawa & Shoya sp. nov.

Holotype. Specimen No. 94081405S-1 (Figs. 6A, C, D)

Paratypes. Specimens No. 94081405A-1 (Figs. 6B, 7A),  
94081405O-1 (Fig. 7C), 94081405S-7 (Figs. 9A,  
B), 950714B-1 (Fig. 9E)

Horizon. Layer S1, Mosanru Formation, Shimokawa  
Group, late Middle Miocene

Locality. PO-1 in the riverbed of the Ponmosanru  
River, Shimokawa Town, Kamikawa District,  
central Hokkaido, Japan

Depository. Laboratory of Paleontology, Department

of Earth Sciences, Faculty of Science, Chiba  
University

Diagnosis. Seeds anatropous, wingless, ob-pyramidal, corners slightly angular, outer surface slightly rugose in cross section (Figs. 5A, 6, 7, 9). Micropylar end narrow; chalazal end broader in longitudinal section (Figs. 5B, 8). Integument composed of three zones; outer zone of the integument consisting of rectangular cells, 8-10  $\mu\text{m}$  in diameter, thick walled and occluded with dark contents (Figs. 6B, 9C); middle zone of the integument, multilayered isodiametric cells with fine pits, 15-20  $\mu\text{m}$  in diameter (Figs. 6B, 9A, C, E); inner zone of the integument, thicker than outer zone of the integument, three to five layers of thick fibrous cells with crystalline contents and helical thickenings (Fig. 9E, arrow). Ventral germination valve with rugose

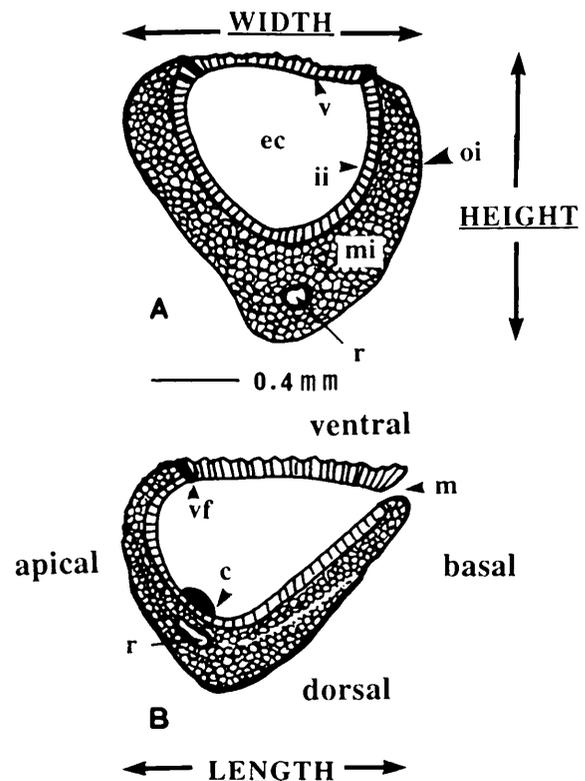
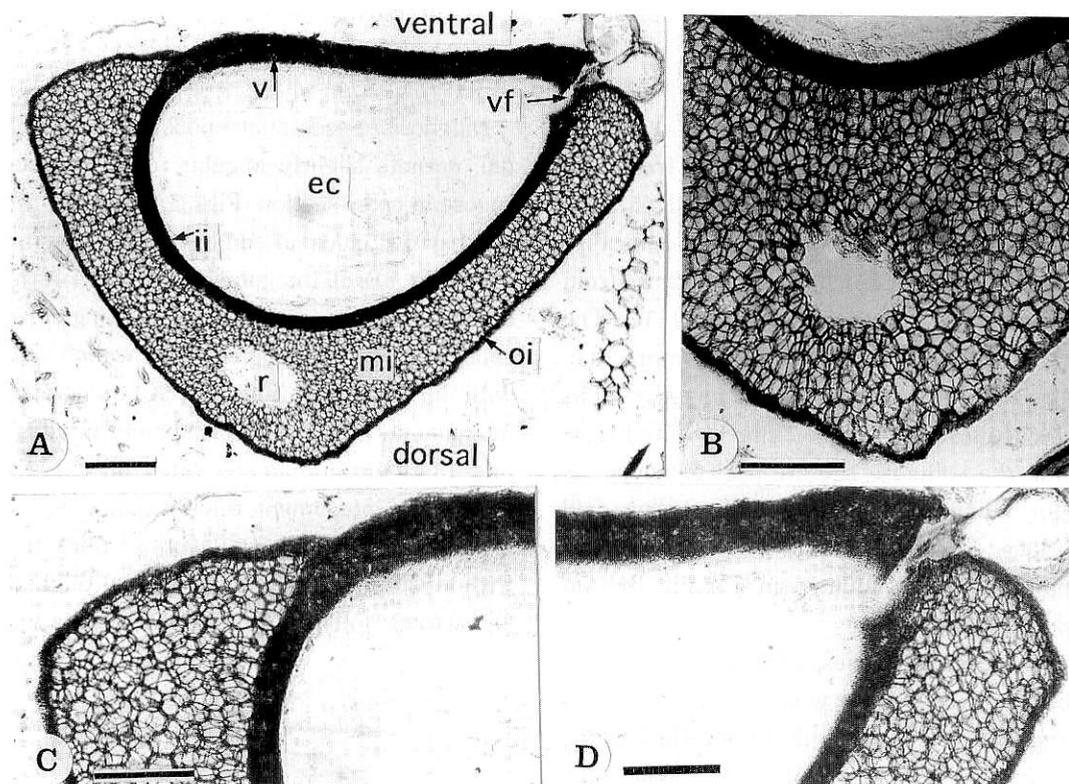


