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FOSSIL MEGASPORES OF MARSILEALES AND SELAGINELLALES FROM THE UPPER CONIACIAN TO LOWER SANTONIAN (UPPER CRETACEOUS) OF THE TAMAGAWA FORMATION (KUJI GROUP) IN NORTHEASTERN JAPAN

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Bulk sieving of sedimentary samples from upper Coniacian to lower Santonian (Upper Cretaceous) of the Tamagawa Formation (Kuji Group) in northeastern Japan has yielded more than 600 fossil megaspores, which comprise the first megaspore assemblage to be described from the Cretaceous of Japan. Megaspores were studied in detail with scanning electron microscopy, including fractures that allow examination of the wall structure. *Molaspora* (Marsileales) is the most distinctive component of the assemblage, with a spirally twisted acrolamella. The other megaspores share three laesurae and a granular exospore structure that is ordered to varying degrees. The most abundant megaspores are *Erlansonisporites* and *Verrutriletes*, followed by *Bacutriletes* and *Trileites*. The regular orientation of exospore granules in *Erlansonisporites* suggests a selaginellalean affinity. Evidence from the new assemblage indicates that the Marsileales and Selaginellales were components of the late Cretaceous paleoflora on the eastern side of Eurasia and expands previous knowledge of the Cretaceous vegetation of this region.

Keywords: bulk sieving, Cretaceous, Kuji Group, Tamagawa Formation, Marsileales, megaspores, Selaginellales.

Introduction

Plant fossils from Upper Cretaceous sediments in northeastern Japan have provided important data on the Cretaceous paleoflora and vegetation of eastern Asia. In particular, a rich and well-preserved assemblage of fossil plants has been recovered from marine deposits of the Yezo Group (Turonian-Santonian) in Hokkaido (Nishida 1991), and most recently, studies of small charcoalified or lignitized plant mesofossils (the Kamikitaba assemblage) from alluvial fan deposits in the Futaba Group (Coniacian-Santonian) have further extended the information available on Cretaceous pteridophytes, conifers, and angiosperms from northeastern Japan (Takahashi et al. 1999*a*, 1999*b*).

The Kuji Group (upper Coniacian–upper Campanian) outcrops in the vicinity of Kuji city in northern Honshu, Japan. Miki (1972) demonstrated that the palynoflora from the Tamagawa Formation of the Kuji Group was composed of spores of bryophytes and pteridophytes (58%), gymnosperm pollen (16%), and angiosperm pollen (22%) in terms of abundance. *Balmarisporites minutus* (= *Ghoshispora longirimosa*) was the only fossil megaspore recovered (Miki 1972). A comprehensive account of the leaf floras of the Kuji Group documented impression fossils of 11 pteridophytes, six conifers, and 10 angiosperms (Tanai 1979). Among pteridophytes, the fossil leaf impressions suggested the occurrence of Osmundaceae, Gleicheniaceae, and Aspleniaceae. This article describes, for the first time, an assemblage of dispersed megaspores from Japan based on material from the Upper Cretaceous (upper Coniacian–lower Santonian) Tamagawa Formation (Kuji Group). More than 600 specimens of dispersed megaspores were recovered, and the presence of five genera significantly extends previous knowledge of the pteridophyte component in the flora of the Kuji Group.

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Material and Methods

Fossil megaspores were isolated from ca. 50 kg of carbonaceous black, poorly sorted siltstone collected along the Tamagawa coast at Noda village, Iwate Prefecture, northern Honshu, Japan (lat. 40°5′N, long. 141°48′E). Samples were from the middle part of the Tamagawa Formation.

The Kuji Group comprises a sequence of sandy to subordinately silty clastics deposited in fluvial to shallow-marine environments on the western margin of a matured forearc basin (Ando 1997). The sediments outcrop in the North Kitakami-Oshima Belt of northern Honshu close to the Pacific Coast. The Kuji Group unconformably overlies a Lower Cretaceous granite (110–120 million years before present; Kawano and Ueda 1966) and is itself overlain by the Lower Paleogene Noda Group (Ando 1997).

The Tamagawa Formation is the lowermost of three formations that comprise the Kuji Group. In its basal part, the Tamagawa Formation is characterized by alluvial fan conglomerates with lacustrine mudstones. Above, the bulk of the formation comprises a few fluvial sequences consisting of sandstone and mudstone intercalating with lagoonal sandy mudstones and nearshore sandstones. Black carbonaceous siltstones and mudstones at this level often contain amber, rarely with some insects. Above the Tamagawa Formation, the Kunitan Formation is interpreted as a shallow-marine facies. The uppermost sedimentary unit in the Kuji Group, the Sawayama Formation, is interpreted as fluvial deposits dominated by floodplain facies.

Based on the occurrence of Santonian ammonites (*Texanites collignoni* Klinger et Kennedy and *Texanites pacificus* Matsumoto) from the lower to middle part of the Kunitan Formation, and a species of earliest Campanian inoceramid (*Inoceramus japonicus* Nagao et Matsumoto) from the upper part of the Kunitan Formation, the Kuji Group is thought to range in age from late Coniacian to late Campanian. The age of the megaspore-bearing sediments in the Tamagawa Formation is therefore probably of late Coniacian–early Santonian age (ca. 87–85 million years before present; Gradstein et al. 1995).

