

Barremian palynofloras from the Ashikajima and Kimigahama formations (Choshi Group, Outer Zone of south-west Japan)

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ABSTRACT

The Choshi Group, which crops out in the Outer Zone of south-west Japan, has been extensively studied for its rich macroflora by Makoto and Harufumi Nishida, among others, and was attributed to the Ryoseki-type Floristic Province by Kimura (1987). New microfloras were discovered in muddy, very fine-grained sandstones and mudstones of the marine Ashikajima and Kimigahama formations, representing the base of the Choshi Group. The authors provide a palynological inventory for these lithological units, which have been dated as Barremian on the basis of the ammonites recorded from them, and compare them with the paleofloristic associations of the South-Laurasian Province (Brenner 1976) and Euro-Sinian Region (Vakhrameev 1991). The studied assemblages yielded 53 genera and 89 species of spores and gymnosperm pollen grains, and also marine or freshwater al-

KEY WORDS

Palynology,
Barremian,
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Choshi Group,
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new species.

gae and some epiphyllous fungi. No angiosperm pollen grain was observed. Four new species are described: *Manumia japonica* n. sp., *Foveosporites ryosekiensis* n. sp., *Nodosisporites choshiensis* n. sp. and *N. makotoi* n. sp. Other forms, probably new species, are described here in detail, but the scarcity of the specimens has led us to place them temporarily in open nomenclature. The spatio-temporal distributions of the genus *Manumia* Pocock, reported for the first time in Asia, and *Cicatricosisporites sinuosus* Hunt, 1985 are plotted on paleogeographical maps. With this palynological study, we add new data to the present knowledge of Barremian floras. This assemblage probably corresponds to a taphocenose. The authors suggest that the climate indicated had marked dry and more humid seasons, in accordance with the hypothesis of a moderate migration of the oceanic islands of the Outer Zone before their collision with the Eurasian continent, or moderate climatic change during the Early Cretaceous in Japan.

RÉSUMÉ

Palynoflores barrémiennes des Formations Ashikajima et Kimigahama (Groupe Choshi, Zone Externe du sud-ouest du Japon).

Le Groupe Choshi, appartenant à la Zone Externe du sud-ouest du Japon, est bien connu pour sa riche macroflore étudiée entre autres par Makoto et Harufumi Nishida, et placée dans la Province Floristique « Ryoseki » par Kimura (1987). De nouvelles microflores ont été découvertes dans des grès argileux à grain très fin et argiles compactées provenant des Formations marines Ashikajima et Kimigahama situées à la base du Groupe Choshi. Les auteurs font un inventaire palynologique de ces unités lithologiques datées du Barrémien par les ammonites, et les comparent avec des associations paléofloristiques connues de la Province sud-laurasienne (Brenner 1976) et Région euro-sinienne (Vakhrameev 1991). Les assemblages nous ont livré 53 genres et 89 espèces de spores et grains de pollen de gymnospermes, ainsi que des algues marines ou d'eau douce et quelques champignons épiphylls. Aucune angiosperme n'a été observée. Quatre nouvelles espèces sont définies: *Manumia japonica* n. sp., *Foveosporites ryosekiensis* n. sp., *Nodosisporites choshiensis* n. sp. et *N. makotoi* n. sp. D'autres formes, probablement de nouvelles espèces, sont décrites ici en détails, mais la rareté des individus nous a conduit à les placer provisoirement en nomenclature ouverte. Les répartitions spatio-temporelles du genre *Manumia* Pocock, signalé en Asie pour la première fois, et de *Cicatricosisporites sinuosus* Hunt, 1985 sont replacées sur des cartes paléogéographiques. Cette première étude palynologique permet de compléter la connaissance des flores du Barrémien. Cet assemblage correspond probablement à une taphocénose. Il indique un climat à saison chaude marquée suivie d'une saison plus humide, ce qui est conforme avec les hypothèses d'une migration modérée des îles océaniques de la Zone Externe avant leur collision avec le continent eurasiatique, ou de changements climatiques modérés au cours du Crétacé inférieur au Japon.

MOTS CLÉS

Palynologie,
Barrémien,
Flore Ryoseki,
Groupe Choshi,
SO Japon,
espèces nouvelles.

INTRODUCTION

The backbone of the Japanese archipelago was largely formed during the Early Cretaceous period.

Before the opening of the Sea of Japan during the Miocene (28 My), the Inner and Outer Zones of present-day Japan (Fig. 1) were separated by a marine basin. The Inner Zone (north-western

part, along the Sea of Japan) was connected to the east of the Korean Peninsula and represented the margin of the Eurasian continent. The Outer Zone (south-eastern part, along the Pacific Ocean) of south-west Japan was represented by oceanic islands located further to the south. Due to sinistral strike-slip movements along the Median Tectonic Line (MTL), which began in the Late Jurassic, these islands moved northwards and reached their present latitude to collide with the Inner Zone until the close of the Hauterivian (Yaskawa 1975; Hirooka *et al.* 1983, 1985; Matsukawa & Obata 1993; Matsuoka *et al.* 1997; Otoh 1998; Otoh & Sasaki 1998; Matsukawa & Fukui 2009). It should be noted, however, that there are many different interpretations of the speed and period of their migration and on the position of the Outer Zone before the strike-slip motion of the plates (Otofujii *et al.* 1985; Kojima 1989; Mitsugi *et al.* 2001; Ishida *et al.* 2003; Lee & Kim 2005; Lee 2008). Some authors even doubt the existence of the terranes constituting the Outer Zone (Isozaki 1996, 1997; Maruyama *et al.* 1997; Isozaki *et al.* 2010). Thus, the developmental history of the Japanese archipelago is still open to question.

The paleoflora of the Outer Zone is called “Ryoseki-(Gondwanian)-type”. It is widely accepted that it flourished under a seasonally dry climate based on the abundance of microphyllous conifers and bennettitoid foliage such as *Zamites* Brongniart emend. Harris and *Ptilophyllum* Morris (Kimura 1958, 1987). This flora is markedly different from the warm temperate “Tetori-(Siberian)-type” flora found in the Tetori Group of the Inner Zone, which is characterized by abundant ferns, ginkgos and macrophyllous conifers (Kimura & Sekido 1976, 1978; Kimura 1987; Kimura & Ohana 1997). Such pronounced phytogeographical differences are often referred by proponents of the strike-slip hypothesis as evidence supporting the low-latitude origin of the Outer Zone terranes (Fig. 2). However, similar age of these floras has been increasingly challenged by recent stratigraphic and paleobotanical studies (Yamada & Uemura 2008; Yamada 2009). Furthermore, the paleoclimates noted above were inferred empirically from the foliar fossils, although these are often difficult

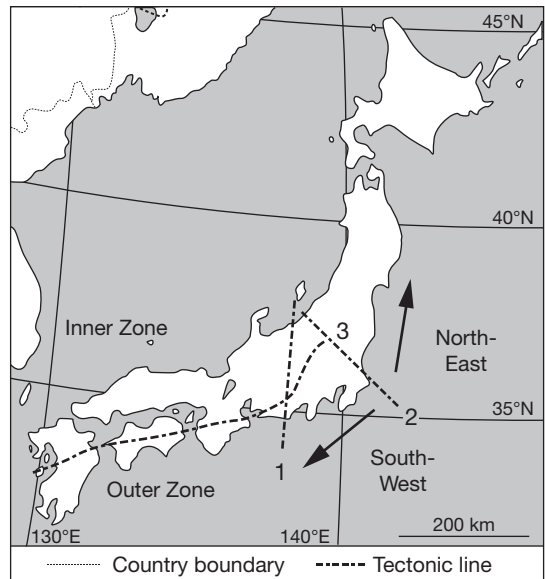


FIG. 1. — Geological setting of Japan: 1, Itoigawa-Shizuoka tectonic line; 2, Kashiwazaki-Choshi tectonic line; 3, Median tectonic line. Map modified from Geological Survey of Japan (2010).

to classify even at the generic level because of the diagenetic loss of their cuticle in Japanese Upper Jurassic to Lower Cretaceous sediments.

Palynological studies provide stratigraphic and climatic clues, but few palynological investigations have been carried out on Lower Cretaceous sediments in Japan until now (e.g., Umetsu & Matsuoka 2003; Umetsu & Sato 2007). We describe here palynomorphs from the upper part of the Ashikajima Formation and lower part of the Kimigahama Formation of the marine Choshi Group, located in the most eastern part of the Chiba Prefecture, south-west Honshu. The Choshi Group (Shikama & Suzuki 1972) represents Lower Cretaceous sediments in south-west Japan and is dated as Barremian to early Albian based on the ammonite and other molluscan assemblages (Hayami & Oji 1980; Kase & Maeda 1980; Obata & Matsukawa 2009). This paper presents the first comprehensive description of a pre-Aptian palynological assemblage for the Outer Zone. We compare the assemblage to coeval palynofloras in adjacent areas to infer the paleoclimate of the Ryoseki-type flora in more detail.

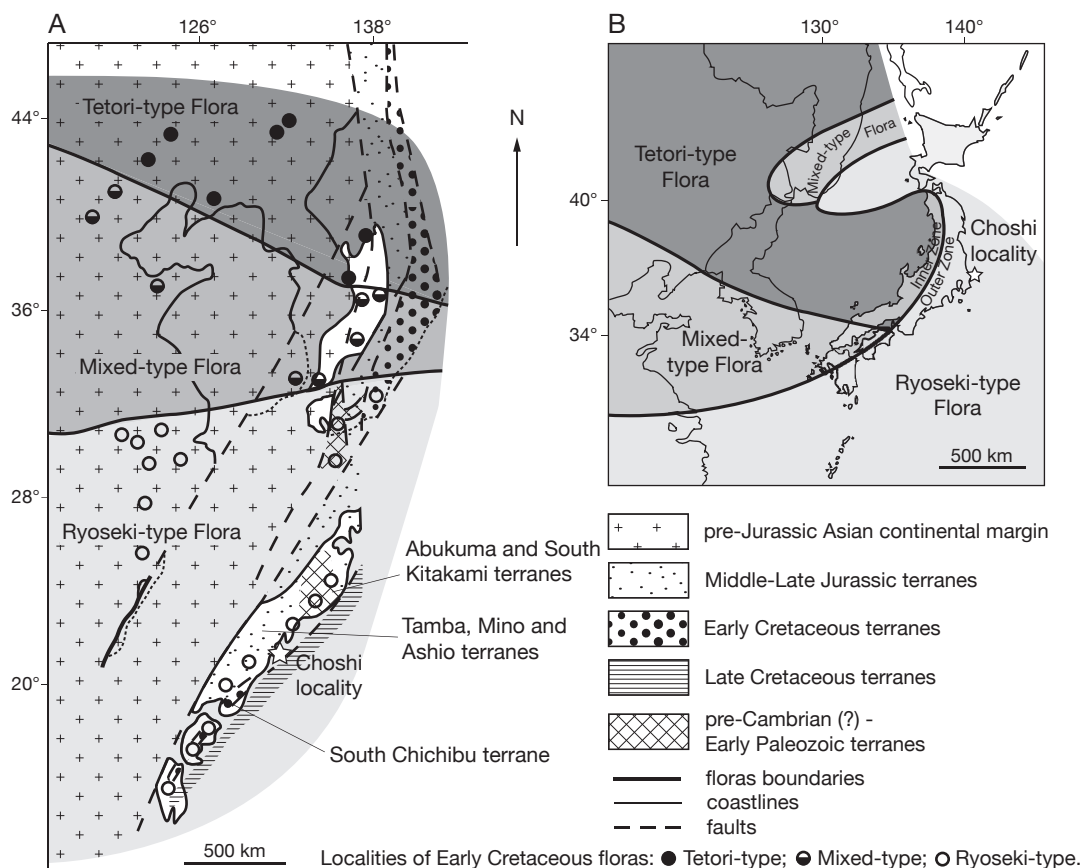


FIG. 2. — Paleofloristic provinces in Japan and eastern Asia during the Late Jurassic-Early Cretaceous period: **A**, on a paleogeographical map, which illustrates the relative locations of the Inner and Outer Zones (modified from Golozoubov *et al.* 1999); **B**, on a present map (from Kimura 1987).