Fig. 5 Generalized cross section of a *Decodon mosanruensis* sp. nov. seed

A : Cross section. B : Longitudinal section.  
c : chalaza. ec : embryo cavity. ii : inner zone  
of the integument. m : micropyle. mi : middle  
zone of integument. oi : outer zone of integu-  
ment. r : raphe. v : germination valve. vf :  
valve flexure.



**Fig. 6** Cross sections of *Decodon mosanruensis* sp. nov. seeds (A, C and D : No.94081405S-1, B : No. 94051405A-1)

A : Cross section of seed showing the integumentary zones (ii, mi, oi), embryo cavity (ec), raphe (r), germination valve (v), and valve flexure (vf). B : Seed showing raphe and three zones of integument. C and D : Enlargement of A, showing outer and inner zones of integuments. Abbreviations are same as those listed in Fig. 5. Scale bars : A=200  $\mu$ m, B-D=100  $\mu$ m.

ventral face, composed of elongate, rectangular, thick-walled cells similar to those of outer zone of the integument (Figs. 5A, B, 9A, B). Raphe running through middle integument (Figs. 5B, 8B).

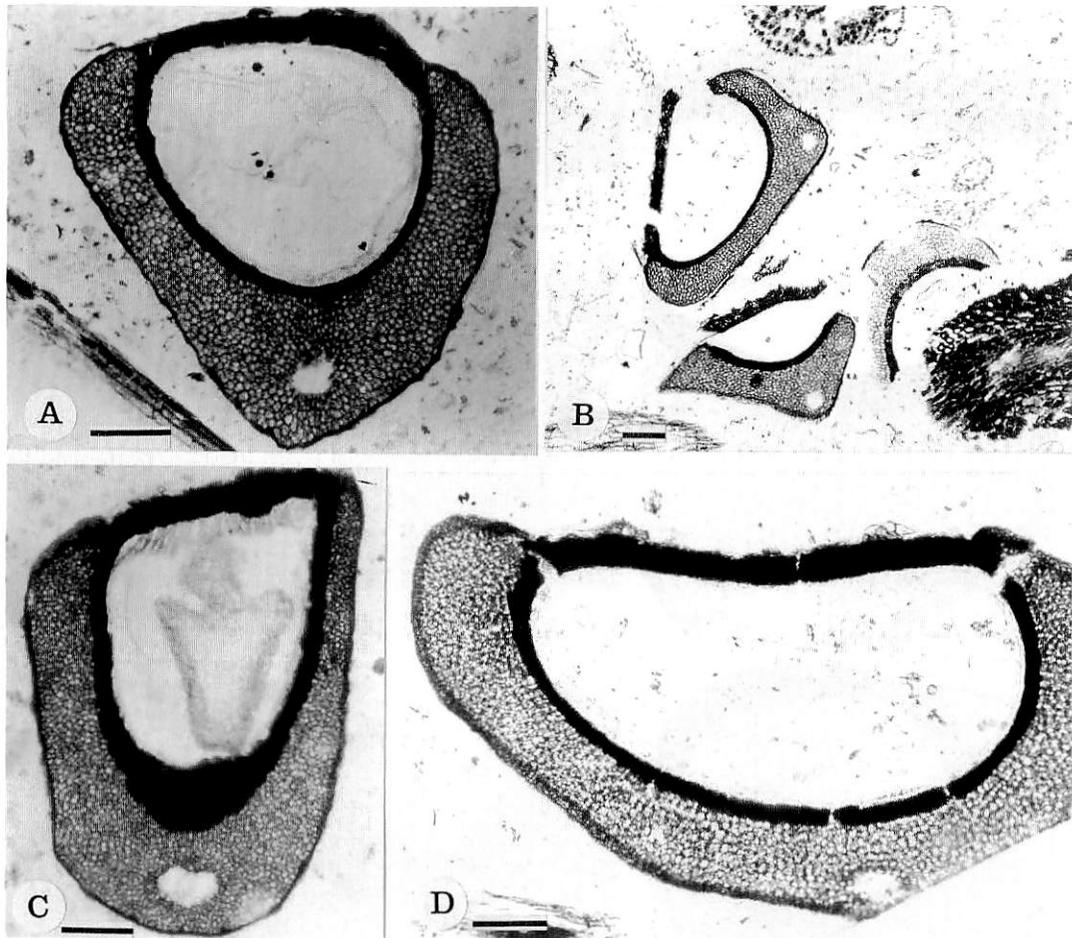
**Description.** The anatropous seeds are ob-pyramidal in shape, possess angular to slightly rounded corners, and lack lateral wings. In cross section, the seeds are triangular to elliptic in shape (Figs. 7A-D). The seeds are 1.0-(1.2)-1.5 mm high, 0.9-(1.0)-1.4 mm wide (Figs. 5A, 6, 7). In longitudinal section, the seeds are 1.0-(1.3)-1.7 mm long and ob-pyramidal with the chalazal and being rounder than the micropylar end (Figs. 5B, 8).

