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Glyptostrobus rubenosawaensis sp. nov., a new permineralized conifer species from the Middle Miocene, Central Hokkaido, Japan

MIDORI MATSUMOTO[1], **TAKESHI ASAKAWA OHSAWA**[2], **MAKOTO NISHIDA**[3], and **HARUFUMI NISHIDA**[4]

[1] *Department of Earth Sciences, Faculty of Science, Chiba University, 1-33 Yayoicho, Inage-ku, Chiba, 263 Japan*
[2] *Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, 1-33 Yayoicho, Inage-ku, Chiba, 263 Japan*
[3] *Research Institute of Evolutionary Biology, 2-4-28 Kamiyoga, Setagaya-ku, Tokyo, 158 Japan*
[4] *Faculty of Science, Chuo University, 1-13-27 Kasuga, Bunkyo-ku, 112 Japan*

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Abstract. Anatomically well preserved fertile and vegetative remains of *Glyptostrobus rubenosawaensis* sp. nov. (Coniferae-Taxodiaceae) have been recovered from silicified lacustrine deposits of the late Middle Miocene Shimokawa Group near Shimokawa Town, Kamikawa district, Central Hokkaido. Vegetative remains include shoots bearing polymorphic leaves. Fertile remains include seed and pollen cones. The fossil remains closely resemble living *Glyptostrobus pensilis* (D. Don) K. Koch in gross morphology, but differ in possessing larger cones and a prominent abaxial projection of the bract.

Previous reports of fossil *Glyptostrobus* were limited to compression floras. This report is the first to use permineralized remains to reconstruct fossil *Glyptostrobus* and document the internal anatomical features of the genus to allow meaningful comparison with the living representative, *G. pensilis.*

Abundant remains of *Glyptostrobus* indicate wetland as the paleoecological setting, based on the co-occurrence of wetland taxa such as *Decodon* (Lythraceae), *Osmunda* and *Alnus*, and mountainous taxa such as *Picea* and *Tsuga*, and using permineralized plant fossils. We can reconstruct an ecological setting in a lake.

Key words: Anatomy, conifer, *Glyptostrobus*, Hokkaido, Miocene, permineralization

Introduction

In a number of previous reports, Matsumoto *et al.* (1994, 1995, 1996) and Nishida (1990) reported on the occurrence of permineralized leaves of *Picea* Dietrich and *Tsuga* (Endlicher) Carrière, seeds of *Decodon* Gmelin and *Osmunda* L. rhizomes from the late Middle Miocene sediments of the Shimokawa Group near Shimokawa town, Kamikawa district, Hokkaido, Japan. In addition, others such as Uemura (1991), Sato (1992), Tanai *et al.* (1992) and Igarashi *et al.* (1993) discussed the regional paleovegetation based on compression fossils or palynological remains from the Middle to Late Miocene deposits near our study area.

This is the third report on the permineralized conifers contained within the silicified lacustrine deposits of the Shimokawa Group. Here we describe a new species of fossil *Glyptostrobus* Endlicher. Extant *Glyptostrobus pensilis* (D. Don) K. Koch is monotypic and a rare endemic to southern Guangdong, northern and southern Fujian, southern Guangxi, and southeastern Yunnan provinces in China. Understanding of the ecological tolerance and attempting to determine the natural geographic distribution of *Glyptostrobus pensilis* have been made difficult because extensive deforestation throughout China has left few, if any, natural stands. Nevertheless, where present, *Glyptostrobus pensilis* occurs in small groves and is restricted to the subtropical and mixed mesophytic forests where climate is warm, humid, and rich in rainfall (Wang, 1961).

Fossil remains of *Glyptostrobus* have been found in the Cretaceous (Bell, 1949, 1957; Brown, 1962). Tertiary fossil remains of *Glyptostrobus* have been found in Eocene to Pliocene age deposits throughout the northern hemisphere (Florin, 1963). Its present distribution is probably a Plio-Pleistocene relict outpost with phylogenetic affinities to a much larger Late Tertiary Asian population (Florin, 1963). LePage and Basinger (1991, 1995), using features of seed cones, reported that some coniferous taxa such as *Larix* Mill and *Pseudolarix* Gordon were present as a high-latitude forest constituent during the early Tertiary. They provide insight into the early evolution and distribution of those two genera.

Conventional thought suggests that all fossil remains of *Glyptostrobus* are in fact representatives of living *G. pensilis* (Christophel, 1976 ; Endo and Okutsu, 1936 ; *etc.*). The discovery of *Glyptostrobus rubenosawaensis* sp. nov. provides significant data for interpreting the evolutionary history of this genus.

Geologic setting

The study site is located near the town of Shimokawa, 15 km east of Nayoro City, Kamikawa district, Central Hokkaido, Japan (Figure 1A). This area has been studied by Sako and Osanai (1955), Sako *et al.* (1960), Suzuki and Matsui (1975) and Yamaguchi *et al.* (1990). In the Shimokawa area the following three stratigraphically distinct units are recognized in an ascending order : (1) Sandstone, mudstone and chert rocks of the pre-Tertiary Hidaka Group ; (2) Volcaniclastic rocks, lacustrine deposits of the Miocene Shimokawa Group ; and (3) Volcanic rocks and fluvial deposits of Pliocene to Quaternary age (Figures 1A-C, 2). The boundaries between these units exhibit unconformable relation. As all specimens analyzed in this study were collected from the Shimokawa Group, we present further information about it.

The Shimokawa Group covers an area of approximately 600 km^2, extending 30 km wide in N-direction, and 20 km wide in E-direction. Its total thickness reaches 500 to 600 m. As *Glyptostrobus*-bearing beds occur in the eastern region, we make a brief stratigraphic description only in this region in an ascending order : the Sanru Lava, the Mosanru and the Ninohashi Formations (Suzuki and Matsui, 1975). The Sanru Lava is exposed widely and consists of volcaniclastic rocks; welded tuff, lava and voluminous pyroclastic flow. The Mosanru Formation is recognized as lacustrine deposits including conglomerate, sandy conglomerate, sandstone, and mudstone (Sako and Osanai, 1955 ; Sako *et al.*, 1960 ; Suzuki and Matsui, 1975). As the mudstone is strongly silicified, abundant macro- and micro-permineralized plants have been well preserved in it. The Ninohashi Formation consists of tuffaceous conglomerate containing gravels derived from underlying silicified rocks. The similar successions are also found in the southern and western regions. The main Formation names are summarized in Figures 1C and 2.

The *Glyptostrobus* specimens analyzed in this study were collected primarily from the western outcrop in the Mosanru Formation (Figures 1B, 3). Four silicified mudstone layers (S1-S4) and two agate mudstone layers (A1, A2) are found from the three outcrops of the Formation (Figures 1A, B, 3). The facies analysis of this lacustrine sediments indicates fining-upwards system (Figure 3). *Glyptostrobus rubenosawaensis* were collected at one horizon (S1) in the Mosanru Formation. The upper agate mudstone layers (A1, A2) do not contain plant mega-fossils but contain pollen grains and spores. As the grain size of this mudstone is very fine, their depositional condition seems to be that of topmost supernatant.

Fission track and K-Ar analysis indicate that the age of the volcaniclastic rocks such as the Furebetsu and the Futamata Volcanics, the Sakingawa and the Sanru Formations ranges from 11-13 Ma, while the age of upper volcaniclastic rocks, the Fureppu Lava is from 10-12 Ma (Table 1, Figure 2 ; Watanabe *et al.*, 1991 ; *etc.*). These data show

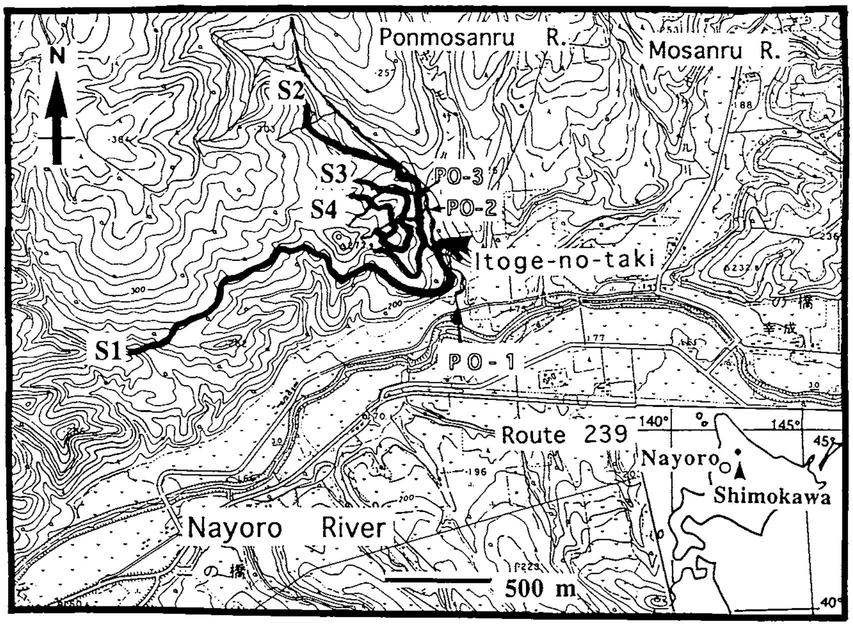


Figure 1A. Locality map of study area (using the topographical map "Shimokawa", scale 1 : 25,000 published by Geographical Survey Institute of Japan) showing the four silicified layers and study sites.

