Int. J. Plant Sci. 155(6):806–815. 1994.

1058-5893/94/5506-0020$02.00

UPPER CRETACEOUS ARAUCARIAN CONES FROM HOKKAIDO AND SAGHALIEN: ARAUCARIA NIPPONENSIS SP. NOV.

RUTH A. STOCKEY,[1] HARUFUMI NISHIDA, AND MAKOTO NISHIDA

Department of Botany, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada; The International Budo University, 841-Shinkan, Katsuura City, Chiba 299-52, Japan; and Research Institute of Evolutionary Biology, 2-4-28 Kamiohga, Setagaya 158, Japan

Six ovulate, permineralized cones, four cone-scale complexes, and one isolated seed are described from the Upper Cretaceous Upper Yezo and Miho Groups from Hokkaido, Japan, and Saghalien, Russia. Cones are spherical, 3.5–6.0 cm in diameter, with prominent thick bracts. Thick ovuliferous scales are almost completely united with the bracts and are not readily distinguishable on all scales. Cone-scale tissues consist of prominent abaxial and adaxial sclerenchyma bands with a central zone of thin-walled cells filled with dark contents that are often missing in abraded cones. Cone-scale vasculature is located in the thin-walled cells of this central zone. There is one large ovule per cone-scale complex with a thick sclerotesta showing a zigzag sclereid pattern. The nucellus is free from the integument except at the chalaza and shows a prominent wavy apex. Megagametophytes and embryos with two cotyledons are poorly preserved but are present in a few seeds. The presence of pollen tubes in the nucellar tissues of a fossil araucarian is demonstrated for the first time in these cones. Cones can be distinguished from those of *Araucaria nihongii* by a larger overall size at maturity, the structure of the cone-scale and its tissue composition, the lack of a bract abscission layer, and a thicker ovuliferous scale without a prominent "ligular sulcus." These cones show similarities to the South American section *Araucaria* (= *Columbea*) species and are known to have shed their scales at maturity.

Introduction

The conifer family Araucariaceae, while mostly confined to the Southern Hemisphere today, has an extensive fossil record in the Northern Hemisphere during the Mesozoic (Stockey 1982). Araucarian ovulate cones, in particular, have been reported in England (Stockey 1980*a*, 1980*b*), Japan (Stockey et al. 1993), and the United States (Stockey 1993). While leaf remains of this family must have cuticular remains preserved to be positively described as araucarian (Stockey and Ko 1986; Stockey and Atkinson 1993), cone material is best identified from permineralized specimens.

In this study we describe several permineralized cones, isolated cone-scale complexes, and one seed from the Upper Cretaceous of Japan and Saghalien. These constitute the second report of permineralized araucarian cone remains from Asia and their excellent preservation has allowed close comparison with extant araucarian cones and the description of a new species, *Araucaria nipponensis* Stockey, Nishida, et Nishida.

Material and methods

Six cones or cone fragments, four isolated cone-scale complexes, and one isolated seed have been identified from several localities in the Late Cretaceous Upper Yezo and Miho Groups from the islands of Hokkaido, Japan, and Saghalien, Russia (table 1; fig. 1). Cone material is permineralized in calcite nodules with varying amounts of silica (Stopes and Fujii 1910). Nodules have been eroded from shales in stream beds and are dated as Turonian, Coniacian, and Santonian based on the included ammonites and inoceramids (Matsumoto 1938, 1954, 1977; Matsumoto et al. 1976; Hirano et al. 1977; Nishida and Nishida 1986).

Plant material in these deposits is mostly debris that probably has been carried some distance from its original growth habitat. Bored wood fragments, short segments of foliage, and the absence of cuticle, epidermis, and often hypodermis on leaves of *Pinus* and other conifers have been noted (Stockey and Nishida 1986; Stockey and Ueda 1986). Several of the specimens here show evidence of erosion and some missing tissues because of transport and abrasion prior to final deposition.

Nodules containing cone material were studied using the cellulose acetate peel technique (Joy et al. 1956). Peel sections were mounted with Entellan or Eukitt rapid mounting media for microscopic examination. All specimens are housed in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, Chiba 260, Japan.

Systematics

ORDER — CONIFERALES

FAMILY — ARAUCARIACEAE

GENUS — ARAUCARIA

SPECIES — A. NIPPONENSIS SP. NOV. STOCKEY, NISHIDA, ET NISHIDA

DIAGNOSIS. Spherical to subspherical cones, 3.5–6.0 cm in diameter, terminal on vegetative

[1] Author for correspondence and reprints.

Manuscript received February 1994; revised manuscript received May 1994.