The raphe bundle is circular to elliptic, 100-200  $\mu$ m in diameter, and is situated near the center of the middle zone of integument in cross section (Figs. 5A, 6A, B). The endosperm, nucellus, hypostases, and embryo are not preserved. All that remains is a black substance at the chalazal end of the embryo

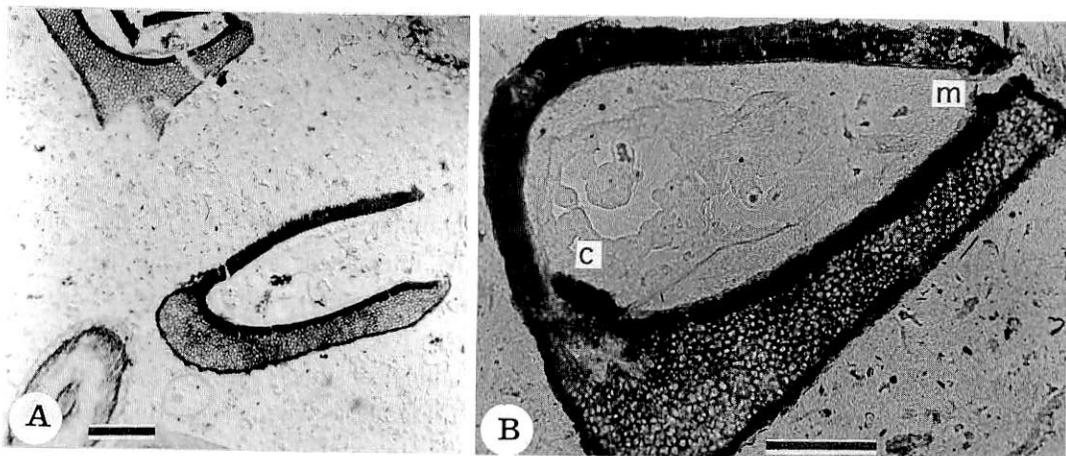
cavity (Figs. 8B, 9C). The shape of the embryo cavity varies from circular to elliptic, except in the region where the germination valve occurs in cross section. Here the embryo cavity is more flattened and is framed by the germination valve (Figs. 5A, 6A, 7A-D).

The germination valve ranges from 40-80  $\mu$ m in thickness and occupies less than three quarters of the width of the ventral face of the seed (Figs. 6A, 7). The outer surface of the valve is marked by ten to fifteen longitudinal ridges (Figs. 9A, B). At maturity, the valve separates along the valve flexure (Figs. 6A, 7B, D, 8A). The surface of the valve on the ventral face of the seed is commonly slightly convex ; 70% of the seeds were convex (Fig. 7A), 8% were concave (Fig. 7D), and 6% were straight (Fig. 6A). The micropyle is visible near the tip of the germination valve in longitudinal section (Figs. 5B, 8B).