GEOLOGICAL SETTING

The Lower Cretaceous strata of the Choshi Group crop out along the eastern coast of the Choshi Peninsula, Chiba Prefecture (Fig. 3). This group has been subdivided lithologically into five formations, in ascending order: the Ashikajima, Kimigahama, Inubouzaki, Toriakeura and Nagasakihana formations (Obata *et al.* 1975, 1982; Kase & Maeda 1980). Type biozones were established for the ammonites of the Lower Cretaceous of southwest Japan and enabled the age of the Choshi Group to be determined as Barremian to early Albian (Obata *et al.* 1975; Obata & Matsukawa

2009). It was deposited in an offshore to shallow marine environment (Katsura *et al.* 1984; Ito & Matsukawa 1997). Plant macrofossils have been described from the Ashikajima, Kimigahama, and Toriakeura formations and contain typical species of the Ryoseki-type flora, such as the cyatheaceous fern *Ptilophyllum cuchense* Morris, and the gymnosperm *Brachyphyllum expansum* (Sternberg) Seward (e.g., Nishida 1960, 1962; Kimura & Ohana 1985; Kimura *et al.* 1991).

The Ashikajima Formation overlies unconformably the pre-Cretaceous rocks, and is overlain conformably by the Kimigahama Formation (Fig. 4). Its base is mainly composed of conglomerates with

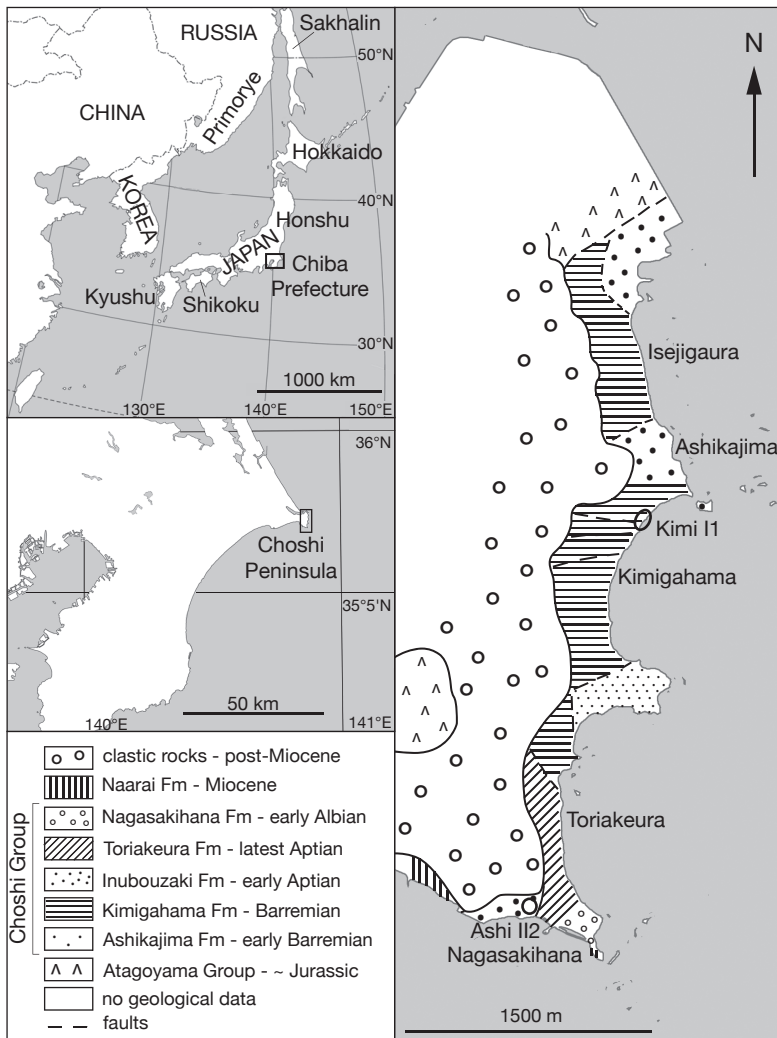


FIG. 3. — Location map of the outcrops and geology of the eastern coast of the Choshi Peninsula (modified from Obata *et al.* 1975, 1982; Ito & Matsukawa 1997; Obata & Matsukawa 2009).

siliceous pebbles, above which are coarse-grained sandstones with intercalated mudstones, becoming thinner towards the top (Obata *et al.* 1975, 1982; Obata & Matsukawa 2009). The formation is about 200 m thick. It is dated as Barremian based on the ammonite and belemnite assemblages (Obata *et al.* 1975; Hayami & Oji 1980). We took our samples from the muddy, very fine-grained sandstones of the Hatoyama locality, in the south-eastern part of the Choshi Peninsula (35°41'N, 140°51'E).

The Kimigahama Formation is overlain unconformably by the Inubouzaki Formation. It is mainly composed of alternating beds of sandstones and mudstones, containing many calcareous nodules. The foraminifer and ammonite assemblages have enabled the assignment of a Barremian age to the formation (Obata *et al.* 1975; Hayami & Oji 1980; Kase & Maeda 1980; Obata & Matsukawa 2009). We collected our samples from the mudstones along Kimigahama beach (35°43'N, 140°52'E).

MATERIAL AND METHODS

The samples, first cleaned under running water and scrubbed with brush, were left for a few days in the open air and then broken in a mortar. The ground samples were sieved and the fraction between 1 and 3 mm in grain diameter was soaked to 10% aqueous hydrochloric acid until the end of the effervescence to remove calcareous materials. After washing in water, the samples were submerged in 70% hydrofluoric acid for one day and washed again. The residues were then decanted, covered by a small amount of 10% hydrochloric acid and heated. When boiling point was reached they were cooled and then washed. After sieving, the fraction of each sample with a diameter between 5 and 100 μm was kept, diluted in water and submitted to treatment with nitric acid while heating in a double boiler. The residue was sieved again, and the fraction with a diameter up to 5 μm was decanted into a test tube and centrifuged for 10 minutes at 1200 revolutions per minute. The residue was then fixed on a slide using a film of Cellosize and mounted in Canada balsam.

Photographs of the palynomorphs were obtained using a Nikon D300 digital camera linked to a Nikon Eclipse 80i microscope, and SEM micrographs were obtained using a Hitachi TM-1000 tabletop microscope. The formation, the level, the number of the slide and the graticule (England Finder) are indicated in the legend for each specimen illustrated in this paper.

Since it is difficult to compare the fossil spores and pollen grains to genera of plants living today, we followed the classification of *sporae dispersae* defined by Potonié & Kremp (1954, 1955). For some palynomorphs, we followed slightly modified version of Potonié & Kremp (1954, 1955) by Dettmann (1963), Potonié (1956, 1958, 1960, 1966, 1970a, b, 1975), and Pflug (1953). These classifications are based on the external morphology. However, we tried to determine the presumed botanical affinities when possible.

SYSTEMATIC DESCRIPTIONS

We present species that have been identified during this investigation (Table 1). The preparations are housed in the Collection de Paléobotanique

of the Université Pierre et Marie Curie (UPMC), Paris (France). Only new species and taxa in open nomenclature are described.

Anteturma PROXIMEGERMINANTES

Genus *Converrucosisporites* Potonié & Kremp, 1954

TYPE SPECIES. — *Converrucosisporites triquetrus* (Ibrahim, 1933) Potonié & Kremp, 1954.

Converrucosisporites sp.

(Fig. 5N, O)

Converrucosisporites sp. A, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 136, pl. III, fig. 2 (2009).

OCCURRENCE. — Ashikajima Fm (rare).

DESCRIPTION

Trilete microspore. Amb rounded triangular. The laesurae are long, rather indistinct, and seem to extend to the 3/4 of the spore radius. The two faces are covered by rounded verrucae of various sizes (0.5 to 3 μm high and 1 to 6 μm in diameter), distributed side by side or sometimes contiguous. Near the equator, some elongated verrucae can be sparsely observed. The exine is about 0.5 μm thick. Equatorial diameter = 30–35 μm .

BOTANICAL AFFINITIES

Cyatheales?

Genus *Manumia* Pocock, 1970

TYPE SPECIES. — *Manumia verrucata* Pocock, 1970.

Manumia japonica

Legrand, Pons, Nishida & Yamada n. sp.

(Fig. 6A–F, I, J)

Manumia sp. A, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces*

paléofloristiques du sud-est asiatique: 138, 139, pl. III, figs 8-10 (2009).

TYPE MATERIAL. — Site II, horizon 2, slides b, g; slide SEM-b; holotype (II2g-O68; Fig. 6C, F), paratypes (SEM-II2b, SEM-II2b, II2b-N21/4, II2c-K65g; Fig. 6A, B, D, E, I, J).

Collection de Paléobotanique - UPMC, Paris, France.

ETYMOLOGY. — The species name is after Japan, where the Choshi Group is located.

OCCURRENCE. — Ashikajima and Kimigahama Fm.

TYPE LOCALITY. — Hatoyama, SE Choshi Peninsula, Chiba Prefecture, Japan.

STRATIGRAPHIC HORIZON. — Ashikajima Fm (Barremian).