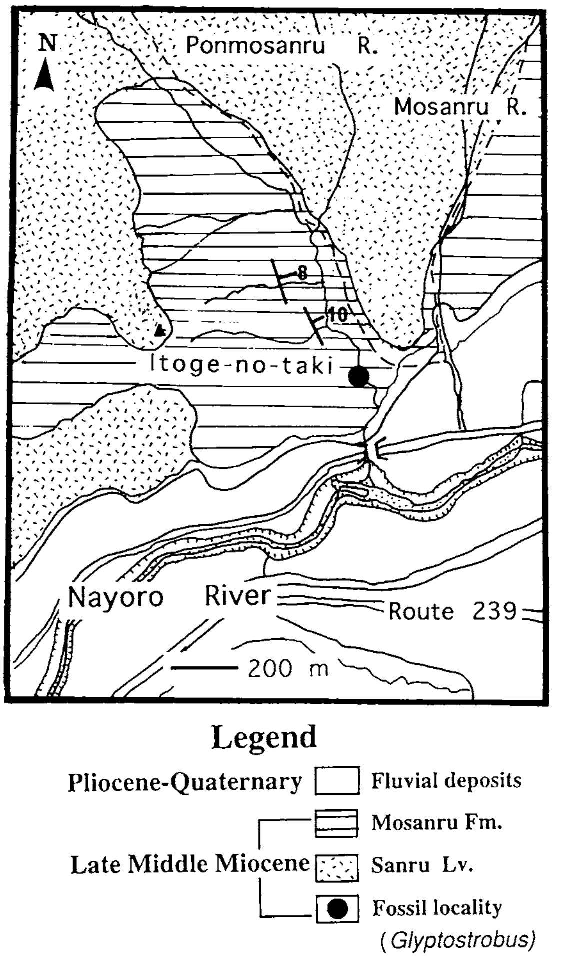


Figure 1B. Geologic map of Shimokawa district including the distribution of the plant-fossiliferous lacustrine deposits, in the Mosanru Formation, Shimokawa Group. Fm.: Formation, Lv.: Lava.

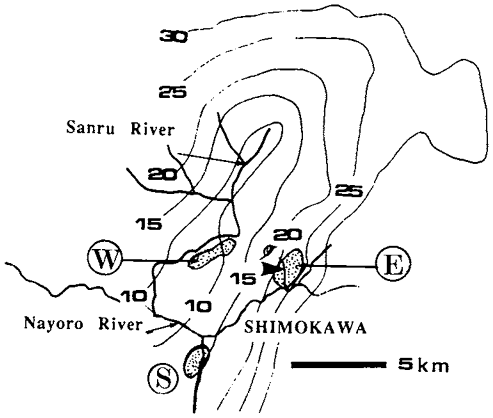


Figure 1C. Map showing the permineralized plant-bearing localities and gravity contours. Bouguer anomalies based on the Normal Gravity Formula (Yamaguchi *et al.*, 1990), which is assumed to be 2.0 g/cm^3. Contour intervals 5 milligals. E: Eastern region is mainly located along the Ponmosanru River, W: Western region is located along the Sanru River, S: Southern region is located along the Shimokawa Panke River

Age	*Stratigraphic Units Western R.	Eastern R.	Southern R.	Main Lithology	Thickness
Quaternary - Pliocene				Fluvial deposits and volcanic rocks	>50m
Late Middle Miocene	Fureppu Lv.	Ninohashi Fm.		Lv., Pyroclastic rocks	ca.300m
	Penke Fm. Sanru Fm.	**Mosanru Fm.	Panke Fm.	Lacustrine deposits	ca.50-80m
	Sanru Lv. Sakingawa Fm.		Furebetsu Fm. Futamata V.	Welded Tf., Lv., Py-flow	ca.200m
Pre-Tertiary	Hidaka Gp.			Sandstone, mudstone, chert rocks	

Figure 2. Stratigraphic sequence of the pre-Tertiary, late Middle Miocene, Pliocene and Quaternary in the Shimokawa region. Three regions are referred to Figure 1C. Fm.: Formation, Gp.: Group, Lv.: lava, Py: pyroclastic, R: region, Tf: tuff, V.: volcanics, *: see to Suzuki and Matsui (1975) and Yamaguchi *et al.* (1990), **: this study

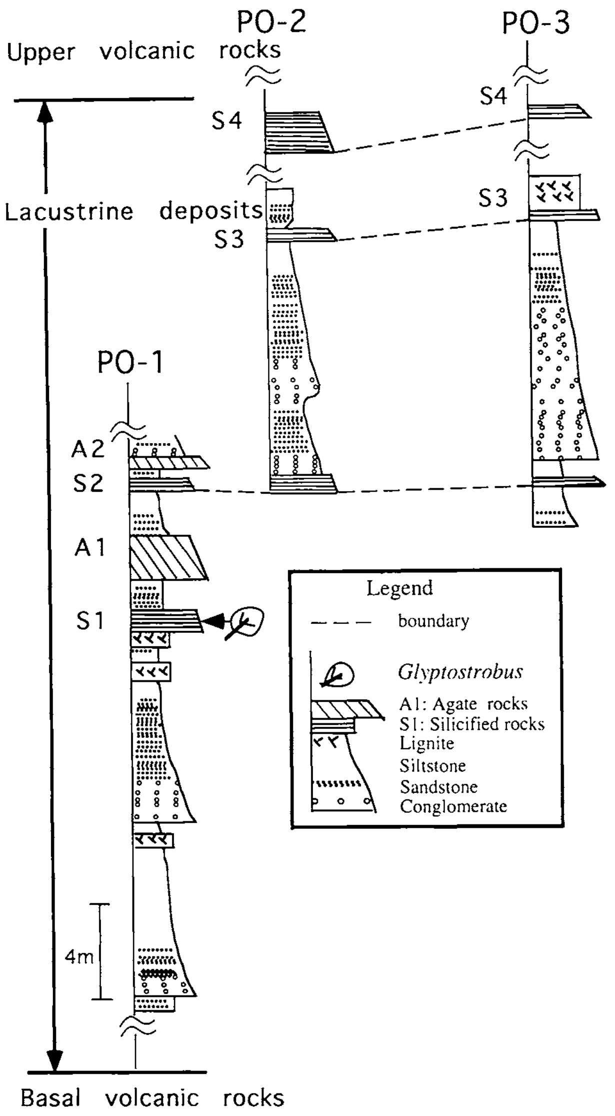


Figure 3. Columnar sections of the Mosanru Formation at Itoge-no-taki, in Shimokawa town.

that deposition of the Shimokawa Group probably occurred without significant interruption and that the age of the plant-bearing horizon is the late Middle Miocene.

Floristic setting

Based on the quality of preservation the plants grew and were preserved *in situ* under the low-energy condition associated with a swamp or lake (Yamaguchi *et al.*, 1990). Such depositional environments and preservational conditions are commonly associated with volcanic terrains (Tiffney, 1981 ; Cevalloz-Ferriz *et al.*, 1988). The deposits containing the plant fossils roughly correspond to a low-gravity area and a caldera lake is suggested as a possible depositional environment (Figures 1C, 4). Megafloral remains associated with the lacustrine deposits include *Picea, Tsuga, Glyptostrobus, Alnus* P. Miller, *Decodon*, and *Osmunda* (Nishida, 1990 ; Matsumoto *et al.*, 1994, 1995, 1996). This assemblage suggests a possible candidate for the sedimentary environment of the lacustrine deposits. Thus we offer a schematic drawing of the paleo-vegetation (Figure 4).

Throughout the high-latitude regions of the northern hemisphere *Glyptostrobus* was a common constituent of the warm-temperate forests (Budanstev, 1992). Extant *Glyptostrobus pensilis* is very sensitive to frost, requires high humidity during the winter months, and will not tolerate temperatures below 0°C. Similar conditions are inferred for Hokkaido during the late Middle Miocene.

Occurrence of fossil plants

The plants occur in a 1.0-1.5 m thick silicified mudstone (S1) that crops out near Itoge-no-taki, a small waterfall on the Ponmosanru River (also called Rubeno Sawa), a tributary of the Nayoro River (Figures 1A-C, 3). The columnar section (PO-1) of the outcrop is shown in Figure 3 and their strike and dip are N40°W and 10°N, respectively (Figure 1B). Another two columnar sections (PO-2, 3) are also indicated in Figure 3.

The rock consists largely of chalcedonic quartz and includes abundant anatomically and morphologically well-preserved plant remains (Figures 5A-C). Preserved shoots are commonly orientated perpendicular to the bedding plane,

Table 1. Ages of formations of the Shimokawa Group

Formation	Rock	Methods	Age (Ma)	References	
Fureppu Lv.	Andesite	K-Ar	12.8±0.6	Watanabe et al.	1988
Fureppu Lv.	Andesite	K-Ar	10.0±0.5	Watanabe et al.	1988
Furebetsu V.	Andesite	K-Ar	11.2±0.3	Sugawara et al.	1992
Sakingsawa Fm.	Andesite	K-Ar	11.2±0.5	Watanabe et al.	1988
Sanru Fm.	Altered volcanics	FT	11.3±0.7	Koshimizu et al.	1987
Sanru Fm.	Rhyolite, Dacite	K-Ar	12.1±0.6	Watanabe et al.	1988
Futamata V.	Basalt	K-Ar	12.1±0.7	Sugawara et al.	1992
Sakingawa Fm.	Altered volcanics	FT	12.1±0.9	Koshimizu et al.	1987
Futamata V.	Basalt	K-Ar	12.4±1.3	Watanabe et al.	1991
Sakingawa Fm.	Green tuff	FT	13.9±1.1	Koshimizu et al.	1986
Futamata V.	Basalt	K-Ar	15.2±1.6	Watanabe et al.	1991

Fm.: Formation, FT: fission track, Lv.: Lava, V.: Volcanics

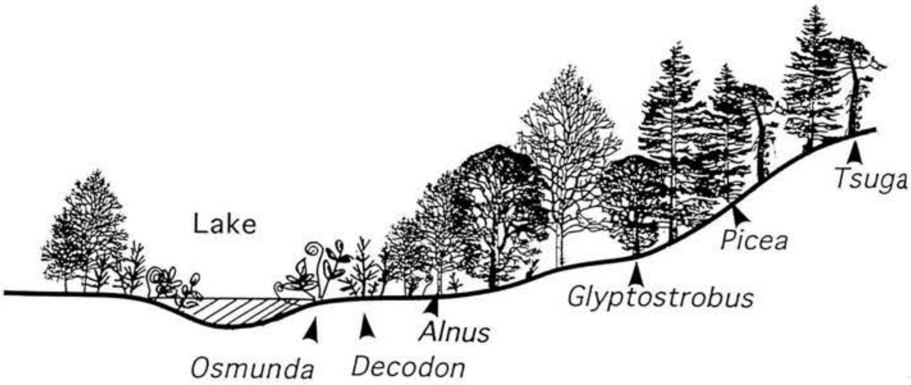


Figure 4. Generalized reconstruction of the region showing the environmental setting and inferred relationship of floristic constituents within a larger vegetational mosaic.