After drying in the laboratory, the samples were disaggregated in water and sieved through 125-μm mesh. The recovered carbonaceous debris was then cleaned of adhering mineral material by treatment with hydrofluoric and hydrochloric acids, thoroughly rinsed in water, and dried in air. Individual megaspores were then separated by visual identification and picking under the dissecting microscope. Specimens selected for scanning electron microscopy were mounted on polished aluminum scanning electron microscope stubs with nail polish, sputter-coated with platinum-palladium, and examined in a Hitachi S-800 field emission scanning electron microscope (FE-SEM). All specimens are deposited in the Department of Geology and Paleontology, National Science Museum (NSM-PP), Tokyo 169-0073, Japan.

Results

Molaspora Schemel, Emend. Hall

Molaspora lobata (Dijkstra) Hall (Fig. 1)

Megaspores are represented by 72 specimens. Megaspores are spheroidal in shape, 380–550 μm in diameter, with the apertural region forming a porelike structure (fig. 1*A*, 1*B*). The aperture is circular in outline and surmounted by a terminal acrolamella. The acrolamella is composed of six to seven spirally twisted units 70 μm high and 100 μm broad at the base (fig. 1*C*). Exospore sculpture is verrucate, composed of closely spaced papillate protuberances (fig. 1*D*). Each protuberance is ca. 15 μm in diameter and almost circular in cross section with some puncta in the surface (fig. 1*E*). Exospore is 2.5–3.5 μm thick and has an irregularly crumpled and vacuolated or corrugated internal structure. The exospore consists of inner granules and rodlets from which the papillate extend perpendicular to the outer wall to form radially aligned chambers (fig. 1*F*).

Comments. Five species of *Molaspora* have been described from the Cretaceous: *M. fibrosa* Singh, *M. reticulata* Campbell et Untergasser, *M. lobata* (Dijkstra) Hall, *M. hallii* (Lachkar) Batten, and *M. salinum* Kovach and Dilcher. *Molaspora salinum* has reticulate ornamentation that differs from that of *M. lobata*. Detailed comparison among the other species has been undertaken by Batten (1988), and the material from the Tamagawa Formation is clearly referable to *M. lobata*. *Molaspora* is assignable to the heterosporous water fern family Marsileaceae by its unique megaspore wall and the presence of an acrolamella, as suggested by Dijkstra (1959).

Previous records. *Cenomanian*: Kansas (Kovach 1988; Kovach and Dilcher 1988), Iowa (Schemel 1950), Minnesota (Hall and Peake 1968), Canada (Singh 1983), France (Colin 1975); *Santonian*: Georgia (Lupia et al. 2000), Germany (Vangerow 1954), Netherlands (Dijkstra 1949, 1959; Batten 1988), Belgium (Batten 1988). *Maastrichtian*: Canada (Gunther and Hills 1972; Sweet 1979).

Erlansonisporites Potonié

Erlansonisporites scanicus Koppelhus et Batten (Fig. 2)

Megaspores are represented by 190 specimens. Megaspores are trilete and circular to subcircular in equatorial outline, 620–750 μm in diameter (fig. 2*A*, 2*B*). The trilete laesura is unclear and difficult to distinguish from constricted muri of the robust reticulum at the proximal pole. Exospore sculpture is a reticulum, ranging from open and more or less rugulate to closed. The muri are undulating, 15–25 μm high (fig. 2*C*). The surface of the reticulum is composed of membranous layers with irregular puncta (fig. 2*D*). The membranous layer has a smaller-scale fine structure comprising a fine regular spongelike meshwork (fig. 2*E*). Exospore is 80 μm thick at the muri and 18 μm at the lumina, and is composed of two different layers (fig. 2*F*, 2*G*). The outer exospore is composed of undulating lamellae forming a spongy structure that is particularly well developed in the muri (fig. 2*H*). The inner exospore consists of a distinctive regularly ordered granular structure (fig. 2*I*). Units comprising the granular structure are 0.1–0.2 μm in diameter and arranged in tightly packed laminae, different levels of which are placed perpendicular to one another.

Comments. *Erlansonisporites* is composed of 27 species, ranging from Triassic to Cretaceous in age (Batten and Kovach 1990). Comparisons among some of the species are presented by Kovach and Dilcher (1988). The material from the Tamagawa Formation is most similar to *E. scanicus* from the late Santonian or early Campanian of Scania, southern Sweden (Koppelhus and Batten 1989). The type specimen of *E. scanicus* is ca. 500 μm in diameter, with a robust reticulum (Koppelhus and Batten 1989). The megaspores assigned to *E. scanicus* from the Kuji Group are somewhat larger with a slightly more delicate reticulum, but we consider that these differences are not sufficient to justify the recognition of a new species. The ordered granular wall structure clearly indicates that the affinity of *Erlansonisporites* lies with the Selaginellales (Bergad 1978; Kovach and Dilcher 1988; Koppelhus and Batten 1989; Collinson 1991; Hemsley et al. 1992).

Previous records. *Santonian-Campanian*: Sweden (Koppelhus and Batten 1989).