DIAGNOSIS

Trilete microspore. Amb rounded triangular. The laesurae are straight and extend to the $\frac{3}{4}$ of the spore radius. They are bordered by raised lips with irregular margins (3 to 7 μm wide) that can be continuous in the apices areas. The ornamentation of the exine is scabrate to granulate, with isolated verrucae (3-7 μm in diameter) irregularly distributed along the laesurae of the proximal face, wider (3-7 μm) in the interradian areas. At the equator, some circular or elongated verrucae are randomly distributed near the angles or between the laesurae. On the distal face, verrucae are more or less densely distributed. The exine is thick (about 2-3 μm). Equatorial diameter = 50-55 μm .

REMARKS

A wide range is noted in the ornamentation of this new species. The laesurae can extend to the $\frac{3}{4}$ of the spore radius or nearly to the equator. On the proximal face of the largest specimens (Fig. 6A, D), verrucae can sometimes be coalescent in the inter-radian areas to form ridges parallel to the equator. At the equator also, the elongated verrucae can gather to form an equatorial thickening (Fig. 6D, I). On the distal face, depending of the specimen, verrucae or tubercles can be isolated (Fig. 6F) or more or less densely distributed and coalescent (Fig. 6B, J). The equatorial diameter ranges from 40 to 55 μm .

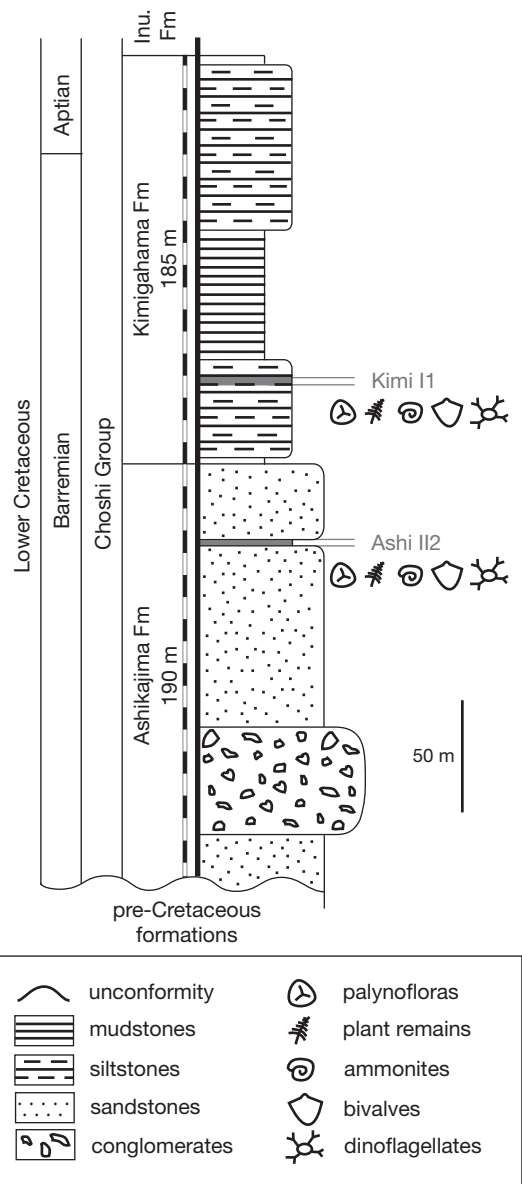


FIG. 4. — Synthetic stratigraphical column of the Ashikajima and Kimigahama formations, between the pre-Cretaceous formations and the Inubou Formation (modified from Obata *et al.* 1975; Obata & Matsukawa 2009).

The genus *Manumia* is generally characterized by strong equatorial thickenings and/or coarse tubercles more or less fused into ridges. The faces are unequal, with different ornamentations.

Four species have been defined for the genus *Manumia*: *M. delcourtii* (Pocock, 1970) Dybkjær, 1991, *M. irregularis* Pocock, 1970, *M. variverrucata* (Couper, 1958) Hoelstad, 1985, and *M. verrucata* Pocock, 1970. The Japanese species can be distinguished from the other species of the genus by the shape and distribution of its verrucae. Concerning *M. variverrucata*, Hoelstad (1985) defined it on the basis of an emendation and new combination of *Concavisorites variverrucatus* Couper, 1958. However, as the diagnosis made by Couper (1958) does not fit that made by Pocock (1970) for the genus *Manumia*, particularly about the ornamentation, we can suggest that the definition of a new species would have been more suitable than the new combination proposed by Hoelstad (1985).

This spore genus was previously reported from the Jurassic of Canada (Pocock 1970), Greenland (Lund & Pedersen 1984; Koppelhus & Hansen 2003), Alaska (Bjærke 1993), and northern Europe (Couper 1958; Schulz 1967; Guy 1971; Herngreen & de Boer 1974; Hoelstad 1985; Dybkjær 1991; Koppelhus 1992; Seidenkrantz *et al.* 1993; Koppelhus & Nielsen 1994; Koppelhus & Dam 2003; Bøe *et al.* 2005; Lindström & Erlström 2007; Stefanowicz 2008), and the Lower Cretaceous of Norway (Bøe *et al.* 2005). It was also reported from the Lower to Middle Jurassic of Afghanistan (Schweitzer *et al.* 1987). It seems to characterize the South Laurasian Province of Brenner (1976). Legrand (2009: 139, pl. III, fig. 11) distinguished a second form, morphologically similar but smaller (30–35 µm) and with a thinner exine, that could correspond to a variation of *M. japonica*.

BOTANICAL AFFINITIES

Even if the ornamentation suggests an affinity with the present Polydiales (Pteridaceae), particularly *Pteris* Linnaeus or *Pityrogramma* Link figured by Tryon & Lugardon (1991), the absence of any cingulum should distinguish them.

Genus *Uvaesporites* Döring, 1965

TYPE SPECIES. — *Uvaesporites glomeratus* Döring, 1965.

Uvaesporites sp.

Uvaesporites sp. B, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 141, pl. IV, fig. 4 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb circular. The laesurae are thin, straight, slightly raised, and extend to the cingulum. Proximal face psilate. The equator is ornamented by verrucae joined at their base (3–4 µm high and 3–7 µm in basal diameter). The distal face is covered by verrucae of various sizes, bigger near the equator than at the pole, often joined, making irregular and very small closed spaces. Equatorial diameter = 28 µm; width of the «cingulum» = 3–4 µm.

BOTANICAL AFFINITIES

Cyatheales (Cyatheaceae) or Lycopsida (Selaginellaceae) (Takahashi 1988).

Genus *Baculatisporites*

Pflug & Thomson *in* Thomson & Pflug, 1953

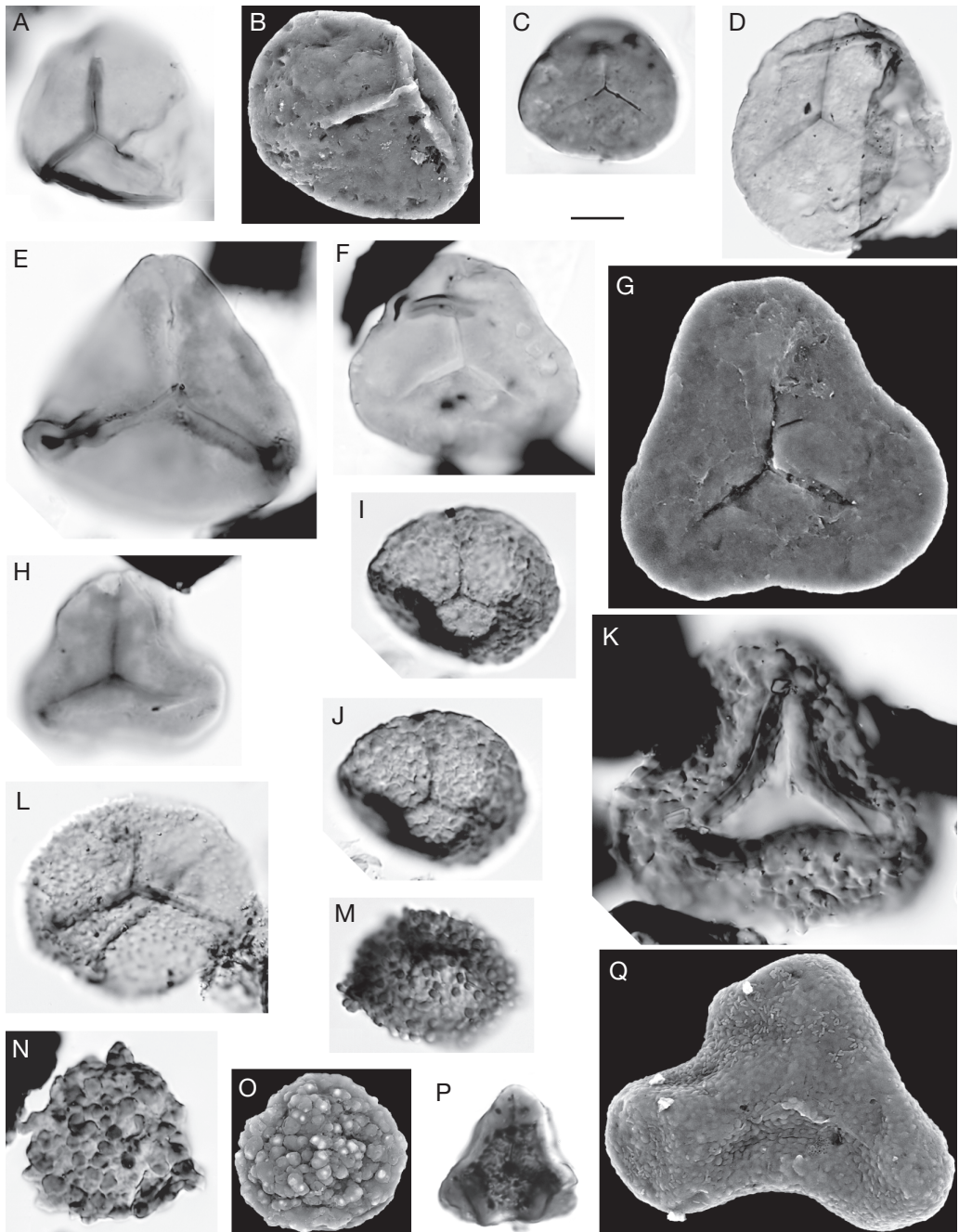
TYPE SPECIES. — *Baculatisporites primarius* (Wolff, 1934) Pflug & Thomson *in* Thomson & Pflug, 1953.

Baculatisporites sp.