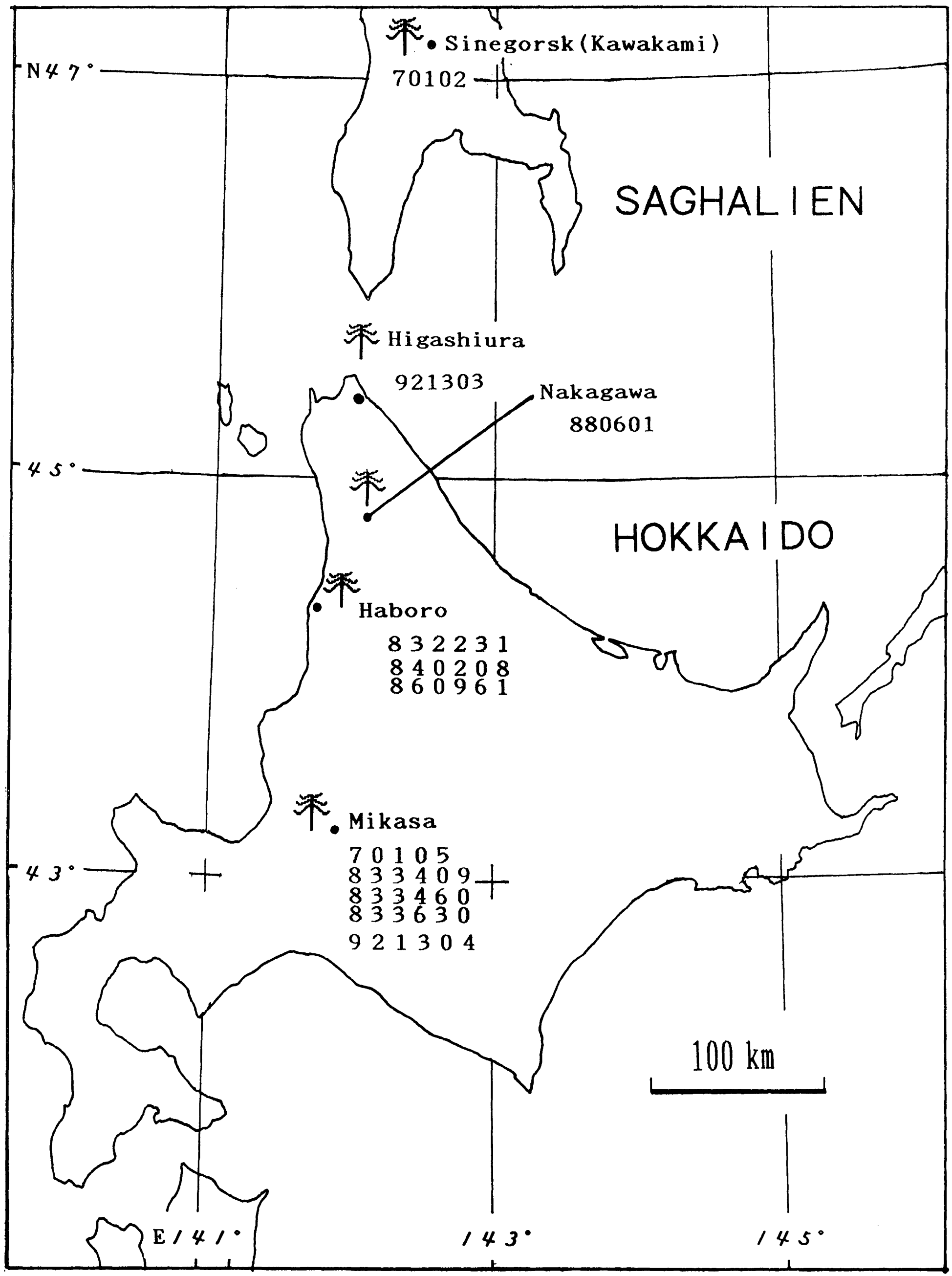


Fig. 1 Localities from which *Araucaria nipponensis* are known are indicated by tree symbols. Specimen numbers are listed beneath.

branches. Cone peduncle with small rhomboidal leaves, 2.5–3.0 mm long, grading into cone scales. Pith of cone axis parenchymatous with scattered sclereid nests. Resin canals and sclereid nests numerous in cortex of cone axis, lacking in xylem. Primary xylem with helical secondary wall thickenings; secondary xylem with uniseriate to biseriate, alternate circular bordered pits. Helically arranged cone-scale complexes. Bracts winged, ovuliferous scales fused to bract, with small or no ligular sulcus. One deeply sunken ovule per cone-scale complex, micropyle facing cone axis. Sclerotesta of branched sclereids in zigzag pattern. Nucellus free from integument except at base, apex wavy. Embryo dicotyledonous.

Holotype. Specimen no. 921303.

Paratypes. 70102, 70105, 832231, 833409, 832460, 833630, 840208, 860961, 880601, 921304.

Locality of holotype. Higashiura, Wakkanai-shi, Hokkaido, Japan.