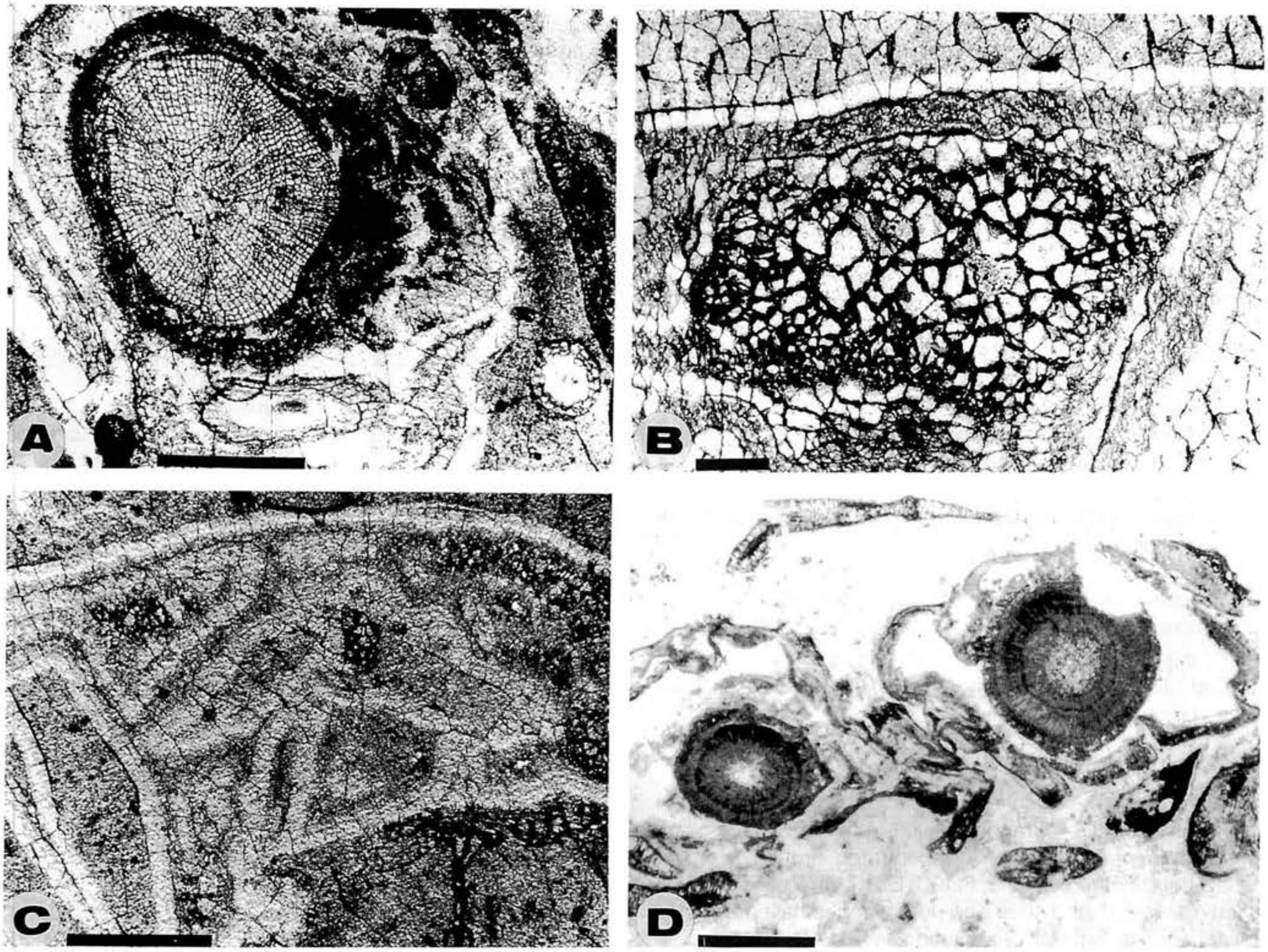


Figure 5. Hand-ground thin sectioned rock samples (A–C) from Itoge-no-taki (S1 layer, #95061501C), and peel section (D). **A, B.** Silicified rock and quartz vein enclosing plant fragments. **C.** Lowermost rocks from the plant bearing horizon. **D.** Peel of shoots and leaves of *Glyptostrobus rubenosawaensis* sp. nov. in transverse section (#93081402). Scale bars : A, C=0.5 mm ; B=0.1 mm ; D=2 mm.

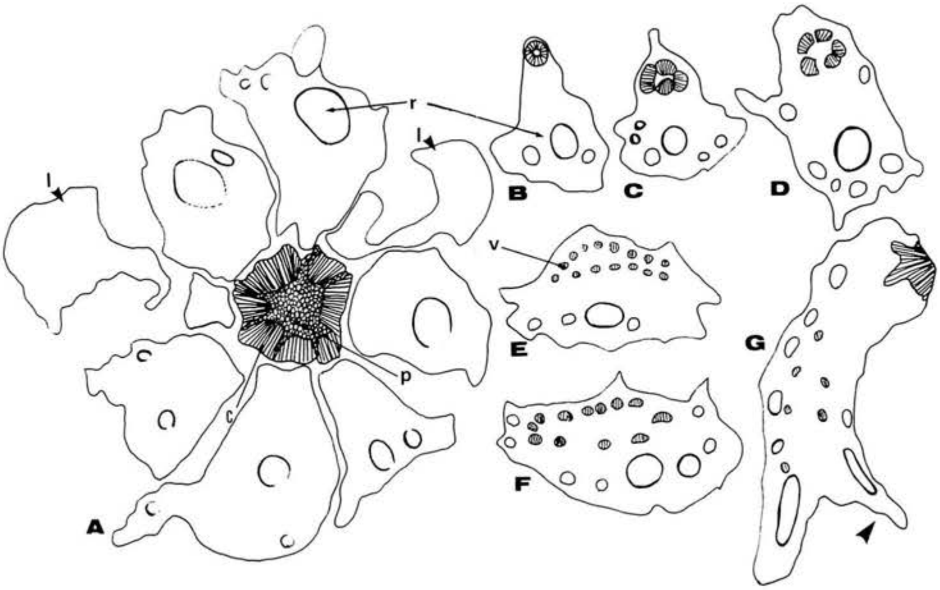


Figure 6-1. Camera lucida drawings showing the arrangement of the vascular bundles and resin canals within the bract-scale complexes of *Glyptostrobus rubenosawaensis* sp. nov. **A-F.** Transverse sections. **G.** Longitudinal section. Note the arrow showing the prominent bract. c : cortex, l : leaf, p : pith, r : resin canal, v : vascular bundle.

Table 2. Measurements (mm) of extant and fossil *Glyptostrobus* cones

Species	Cone		b-s complex		Measured no. of specimes	Locality
	Length	Diameter	Length	Width		
Glyptostrobus rubenosawaensis sp. nov.	26.2	18.8	20.1	7.0	22	Hokkaido, Japan
G. pensilis Endl.	20.9	17.5	11.5	5.5	11	Chiba, Japan
G. pensilis Endl.	22.4	16.8	16.5	6.2	103	Shizuoka, Japan
G. pensilis Koch.	21.0	16.0	11.5	4.8	?	Many places, Honsyu, Japan
G. pensilis Endl.	19.1	12.5	16.1	4.0	45	Aichi, Japan
G. orientalis Endo	16.0	10.5	10.5	6.0	1	Kyushin, Korea
G. nordenskioeldii (Heer) Brown	13.5	10.6	—	—	1	Axel Heiberg Island, Canada
G. nordenskioeldii (Heer) Brown	14.7	10.9	7.5	5.0	13	Smoky Tower, Canada
G. nordenskioeldii (Heer) Brown	10.0	10.0	—	—	?	Alberta, Canada
G. europaeus (Brong) Heer	24.0	19.0	—	—	1	Gifu, Japan
G. europaeus (Brong) Heer	17.0	12.3	—	—	3	Hokkaido, Japan
G. europaeus (Brong) Heer	18.0	14.0	8.0	4.0	1	Hokkaido, Japan
G. europaeus (Broug) Heer	22.0	16.0	—	—	2	Akita, Japan
G. europaeus (Brong) Heer	18.5	11.5	9.2	4.7	4	Germany

* : this paper ; ** : collector

Cret : Cretaceous, E : Early, L : Late, M : Middle, Pal : Paleocene, Eoc : Eocene, Mio : Miocene, Pli : Pliocene, U : Upper, b-s : bract-scale, Ex : Extant

indicating that plant burial and preservation was rapid and *in situ* (Figures 5A, D). Branches with attached leaves and cones of *Glyptostrobus* are concentrated around some of these shoots (Figures 7A, B, F, 10C-E). Many organs, such as leaves, shoots and seed and pollen cones have kept their original shapes without deformation.