(Fig. 6N)

Baculatisporites sp. B, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et*

Fig. 5. — Spores from the Barremian of south-west Japan: **A, B**, *Biretisporites potoniaei* (Delcourt & Sprumont, 1955) Delcourt, Dettmann & Hughes, 1963 (**A**, proximal face, Ashikajima Fm, 112a-U31/3; **B**, proximal face, Kimigahama Fm, SEM-I1a); **C**, *Todisporites miser* Takahashi, 1988, proximal face, Ashikajima Fm, 112b-R25hg; **D**, *Todisporites major* Couper, 1958, proximal face, Ashikajima Fm, 112c-H34/1; **E**, *Incertae sedis in* Hasenboehler (1981), proximal face, Ashikajima Fm, 112a-Q62/3; **F**, *Cyathidites minor* Couper, 1953, proximal face, Ashikajima Fm, 11a-V64; **G**, *Cyathidites australis* Couper, 1953, proximal face, Ashikajima Fm, SEM-II2a; **H**, *Cyathidites rarus* (Bolikhovitina, 1953) Deák, 1964, proximal face, Ashikajima Fm, 112a-G59/1; **I, J**, *Verrucosisporites densus* (Bolikhovitina, 1956)



Pocock, 1970, proximal and distal faces, Ashikajima Fm, Il2h-H49g; **K**, *Concavissimisporites variverrucatus* (Couper, 1958) Brenner, 1963, proximal face, Ashikajima Fm, Il2c-K43-1; **L**, *Osmundacidites wellmanii* Couper, 1953, proximal face, Ashikajima Fm, Il2b-P32/4; **M**, *Trilites bossus* Couper, 1958, Ashikajima Fm, Il2f-H29/1; **N**, **O**, *Converrucosisporites* sp. (**N**, Ashikajima Fm, Il2f-V27/3; **O**, Ashikajima Fm, SEM-II2c); **P**, *Cibotiumspora paradoxa* (Maljavkina, 1949) Chang, 1965, proximal face, Kimigahama Fm, I1a-F40-g; **Q**, *Concavissimisporites punctatus* (Delcourt & Sprumont, 1955) Brenner, 1963, proximal face, Ashikajima Fm, SEM-II2c. Scale bar: 10 μ m.

provinces paléofloristiques du sud-est asiatique: 142-143, pl. IV, fig. 8 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb circular. The laesurae are straight and extend to the 3/4 of the spore radius. The contact area is psilate. Small verrucae, coni and bacula (less than 1 µm long) are sparsely distributed near the equator and on the distal face. The exine is 1 µm thick. Equatorial diameter = 40-45 µm.

BOTANICAL AFFINITIES

Osmundales, Osmundaceae (Dettmann 1963, 1994).

Genus *Neoraistrickia* Potonié, 1956

TYPE SPECIES. — *Neoraistrickia truncatus* (Cookson, 1953) Potonié, 1956.

Neoraistrickia sp. 1 (Fig. 7A, B)

Neoraistrickia sp. A, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 143, pl. IV, fig. 12 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb rounded triangular. The laesurae are straight, slightly raised, and extend to the 3/4 of the spore radius. The two faces are densely covered by rounded to slender bacula mingled with some sharpened coni (3 to 7 µm high). The exine is 1.5 to 2 µm thick. Equatorial diameter = 50 µm with the ornamentation.

BOTANICAL AFFINITIES

Bryophyta or Lycopsidea (Selaginellaceae)?

Neoraistrickia sp. 2 (Fig. 7C, D)

Neoraistrickia sp. B, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et*

provinces paléofloristiques du sud-est asiatique: 144, pl. IV, fig. 14 (2009).

OCCURRENCE. — Ashikajima Fm (rare).

DESCRIPTION

Trilete microspore. Amb circular. The laesurae are straight and extend to the 2/3 of the spore radius. The contact area is psilate, followed by more or less coarse bacula and some elongated, sometimes joined (particularly at the equator) coni near the equator and on the distal face. The exine is about 1.5 µm thick. Equatorial diameter = 45-50 µm.

BOTANICAL AFFINITIES

Bryophyta or Lycopsidea (Selaginellaceae)?

Neoraistrickia sp. 3 (Fig. 7G, J)

Neoraistrickia sp. C, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 144, pl. IV, figs 11, 15 (2009).

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Trilete microspore. Amb circular. The laesurae cannot be clearly seen; they seem short and raised in a very small contact area. The two faces are densely covered by more or less short and sinuous rugulae topped by bacula, coni, spines or tubercules (4 to 7 µm high), giving to the spore a bristling appearance. The exine is about 3 µm thick. Equatorial diameter = 35-45 µm.

REMARK

The ornamentation of *Neoraistrickia* sp. 3 has similarities with that of *N.* sp. 2, but can be distinguished from the later by its dense and bristling appearance and its thicker exine.

BOTANICAL AFFINITIES

Bryophyta or Lycopsidea (Selaginellaceae)?

Genus *Tuberositriletes* Döring, 1964

TYPE SPECIES. — *Tuberositriletes montuosus* Döring, 1964.

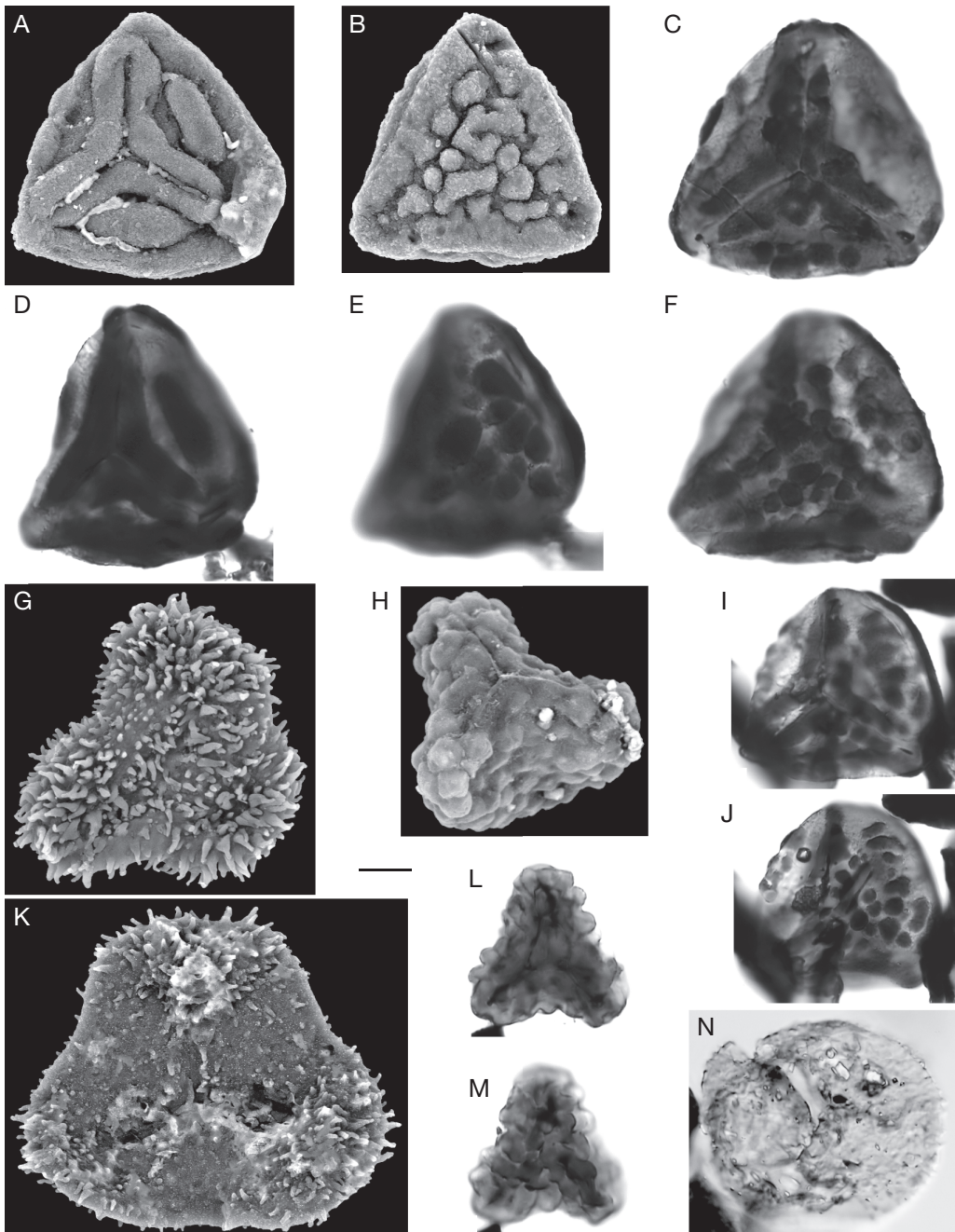


FIG. 6. — Spores from the Barremian of south-west Japan: **A-F, I, J**, *Manumia japonica* n. sp. (**A**, proximal face, Ashikajima Fm, SEM-II2b; **B**, distal face, Ashikajima Fm, SEM-II2b; **C, F**, proximal and distal faces, Ashikajima Fm, II2g-O68; **D, E**, proximal and distal faces, Ashikajima Fm, II2b-N21/4; **I, J**, proximal and distal faces, Ashikajima Fm, II2c-K65g); **G**, *Pilosisorites verus* Delcourt & Sprumont, 1955, distal face, Ashikajima Fm, SEM-II2c; **H, L, M**, *Tuberositriletes* sp. (**H**, proximal face, Ashikajima Fm, SEM-II2a; **L, M**, proximal and distal faces, Ashikajima Fm, II2b-U45/4); **K**, *Pilosisorites brevis* Delcourt & Sprumont, 1955, proximal face, Ashikajima Fm, SEM-II2c; **N**, *Baculatisporites* sp., proximal face, Ashikajima Fm, II2b-Z40/3. Scale bar: 10 μ m.

Tuberositriletes sp.
(Fig. 6H, L, M)

OCCURRENCE. — Ashikajima Fm (rare).

DESCRIPTION

Trilete microspore. Amb triangular with concave sides. The laesurae extend to the 3/4 of the spore radius. On the proximal face, the contact area is psilate, followed by one row of big welded verrucae (2-4 µm high, 2.5-5 µm in basal diameter) near the equator. The distal face is ornamented by welded and wavy rugulae, which are topped by verrucae. The rugulae are separated by small irregular spaces that can connect. Equatorial diameter = 28 µm.

BOTANICAL AFFINITIES

Filicopsida.

Genus *Cicatricosisporites*

Potonié & Gelletich, 1933 emend. Potonié, 1966

TYPE SPECIES. — *Cicatricosisporites dorogensis* Potonié & Gelletich, 1933.