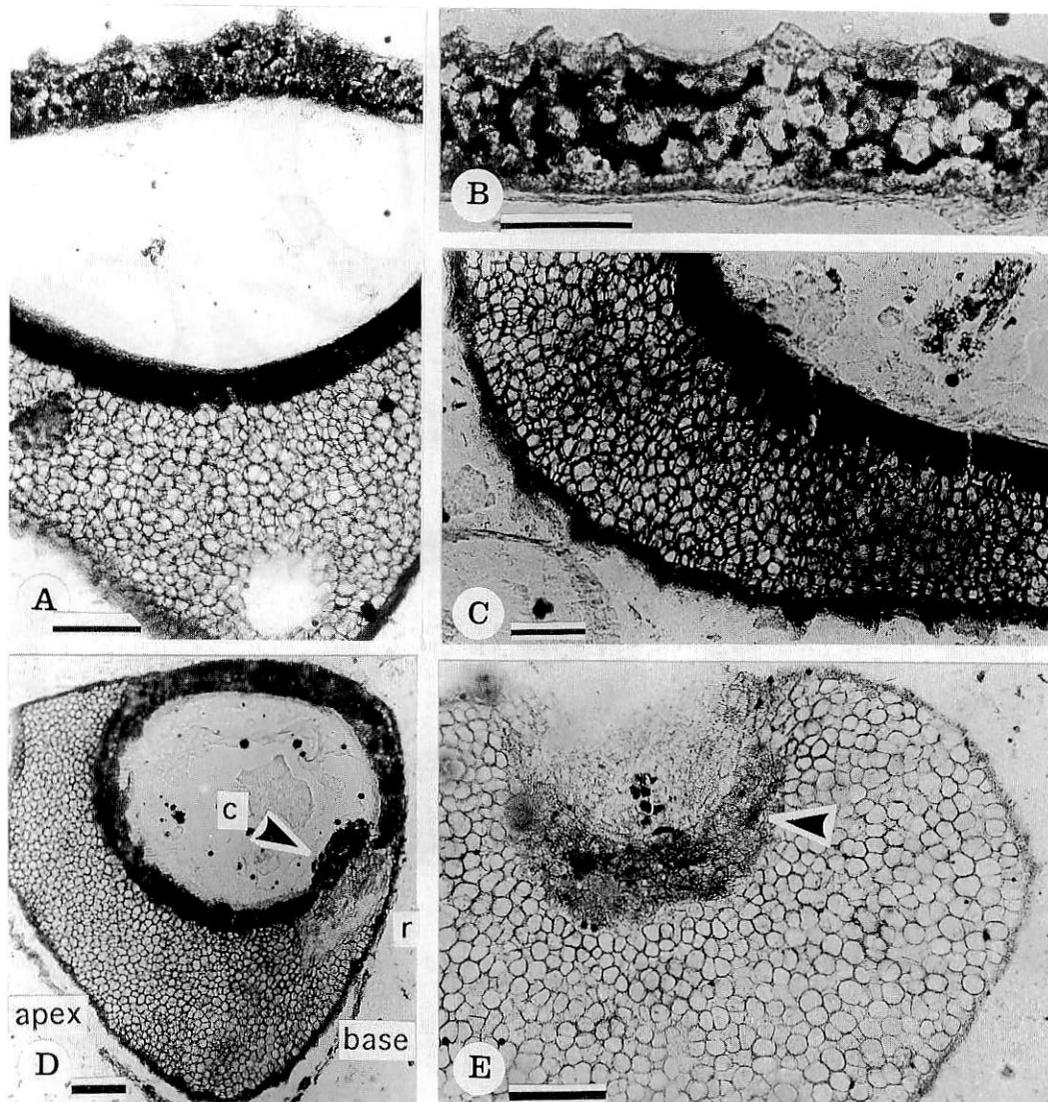
With the exception of the germination valve, the



**Fig. 7** Cross sections of *Decodon mosanruensis* sp. nov. seeds showing their variation in size and shape  
 A : No.94081405A-2. B : No.94080405S-2,3,4. C : No.94081405O-1. D : No.94081405O-2.  
 Scale bars : A, C, D=50  $\mu$ m, B=200  $\mu$ m.