Microscopic observations of thin-sectioned rocks show the textures of the well preserved shoots, branches and fragments of plants. Numerous quartz network veins surround the plant fragments preserving their structure (Figures 5A-C).

Materials and Methods

Twelve fossiliferous rocks (No. 903000, 903001, 903005, 931122, 94081401, 94081402, 94081403, 94081406, 94081407, 95052802, 95061501C, and 95071401) were collected by Isekichi Nakauchi of Shimokawa, Kamikawa district, Central Hokkaido, and the authors from the riverbeds of the Ponmosanru River, tributary of the Nayoro River (Figures 1A-C).

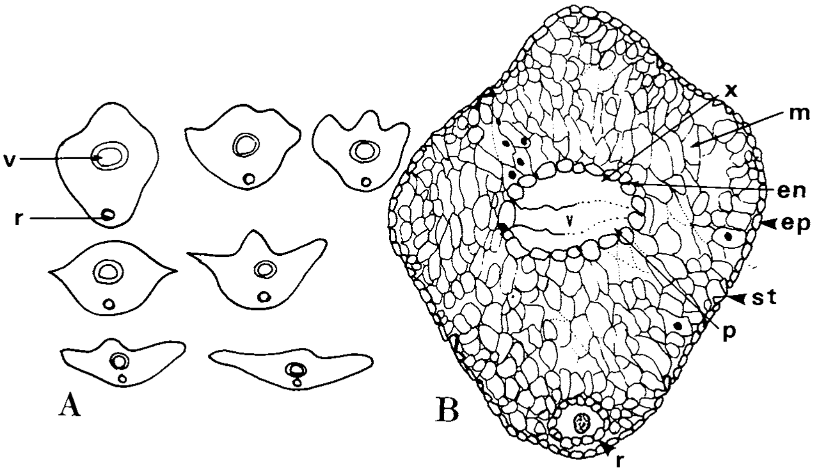


Figure 6-2. Camera lucida drawings showing the internal anatomy of leaves of *Glyptostrobus rubenosawaensis* sp. nov. in transverse section. **A.** Note that the shape of the leaf changes at different levels. **B.** Transverse section of a rhomboid-shaped leaf (#93081403). en : endodermis, ep : epidermis, m : mesophyll, p : phloem, r : resin canal, st : stomata, v : vascular bundle, x : xylem.

and bract-scale complex

Age	Source
Mio.	I. Nakauchi, M. Matsumoto & T. Ohsawa*
Ex	M. Matsumoto & T. Ohsawa*
Ex	M. Matsumoto*
Pli.	S. Miki (1950)
L. Mio.-Pli.	K. Uemura (1982)**
E. Mio.	S. Endo & H. Okutsu (1936)
Eoc.	J.F. Basinger (1991)
Pal.	D.C. Christophel (1976)
U. Cret.	W. Bell (1949)
M. Mio.	T. Tanai & N. Suzuki (1961)
M. Mio.	T. Tanai & N. Suzuki (1961)
M. Mio.	T. Tanai & N. Suzuki (1961)
E. Mio.	K. Huzioka (1964)
Tertiary	O. Heer (1855-59)

The fossils are preserved as silica permineralizations.

Rocks were sliced by a rock cutter, at intervals of 1-2 cm. All specimens were prepared using the cellulose acetate peel method which has been modified for silicifications with 25-45% hydrofluoric acid as the etching reagent (Joy *et al.*, 1956 ; Basinger, 1981). The peels were mounted in a xylene-soluble Canada balsam suitable for light microscopy. We also made thin sections of rocks for microscopic observation and examined textures.

With the exception of specimen No. 94081407, all specimens are housed in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, Japan. Specimen No. 94081407 is housed in the Board of Education Office, Shimokawa, Hokkaido, Japan.

Leaves, shoots and seed and pollen cones of extant *Glyptostrobus pensilis* were examined anatomically for comparison purposes. These specimens were collected from a number of localities throughout Japan (Table 2), fixed in FAA, and embedded in Palaplast. The leaves, shoots, and pollen cones were then sectioned with a rotary microtome in 12.0-20.0 μm thick, stained with safranine and fastgreen, and mounted on glass slides. The seed cones, both attached and detached, were either fixed with a glycerin-alcohol mixture or air dried, and sectioned by hand using a razor.

A number of fossil *Glyptostrobus* specimens were studied for comparative purposes (Table 2). Unfortunately, it was not possible to examine some of these specimens and the taxonomic information was, from necessity, obtained from the literature.

Description

Systematic treatment
Order Coniferae Jussieu, 1789
Family Taxodiaceae Warming, 1884
Genus **Glyptosrobus** Endlicher, 1847

Type species.—*Glyptostrobus pensilis* Endlicher, Syn. Conif., 1847

Glyptostrobus rubenosawaensis sp. nov.

Occurrence.—Itoge-no-taki ; S1 Bed of the Mosanru For-

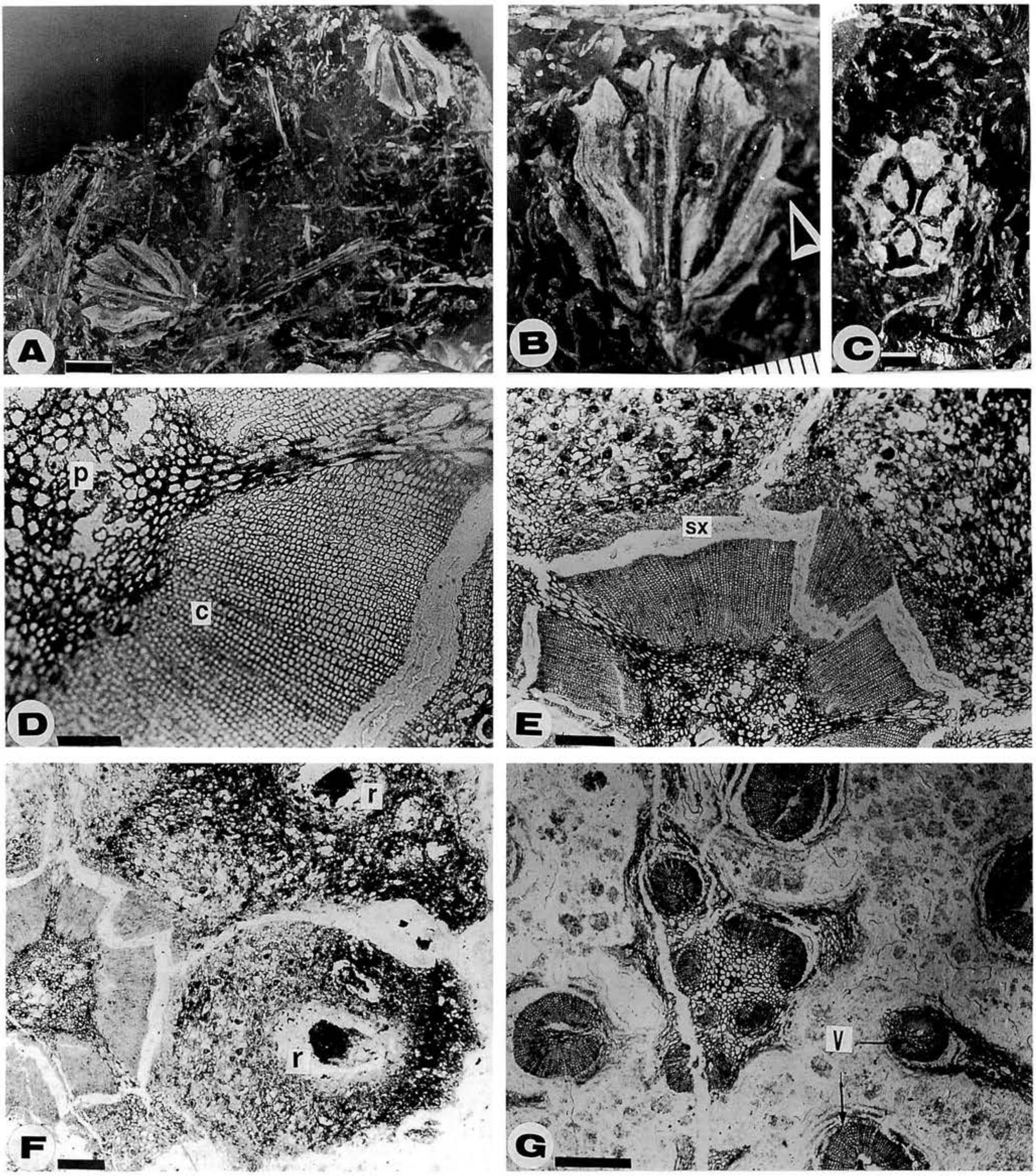


Figure 7. Transverse and longitudinal sections of the bract-scale complex of *Glyptostrobus rubenosawaensis* sp. nov. **A.** Seed cones in longitudinal section showing the individual bract-scale complexes (#94081407). **B.** Enlargement of specimen in Figure 7A. Note the prominent bract (arrow, #94081407). **C.** Cross section of seed cone (#95071401). **D.** Transverse section of cone axis showing pith (p), cortical tissues (c) (#94081403). **E.** Transverse section of cone axis showing pith, cortical tissues, and bract-scale complexes with large resin canals (#94081403). **F.** Transverse section of cone axis and bract-scale complex showing large resin canals (#94081403). **G.** Transverse section of cone axis showing cylindrical units (#94081403). c: cortex, p: pith, r: resin canal, sx: secondary xylem, v: vascular bundle. Scale bars: A, C=10.0 mm; D=150 μm; E-G=400 μm.

mation of the Shimokawa Group.