Cicatricosisporites sinuosus Hunt, 1985
(Fig. 8K, L, S, T)

Pollen et Spores 27: 427-428, 430, pl. 2, figs 1-3 (1985). — Omran *et al.*, *Review of Palaeobotany and Palynology* 66: 301, pl. 1, fig. 4 (1990). — Schrank & Ibrahim, *Berliner Geowissenschaftliche Abhandlungen, Reihe A* 177: 16, 17, pl. 1, fig. 14 (1995). — Ibrahim, *Review of Palaeobotany and Palynology* 94: 151 (1996). — Al-Ameri *et al.*, *Cretaceous Research* 22: 738 (2001). — Ibrahim *et al.*, *Journal of African Earth Sciences* 32 (2): 276 (2001). — Mahmoud & Deaf, *Rivista Italiana di Paleontologia e Stratigrafia* 113 (2): 218 (2007). — Mahmoud *et al.*, *Revista Española de Micropaleontología* 39 (3): 176, pl. 5, fig. 14 (2007). — Mejia Velasquez, *Floral composition of a Lower Cretaceous paleotropical ecosystem inferred from quantitative palynology*: 60, pl. VIII, fig. 81 (2007). — Peyrot *et al.*, *Revista Española de Micropaleontología* 39 (1-2): 142 (2007). — Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 156, 157, pl. VIII, figs 2-4 (2009).

Camarozonosporites insignis Norris, 1959, Saad, *Pollen et Spores* 20 (2): 274, pl. III, figs 5, 6 (1978).

Reticulisporites sp. *sensu* Batten & Uwins (1985), Batten & Uwins, *Journal of Micropalaeontology* 4 (1): pl. 67, figs 1, 2 (1985). — Uwins & Batten, *Subsurface Palynostratigraphy of Northeast Libya*: 219, 224, pl. 43, fig. 12 (1988). — Masure *et al.*, *Géologie Méditerranéenne* 25 (3-4): 273, pl. 2, fig. 20 (1998).

Reticulisporites sp., Pons *et al.*, *Géologie de l'Afrique et de l'Atlantique Sud: Compte rendu des Colloques de géologie d'Angers*: 390 (1996).

Cicatricosisporites daxinganlingensis Pu & Wu, 1985, Umetsu & Sato, *Review of Palaeobotany and Palynology* 144 (1-2): pl. 1, fig. 7 (2007).

OCCURRENCE. — Ashikajima and Kimigahama Fm (common).

DISTRIBUTION. — **North Tethys.** Upper Jurassic to Lower Cretaceous of England (Hunt 1985). This species is known in Japan under the name *Cicatricosisporites daxinganlingensis* Pu & Wu, 1985 (Aptian-Albian, Umetsu & Sato 2007). It was also reported from the early Aptian of France (Masure *et al.* 1998), and late Aptian-early Albian of Spain (Peyrot *et al.* 2007).

South Tethys. This species is known in the ?late Hauterivian-?middle Barremian and early to middle Albian of Libya under the name *Reticulisporites* sp. *sensu* Batten & Uwins (1985) (Uwins & Batten 1988). It was also reported in the Barremian of Lebanon (Dejax, personal communication), early Aptian of Colombia (Mejia Velasquez 2007), late Aptian of Brazil (Pons *et al.* 1996, under the name *Reticulisporites* sp.), Aptian-Albian of Egypt (Saad 1978, under the name *Camarozonosporites insignis* Norris, 1959; Omran *et al.* 1990; Schrank & Ibrahim 1995; Ibrahim 1996; Ibrahim *et al.* 2001; Mahmoud & Deaf 2007; Mahmoud *et al.* 2007), Albian of Tunisia (Pons, personal communication), and Albian-early Cenomanian of Iraq (Al-Ameri *et al.* 2001).

DESCRIPTION

Trilete microspore. Amb rounded triangular. The laesurae are straight, bordered by lips (1-1.5 µm wide), and extend to the 3/4 of the spore radius. Exine striate. Striae (0.5-1.5 µm wide; 0.5-1 µm high) are separated by spaces 0.5 to 3 µm wide; they are oblique to perpendicular to the equator, more or less sinuous and parallel, can bifurcate, and run irregularly on both faces. On the proximal face, each interradial area contains 4 to 9 striae. The exine is about 1 µm thick. Equatorial diameter = 20-35 (40) µm.

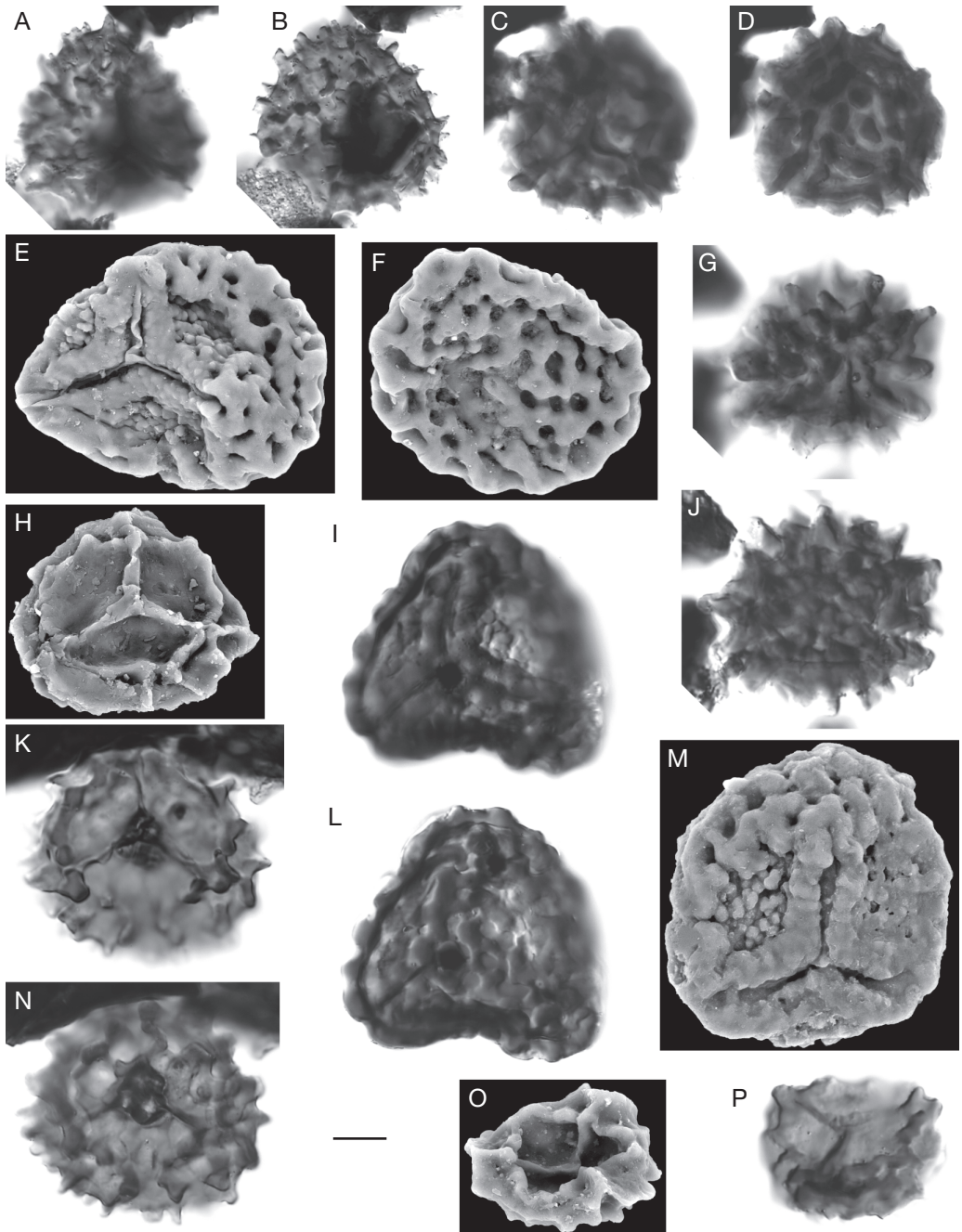


FIG. 7. — Spores from the Barremian of south-west Japan: **A, B**, *Neoraistrickia* sp. 1, proximal and distal faces, Ashikajima Fm, Il2c-U62/3d; **C, D**, *Neoraistrickia* sp. 2, proximal and distal faces, Ashikajima Fm, Il2c-H33/4; **E, F, I, L, M**, *Klukisporites variegatus* Couper, 1958 (**E**, proximal face, Kimigahama Fm, SEM-I1a; **F**, distal face, Kimigahama Fm, SEM-I1a; **I, L, M**, proximal and distal faces, Kimigahama Fm, I1a-H48/1a; **M**, proximal face, Ashikajima Fm, SEM-II2c); **G, J**, *Neoraistrickia* sp. 3, proximal and distal faces, Kimigahama Fm, I1b-S68g; **H, K, N-P**, *Lycopodiumsporites dentimuratus* Brenner, 1963 (**H**, proximal face, Kimigahama Fm, SEM-I1c; **K, N**, proximal and distal faces, Ashikajima Fm, Il2f-M56/2; **O**, lateral view, Kimigahama Fm, SEM-I1a; **P**, lateral view, Ashikajima Fm, Il2e-R56/2). Scale bar: 10 μ m.

REMARKS

Hunt (1985) attributed this species to *Cicatricosporites*. However, it differs from all other species already described in this genus, by its striae perpendicular to the equator on the proximal face. De Haan (1997) proposed in his thesis a new form-genus, *Huntisporis*, and a new combination, *Huntisporis sinuosus* (Hunt, 1985) de Haan, 1997, but both are not valid because unpublished.

Cicatricosporites curvatus Pu & Wu, 1982 (417, pl. 8, figs 19, 20), reported from the ?Valanginian-Barremian of the Heilongjiang Province of North China, has a similar size (34-42 µm in diameter) and distribution of the striae, but the laterals are larger (2-3 µm) than those of *C. sinuosus* (0.5-1.5 µm).

Cicatricosporites sinuosus, reported from the Neocomian-Barremian of Portugal by Trincão (1990: 155, pl. 19, figs 4, 5, 9), shows a proximal face with ridges perpendicular to the equator and a distal face rugate-reticulate, different from *C. sinuosus*.

BOTANICAL AFFINITIES

Cicatricosporites sinuosus shows similarities with spores of the genus *Saccoloma* Kaulfuss (Polypodiales, Saccolomataceae) (Murillo & Bless 1974; Tryon & Tryon 1982; Tryon & Lugardon 1991).