Table 1

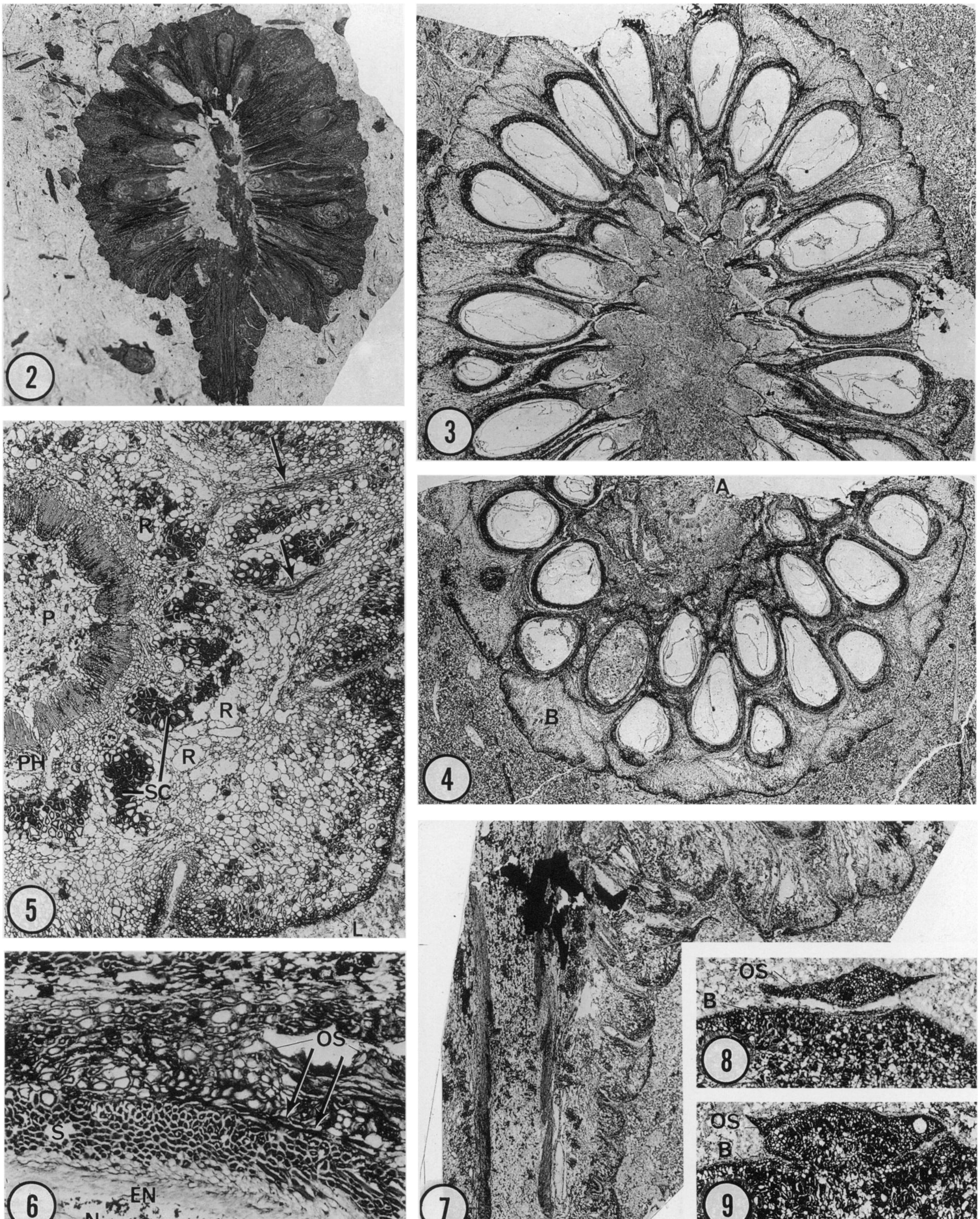
ARAUCARIAN CONES FROM HOKKAIDO AND SAGHALIEN

Specimen	Locality	Collector	Age
70102, cone	Saghalien, near Kawakami coal mine	S. Mabuchi	Lower Turonian-Santonian, Miho Group
70105, cone	Horomoizawa, Ikushumbetsugawa, Mikasa	M. Koshisaka	Coniacian-Santonian, Upper Yezo Group
832231, cone scale	Sankebetsugawa, Haboro	H. Nishida and M. Nishida	Santonian Upper Yezo Group
833409, seed	Kumaoizawa, near Lake Katsurazawako, Ikushumbetsu, Mikasa	T. Ohsawa, H. Nishida and M. Nishida	Coniacian, Upper Yezo Group
833460, cone scale	Kami-ichinosawa, near Lake Katsurazawako, Ikushumbetsu, Mikasa	H. Nishida and M. Nishida	Lower Turonian-Santonian Upper Yezo Group
833630, cone scale	Ashiyachizawa, near Lake Katsurazawako, Mikasa	H. Nishida and M. Nishida	Coniacian Upper Yezo Group
840208, cone scale	Sankebetsugawa, Haboro	M. Nishida	Santonian Upper Yezo Group
860961, broken cone	Pissiri-do, Sankebetsugawa, Haboro	T. Yokoi	Santonian Upper Yezo Group
880601, nearly complete cone x.s.	Nigorigawa, Nakagawamachi	M. Nihongi	Coniacian-Santonian Upper Yezo Group
921303, nearly complete cone w/attached branch	Higashiura, Wakkanai-shi (holotype)	T. Hasekura	Turonian Upper Yezo Group
921304, ½ cone	Kumaoizawa, Mikasa	M. Nihongi	Coniacian Upper Yezo Group

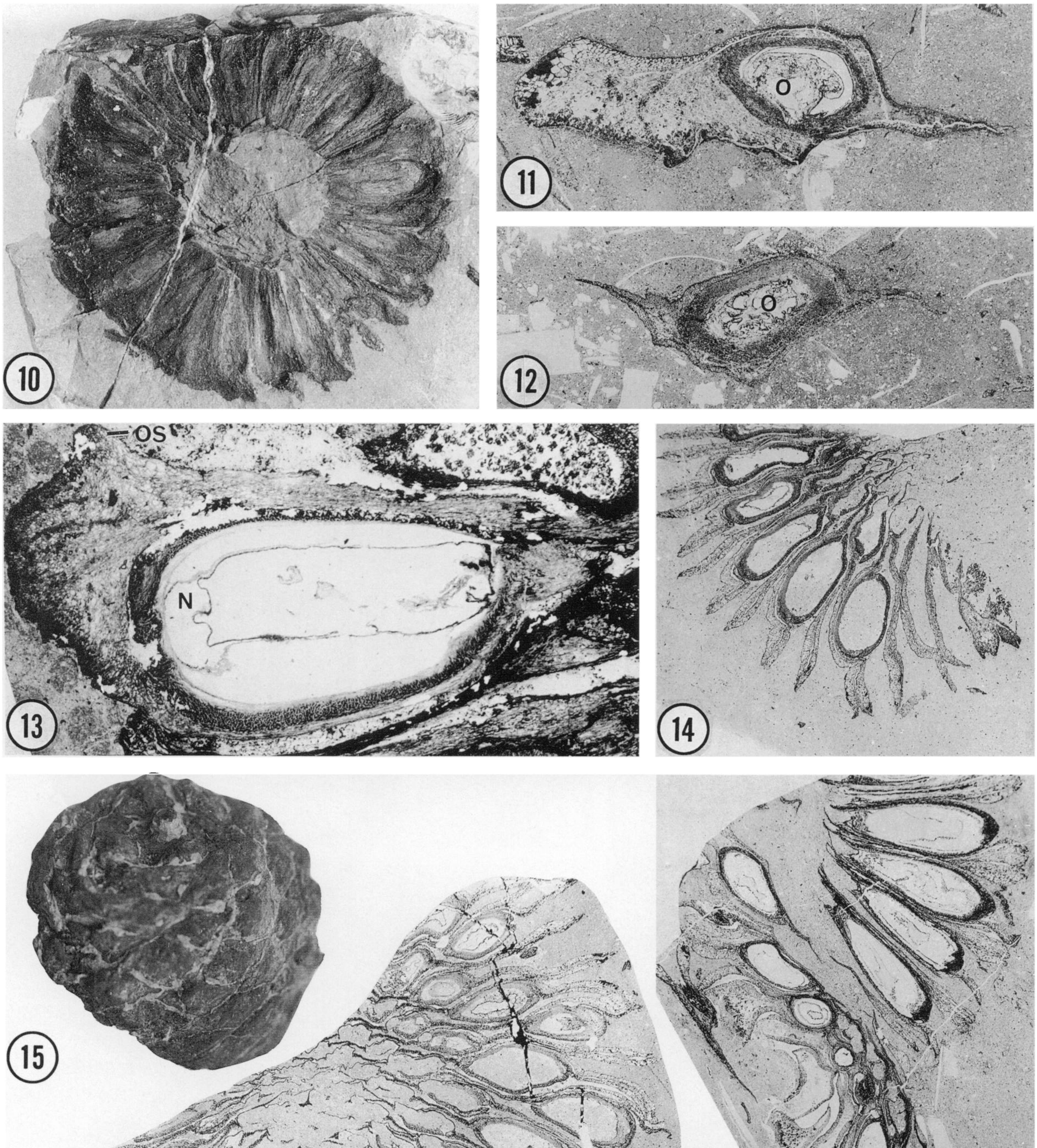
STRATIGRAPHY. Upper Cretaceous, Upper Yezo Group (Turonian).