**Fig. 8** Longitudinal sections of *Decodon mosanruensis* sp. nov. seeds  
 A : No.94081405S-5. B : No.94081405S-6. m : micropyle. c : chalaza. Scale bars : A, B=50  $\mu$ m.



**Fig. 9** Cross sections of *Decodon mosanruensis* sp. nov. seeds  
 A and B : Ventral face of the seed showing the rugose surface of germination valve (No. 94081405S-7). C : Dorsal face of the seed showing the slightly rugose surface of the outer zone of integument (No.94081405A-3). D : Seed showing the chalaza (c) attached to raphal bundle (No.94081405A-4). E : Seed showing the thick walled cells of the inner zone of integument (arrow head) (No.950714B-1). Scale bars: A, D, E=100  $\mu$ m, B, C=50  $\mu$ m.

integument can be divided into three tissue zones (Fig. 6). The outer zone of the integument is 10-15  $\mu$ m thick and consists of a single layer of more or less elongate epidermal cells that are up to 10  $\mu$ m long and 8  $\mu$ m wide and contain a dark substance (Figs. 6B, 9C). The outer zone of the integument is connected to the inner one near the germination valve. The middle zone of the integument on the dorsal and lateral faces of the seed are 200-300  $\mu$ m thick and composed of finely pitted, isodiametric cells that are between 15-20

$\mu$ m in diameter (Figs. 6B, 9A, C, E). The inner zone of the integument surrounding the embryo cavity ranges from 40-80  $\mu$ m in thickness and composed of three to five layers of polygonal cells that contain a crystalline substance and possess helically-thickened walls (Fig. 9E). The germination valve is composed of elongate rectangular thick-walled cells that are 15-20  $\mu$ m in diameter and resemble those of the outer zone of integument (Fig. 9B).

**Etymology.** The specific epithet is based on the

name of the Mosanru River, the type locality of the Mosanru Formation (Sako & Osanai, 1955).

### Affinities and Discussion

#### Comparison with extant families and genus

In general, the morphology of our seeds resembles that seen in Combretaceae, Lythraceae, Onagraceae, Punicaceae, Sonneratiaceae, and Trapaceae in possession of three well-developed integument zones (Cevallos-Ferriz & Stockey, 1988). Our specimens possess a middle zone of integument that is composed of well-developed isodiametric cells and can be distinguished from seeds of Onagraceae which possess an aerenchymatous middle zone that becomes crushed at maturity (Cevallos-Ferriz & Stockey, 1988). Combretaceae possesses seeds that have a middle integumentary layer composed of thin-walled cells, with scattered sclerotic cells, and in some cases spiral or annual thickenings and cannot be confused with our seeds. The presence of a watery, translucent sarcotesta in Punicaceae precludes any relationship with our fossil seeds. The inner zone of the integument of Sonneratiaceae is composed of pitted lignified fibers, instead of the helically thickened fibers seen in our material. Representatives of Trapaceae possess a multicellular outer zone of integument which differs significantly from the single layer seen in our samples. Consequently, through the process of elimination and comparison with extant and fossil representatives, our fossil appears to be closely related to Lythraceae.

Koehne (1903) divided Lythraceae into two tribes: Lythraceae which possess an incomplete fruit septa and Nesaeae which possess a complete fruit septa. Nesaeae is further divided into two subtribes based mainly on the development of wings on the seed. Those that are wingless are assigned to Nesaeinae, while those that are winged are assigned to Lagerstroemiinae. The extant genera, *Crenea* Aubl., *Nesaea* Comm., *Heimia* Link et Otto, *Decodon*, *Grislea* L., *Adenaria* H. B. K., *Tetrulaxis* Hook., and *Ginoria* Jacq., have wingless seeds and are included in subtribe Nesaeinae (Cevallos-Ferriz & Stockey, 1988). Our fossil seeds fall into wingless Nesaeinae and resemble the ob-pyramidal to ellipsoid seeds of *Decodon* and *Heimia*. However, it is unlikely that our material has affinity with *Heimia* because for the seeds of this

genus are only 0.8 mm long and remain significantly smaller than the 1.0-1.7 mm long seeds of our fossil specimens.

#### Comparison with fossil and extant *Decodon*

Thirteen fossil species of *Decodon* are described based on compressions of dispersed seeds (Dorofeev, 1977; Tiffney, 1981; Manchester, 1994), one record is based on anatomically preserved fruits and seeds (Cevallos-Ferriz & Stockey, 1988), and another is represented by an impression of a fossil leaf (Wolfe & Tanai, 1980).