Cicatricosporites sp. 1

(Fig. 9A, B)

Cicatricosporites sp. B, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 159, pl. X, fig. 2 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb rounded triangular. The laesurae are slightly undulating, bordered by lips, and extend to the $\frac{2}{3}$ of the spore radius. Exine

canaliculate. The proximal face is ornamented by 3 sets of 4 muri parallel to the equator and to the laesurae. The distal face shows 8 to 10 muri, 3 to 5 µm wide and separated by less than 0.5 µm, which are parallel among them and to one side (Fig. 11). The exine is thick at the equator (about 3 µm). The ornamentation of this form corresponds to the type VI-B defined by Krutzsch (1963). Equatorial diameter = 40-55 µm.

BOTANICAL AFFINITIES

Schizaeales, Anemiaceae. Couper (1958) suggested an affinity of *Cicatricosporites* with spores produced by *Ruffordia* Seward, and Skog (1980, 1982) an affinity with *Pelletixia* Watson & Hill (Schizaeaceae).

Cicatricosporites sp. 2

(Fig. 9C, D)

Cicatricosporites sp. D, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 159, 160, pl. VIII, fig. 5 (2009).

OCCURRENCE. — Ashikajima Fm.

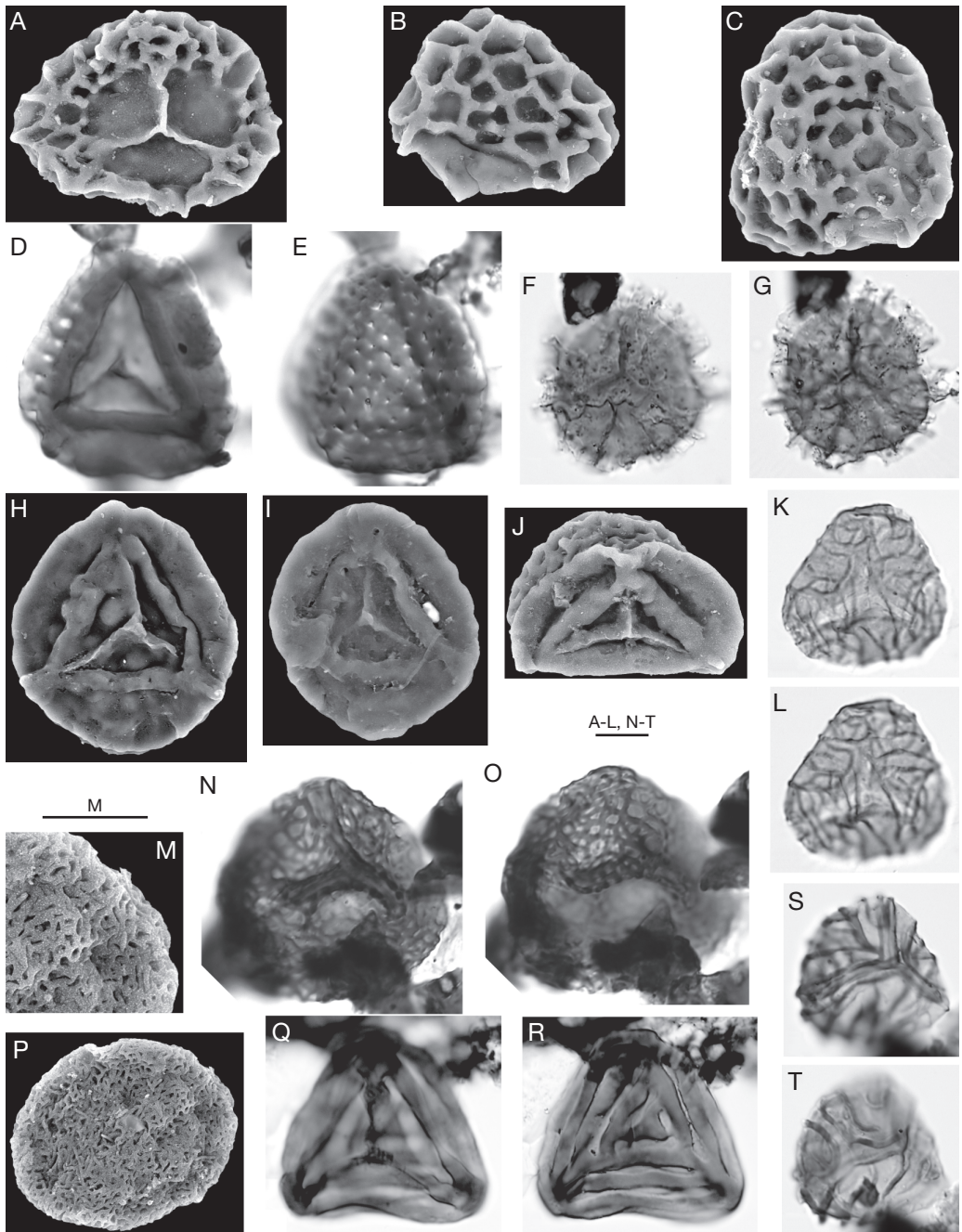
DESCRIPTION

Trilete microspore. Amb rounded triangular with convex sides. The spore is bordered by a thin carina. The laesurae are raised, bordered by a small thickening, and extend to the equator of the spore. Exine cicatricose. The proximal face is tetrahedral and psilate. On the distal face, 3 sets of 4 muri (2 to 4 µm wide, separated by spaces 2 to 5 µm wide) parallel to the equator form equilateral triangles centered on the distal pole, where they delimit a wide triangle (side 15 to 20 µm long) (Fig. 11). The exine is about 4 µm thick. The ornamentation of this form corresponds to the type I-A defined by Krutzsch (1963). Equatorial diameter = 45 µm.

BOTANICAL AFFINITIES

Schizaeales, Anemiaceae.

Fig. 8. — Spores from the Barremian of south-west Japan: **A-C**, *Retitriteles* sp. (**A**, proximal face, Kimigahama Fm, SEM-I1a; **B**, lateral view, Kimigahama Fm, SEM-I1a; **C**, distal face, Kimigahama Fm, SEM-I1c); **D, E, H-J**, *Foveosporites ryosekiensis* n. sp. (**D, E**, proximal and distal faces, Ashikajima Fm, I12a-U63; **H**, proximal face, Ashikajima Fm, SEM-I12a; **I**, proximal face, Ashikajima Fm, SEM-I12b; **J**, lateral



view, Kimigahama Fm, SEM-I1c); **F, G**, *Retitriletes austroclavatidites* (Cookson, 1953) Döring, Krutzsch, Mai & Schulz *in* Krutzsch, 1963, proximal and distal faces, Ashikajima Fm, I12b-O45/3; **K, L, S, T**, *Cicatricosisporites sinuosus* Hunt, 1985 (**K, L**, proximal and distal faces, Ashikajima Fm, I12d-D55/4; **S, T**, proximal and distal faces, Ashikajima Fm, I12b-N33/1); **M, P**, *Microreticulatisporites* sp. 1, distal face with detail, Kimigahama Fm, SEM-I1a; **N, O**, *Microreticulatisporites* sp. 2, proximal and distal faces, Ashikajima Fm, I12b-T23d; **Q, R**, *Cicatricosisporites hughesi* Dettmann, 1963, proximal and distal faces, Ashikajima Fm, I12h-E52/1. Scale bars: 10 μ m.

Cicatricosisporites sp. 3
(Fig. 9E, F)

Cicatricosisporites sp. E, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 160, pl. IX, fig. 8 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb triangular with convex sides. Tops are slightly raised. The laesurae are thin, raised, slightly undulating, and bordered by lips in the contact area. Exine cicatricose. On the proximal face, we can observe 3 sets of 4 muri which can fork in each interradian area. Those muri often roll up slightly before joining with the laesurae. The distal face shows muri which form triangles centered on the distal pole; however, those muri are undulating and intersect the bisecting line, alternating from one to another (Fig. 11). Equatorial diameter = 40–60 μm .

BOTANICAL AFFINITIES

Schizaeales, Anemiaceae.

Cicatricosisporites sp. 4
(Fig. 9G, H)

Cicatricosisporites sp. C, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 159, pl. VIII, fig. 7 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb rounded triangular with convex sides. The laesurae are raised, slightly undulating, and extend to the 3/4 of the spore radius. Exine cicatricose. On the proximal face, a small and psilate contact area is followed by 3 sets of about 9 narrow muri (about 0.5 μm wide, separated by furrows of the same width) parallel to the equator. On the distal face, many narrow muri are more or less parallel to one set of the proximal face, and they go from one to another top of the spore (Fig. 11). The ornamentation of this

form corresponds to the type VI-B defined by Krutzsch (1963). Equatorial diameter = 40–45 μm .

BOTANICAL AFFINITIES

Schizaeales, Anemiaceae.

Genus *Foveosporites* Balme, 1957

TYPE SPECIES. — *Foveosporites canalis* Balme, 1957.

Foveosporites ryosekiensis

Legrand, Pons, Nishida & Yamada n. sp.
(Fig. 8D, E, H–J)

Foveosporites sp., Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 149, pl. V, fig. 16; pl. VI, figs 1, 2 (2009).

TYPE MATERIAL. — Site II, horizon 2, slide a; slides SEM-a, SEM-b; holotype (II2a-U63; Fig. 8D, E); paratypes (SEM-II2a, SEM-II2b; Fig. 8H, I).
Collection de Paléobotanique-UPMC, Paris, France.

ETYMOLOGY. — The species name is after the Ryoseki-type Province of Japan, of which this species seems to be characteristic.

OCCURRENCE. — Ashikajima and Kimigahama Fm (common).

TYPE LOCALITY. — Hatoyama, SE Choshi Peninsula, Chiba Prefecture, Japan.

STRATIGRAPHIC HORIZON. — Ashikajima Fm (Barremian).