Bacutriletes (van der Hammen) ex Potonié

Bacutriletes arnoldii (Miner) Potonié (Fig. 3)

Megaspores are represented by 124 specimens. Megaspores are trilete and circular to subcircular in equatorial outline, 650–700 μm in diameter (fig. 3*A*). The trilete laesura extends

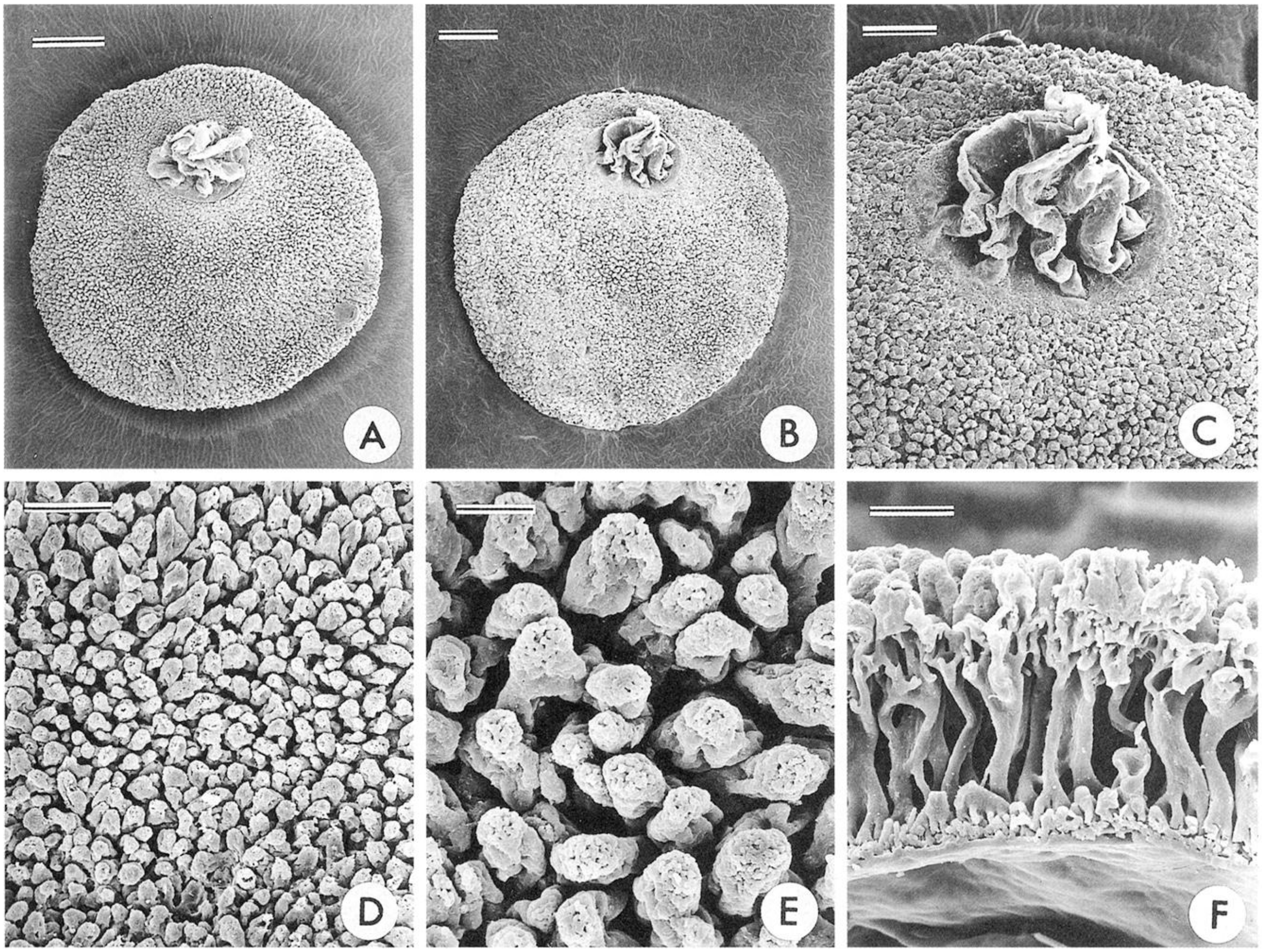

Fig. 1 *Molaspora lobata* (Dijkstra) Hall. *A*, Megaspore, oblique view of proximal face (NSM-PP12002); ×97. Bar scale = 100 μm. *B*, Megaspore, oblique view of proximal face (NSM-PP120001); ×80. Bar scale = 100 μm. *C*, Acrolamella (NSM-PP12001); ×200. Bar scale = 50 μm. *D*, Verrucate exospore (NSM-PP12002); ×580. Bar scale = 20 μm. *E*, Verrucate exospore (NSM-PP12002); ×2000. Bar scale = 20 μm. *F*, Exospore structure in transverse section showing vacuolated corrugated appearance (NSM-PP12003); ×1175. Bar scale = 10 μm.

to one-half the radius of the spore but is sometimes difficult to distinguish and is covered by the exospore sculpture. The exospore surface is covered with vermiculate protrusions that have a rounded tip (fig. 3*B*). The fine sculpture of the surface of each protrusion and the exospore to which it is attached at the base is punctate with numerous densely packed and more or less evenly distributed perforations, less than 0.5 μm in diameter (fig. 3*C*, 3*D*). The exospore is 15–17 μm thick and consists of a mass of variably fused granules (fig. 3*E*). Each granular unit is 0.7 μm in diameter. The arrangement of granules is relatively irregular, and particularly toward the outside they are often tightly packed and generally more or less fused (fig. 3*F*).

Comments. More than 25 species of *Bacutriletes* have been described from the Triassic to the Cretaceous. *Bacutriletes arnoldii* is distinguished from the other species by the longer, thinner vermiculate protrusions. The exospore structure of *B. majorinus* (Koppelhus and Batten 1989) is similar to that of *B. arnoldii* and has been interpreted as indicating a probable selaginellalean affinity. However, this conclusion is much less certain than for *Erlansonisporites*.