Geologic age.—The late Middle Miocene.

Diagnosis.—Foliaged-bearing shoots bearing cryptomeroid, taxodioid, and cupressoid-like leaves (Figures 6-2A, 10D, E, 11A). Leaves bifacially flattened or four-sided, stomata present in two to three rows on all surfaces (Figures 6-2B, 11A). Epidermis one cell-layer thick and consisting of elliptical to rounded cells, 7.0-15.0 μm wide, 5.0-7.5 μm high. Hypodermis not discernible (Figure 11A). Endodermis composed of isodiametric parenchyma cells, 90.0-130.0 μm in diameter and forming a continuous sheath around the vascular bundle (Figures 6-2B, 11A). Single resin canal 40.0-65.0 μm in diameter located just on the abaxial surface near the epidermis and encircled by one layer of epithelial cells (Figures 6-2B, 11A). One single centrally located vascular bundle. Mesophyll undifferentiated, elliptic to isodiametric in shape, 10.0-25.0 μm long, 15.0-40.0 μm wide.

Seed cones obovate in outlook. Ovuliferous scale wedge-shaped and fused with bract basally; bract free apically. Free portion of the bract is up to 2.0 mm long, conspicuous, and forming a 90° angle with ovuliferous scale (Figures 6-1G, 7B, 9A). Bract-scale complex wedge-shaped, narrowing toward the basal part (Figures 6-1G, 7A, B, 8F, G, 9A). Bract width is about one half the length of the bract-scale complex.

Pollen cones composed of four to five microsporophylls, each bearing 4-8 microsporangia (Figures 11D-F). The arrangement of microsporophyll and subtending scale-leaves helical.

Type and deposition.—Specimen including leaves, seeds and pollen cones.

Holotype: Specimen No. 94081402

Paratypes: Specimens Nos. 903000, 903001, 903005, 931122, 94081401, 94081403, 94081404, 94081407, 95052802, 95061501C, and 95071401

Extant material: Specimen Nos. 950529 and 941125.

Etymology.—The specific epithet is named after this fossil locality, Rubeno-Sawa.

Detailed description

Descriptive terms.—The terminology used here concerning coniferous seed cones are after Miller (1975). The terms bract-scale complex, scale, and bract signify the cone-scale complex, ovuliferous scale, and bract-scale of Florin (1951), respectively. We describe the term cone as seed cone.

Shoots and leaves.—The leafy twigs bear cryptomeroid and taxodioid leaves distally and cupressoid leaves proximally (Christophel, 1976) (Figure 10E). Shape of leaf is acute-acuminate-obtuse or rotundate in cross section; their width and thickness are various in size, ranging from 0.4-1.1 mm wide, 0.3-0.9 mm thick (Figures 6-2A, B, 10C-E, 11A).

The epidermis consists of a single layer of elliptical to rounded cells in cross section, 7.0-15.0 μm wide, 5.0-7.5 μm high, with cell walls 1.0-2.0 μm thick (Figures 6-2B, 11A).

Stomata are arranged in two to three rows on each face (Figures 6-2B, 11A). We did not examine the hypodermis on these specimens. Mesophyll cells are not differentiated into palisade and spongy tissues. These cells are elliptical to isodiametric in shape, with round corners in cross section and 10.0-25.0 μm thick, 15.0-40.0 μm wide with cell walls 1.0-2.5 μm thick (Figures 6-2B, 11A).

Cell of the endodermis are isodiametric, 90-130 μm in diameter, and form a single layer that completely encircles the vascular bundle (Figures 6-2B, 11A). Endodermal cells are not well preserved, about 20 cells in number. Details of their anatomy are obscured (Figures 6-2B, 11A). The diameter of endodermis is about 150-180 μm. The median vascular bundle is poorly preserved and details of its anatomy are obscured (Figures 6-2A, B, 11A).

A single resin canal 40.0-65.0 μm in diameter and encircled by one layer of epithelial cells is located on the abaxial surface near the epidermis. Epithelial cells are 10-16 in number (Figures 6-2A, B, 11A).

Cones.—The seed cones are obovate in outline, 26.2 mm long and 18.8 mm wide on average (Table 2, Figures 7A, B). Each cone is composed of approximately 15 bract-scale complexes arranged helically on a central cone axis. Seven to nine bract-scale complexes are visible in lateral view in longitudinal section (Figures 7A-C). The ovuliferous scale is fused with the bract basally, but free apically (Figures 7A, B). The shape and size of the cone scales vary with positions. Those near the base of the cone are spatulate, 3.5-6.7 mm wide, and 1.5-2.7 mm thick, those near the middle are peltate, 1.3-3.8 mm wide, and 1.9-4.4 mm thick, while those near the top are cuneate, 0.5-2.0 mm wide, and 1.9-2.4 mm thick (Figure 7B). The cone scales are wedge-shaped, narrow at the base and reaching a maximum width of 7.0-8.0 mm near the apex, and range from 17.0-23.0 mm in length (Figure 7B).

The centrally located cone scales diverge from the central axis at 22-26°, while the basal scales diverge from the central axis at 45-52° and turn upwards at a 20° angle (Figures 7A, B, 8F, G, 9A). The basal scales are somewhat furrowed and possess wavy margins (Figures 7A, B, 10A). The free portion of the bract is up to 2.0 mm long, conspicuous, and forming a 90° angle with the ovuliferous scale (Figures 6-1G, 7A, B, 8F, G, 9A). Bract width is about one half the length of the bract-scale complex (Figures 6-1G, 7B, 8F, G, 9A).

Cone axis.—The cone axis is 2.7-3.0 mm in diameter with a central vascular cylinder 0.5-0.6 mm in diameter (Figures 6A, 7D-F). The pith is 1.0-1.2 mm in diameter and composed of thick-walled isodiametric parenchyma cells, 25.0-50.0 μm in diameter and 100-125 μm in length (Figures 6-1A, 7D-F). The vascular cylinder is 2.2-2.4 mm in diameter and composed primarily of secondary xylem (Figures 6-1A, 7D-F). Secondary xylem tracheids are 8.0-15.0 μm in diameter. The primary xylem is endarch and located at the inner edge of the vascular cylinder (Figures 7D-F).

Cortex.—The cortex of the cone axis is 80.0-120.0 μm thick and composed of isodiametric parenchyma cells that are 10.0-15.0 μm in diameter and cell walls 2.0-2.5 μm thick (Figures 6-1A, 7E, F). Resin canals were not observed in the cortex or surrounding tissues; however, tissues external to the cortex were not well preserved.

Bract-scale complex.—Tissues of the bract-scale complexes consist of epidermis, hypodermis, fundamental tissue, vascular trace and resin canals.

The vascular trace that supplies the bract-scale complex diverges from the central stele in the cone axis as a cylindrical unit (Figures 6-1B, 7G, 8A). A small strand diverges from the trace that enters the complex on the abaxial surface and enters the bract (Figures 6-1C, D, 8B-G). The trace then splits into 14-18 vascular strands in two horizontal rows that supply the scale (Figures 6-1E, F, 9C, 10A, B). Phloem associated with the adaxial vascular strands occurs on the adaxial surface, while that of the abaxial strands is found on the abaxial surface. In the distal part of the bract-scale complex the vascular bundle consists of 7-12 filed xylem cells and 5-7 filled phloem cells (Figure 9F).

Near the base of the bract-scale complex one resin canal, 0.5-1.4 mm in diameter, is present (Figures 6-1A, 7F). This large canal divides acropetally into 14-18 smaller resin canals, 0.1-0.4 mm in diameter, and arranged in two rows on the abaxial side (Figures 6-1A-G, 8A-G, 9A-C, 10A, B). The fundamental tissue consists of parenchyma cells and scattered fibers (Figures 8G, 9B-F). The parenchyma cells are isodiametric and 25.0-70.0 μm in diameter, while the fibers are round to polygonal and 50-90 μm in diameter, with walls 15.0-30.0 μm thick. The fibers are moderately abundant basally and become more prevalent in the apical part of the cone scales (Figures 9D-F).

The epidermis consists of a single layer of thick-walled, elliptical cells, 15.0-25.0 μm in diameter on the adaxial and lateral sides of the distal part of the complex (Figures 9D, G).

The hypodermis is composed of 2-5 layers of thin-walled, isodiametric parenchyma cells, 20.0-35.0 μm in diameter (Figures 9D, G). On the adaxial surface these cells are occluded by an unidentifiable black substances. Adaxially, trichomes are abundant (Figure 9D).

Pollen cones.—The pollen cones are subtended by 3-4 bracts and consist of 4-5 helically arranged microsporophylls bearing 4-8 peltate microsporangia. The microsporangia are 40.0-50.0 μm in diameter and arranged in two rows (Figures 11D-F). A longitudinal dehiscence zone occurs on the abaxial side.

Affinity and Discussion

Comparisons with extant genera of Taxodiaceae

Seed cones.—Taxodiaceous cones are separated into three distinct groups based on bract-scale morphology, the relative size of the ovuliferous scales and bracts, and arrangement of the vasculature traces within the bract-scale complex (Eames, 1913 ; Satake, 1934 ; Hirmer, 1936 ; Dallimore and Jackson, 1966 ; La Pasha and Miller, 1981).