DESCRIPTION. Of the six cones, two are complete or nearly complete (table 1; figs. 2, 10). Four isolated cone scales of the same morphology have been identified (figs. 11, 12), as well as one isolated seed. The holotype has an attached peduncle and was borne terminally on a leafy branch (figs. 2, 7). The holotype specimen (921303) was chosen because it was the most complete cone and also had internal preservation of the cone axis. Most cone specimens lack preservation in the axis region (figs. 10, 14, 17). The holotype, however, is an immature cone (figs. 2–9). The presence of three distinct integumentary layers in the ovules, a sclerotesta that is only partially sclerotized (fig. 6), its small size, and lack of mature embryos probably indicate that this is an immature cone.

Cones are spherical to subspherical, ranging in size from 3.5 to 6.0 cm in diameter (figs. 2, 10). They are borne on the tips of branches with rhomboidal scale-like leaves, 2.5–3.0 mm long, that grade into cone scales (figs. 5, 7). The pith of the cone axis as well as that of the peduncle is parenchymatous with scattered sclereid nests (figs. 5, 7). The cone is vascularized by a ring of slender vascular bundles (fig. 18) and a narrow vascular cylinder in the cone peduncle (figs. 5, 7). Primary xylem is endarch, and tracheids show helical secondary wall thickenings. Secondary xylem in the peduncle, from 12 to 26 tracheids in thickness, contains numerous uniseriate rays (fig. 5). Tracheids show uniseriate to biseriate circular bordered pits on their radial walls. The cortex of the cone axis and peduncle is parenchymatous and like the pith contains numerous scattered sclereid nests (fig. 5). Numerous resin canals occur in the



Figs. 2–9 *Araucaria nipponensis* sp. nov. Holotype. Fig. 2, Longitudinal section of cone in matrix showing attachment to leafy branch; 921303 B; × 1.4. Fig. 3, Longitudinal section of cone showing ovules; 921303 A side #55; × 2.5. Fig. 4, Cross section of cone showing axis and broadly winged bract; 921303 A bot #5; × 2.5. Fig. 5, Cross section of cone bearing branch showing ring of vascular tissues and traces to leaves (arrows); 921303 B bot #1; × 16. Fig. 6, Cross section of ovule embedded in ovuliferous scale tissue showing immature integument. Arrows indicate sarcotesta; 921303 A side #51; × 46. Fig. 7, Longitudinal section of cone peduncle with cone scales grading to small leaves on attached branch; 921303 B/C side #2; × 5. Fig. 8, Tangential section of cone showing separate ovuliferous scale and bract; 921303 A side #12; × 14. Fig. 9, Longitudinal section of cone showing lateral separation of ovuliferous scale and bract; 921303 A side #16; × 14. *A*, axis; *B*, bract; *EN*, endotesta; *L*, leaf; *N*, nucellus; *OS*, ovuliferous scale; *P*, pith; *PH*, phloem; *R*, resin canal; *S*, sclerotesta; *SC*, sclerenchyma.



Figs. 10–17 *Araucaria nipponensis* sp. nov. Fig. 10, Cross section of mature cone with tissue in axis region not preserved; 880601; × 1. Fig. 11, Cone-scale complex in longitudinal section showing one embedded ovule; 832231 C side #25; × 5. Fig. 12, Cross section of winged cone-scale complex showing one embedded ovule; 840208 C top #7; × 5. Fig. 13, Longitudinal section of cone-scale complex showing inverted ovule and ovuliferous scale represented by an adaxial bulge; 70102 A #1; × 8. Fig. 14, Oblique longitudinal section of abraded cone showing sunken ovules; 880601 D #5; × 2. Fig. 15, External surface of cone apex showing winged cone-scale complexes; 70102; × 1. Fig. 16, Tangential section of abraded cone showing lack of cortical preservation at center; 880601 A #5; × 2. Fig. 17, Longitudinal section of crushed cone; 860961 A #19; × 1.6. *O,* ovule; *OS,* ovuliferous scale; *N,* nucellus.

cortex of both the cone axis and peduncle (figs. 5, 18) but are lacking in the pith and the vascular tissues.

Since all of the cones described here probably have been transported some distance prior to their burial and fossilization, it is difficult to describe the external surface completely. Cone-scale complexes are helically arranged. Bracts are winged and fairly thick (figs. 3, 4, 11, 13, 15). Ovuliferous scales are not usually seen in most cone-scale complexes. In others, ovuliferous scales are visible but are fused to the bract completely and represented by a small protrusion on the adaxial side of the bract (fig. 13). In one cone, however, distinct ovuliferous scales were visible (figs. 8, 9). The line of separation of the ovuliferous scale and bract, the "ligular sulcus" (Wieland 1935; Wilde and Eames 1948), is very small. Only the last millimeter or so is free from the bract. In transverse sections of the cone-scale complex, the ovuliferous scale separates from the edges of the bract first (fig. 9). This cone is immature; however, the separate nature of bract and scale was probably not visible in mature cones. Cone-scale tissues are distinctly zoned. There are two broad bands of sclerenchyma cells (abaxial and adaxial) (figs. 19, 21, 23, 30). These tissues are usually preserved even in cones that have been abraded and crushed (figs. 14, 16, 17). The intervening tissues are parenchymatous with scattered sclereid nests (figs. 21, 27). These tissues are usually filled with dark contents (figs. 19, 23) and not preserved in abraded cones.