Previous records. *Albian*: Spain (Busnardo and Taugourdearu-Lants 1964); *Turonian-Campanian*: Greenland (Miner 1932, 1935; Potonié 1956).

Verrutriletes (van der Hammen), ex Potonié, Emend. Binda et Srivastava

Verrutriletes dubius (Dijkstra) Potonié (Fig. 4)

Megaspores are represented by 178 specimens. The megaspores are subcircular to rounded triangular in equatorial outline, proximal face commonly slightly flattened, 650–740 μm in diameter (fig. 4*A*, 4*B*). The prominent trilete laesura, ca. 40 μm wide and 40–50 μm high, extends to the equator (fig. 4*C*). The exospore surface is verrucate, covered with numerous, often closely spaced, rounded to flat-topped verrucae, 20–60 μm high and 10–60 μm in width (fig. 4*D*). The equatorial and

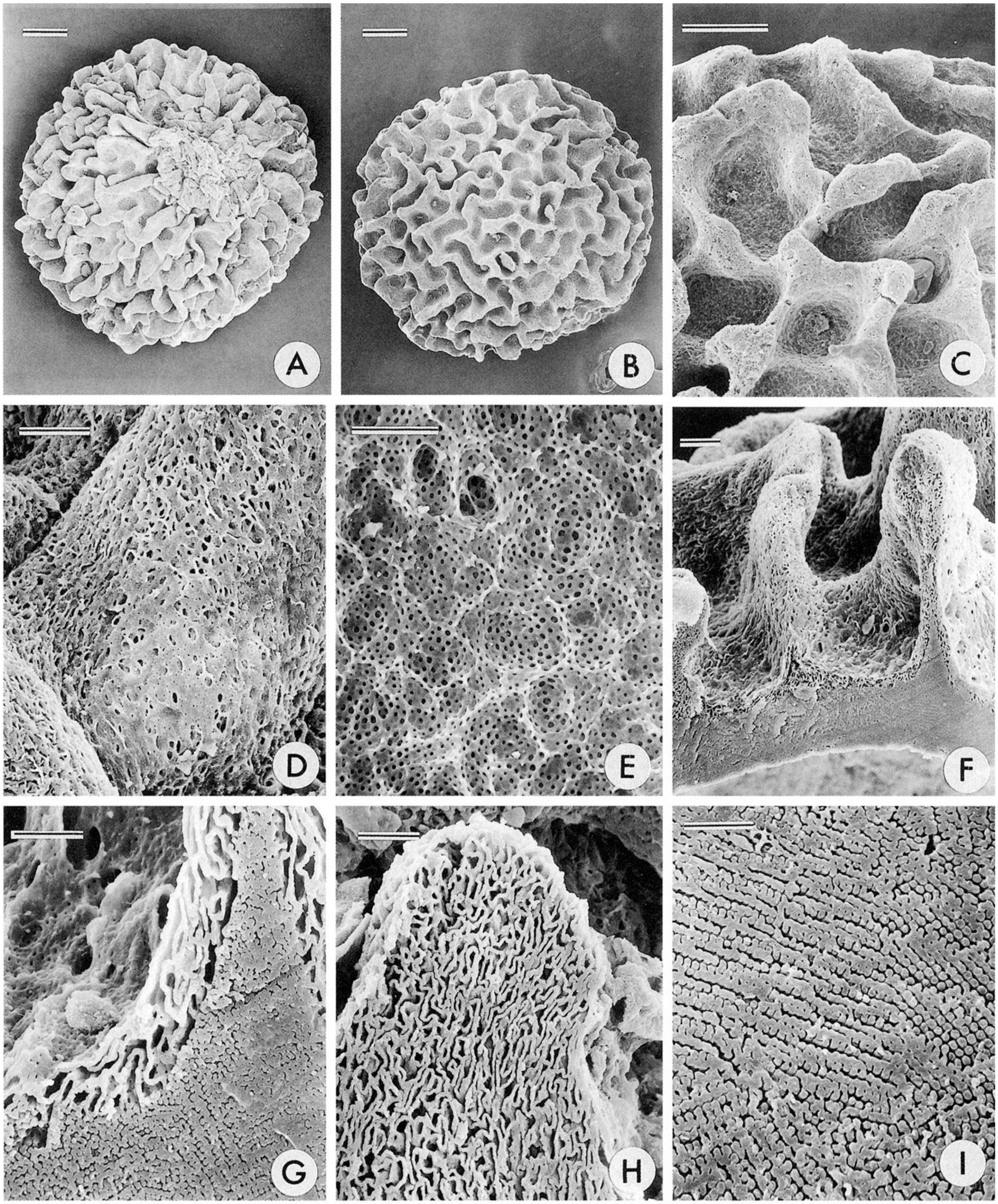

Fig. 2 *Erlansonisporites scanicus* Koppelhus et Batten. *A*, Megaspore, proximal face (NSM-PP12005); × 70. Bar scale = 100 μm. *B*, Megaspore, distal face (NSM-PP12004); × 80. Bar scale = 100 μm. *C*, Reticulate-rugulate exospore (NSM-PP12004); × 300. Bar scale = 50 μm. *D*, Surface of muri (NSM-PP12004); × 1200. Bar scale = 10 μm. *E*, Detail of surface sculpture of muri composed of fine regular meshwork (NSM-PP12004); × 3000. Bar scale = 5 μm. *F*, Fractured exospore structure (NSM-PP12006); × 660. Bar scale = 10 μm. *G*, Detail of exospore structure in transverse section showing the different configurations of the two wall layers (NSM-PP12006); × 3600. Bar scale = 3 μm. *H*, Outer exospore composed of undulating lamellae (NSM-PP12006); × 2100. Bar scale = 5 μm. *I*, Inner exospore consisting of a distinctive-ordered granular structure (NSM-PP12006); × 6000. Bar scale = 2 μm.