The first group includes *Glyptostrobus, Cryptomeria* D. Don, and *Taxodium* Richard. The bract-scale complexes of this group are commonly cuneiform and non-peltate (although peltate in *Taxodium*) and possess small bracts. The vascular trace is of the open type (Satake, 1934 ; La Pasha and Miller, 1981).

The second group, which includes *Sequoia* Endlicher, *Sequoiadendron* Buchholz, and *Metasequoia* Hu et Cheng has peltate bract-scale complexes, equally sized scales and bracts, and possesses a circular trace to the bract-scale complex (Eames, 1913 ; Hirmer, 1936 ; La Pasha and Miller, 1981).

Group three consists of *Cunninghamia* R. Brown and *Taiwania* Hayata and possesses tapering non-peltate bract-scale complexes, large bracts, reduced scales and terete traces (Satake, 1934). *Athrotaxis* D. Don shows wide variation in these features and is commonly not considered in such analyses (Eames, 1913 ; Hirmer, 1936 ; Dallimore and Jackson, 1966).

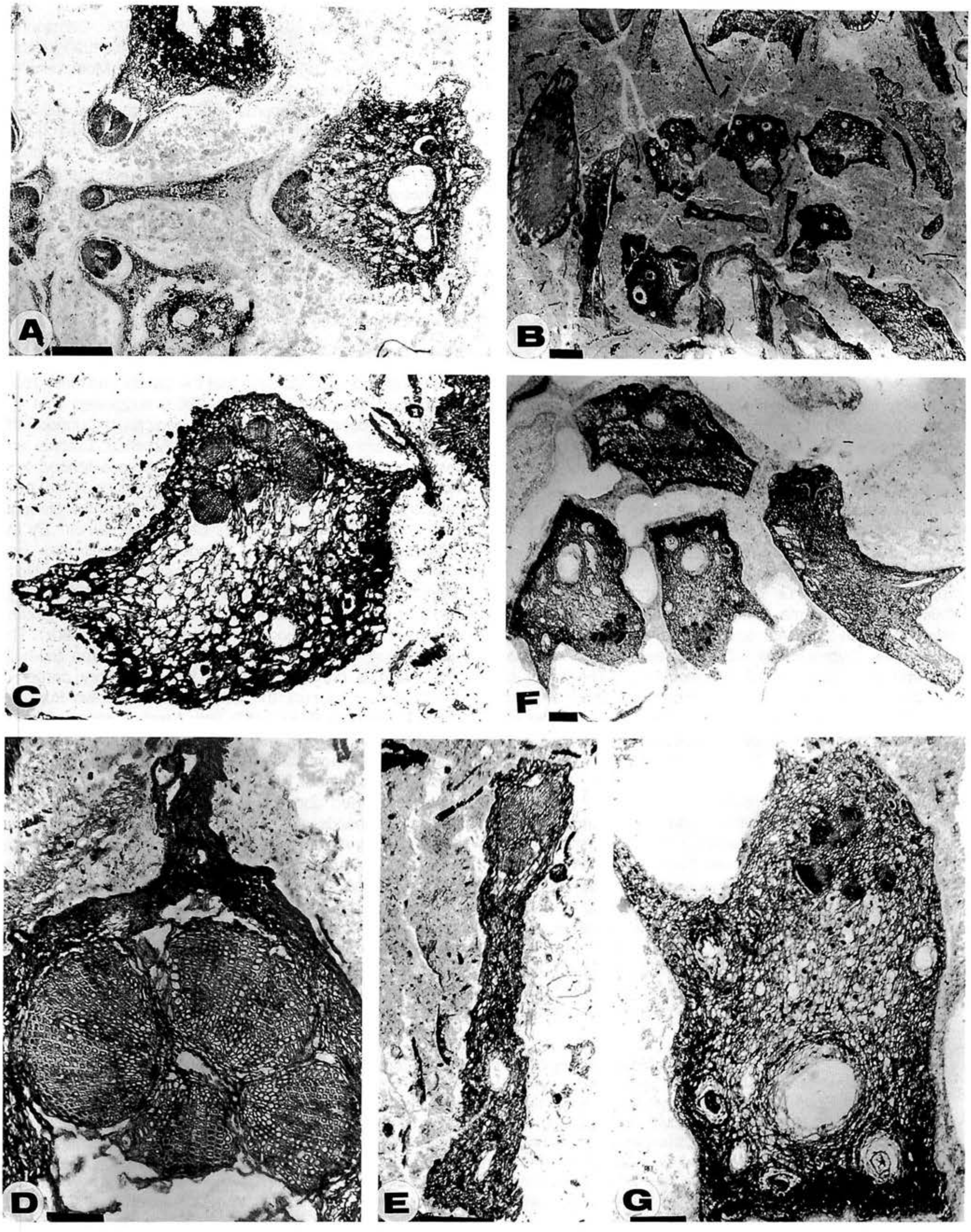
Based on gross morphological features, the shape and size of the bract, the small ovuliferous scale, and degree of fusion between the bract and scale, our fossil material most closely resembles the seed cones of *Glyptostrobus, Cryptomeria* and *Taxodium* (Satake, 1934 ; La Pasha and Miller, 1981).

Although *Cryptomeria* and *Taxodium* resemble our fossil specimens in some aspects, there are significant differences. *Cryptomeria* seed cones are globular, less than 15.0 mm in diameter, and possess wedge-shaped bract-scale complexes with deeply sculptured apical margins. Seed cones of *Taxodium* are ovoid to sub-globose with peltate cone scales.

Pollen cones.—Pollen cones of *Metasequoia* and *Taxodium* are also subtended by a number of bracts, but in *Metasequoia* the arrangement of the bracts, microsporophylls, and subtending scale leaves is decussate and only three microsporangia are present. In *Taxodium* there are 5-9 microsporangia per microsporophyll (Dallimore *et al.*, 1966 ; Rothwell *et al.*, 1979 ; Basinger, 1981) ; usually the microsporangia flattened on the abaxial side. However the microsporangia of *Glyptostrobus* are arranged in a double horizontal lines. The shape of the microsporophylls is peltate with a radial longitudinal downward curve at the abaxial side. Based on these features and comparison of our fossil specimens with those of living *Metasequoia* and *Taxodium* there is no doubt that our material is *Glyptostrobus*.

Shoots and leaves.—The shoots and leaves of *Glyptostrobus rubenosawaensis* are characterized by possession of helically arranged, four-sided, linear to acicular scalelike leaves with stomata on all surfaces. Internally, there is a single resin canal near the epidermis on the abaxial surface, no hypodermis, a single median vascular bundle, and mesophyll which has not been differentiated into palisade tissues or spongy mesophyll. Although *Cryptomeria* (Suzuki, 1979), *Athrotaxis* (Dallimore *et al.*, 1966), and *Taxodium* (Basinger, 1981) possess four-sided, linear to acicular scalelike leaves,

Figure 8. Transverse and longitudinal sections of the bract-scale complex of *Glyptostrobus rubenosawaensis* sp. nov. **A.** Transverse section showing a large and small resin canals (#94081403). **B.** Transverse section of a bract-scale complex (#903005). **C-E.** Enlargement of specimen of Figure 8B (#903005). **F.** Transverse and longitudinal section of bract-scale complex (#94081402). **G.** Enlargement of specimen of Figure 8G (#94081402). ep : epidermis, ph : phloem, r : resin canal, t : trichome, v : vascular bundle, x : xylem. Scale bars : A, B, F=800 μm ; C, E, G=400 μm ; D=150 μm.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with undifferentiated mesophyll, and a single resin canal and bear some similarity to those of *Glyptostrobus rubenosawaensis*, there are notable differences. Leaves of *Taxodium* are broader and possess sclerids abaxial to the vascular bundle. Leaves of *Cryptomeria* and *Athrotaxis* possess a single-layered hypodermis, and a resin canal which is closely associated with the vascular bundle sheath, but not in contact with the epidermis.

Thus our leaf specimens are not assigned to these three genera of Taxodiaceae but belong to *Glyptostrobus*.

Based on anatomical and morphological features of the seed and pollen cones, shoots and leaves our fossil specimens most closely resemble those of extant *Glyptostrobus pensilis* (extant *G. pensilis* : pollen cone- Figure 11C, leaf in cross section-Figure 11B).

Comparisons with extant and fossil *Glyptostrobus*

Specimens of *Glyptostrobus rubenosawaensis* were compared with *G. pensilis* and a number of previously described fossil *Glyptostrobus* (Table 2). *Glyptostrobus rubenosawaensis* differs from *G. pensilis* in having larger seed cones, longer bract-scales, and a prominent bract (Table 2 ; Figures 6-1G, 7B, 8F, G, 9A). The most obvious difference between *Glyptostrobus rubenosawaensis* and the other fossils is the larger cone size and prominent projection of the bract in *G. rubenosawaensis*. The North American *Glyptostrobus nordenskioeldii* (Heer) Brown and Asian *G. orientalis* Endo are significantly smaller, while those of *G. europaeus* Heer and *G. pensilis* are about 25% smaller. Although cone size may not necessarily be a diagnostic feature on which to base a new species, the prominent bract distinguishes *Glyptostrobus rubenosawaensis* from all other fossil and living species of *Glyptostrobus*. The bract of *Glyptostrobus rubenosawaensis* is more than twice as long and wide as in the extant species. This is a major reason why we describe *Glyptostrobus rubenosawaensis* as a new species.