Dorofeev (1977) classified the fossil and extant species of *Decodon* into three groups using general morphological features. These groups are (1) *D. gibbosus* group, (2) *D. globosus* group, and (3) *D. vectensis* group. Seeds of the *D. gibbosus* group have rounded edges, well-developed spongy tissue on the dorsal side, and narrow ventral faces. Those of the *D. globosus* group possess rounded edges, poorly developed dorsal tissues, and broad ventral faces with wide germination valves. In the *D. vectensis* group the seeds are sharply angled and have poorly developed dorsal tissues and narrow ventral faces with wide germination valves.

Tiffney (1981) refined Dorofeev's classification by recognizing that the thickness of the inner and outer zones of the integument are an important diagnostic feature of the genus. Using these criteria Tiffney found that the *D. gibbosus* and *D. globosus* groups have a thicker outer zone of the integuments than the inner ones, while the *D. vectensis* group, *D. allenbyensis* and extant *D. verticillatus* have a thin outer zone of the integuments and thick inner integuments. The seeds of *D. mosanruensis* possess a thin outer zone of the integuments and naturally fall into the *D. vectensis* group, even though the middle zone of the integument is narrower and better developed than that seen in *D. vectensis*.

In order to confirm the relationships that were beginning to emerge among these species of *Decodon*, a phylogenetic analysis of seven of the seed characters was performed using PAUP Macintosh 3.1.1 (Tables 1, 2; Swofford, 1993). In addition to *D. mosanruensis* we chose five additional species of *Decodon* that include *D. gibbosus*, *D. globosus*, *D. vectensis*, *D. allenbyensis*

and *D. verticillatus*. *Lythrum salicaria* L.(Lythraceae) was chosen as an outgroup. Cladograms were calculated with the furthest addition sequence method (Tables 1, 2; Fig. 10). The most parsimonious tree has a length of 9, consistency index of 0.714, and a retention index of 0.800 (Fig. 10). This tree shows *D. gibbosus* occurring basal to all other representatives used in the analysis. *Decodon mosanruensis* occurs as a polytomy with the Eocene species, *Decodon allenbyensis*, and the living specie, *D. verticillatus*.

#### Habitat of *Decodon mosanruensis*

Living *Decodon verticillatus* requires high-humidity levels and commonly grows in and around lakes, swamps, and rivers (Britton & Brown 1970; Manchester, 1994), and it is assumed that *Decodon mosanruensis* grew under a similar climatic regime and habitat. The polygonal cells in the middle zone of the integument are presumed to have aided in flotation and dispersal in an aquatic environment. The abundant and well-preserved seeds from our fossil locality indicates that the plants grew close or at the site of deposition, even if fossil fruits have not yet been recognized (Fig. 7B). The absence of germination in some of the seeds recovered indicates that they were deposited after the seeds had germinated (Fig. 7B).

The plants so far recognized and associated with *Decodon mosanruensis* include *Picea*, *Tsuga*, *Glyptostrobus*, *Alnus* and *Osmunda* (Matsumoto *et al.*, 1994, 1995, 1997). Among these, *Osmunda* is presumed to have grown together with *Decodon* because the *Osmunda* rhizomes frequently occur together with *Decodon* (Fig. 4A). *Glyptostrobus* would have presumably been part of the canopy forest in the lowlands near the lake. *Picea* and *Tsuga* were probably growing in the uplands surrounding the lake; their cones and leaves show signs of transport. A generalized model of the paleovegetation and setting is presented in Figure 11.

#### Biogeography of *Decodon*

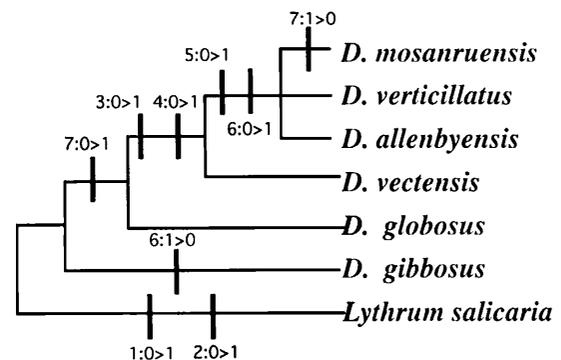
Fifteen species of *Decodon* have been described as occurring between the Middle Eocene and Pliocene (Wolfe & Tanai, 1980; Tiffney, 1981; Cevallos-Ferriz & Stockey, 1988). The earliest occurrence of *Decodon* is that of *D. allenbyensis* from the Middle