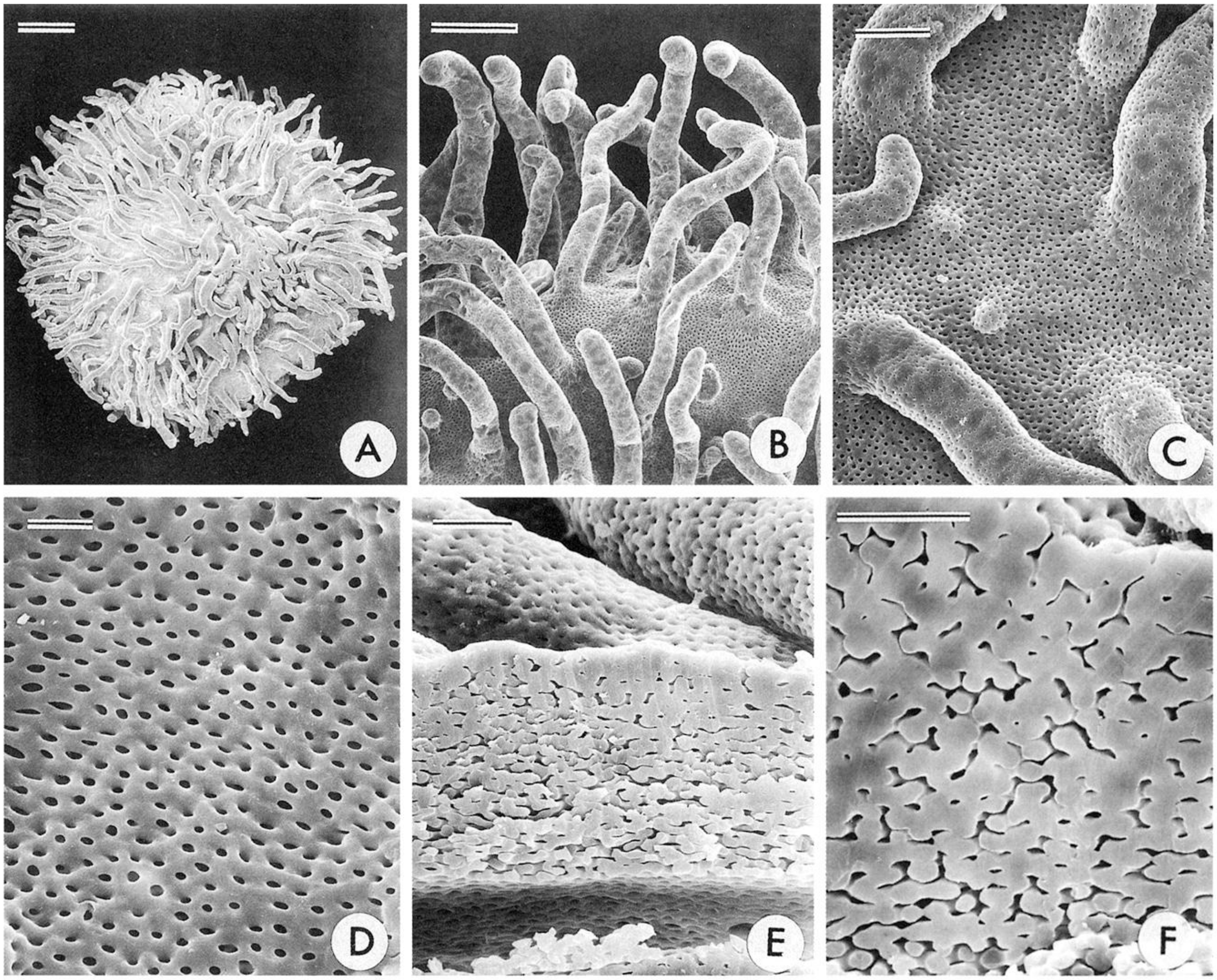

Fig. 3 *Bacutriletes arnoldii* (Miner) Potonié. *A*, Megaspore, oblique view of probable proximal face (NSM-PP12006); ×80. Bar scale = 100 μm. *B*, Exospore surface with the vermiculate protrusions (NSM-PP12006); ×420. Bar scale = 30 μm. *C*, Punctate exospore surface (NSM-PP12006); ×1000. Bar scale = 10 μm. *D*, Detail of punctate surface of exospore (NSM-PP12006); ×3000. Bar scale = 3 μm. *E*, Fractured exospore (NSM-PP12007); ×2100. Bar scale = 100 μm. *F*, Detail of exospore structure in transverse section showing the irregular appearance of the fused granules (NSM-PP12007); ×3600. Bar scale = 5 μm.

distal sculpture is often more prominent than that of the contact area on the proximal face. The fine sculpture of the exospore is reticulate and consists of a three-dimensional network of fine sporopollenin threads (fig. 4*E*, 4*F*). The exospore is typically 35–40 μm thick at the verrucae and 7 μm thick between these protrusions. It consists of a mass of variably fused granules or threads (fig. 4*G*, 4*H*). The granular units, 0.5 μm in diameter, are interconnected but relatively irregular in their arrangement (fig. 4*I*).