Fossil records of *Glyptostrobus*

The first appearance of the genus *Glyptostrobus* was reported from the Upper Cretaceous of northwestern North America (Bell, 1949, 1957 ; Brown, 1962). The fossil record of this genus indicates that the genus was a common forest constituent throughout Europe, North America, Asia, and Japan from the Early Tertiary until the Late Pleistocene (Heer, 1855 ; Endo *et al.*, 1936 ; Shimakura, 1939 ; Miki, 1941, 1950, 1954, 1957 ; Endo, 1953 ; Hantke, 1954 ; Okutsu, 1955 ; Tanai, 1952, 1961, 1970, 1992 ; Tanai *et al.*, 1963, 1972, 1992 ; Wang, 1961 ; Huzioka, 1964, 1972 ; Ferguson, 1967 ; Matsuo, 1967, 1970a, b, 1971, 1972 ; Klipper, 1968 ; Murai, 1968 ; Pabst, 1968 ; Ishida, 1970 ; Schweitzer, 1974 ; Christophel, 1976 ; Basinger, 1981, 1991 ; Uemura, 1988, 1990 ; Ozaki, 1991 ; Budantsev, 1992 ; Yamakawa, 1993 ; Momohara *et al.*, 1993 ; Momohara, 1994a, b).

Although the fossil records of *Glyptostrobus* are relatively extensive, aspects of its evolutionary history and intergeneric relationships within the Taxodiaceae are poorly understood. While most of these reports are based on well-preserved, morphologically informative compression fossils, anatomical data are rare and limited to reports of leaves (Basinger, 1981) and wood (Watari, 1947 ; Suzuki *et al.*, 1989 ; Itoh, 1993). Based on data derived from immunological (Price and Lowenstein, 1989) and DNA analyses (Chase *et al.*, 1993), Ohsawa (1994) concluded that the genus probably first appeared sometime during the early Tertiary.

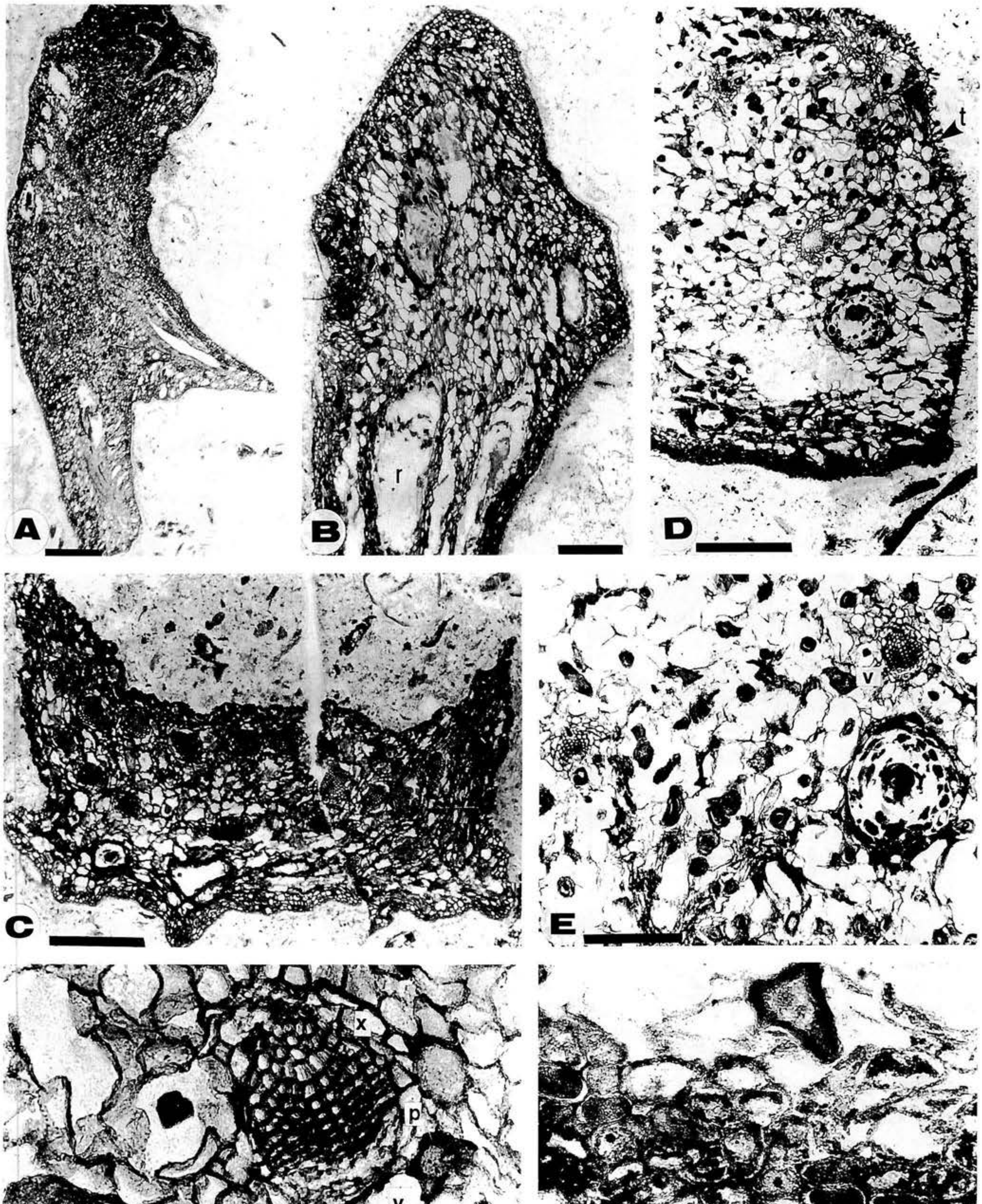
Evolutionary history of *Glyptostrobus*

The fossil records indicate that the genus was much more widespread than today. Florin (1963) suggested that the genus was concentrated in three regions throughout the northern hemisphere : western North America, Europe, and Asia. In western North America the genus extended from Montana to Alaska during the Upper Cretaceous to Lower Paleocene. This was thought to be the center of origin (Bell, 1949, 1957 ; Brown, 1962 ; Christophel, 1976). By the Late Paleogene and Early Neogene *Glyptostrobus* was widespread, but appears to have disappeared from North America by the end of the Miocene (Basinger, 1991).

In Eurasia, *Glyptostrobus europaeus* was widely distributed from the Eocene to Pliocene (Wolfe and Tanai, 1980). The Asian region, including southeastern Siberia, Korea, Sakhalin and Japan is considered to be the secondary center of distribution. In Japan, the genus is well known from the Pliocene deposits (Miki, 1957), with fossil representatives of *Glyptostrobus pensilis* becoming rare in the Early Pleistocene (Momohara *et al.*, 1993). The genus survived into the first warm interglacial of the Pleistocene (Florin, 1963).

We mentioned above that the Eurasian species *Glyptostrobus europaeus* was widely distributed in the northern hemisphere during the Tertiary, and is difficult to distinguish from the North American species, *G. nordenskioeldii* from the Oligocene to Miocene, which are represented by impressions or compressions of foliage and cones. We reconstruct generalized paleogeographic distribution of the genus *Glyptostrobus* in the northern hemisphere of the late Middle Miocene (Figure 12). Data on distribution of fossil and living *Glyptostrobus* include specimens referred to Florin (1963) and previous data.

Figure 9. Transverse and longitudinal sections of the bract-scale complex of *Glyptostrobus rubenosawaensis* sp. nov. **A.** Longitudinal section showing the angle of divergence between the bract and scale (#94081402). **B.** Enlargement of specimen in Figure 8A showing large resin canals and hypodermal cells (#94081402). **C.** Transverse section showing vascular strands arranged in two rows (#903005). **D.** Transverse section of the bract-scale complex showing epidermis, hypodermis, resin canals, vascular bundles, parenchyma, and trichomes (#94081404). Note the 2-5 layers of hypodermis and trichomes on the abaxial surface. **E.** Enlargement of specimen in Figure 9D (#94081404). **F.** Enlargement of specimen in Figure 9D showing vascular bundle. (#94081404). **G.** Enlargement of specimen in Figure 9C showing epidermis and hypodermis (#94081404). ep : epidermis, p : phloem, v : vascular bundle, x : xylem. Scale bars : A=800 μm ; B-D=400 μm ; E=200 μm ; F, G=50 μm.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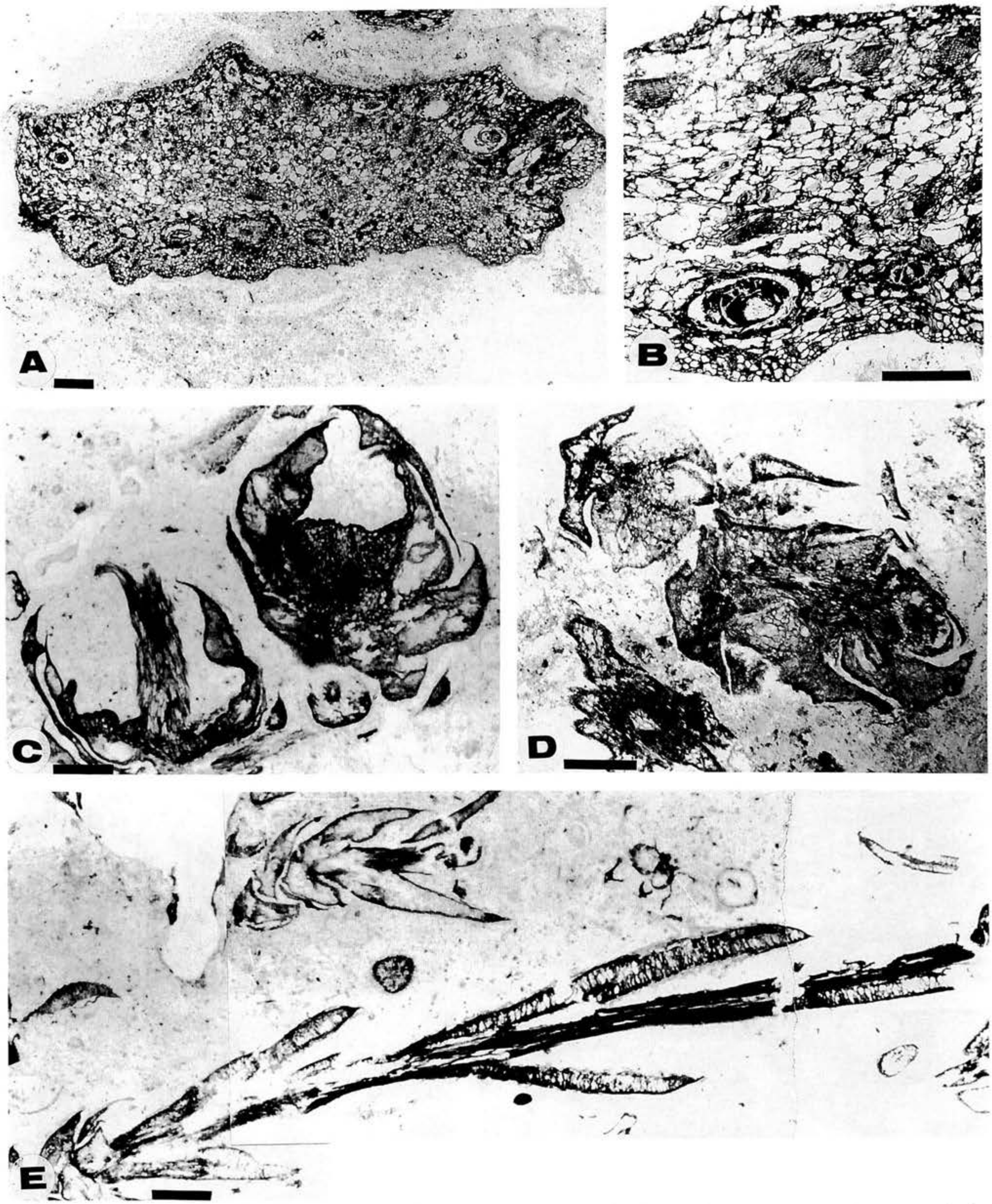