The central parenchymatous zone also contains the vascular system of the cone-scale complex (fig. 27). It is difficult to determine the mode of trace divergence from the axis stele since few specimens have this region preserved. Phloem is usually not preserved, and diagenetic changes to the tissues surrounding the axis region are possible. Since cone axes are primarily parenchymatous and broad, preservation in this zone is less likely than other areas of the cone. In one cone the vascular strand appears to be single (fig. 22), but it rapidly separates into two strands (fig. 24). However, there may, in fact, be two strands at the origin in the axis stele (fig. 22, arrows). A mineral fracture in this zone makes these tissues difficult to interpret. Whether or not there are two strands at the source in the axis stele, separate bract and ovuliferous scale traces appear in the outer cortex (fig. 18). Vascularization of the ovule is seen in some cones, and two vascular strands have been identified in the sclerotesta (fig. 26). There is no vascular plexus at the base of the ovule (fig. 21), as is seen in the cones of *Araucaria* Section *Bunya* (Wilde and Eames 1948).

There is one ovule per cone-scale complex that is deeply embedded in ovuliferous scale tissue with its micropyle directed toward the cone axis (figs. 11–14, 21, 23). Integuments are three-layered with an endotesta of thin-walled cells about four cells thick in immature ovules (fig. 6). The sclerotesta in mature cones is composed of interlocking branched sclereids several cells thick (fig. 20). In immature cones the wall thickening of the inner sclereids is not yet complete (fig. 6), and the endotesta is represented by one to two layers of elongated thin-walled cells (fig. 6, *EN*). This layer is not often visible and is probably crushed in the most mature cones. The integument of the upper surface of the ovule is in contact with the adaxial scale sclerenchyma (fig. 6). Ovules are embedded in the thin-walled parenchyma of the scale (figs. 19, 21).

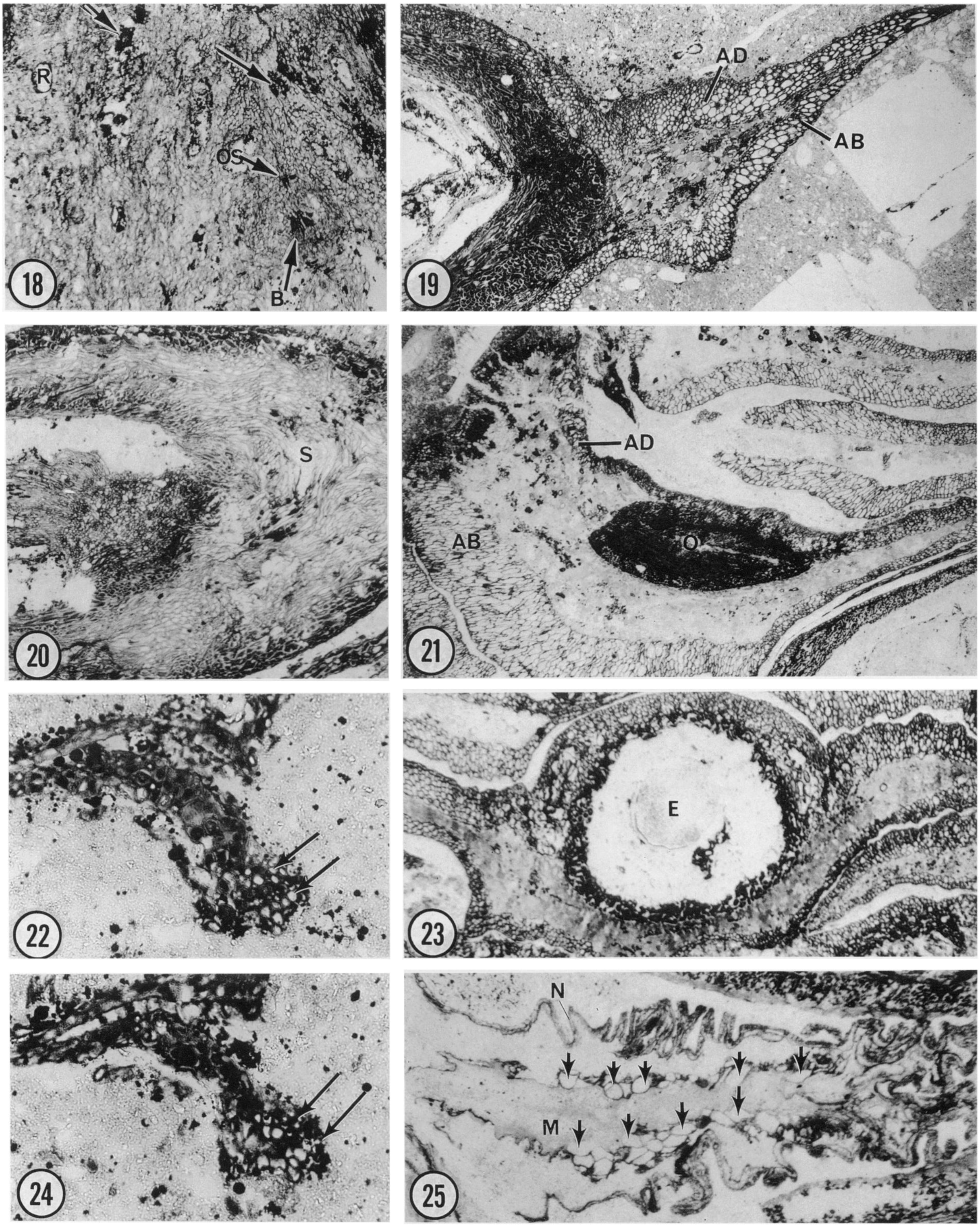
The nucellus is free from the integuments except at the chalaza (fig. 13). The nucellar apex, as in extant araucarians, is wavy and highly folded near the micropyle (figs. 25, 28). The megaspore membrane, as in extant araucarians, is thin in comparison to the thick nucellus (fig. 25). Megagametophyte tissue is present in some seeds; however, cell walls are difficult to discern (figs. 25, 28, 29, 31, 32). Embryos with two laminar cotyledons are also present in several seeds of the mature cones (figs. 23, 28–32).