Comments. More than 30 species of *Verrutriletes* have been reported from the Triassic to the Cretaceous. The material from the Tamagawa Formation is most similar to *V. dubius*. Batten (1988) suggested that the granular exospore of *V. dubius* may indicate a selaginellalean affinity, but this is much less certain than for *Erlansonisporites*.

Previous records. *Cenomanian-Turonian*: France (Colin 1975); *Santonian*: Netherlands (Dijkstra 1949; Batten 1988), Germany (Vangerow 1954).

Trileites Erdtman ex Potonié

Trileites persimis (Harris) Potonié (Fig. 5)

Megaspores are represented by 35 specimens. The megaspores are 600–650 μm in diameter, circular or triangular in polar view (fig. 5*A*, 5*B*). The trilete laesura is prominent and extends to two-thirds of the radius. The exospore surface is psilate (fig. 5*C*). The fine sculpture of the exospore is microreticulate and composed of a three-dimensional network of fine sporopollenin threads (fig. 5*D*). The threads are 0.6 μm in diameter. The exospore is 15–16 μm thick and has irregular granular structure (fig. 5*E*). Granular units, 1 μm in diameter,

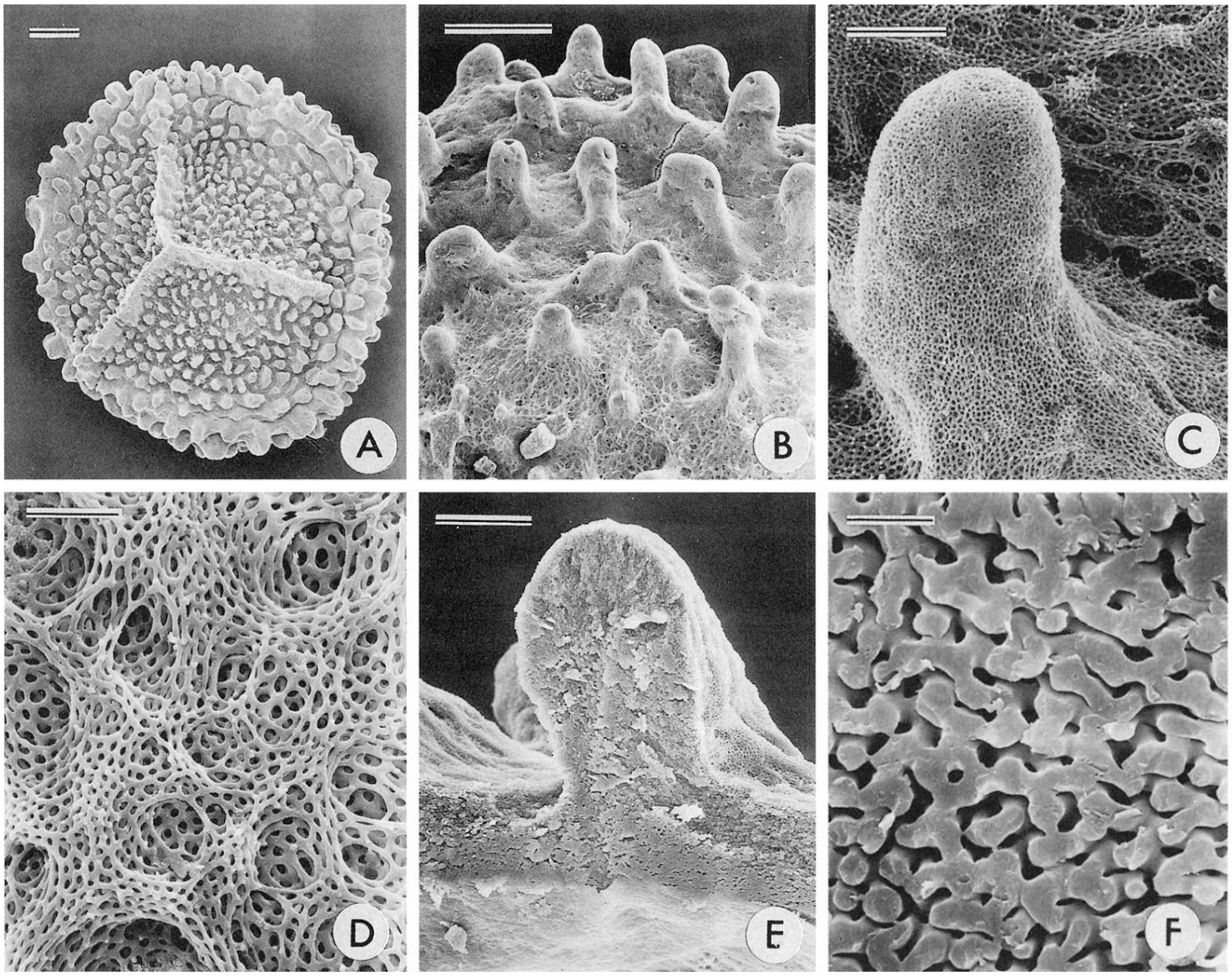

Fig. 4 *Verrutriletes dubius* (Dijkstra) Potonié. *A*, Megaspore, proximal face (NSM-PP12010); ×70. Bar scale = 100 μm. *B*, Verrucate exospore sculpture (NSM-PP12009); ×290. Bar scale = 50 μm. *C*, Verrucate protrusion with three-dimensional network (NSM-PP12009); ×2600. Bar scale = 5 μm. *D*, Detail of verrucate protrusion showing three-dimensional network of exospore surface (NSM-PP12009); ×5800. Bar scale = 2 μm *E*, Fractured exospore showing structure in transverse section (NSM-PP12009); ×1260. Bar scale = 10 μm. *F*, Detail of exospore structure (NSM-PP12011); ×5800. Bar scale = 2 μm.

are loosely organized in the outer part of the wall but more compact and irregularly connected to each other in the inner part (fig. 5*F*).