DIAGNOSIS

Trilete microspore. Amb triangular with straight to slightly convex sides. The laesurae are undulating, slightly raised (1–2.5 μm), and extend to the 3/4 of the spore radius. The contact area is psilate or can sometimes present one tubercule, and is delimited by a triangular thickening of the exine (3–4 μm wide), which overhangs and includes the trilete mark, and can extend to the apices. Beyond this thickening, the exine is psilate on the proximal face and forms a broad equatorial flange. The equator and the distal face are densely pitted to foveolate. On the distal

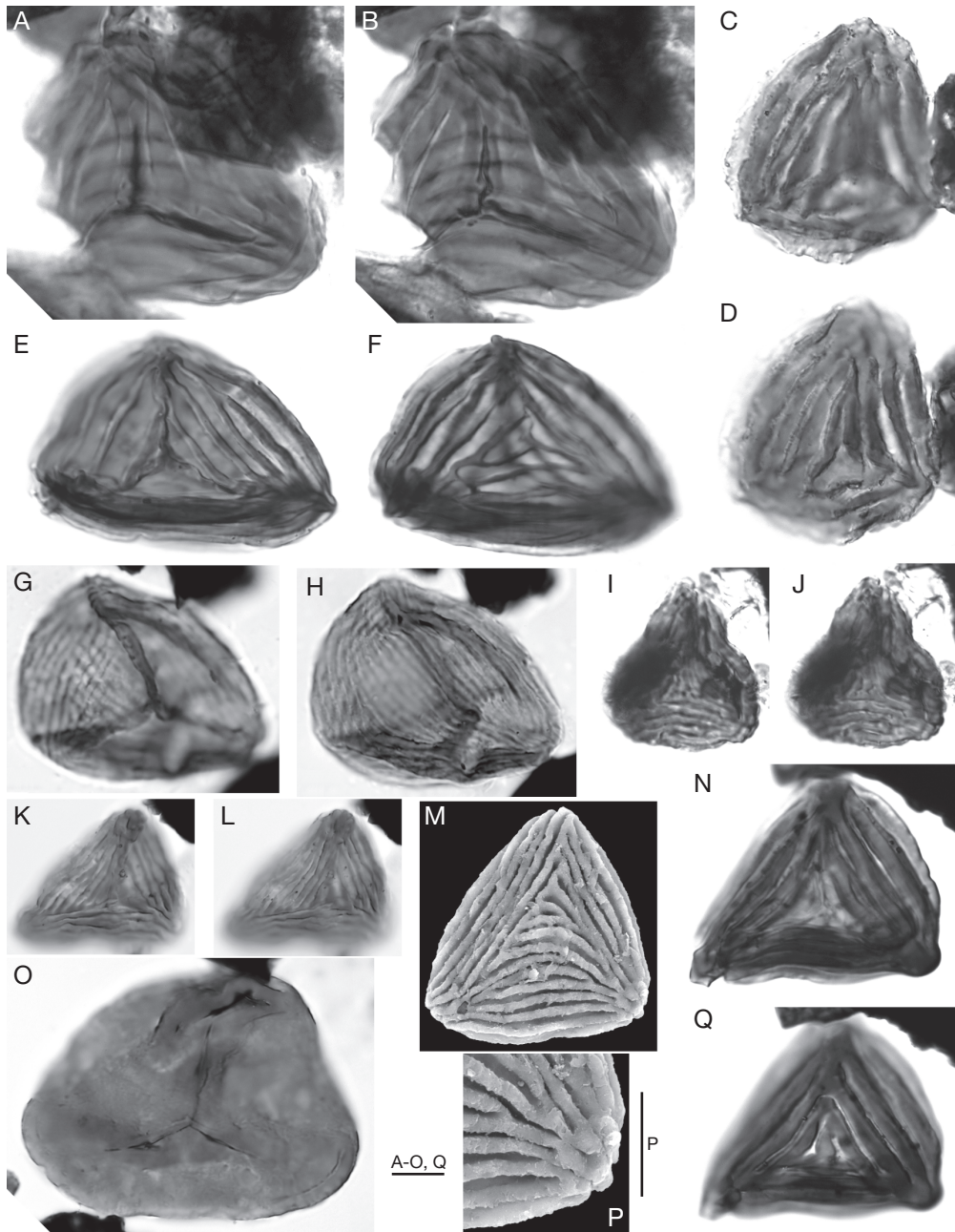


FIG. 9. — Spores from the Barremian of south-west Japan: **A, B**, *Cicatricosisporites* sp. 1, proximal and distal faces, Ashikajima Fm, II2f-U33d; **C, D**, *Cicatricosisporites* sp. 2, proximal and distal faces, Ashikajima Fm, II2a-G40d; **E, F**, *Cicatricosisporites* sp. 3, proximal and distal faces, Ashikajima Fm, II2h-Q57; **G, H**, *Cicatricosisporites* sp. 4, proximal and distal faces, Ashikajima Fm, II2f-Y56/1b; **I, J**, *Cicatricosisporites mohrioides* Delcourt & Sprumont, 1955, proximal and distal faces, Kimigahama Fm, I1a-M55; **K-M, P**, *Ruffordiaspora australiensis* (Cookson, 1953) Dettmann & Clifford, 1992 (**K, L**, proximal and distal faces, Ashikajima Fm, II2c-D62/4; **M, P**, distal face with detail, Kimigahama Fm, SEM-I1a); **O**, *Matonisporites* sp. 2, proximal face, Ashikajima Fm, II2a-J46/4; **N, Q**, *Plicatella* sp., proximal and distal faces, Ashikajima Fm, II2h-J54. Scale bars: 10 µm.

face, the foveolae are more or less rounded, coarser near the equator (0.5 to 1.5 μm wide). The exine is 3 to 4 μm thick. Equatorial diameter = 35-45 μm ; equatorial flange width = 5-7 μm .

REMARKS

Foveosporites labiosus Singh, 1971 has a thickening on its distal face similar to that observed in *F. ryosekiensis*, but its location is different. The equatorial flange reminds the Cyatheales (Lophosoriaceae) figured by Tryon & Tryon (1982).

BOTANICAL AFFINITIES

Lycopodiales, Lycopodiaceae.

Genus *Microreticulatisporites*

Knox, 1950 emend. Potonié & Kremp, 1954

TYPE SPECIES. — *Microreticulatisporites lacunosus* (Ibrahim, 1933) Knox, 1950.

Microreticulatisporites sp. 1

(Fig. 8M, P)

OCCURRENCE. — Kimigahama Fm (one specimen).

DESCRIPTION

Microspore. Amb circular. The laesurae are not seen. Exine microreticulated and finely scabrate. The mesh is polygonal, of various shapes and sizes (lumina 0.2 to 1.5 μm in diameter). The exine is 2 μm thick. Equatorial diameter = 40-45 μm .

BOTANICAL AFFINITIES

The ornamentation of this species shows similarities with that of some Polypodiales (Dennstaedtiaceae) figured by Tryon & Lugardon (1991). Moreover, the genus may have sphenophyte affinities, e.g. with the Noeggerathiales (Knox 1950; Singh 1964).

Microreticulatisporites sp. 2

(Fig. 8N, O)

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb rounded triangular. The laesurae are straight, bordered by lips 1 to 1.5 μm wide, and extend to the $\frac{2}{3}$ of the spore radius. Exine reticulated and slightly rounded. The mesh is polygonal, of various shapes and sizes (lumina 0.5 to 3 μm in diameter). The exine is 2 μm thick. Equatorial diameter = 40-50 μm .

BOTANICAL AFFINITIES

Polypodiales (Dennstaedtiaceae) or Noeggerathiales (Knox 1950; Singh 1964).

Genus *Retitriletes*

van der Hammen, 1956 ex Pierce, 1961 emend. Döring, Krutzsch, Mai & Schulz *in* Krutzsch, 1963

TYPE SPECIES. — *Retitriletes globosus* Pierce, 1961.

Retitriletes sp.

(Fig. 8A-C)

OCCURRENCE. — Kimigahama Fm.

DESCRIPTION

Trilete microspore. Amb rounded triangular. The laesurae are straight, slightly raised, and extend to the $\frac{2}{3}$ of the spore radius. The contact area is psilate, followed by a reticulum with polygonal lumina of various shapes and sizes (3-8 μm in diameter; muri about 2 μm high) near the equator and on the distal face. The exine is about 2.5 μm thick. Equatorial diameter = 40-45 μm .

BOTANICAL AFFINITIES

Döring *et al.* *in* Krutzsch (1963) suggested an affinity of *Retitriletes* with spores produced by the Lycopsida (Lycopodiaceae), for example *Lycopodium* Linnaeus.

Genus *Matonisporites*

Couper, 1958 emend. Dettmann, 1963

TYPE SPECIES. — *Matonisporites phlebopteroides* Couper, 1958.

Matonisorites sp. 1

Matonisorites sp. A, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 164, pl. XI, fig. 6 (2009).

OCCURRENCE. — Kimigahama Fm.

DESCRIPTION

Psilate trilete microspore. Amb rounded triangular with slightly convex sides. The laesurae are straight and extend to the 3/4 of the spore radius. The exine is about 4 µm thick. Equatorial diameter = 90 µm.

BOTANICAL AFFINITIES

Couper (1958) discovered *Matonisorites* spores *in situ* in *Phlebopteris* Brongniart, *Selenocarpus* Schenk and *Matonidium* Schenk (Gleicheniales, Matoniaceae). Ash *et al.* (1982) and Sukh-Dev (1980) also discovered *in situ* *Matonisorites* spores in *Phlebopteris* sporangia, associated with *Dictyophyllidites* Couper, 1958 emend. Dettmann, 1963 spores.

Matonisorites sp. 2 (Fig. 9O)

Matonisorites sp. D, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 165, pl. XII, figs 1, 4 (2009).

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Psilate trilete microspore. Amb rounded triangular. The laesurae are straight, bordered by thickenings (2-4 µm wide), and extend to the 2/3 of the spore radius. The exine is 2 µm thick. Equatorial diameter = 40-55 µm.

BOTANICAL AFFINITIES

Gleicheniales, Matoniaceae.

Genus *Nodosisorites*

Deák, 1964 emend. Dettmann & Clifford, 1992

TYPE SPECIES. — *Nodosisorites costatus* Deák, 1964.

Nodosisorites choshiensis

Legrand, Pons, Nishida & Yamada n. sp.
(Fig. 10G-K)

Nodosisorites sp., Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 166, 167, pl. XIII, figs 3, 5, 6 (2009).

TYPE MATERIAL. — Site I, horizon 1, slides SEM-a, SEM-b; holotype (SEM-a; Fig. 10J); paratype (SEM-b; Fig. 10K).

Collection de Paléobotanique-UPMC, Paris, France.

ETYMOLOGY. — The species name is after the Choshi Group, from which it was reported.

OCCURRENCE. — Ashikajima and Kimigahama Fm.

TYPE LOCALITY. — Kimigahama bay, Choshi Peninsula, Chiba Prefecture, Japan.

STRATIGRAPHIC HORIZON. — Kimigahama Fm (late Barremian).

DIAGNOSIS

Tetrahedral trilete microspore. Amb rounded triangular. Proximal face slightly flattened, with a psilate contact area followed by 1 or 2 muri parallel to the equator. The laesurae are relatively narrow, slightly raised and undulating, and extend to the 3/4 of the spore radius. The exine is cicatricose. The distal face is strongly convex (35 to 40 µm in polar diameter). It shows 3 sets of 3-4 muri parallel to the equator, that join in the apex areas. One of these sets goes on to form a triangle centered on the distal pole (Fig. 11). The muri are raised, 2 to 3 µm wide, and are ornamented by tubercules, verrucae or spines (5 to 7 µm long) regularly distributed. The ornamentation of this form corresponds to the type I-A defined by Krutzsch (1963). Equatorial diameter = 35-50 µm; polar diameter = 35-40 µm.