In one cone, structures that appear to be pollen tubes have been preserved (fig. 25, arrows). Inside of the nucellus and in contact with the megaspore membrane are numerous branched tubes 80–150 μm in diameter that have the general appearance of araucarian pollen tubes. These structures cover the apex of the megagametophyte (fig. 25).

Discussion

The spherical shaped cones, with helically arranged cone-scale complexes, prominently winged bracts, large pith in the cone axis, cortical resin canals, and one seed per ovuliferous scale show the general characteristics of cones from the family Araucariaceae. The presence of a ligular sulcus, or space between the ovuliferous scale tip and the bract, and wingless seeds embedded in ovuliferous scale tissue indicate affinities with the genus *Araucaria.* Not all cones show a distinct separation between bract and scale as is characteristic of all extant *Araucaria,* however. The fusion of bract and scale in the genus *Agathis* has been noted (Eames 1913). However, cones of *Agathis* have winged seeds, unlike the deeply embedded seeds of *Araucaria.* We have observed cone scales of *Araucaria angustifolia* from Brazil, however, in which bract and scale are fused for most or all of their length at maturity. Fossil cones thus fit into the genus *Araucaria.*

The general cone structure with woody winged bracts and thick, but short, ovuliferous scales shows features of both the section *Eutacta* and section *Araucaria* (= *Columbea*). Scales were very woody, based on the abaxial and adaxial scleren-



Figs. 18–25 *Araucaria nipponensis* sp. nov. Fig. 18, Cross section of cone axis region (pith near top) showing small vascular bundles (unlabeled arrows), resin canals (*R*), separate bract (*B*), and ovuliferous scale traces in the outer cortex; 70102 A #4; × 22. Fig. 19, Cross section of cone-scale complex showing sclerotic abaxial (*AB*) and adaxial (*AD*) tissues and intervening parenchyma cells with dark contents; 840208 B bot #23; × 19. Fig. 20, Oblique longitudinal section of ovule showing elongate, tightly packed sclereids of the integument; 880601 A #8; × 25. Fig. 21, Oblique longitudinal section of cone-scale complex showing ovule (*O*) embedded in parenchymatous tissues between abaxial (*AB*) and adaxial (*AD*) sclerenchyma; 860961 A #7; × 9. Fig. 22, Cross section of vascular trace to cone-scale complex. Arrows show the position of two possible traces; 880601 A #10; × 100. Fig. 23, Cross section of cone-scale complex showing seed embedded in parenchymatous tissue with possible embryo (*E*); 860961 A #19; × 20. Fig. 24, Cross section of vascular trace to cone-scale complex. Arrows show the position of

chyma bands, like those of the South American section *Araucaria* species. Bracts are distinctly winged like those of the section *Eutacta* and not as thin and expanded as those of section *Intermedia* from New Guinea. Although these cones have been abraded, there is no indication of a deciduous laminar tip even in the most completely preserved specimens, as is seen in *Araucaria nihongii* from the same localities and preserved under the same conditions. Ovules are vascularized by two strands and do not show a vascular plexus near the chalaza as in section *Bunya* species from Australia or section *Bunya* fossils from England and Argentina (Stockey 1975, 1980*a,* 1982).

Embryos are not as well preserved as those of *A. nihongii* from the same localities. They do have two laminar cotyledons similar to embryos of *Araucaria* Section *Intermedia* or the genus *Agathis* (Rouane and Woltz 1979; Woltz 1986). Some cones of section *Eutacta* have also been reported with two cotyledons (Rouane and Woltz 1980); however, most species have four cotyledons per embryo in this widespread South Pacific group of *Araucaria.* Embryos of section *Bunya,* i.e., *Araucaria bidwillii,* have two cotyledons that fuse into a cotyledonary tube and that separate distally (Rouane and Woltz 1980; Burrows et al. 1992). Unfortunately, preservation of these embryos does not allow as complete a description as that of *A. nihongii* (Stockey et al. 1993). The position of vascular bundles and resin canals are unknown in embryos of *Araucaria nipponensis.*

Araucaria nipponensis cones can be distinguished from those of *A. nihongii* from the same localities by their overall larger size at maturity, the presence of sclerenchymatous cone-scale tissues, the apparent lack of a deciduous laminar tip on the bract, and a thicker ovuliferous scale with little or no ligular sulcus at maturity. Cones of *A. nihongii* have papery thin ovuliferous scales like those of section *Eutacta* and *Intermedia.* Therefore, we have designated the current suite of cones as representing a new species.

Araucaria nipponensis, like *A. nihongii* and *Araucaria brownii* from the Jurassic of England, shows characters of several sections of the genus. Stockey et al. (1993) suggested that these cones represented a generalized araucarian cone type that was present in the Northern Hemisphere in the Jurassic and Cretaceous showing characters of at least three of the four sections of the genus. Unlike cones of section *Bunya,* a group that includes extant *A. bidwillii,* the fossils *Araucaria sphaerocarpa, Araucaria mirabilis,* and probably *Araucarites bindrabunensis* (Vishnu-Mittre 1954), these cones lack a vascular plexus at the base of the ovule, a vascularized ovuliferous scale tip, and perhaps a double vascular strand, although this character is extremely difficult to interpret in fossil cones. Leaves borne on the branches that bear these cones are rhomboidal in outline and similar to adult foliage of *Araucaria* section *Eutacta* (Stockey 1982).