Comments. Nearly 30 species of *Trileites* have been described from the Triassic to the Cretaceous. Discriminative features for the species of *Trileites* include the length of laesurae and sizes. The material from the Tamagawa Formation is most similar to *T. persimis*. A selaginellalean affinity has been suggested by Koppelhus and Batten (1989) based on the fused granular exospore structure, but this is much less certain than for *Erlansonisporites*.

Previous records. *Barremian*: France (Taugourdeau-Lants and Donze 1971); *Albian*: Spain (Busnardo and Taugourdeau-Lants 1964), Canada (Singh 1964); *Cenomanian*: Spain (Floquet and Lachkar 1979); *Santonian*: Netherlands (Dijkstra 1949; Batten 1988), Germany (Vangerow 1954); *Santonian-Campanian*: Sweden (Koppelhus and Batten 1989). Also *Triassic*: Greenland (Harris 1935).

Discussion

The Paleoflora of the Kuji Group

Previous paleobotanical studies of the Kuji Group have focused either on the dispersed palynoflora (Miki 1972) or on fossil leaf compressions (Tanai 1979). Palynological samples from the Tamagawa Formation were dominated (ca. 57%–58% of the 200 spores/pollen counted) by ca. 70 species of pteridophytes (Miki 1972), among which probable polypodiaceous monolete spores (*Laevigatosporites*) were especially prominent. The distinctive spores of the Schizaeaceae were also present. Saccate podocarpaceous-pinaceous grains and inaperturate probable taxodiaceous grains were also prominent with lesser amounts of pollen of putative Araucariaceae (Miki 1972). Pollen of *Classopollis* and ephedroid grains were consistently present, while monosulcate pollen of presumed nonconifer gymnosperms (e.g., cycads, Bennettitales,