**Table 1** Characters used in phylogenetic analysis of fossil and living *Decodon* seeds

1	average seed length
	0=less than 1.0mm, 1=more than 1.0mm
2	shape of seed in outline
	0=obvoid, 1=ob-pyramidal
3	thickness of outer and inner zones of integument
	0=outer is thicker than inner, 1=outer is thinner than inner
4	angle of outline at ventral face in cross section
	0=rounded, 1=angular
5	valve width
	0=wide, 1=narrow
6	thickness of middle zone of integument
	0=weak developed, 1=well developed
7	valve shape
	0=convex, 1=concave

**Table 2** Character state distribution of the seeds of *Decodon* and the outgroup *Lythrum*

Species	Character numbers						
	1	2	3	4	5	6	7
<i>Decodon mosanruensis</i>	1	1	1	1	1	1	0
<i>D. allenbyensis</i>	1	1	1	1	1	1	1
<i>D. gibbosus</i>	1	1	0	0	0	1	0
<i>D. globosus</i>	1	1	0	0	0	0	1
<i>D. vectensis</i>	1	1	1	1	0	0	1
<i>D. verticillatus</i>	1	1	1	1	1	1	1
<i>Lythrum salicaria</i>	0	0	0	0	0	0	0



**Fig. 10** Most parsimonious cladogram generated on the basis of seven seed characters of fossil and living species of *Decodon*. All character states are unambiguously rearranged. Characters and character states are provided in Tables 1 and 2.

Eocene Princeton chert from southern British Columbia, Canada (Cevallos-Ferriz & Stockey, 1988) and *D.* sp. from the Middle Eocene Clarno nut beds in Oregon

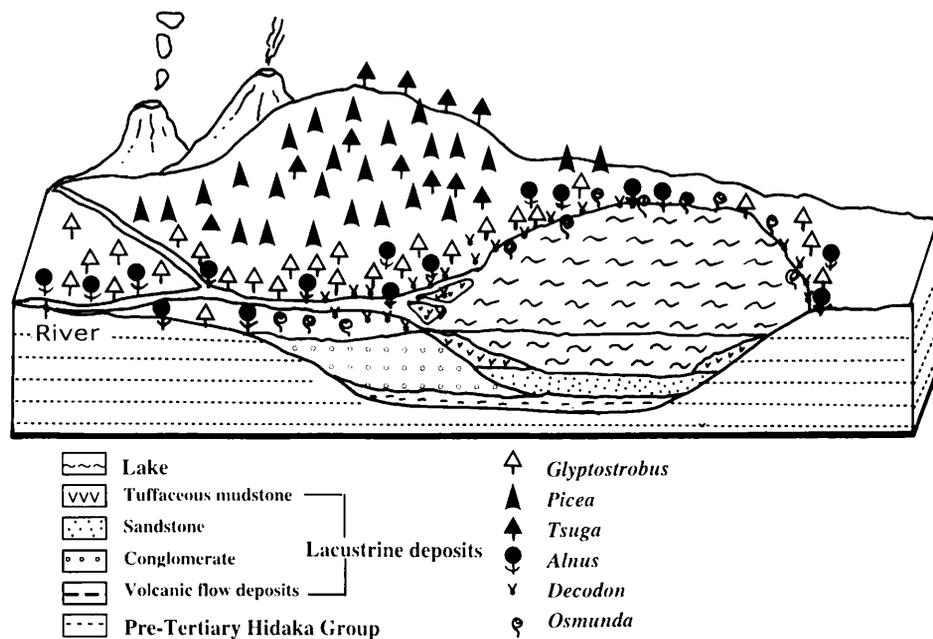


Fig. 11 Generalized reconstruction of the paleovegetation of Shimokawa region in the late Middle Miocene

(Manchester, 1994). By the Late Eocene and Oligocene the genus had spread into Europe and western Siberia (Reid & Chandler, 1933; Chandler, 1960; Tiffney, 1981; Fig. 12), with continued expansion of its range east into eastern Siberia, Japan, and Alaska until Miocene. The Pliocene distribution of the genus shows that only four species remained and that they had become restricted to western Siberia and southern Europe in response to climatic cooling and drying. Continued cooling eliminated *Decodon* from Eurasia by Pleistocene time.