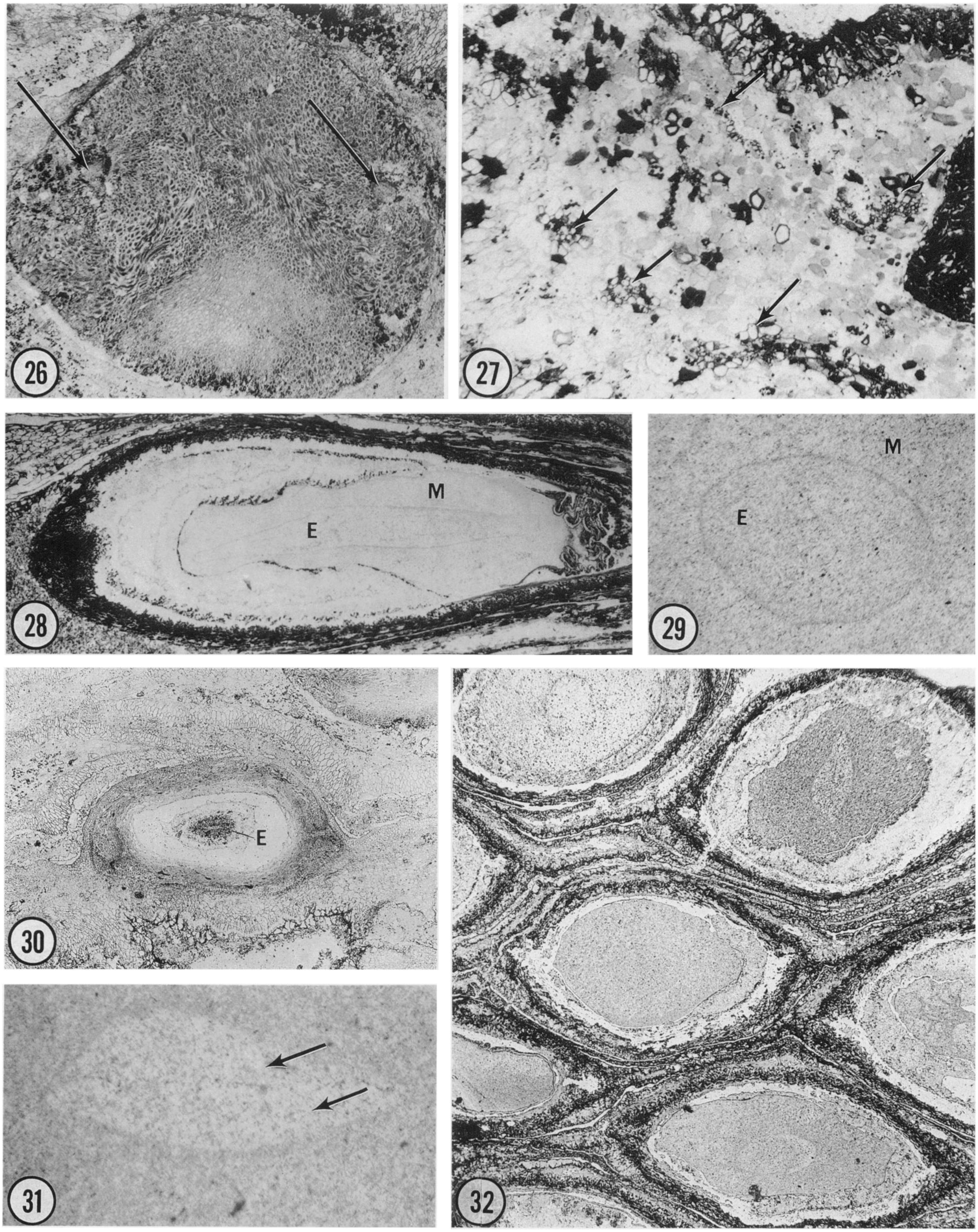
Cone scales were shed as a unit, as in most living araucarians (Stockey 1980*b*). Isolated scales of this type are common at some Hokkaido localities, such as Kumaoizawa. The lack of an obvious ovuliferous scale on these cone scales would make them appear similar to those dispersed compression/impression specimens described by White (1981) from Australia, Brown (1977) from South Africa, and Berry (1926) from the Atlantic Coastal Plain. These fossils, however, are not anatomically preserved, and their affinities must remain in doubt at the present time.

The presence of pollen tubes in the nucellar tissues of *A. nipponensis* is noteworthy, as this is, to our knowledge, the first report of pollen tubes in fossil conifer cones. Although fossil pollen tubes have been reported in gymnosperms of Pennsylvanian age (Rothwell 1972), this is indeed a rare occurrence in the fossil record. In extant araucarians, Eames (1913, pl. 1, figs. 9, 10) illustrated the pollen tubes of *Agathis australis* and discussed the corrosive nature of these tubes to the cone tissues and their branched nature. Pollen tubes of *A. angustifolia* (= *A. brasiliensis*) described by Burlingame (1914, pl. 26, figs. 28, 29) are similar in appearance to those in the fossil material and in the same size range. Occasional branching is reported in this extant species. Of the 11 specimens described here, only one shows pollen tubes preserved. These tubes appear to branch as in *A. angustifolia, Ginkgo biloba* (Friedman 1987), and *Zamia furfuracea* (Choi and Friedman 1991).

The new taxon shows characters of *Araucaria* Sections *Eutacta, Intermedia,* and *Araucaria* with closest similarities to section *Araucaria* species. The complete fusion of bract and scale in most specimens is similar to that reported for *Agathis* and at least one *Araucaria* species, but all other characters are *Araucaria*-like. This second report of permineralized *Araucaria* from the Cretaceous of Hokkaido and Saghalien shows the importance of these Cretaceous localities to our understanding of the diversity of these conifers and their past distributions.

←

two possible traces with intervening mineral fracture; 880601 A #9; × 100. Fig. 25, Longitudinal section of nucellar apex showing pollen tubes (arrows) surrounding the megagametophyte (*M*); 860961 A #2; × 22. *B,* bract trace; *N,* nucellus; *OS,* ovuliferous scale trace.



Figs. 26–32 *Araucaria nipponensis* sp. nov. Fig. 26, Cross section of ovule near chalaza showing two vascular strands (arrows) in sclerotesta; 70102 B #4; × 18. Fig. 27, Oblique longitudinal section of cone-scale parenchyma showing scattered sclereids and vascular strands near base of ovule (at right); 860961 A #7; × 27. Fig. 28, Longitudinal section of seed with embryo (*E*); 860961 A #19; × 8. Fig. 29, Cross section of embryo (*E*) in megagametophyte (*M*) tissue; 860961 A #1; × 30. Fig. 30, Cross section of cone-scale complex showing abaxial and adaxial sclerenchyma and seed with cellular embryo tissue in center; 70102 A side #4; × 8. Fig. 31, Cross section of embryo with two laminar cotyledons (arrows); 860961 A #1; × 30. Fig. 32, Cross sections of seeds with embryos; 860961 A #1; × 8. *E*, embryo; *M*, megagametophyte.