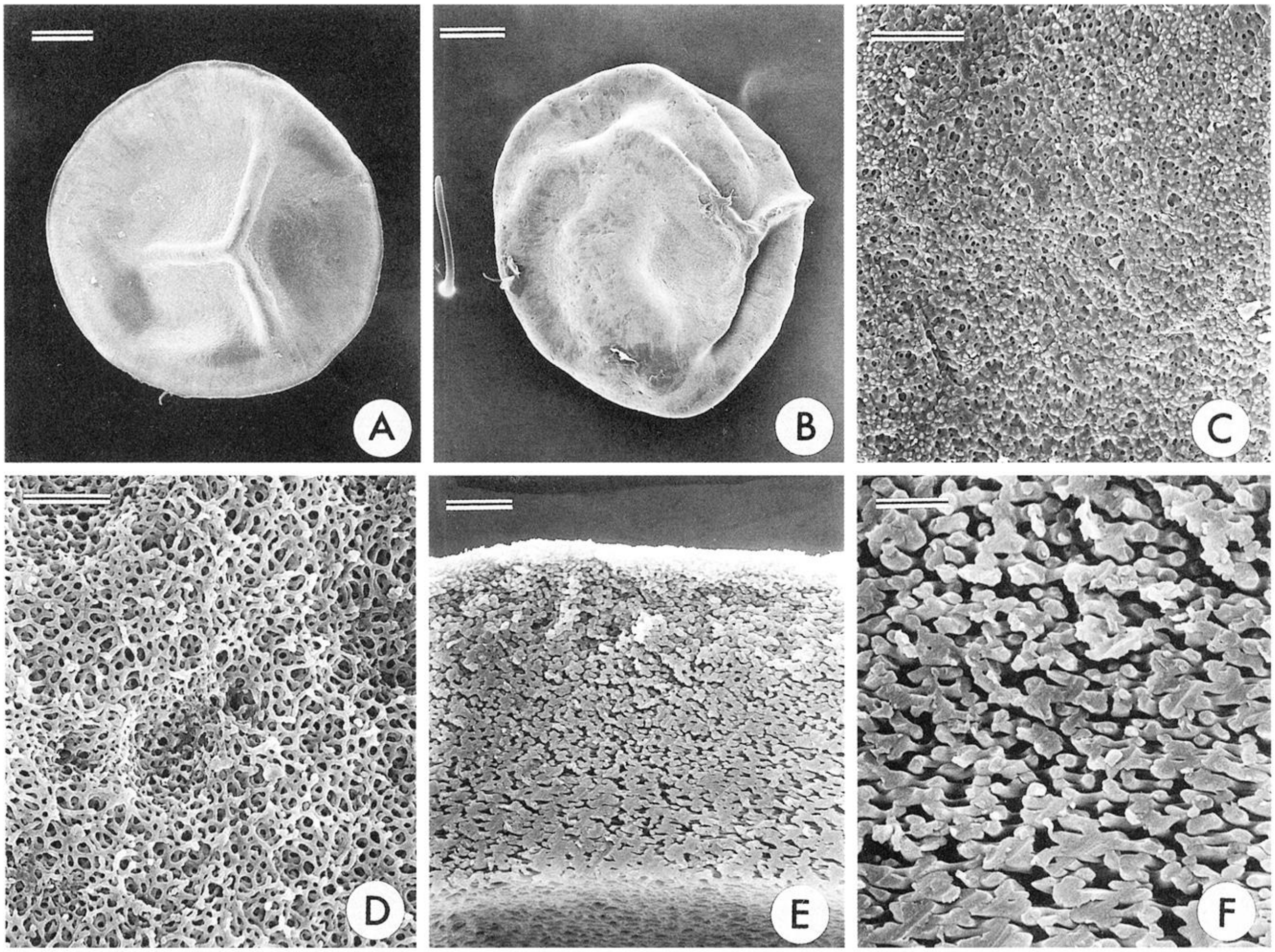

Fig. 5 *Trileites persimis* (Harris) Potonié. *A*, Megaspore, proximal face (NSM-PP12013); × 70. Bar scale = 100 μm. *B*, Megaspore, oblique view of proximal face (NSM-PP12012); × 80. Bar scale = 100 μm. *C*, Exospore showing surface sculpture (NSM-PP12012); × 1170. Bar scale = 10 μm. *D*, Detail of exospore sculpture, showing the three-dimensional network of fine threads (NSM-PP12012); × 5800. Bar scale = 2 μm. *E*, Fracture of exospore structure showing the loosely granular organization in the outer part of the wall (NSM-PP12014); × 2900. Bar scale = 3 μm. *F*, Detail of exospore structure in transverse section (NSM-PP12014); × 8700. Bar scale = 1 μm.

Ginkgo, Gnetales, and extinct groups) were significant in some samples (Miki 1972). Based on palynological samples, angiosperms were the second most abundant group in the Tamagawa Formation, with 30 species accounting for ca. 22% of the spores/pollen counted. Monosulcate grains were significant in some samples, but especially prominent were a variety of small tricolpate and tricolporate grains. Triprojectate grains of *Aquilapollenites* were also recovered (Miki 1972).

Fossil leaf compressions have been recovered from both the Tamagawa and Sawayama Formations, the lowermost and uppermost of the three formations that comprise the Kuji Group (Tanai 1979). The leaf flora described from the Tamagawa Formation consists of 17 species of pteridophytes, six species of conifer, and 10 species of angiosperms (Tanai 1979).

Neither previous palynological studies nor the paleobotanical work on fossil leaf impressions has previously provided any evidence of the presence of heterosporous pteridophytes in the Tamagawa Formation. The megaspore assemblage described here is the first to document the occurrence of the Marsileales and the Selaginellales from the Kuji Group. Also noteworthy is the apparent absence of spores assignable to the Isoetales in the Tamagawa Formation. This contrasts with the situation in Europe and North America where dispersed isoetalean megaspores are very common in these kinds of Upper Cretaceous sediments (Collinson 1991; Hemsley et al. 1999).

Marsileales

The order Marsileales comprised the single family Marsileaceae with three extant genera, *Marsilea*, *Regnellidium*, and *Pilularia*. In the fossil record, the group is known from the Tertiary megaspore, *Rodeites*, and two extinct Cretaceous form-genera of megaspores, *Molaspora* and *Arcellites*, with an associated microspore form-genus *Crybelosporites* (Lupia et al. 2000). There is also an important macrofossil record of the group from the mid-Cretaceous of central Kansas (Skog and Dilcher 1992). *Molaspora* is assigned to the Marsileales based on the presence of a prominent proximal neck made up of six spiral twisting units (acrolamella). These distinctive megaspores have been recovered previously from the Upper Cretaceous of Europe and the United States (Dijkstra 1949; Campbell and Untergasser 1972; Gunther and Hills 1972; Singh 1983; Batten 1988; Kovach and Dilcher 1988; Collinson 1991; Lupia et al. 2000), but the megaspores of *Molaspora lobata* from the Kuji Group are the first report of this genus from Asia. The occurrence of *Molaspora* in Asia, Europe, and North America during the late Cretaceous indicates that despite the vegetational differences between these areas inferred from definitions of floristic provinces based on fossil pollen, the Marsileales were widespread across middle paleolatitudes at this time. A floodplain marsh to lacustrine habitat may be inferred as the source for some of the sediments of the Tamagawa Formation based on the presumed relationships between *Molaspora* and the Marsileales.

Selaginellales

Extant selaginellalean megaspores show various structural types (Minaki 1984). Taylor (1989) divided the structure of the megaspore wall into three types: an ordered granular type, a laterally fused type, and a laminar type. The ordered granular type has been variously described as a highly ordered patchwork pattern (Taylor and Taylor 1988), a compact framework of regularly distributed spherical elements (Koppelhus and Batten 1989), or interconnected granular layers in a sporopollenin gridlike structure (Batten 1988), but there is clear evidence that this indicates a close relationship to the Selaginellales. The regular orientation of exospore granules in *Erlansonisporites* suggests a selaginellalean affinity.

Most extant selaginellalean megaspores have a laterally fused exospore structure that is less distinctive and more difficult to distinguish from that of other megaspores. Three of the fossil genera, *Bacutriletes*, *Verrutriletes*, and *Trileites*, described from the Tamagawa Formation also have the laterally fused exospore structure. Their relationships may also be with the Selaginellales, but establishing this with certainty will require additional information from other parts of these fossil plants.

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