Figure 10. Transverse and longitudinal sections of seed cones and shoots of *Glyptostrobus rubenosawaensis* sp. nov. **A.** Cross section of cone scale showing vascular strands and resin canals on abaxial and adaxial surfaces (#94081402). **B.** Cross section of cone scale showing arrangement of vascular bundles and resin canals (#903005). **C.** Longitudinal section of the basal region of a cone scale (#94081402). **D.** Transverse section of the basal region of a cone scale (#94081402). **E.** Longitudinal and slightly oblique section of a cone scale and shoots (#94081402). Scale bars : A–D=400 μm ; E=800 μm.

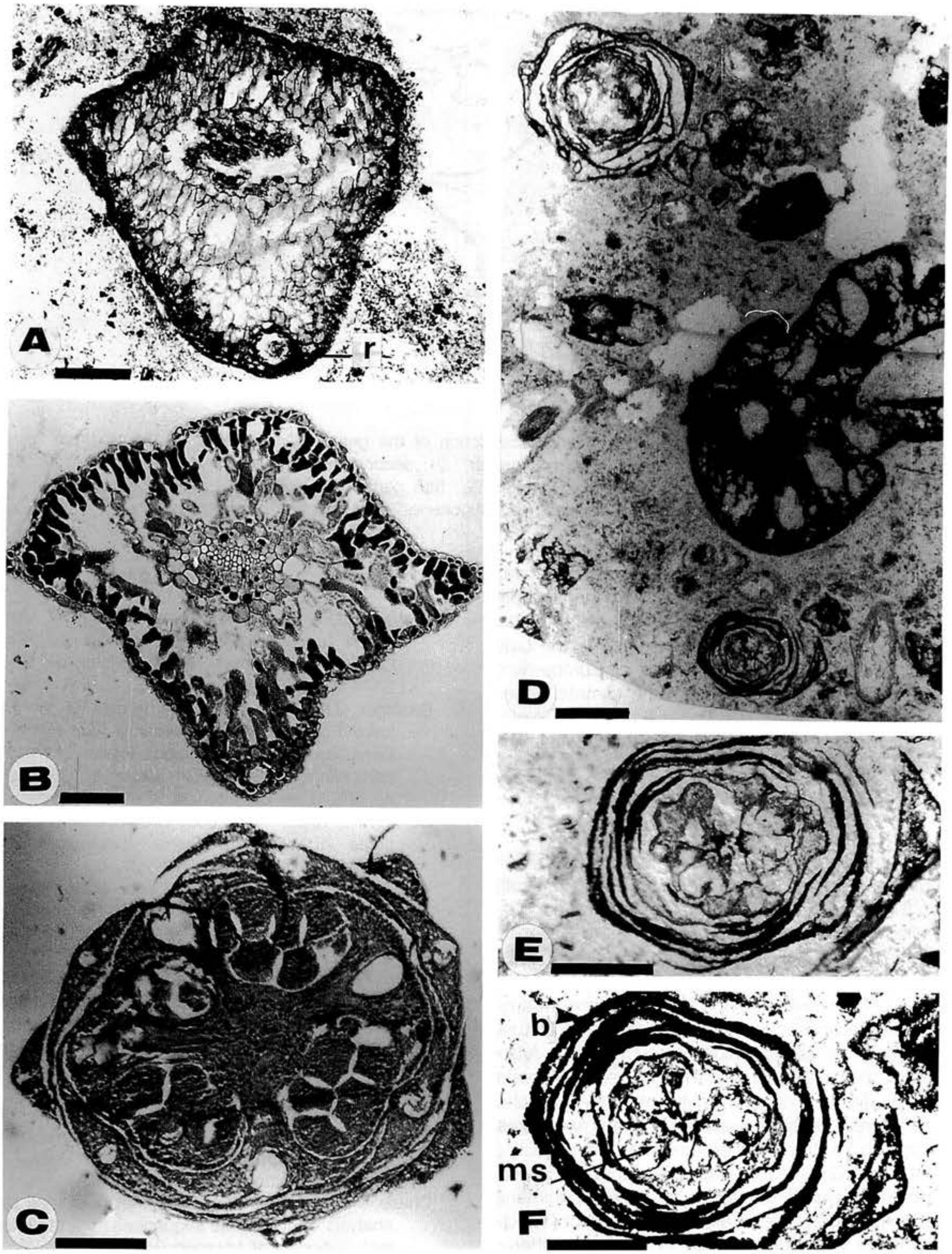

Figure 11. Transverse section of leaves and pollen cones of *Glyptostrobus rubenosawaensis* sp. nov. and leaf of *G. pensilis*. **A.** Leaf showing resin canal and vascular bundle (#94081402). Compare with Figure 11B. **B.** Leaf of living *Glyptostrobus pensilis* showing resin canal and vascular bundle (#950529). Compare with Figure 11A. **C.** Pollen cone showing the microsporophyll and microsporangia (#941125). **D.** Pollen cones. (#903000). **E-F.** Enlargement of specimens Figure D (#903000). b : bract, ms : microsporangia, r : resin canal. Scale bars : A, B=100 μm ; C, E=400 μm ; F=800 μm.

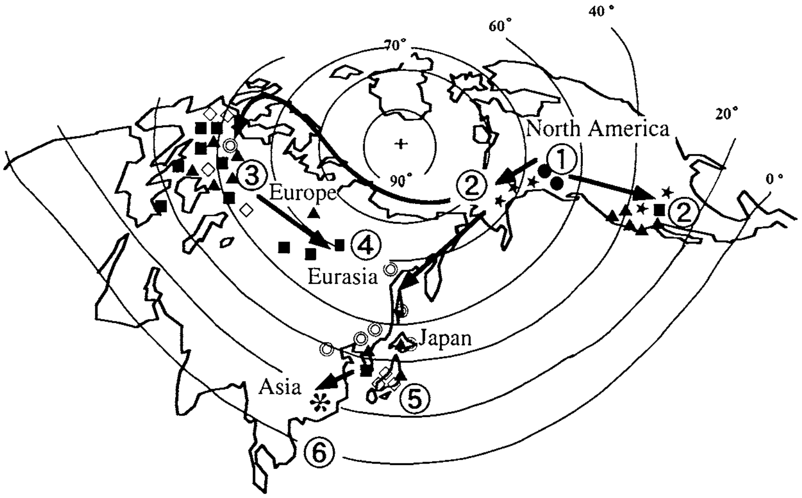

Figure 12. Generalized paleogeographic reconstruction of the genus *Glyptostrobus* in the northern hemisphere, showing the distribution orders. ①: first center, ②: second center, ③: third center through Thulian Route, ④: fourth center through Beringian Corridor, ⑤: fifth center, in Japan, ⑥: present distribution. ●: Upper Cretaceous, ★: Paleocene, ◎: Eocene, ■: Oligocene, ▲: Miocene, ◇: Pliocene, ＊: Present.

By the Miocene, the distribution of *Glyptostrobus* was becoming restricted as climate in the northern hemisphere cooled (LePage and Basinger, 1995). In North America, *Glyptostrobus* appears to have become extinct by the Late Miocene. *Glyptostrobus* became extinct in Europe and Japan at the end of the Pliocene when the climate turned more arid (Figure 12; Miki, 1957). The discovery of *Glyptostrobus rubenosawaensis* suggests diversification within the genus in the Tertiary.

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