Acknowledgments

We thank Gar W. Rothwell and Takeshi Ohsawa for the use of laboratory facilities. This research was supported in part by Natural Sciences and Engineering Research Council of Canada grants A6908 and ICR145941 to Ruth A. Stockey and Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan no. 04640644 to Harufumi Nishida.

Literature cited

Berry EW 1926 Some araucarian remains from the Atlantic coastal plain. Bull Torrey Bot Club 35:249–260.

Brown JT 1977 On *Araucarites rogersii* Seward from the Lower Cretaceous Kirkwood Formation of the Algoa Basin, Cape Province, South Africa. Palaeontol Afr 20:47–51.

Burlingame LL 1914 The morphology of *Araucaria brasiliensis.* II. The ovulate cone and female gametophyte. Bot Gaz 56:490–508.

Burrows GE, TS Boag, RA Stockey 1992 A morphological investigation of the unusual cryptogeal germination strategy of bunya pine (*Araucaria bidwillii*)—an Australian rain forest conifer. Int J Plant Sci 153:503–512.

Choi J, WE Friedman 1991 Development of the pollen tube of *Zamia furfuracea* (Zamiaceae) and its evolutionary implications. Am J Bot 78:544–560.

Eames AJ 1913 The morphology of *Agathis australis.* Ann Bot 27:1–38.

Friedman WE 1987 Growth and development of the male gametophyte of *Ginkgo biloba* with the ovule (*in vivo*). Am J Bot 74:1797–1815.

Hirano H, T Matsumoto, K Tanabe 1977 Mid-Cretaceous stratigraphy of the Oyubari area, Central Hokkaido. Pages 1–10 *in* T Matsumoto, ed. Mid-Cretaceous Event-Hokkaido Symposium, 1976. Palaeontological Society of Japan Special Paper 21.

Joy KW, AJ Willis, WS Lacey 1956 A rapid cellulose peel technique in paleobotany. Ann Bot, NS, 20:635–637.

Matsumoto T 1938 A biostratigraphic study on the Cretaceous deposits of the Naibuti Valley, South Karahuto. Proc Imp Acad Jpn 14:190–194.

——— 1954 The Cretaceous system in the Japanese Islands. Japanese Society for Promotion of Scientific Research, Tokyo. 324 pp, 36 pls.

——— 1977 Zonal correlation of the Upper Cretaceous of Japan. Palaeontol Soc Jpn Spec Pap 21:63–74.

Matsumoto T, H Okada, H Hirano, K Tanabe 1976 Mid-Cretaceous Zonation in Japan. Ann Mus Hist Nice 33(4): 1–5.

Nishida M, H Nishida 1986 Structure and affinities of the petrified plants from the Cretaceous of northern Japan and Saghalien. III. Petrified plants from the Upper Cretaceous of Saghalien (1). Bot Mag Tokyo 99:191–204.

Rothwell GW 1972 Evidence of pollen tubes in Paleozoic pteridosperms. Science 175:772–774.

Rouane ML, P Woltz 1979 Apport de l'étude des plantules pour la taxonomie et l'évolution des Araucariacées. Bull Soc Bot Fr 126, Actual Bot 3:67–76.

——— 1980 Intéret des plantules pour la systématique et l'évolution des Araucariacées. Bull Soc Hist Nat Toulouse 116(1–2):120–136.

Stockey RA 1975 Seeds and embryos of *Araucaria mirabilis.* Am J Bot 62:856–868.

——— 1980*a* Anatomy and morphology of *Araucaria sphaerocarpa* Carruthers from the Jurassic Inferior Oolite of Bruton, Somerset. Bot Gaz 141:116–124.

——— 1980*b* Jurassic araucarian cone from southern England. Paleontology 23:657–666.

——— 1982 The Araucariaceae: an evolutionary perspective. Rev Palaeobot Palynol 37:133–154.

——— 1993 Mesozoic Araucariaceae: morphology and systematic relationships. XV International Botany Congress, Yokohama, Japan. Abst. p. 27.

Stockey RA, IJ Atkinson 1993 Cuticle micromorphology of *Agathis* Salisbury. Int J Plant Sci 154:187–225.

Stockey RA, H Ko 1986 Cuticle micromorphology of *Araucaria* de Jussieu. Bot Gaz 147:508–548.

Stockey RA, M Nishida 1986 *Pinus haboroensis* sp. nov. and the affinities of permineralized leaves from the Upper Cretaceous of Japan. Can J Bot 64:1856–1866.

Stockey RA, H Nishida, M Nishida 1993 Upper Cretaceous araucarian cones from Hokkaido: *Araucaria nihongii* sp. nov. Rev Palaeobot Palynol 72:27–40.

Stockey RA, Y Ueda 1986 Permineralized pinaceous leaves from the Upper Cretaceous of Hokkaido. Am J Bot 73: 1157–1162.

Stopes MC, K Fujii 1910 Studies on the structure and affinities of Cretaceous plants. Philos Trans R Soc Lond B Biol Sci 210:1–90.

Vishnu-Mittre 1954 *Araucarites bindrabunensis* sp. nov. a petrified megastrobilus from the Jurassic of Rajmahal Hills, Bihar. Palaeobotanist 3:103–108.

White ME 1981 Revision of the Talbragar Fish Bed Flora (Jurassic) of New South Wales. Rec Aust Mus 33:695–721.

Wieland GR 1935 The Cerro Cuadrado petrified forest. Carnegie Institute of Washington Publication 449. Carnegie Institute of Washington, Stanford, Calif.

Wilde MH, AJ Eames 1948 The ovule and 'seed' of *Araucaria bidwilli* with discussion of the taxonomy of the genus. I. Morphology. Ann Bot 12:311–326.

Woltz P 1986 Les *Podocarpus* (s.l.), origines et évolution. Étude des plantules; comparaison avec les familles de conifères de l'hémisphère sud. Thesis. Université Aix-Marseille III (St-Jérome).