The fossil record indicates that the genus first appears in western North America and migrated into western Europe prior to the Late Eocene. Movement of flora and fauna between North America and Eurasia was possible through three land bridges that existed at this time (Tiffney, 1985; LePage & Basinger, 1995). These land bridges are: (1) DeGeer route between northern Greenland and Fennoscandia; (2) Thulian route between southern Greenland and western Europe; and (3) Beringian Corridor between North America and Asia (Fig. 12). Among these, it appears that *Decodon* utilized the more southern North Atlantic Thulian route. The spread of *Decodon* to the east is coincident with the retreat of

the Turgai Strait which physically isolated eastern and western Eurasia until Oligocene time.

By Miocene the distribution of *Decodon* had extended into eastern Siberia. Dorofeev describes three species of *Decodon*, *Decodon gibbosus*, *D. globosus* and *D. sibiricus*, from the Miocene Mammoth Mountain (Dorofeev, 1969) and *D. globosus* and *D. sibiricus* from Omoloi River localities (Dorofeev, 1972). Among these taxa, *D. sibiricus* was included under his *D. globosus* group (Dorofeev, 1977).

*D. mosanruensis* appears to be more related to the North American fossil *D. allenbyensis* and extant *D. verticillatus* than the eastern Siberia species, *D. gibbosus* and *D. globosus*. Although it is tempting to conclude that *D. mosanruensis* evolved from the North American population and migrated into Japan through the Beringian Corridor, further detailed comparison with the other known fossil species is essential. Nevertheless, the presence of *D. alaskana* leaves from the Miocene of Alaska provides a possible link between North America and northern Japan (Wolfe & Tanai, 1980). The populations in and around Eurasia became extinct since the Late Miocene by the Late Pliocene through the climatic changes such as drying and cooling. The present range of *D. verticillatus* is

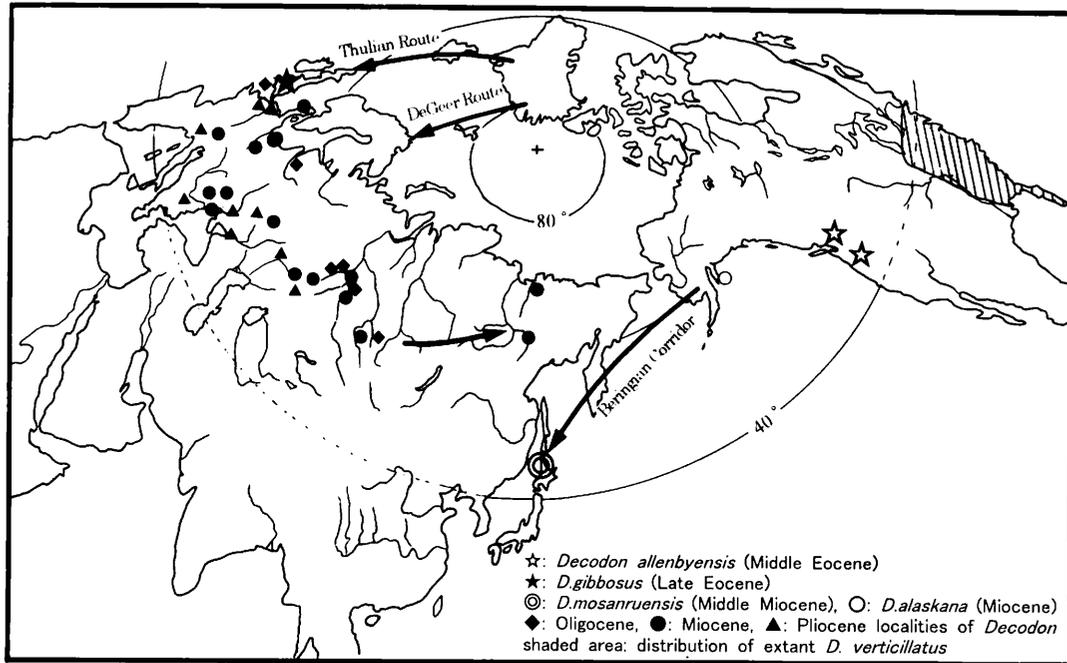


Fig. 12 Distribution of fossil and extant species of *Decodon* and the inferred migration routes of the genus between North America to Eurasia. Fossil localities are after Dorofeev (1969, 1972), Wolfe & Tanai (1980), Tiffney (1981), Cevallos-Ferriz & Stockey (1988) and Manchester (1994). Distribution of *D. verticillatus* after Britton & Brown (1970).

restricted to eastern North America and may be a possible remnant of the population that is thought to have given rise to *D. mosanruensis* during the Miocene (Fig. 12).

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