REMARKS

Appendicisporites spinosus Pocock, 1964 shows supramural bacula, verrucae or spines as observed in *Nodosisorites*, but differs from the later in that these elements are not evenly distributed. Cicatricose or canaliculate genera *Cicatricosisporites* and *Plicatella* also show some morpho-

logical similarities, but both lack supramural elements.

BOTANICAL AFFINITIES

Schizaeales, Anemiaceae (Dettmann & Clifford 1992).

Nodosisporites makotoi

Legrand, Pons, Nishida & Yamada n. sp.
(Fig. 10A-F)

Nodosisporites sp., Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 166, 167, pl. XIII, figs 1, 2, 4, 7; pl. XIV, fig. 7 (2009).

TYPE MATERIAL. — Site II, horizon 2, slides a, b; holotype (II2a-L58/2; Fig. 10A, D); paratypes (II2b-E56/3, II2b-U33; Fig. 10B, C, E, F).
Collection de Paléobotanique-UPMC, Paris, France.

ETYMOLOGY. — The species is named in honour of Prof. Makoto Nishida, who first studied fossil plants from the Choshi Group.

OCCURRENCE. — Ashikajima and Kimigahama formations.

TYPE LOCALITY. — Hatoyama, SE Choshi Peninsula, Chiba Prefecture, Japan.

STRATIGRAPHIC HORIZON. — Ashikajima Formation (Barremian).

DIAGNOSIS

Tetrahedral trilete microspore. Amb rounded triangular. Proximal face slightly flattened, with a psilate contact area followed by 1 or 2 muri parallel to the equator. The laesurae are relatively narrow, raised (about 3 µm), undulating, and extend to the 3/4 of the spore radius or to the equator; they are smooth or ornamented by small spines (0.5-1 µm high and 1-3 µm in basal diameter). Near the apices, 5-6 big spines (3-5 µm high) are present. A translucent equatorial zona with a dentate margin can be seen. The exine is cicatricose. The distal face shows 3 sets of 3-4 muri sinuous but parallel to the equator. One of these sets goes on to form a triangle (sometimes, more or less a network) centered on the distal

pole (Fig. 11). The ornamentation of this form corresponds to the type I-A defined by Krutzsch (1963). Equatorial diameter = 40-45 µm.

REMARKS

Appendicisporites dentimarginatus Brenner, 1963 shows similarities with *Nodosisporites makotoi*, but lacks spines on the apices.

BOTANICAL AFFINITIES

Schizaeales, Anemiaceae (Dettmann & Clifford 1992). The ornamentation shows similarities with that of *Anemia phyllitidis* (Linnaeus) Swartz from Brazil, figured by Tryon & Lugardon (1991).

Genus *Plicatella*

Maljavkina, 1949 emend. Burden & Hills, 1989

TYPE SPECIES. — *Plicatella trichacantha* Maljavkina, 1949.

Plicatella sp.
(Fig. 9N, Q)

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb triangular with straight to slightly convex sides and raised tops. The laesurae are thin, straight, raised, and extend to the 3/4 of the spore radius. Exine canaliculate. The proximal face shows a small psilate contact area, followed by 3 sets of 3-4 muri (1.5 to 4 µm wide) parallel to the equator; the muri join at the tops. The distal face is ornamented by 3 sets of 4 wavy muri parallel to the equator, distributed in a slight interval to form concentric triangles centered on the distal pole (Fig. 11). The ornamentation of this form corresponds to the type I-B defined by Krutzsch (1963). Equatorial diameter = 40-50 µm.

BOTANICAL AFFINITIES

Schizaeales, Schizaeaceae (Dettmann & Clifford 1992).

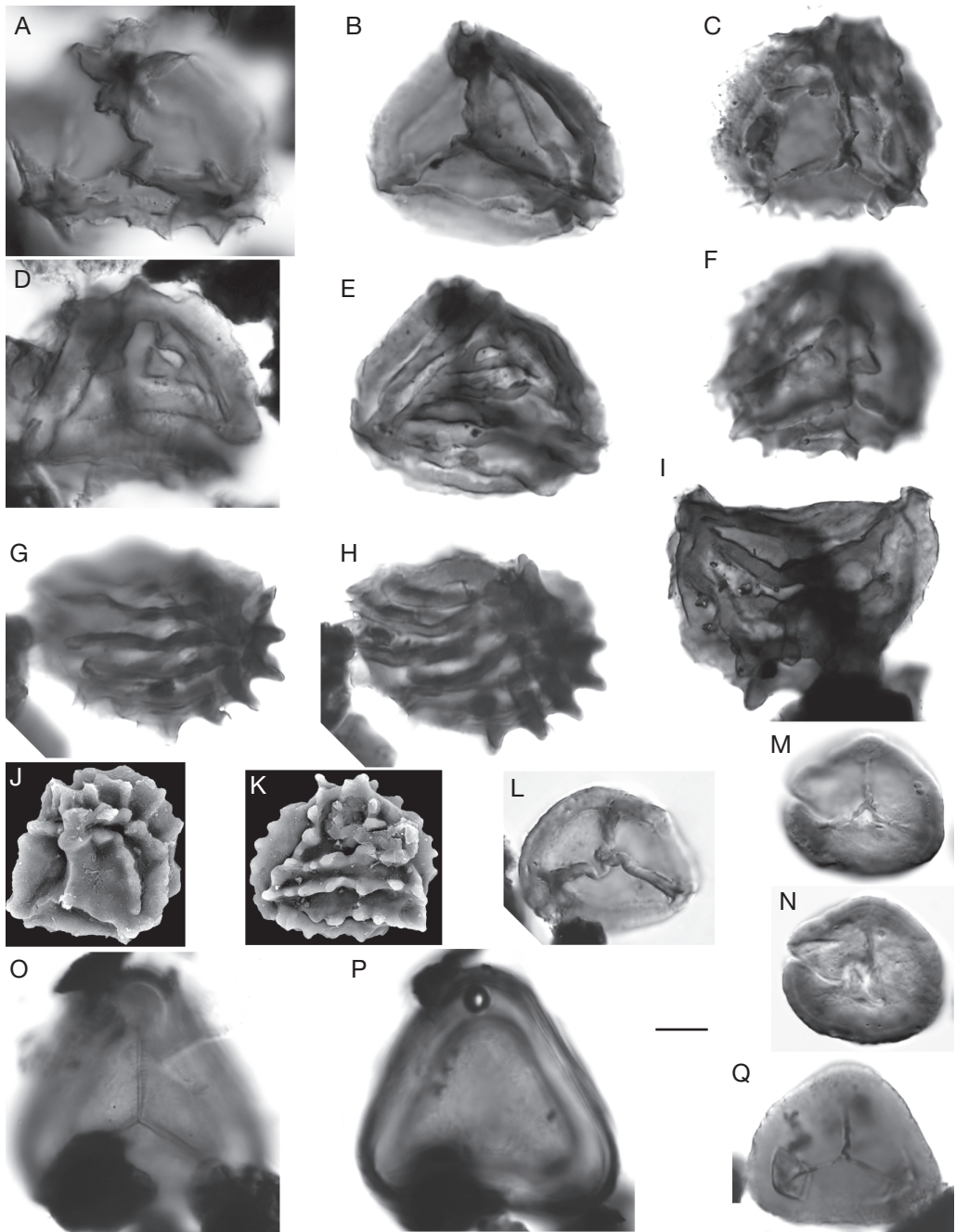


FIG. 10. — Spores from the Barremian of south-west Japan: **A-F**, *Nodosisporites makotoi* n. sp. (**A, D**, proximal and distal faces, Ashikajima Fm, I12a-L58/2; **B, E**, proximal and distal faces, Ashikajima Fm, I12b-E56/3; **C, F**, proximal and distal faces, Ashikajima Fm, I12b-U33); **G-K**, *Nodosisporites choshiensis* n. sp. (**G, H**, lateral view, Ashikajima Fm, I12b-K22/2; **I**, lateral view, Ashikajima Fm, I12b-E40b; **J**, proximal face, Kimigahama Fm, SEM-I1a; **K**, distal face, Kimigahama Fm, SEM-I1b); **L-N**, *Cingulatisporites* sp. 1 (**L**, proximal face, Kimigahama Fm, I1b-R41; **M, N**, proximal and distal faces, Ashikajima Fm, I12c-J26/3); **O, P**, *Cingulatisporites psilatus* Groot & Penny, 1960, proximal and distal faces, Kimigahama Fm, I1a-W67g; **Q**, *Cingutriteles* sp., proximal face, Ashikajima Fm, I12a-H67g. Scale bar: 10 μ m.

Genus *Cingulatisporites*
Thomson in Thomson & Pflug, 1953
emend. Potonié, 1956

TYPE SPECIES. — *Cingulatisporites levispeciosus* Pflug in Thomson & Pflug, 1953.

Cingulatisporites sp. 1
(Fig. 10L-N)

Cingulatisporites sp. B, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 168, pl. XIV, figs 4-6 (2009).

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Cingulate trilete microspore. Amb rounded triangular. The laesurae are undulating and extend to the cingulum, where they divide into two ends. Exine scabrate. Equatorial diameter = 30-35 μ m; cingulum thickness = 3-5 μ m.

BOTANICAL AFFINITIES

Filicopsida.

Cingulatisporites sp. 2
(Fig. 12A)

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Cingulate trilete microspore. Amb rounded triangular. The laesurae are raised, undulating, and extend to the cingulum. Exine scabrate. Equatorial diameter = 45-50 μ m; cingulum thickness = 5-8 μ m.

BOTANICAL AFFINITIES

Filicopsida.

Genus *Cinguriletes*
Pierce, 1961 emend. Dettmann, 1963

TYPE SPECIES. — *Cinguriletes congruens* Pierce, 1961.

Cinguriletes sp. (Fig. 10Q)

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Cingulate trilete microspore. Amb rounded triangular with straight to convex sides. The laesurae are straight and extend to the $\frac{2}{3}$ of the spore radius (a little before the cingulum). The cingulum is wide (4-5 μ m, that is to say more than $\frac{1}{5}$ of the spore radius). Exine psilate. Equatorial diameter = 30-35 μ m.

BOTANICAL AFFINITIES

Filicopsida (Couper 1958), Lycopsida (Selaginellaceae?) (Pierce 1961).

Genus *Distaltriangulisporites* Singh, 1971

TYPE SPECIES. — *Distaltriangulisporites perplexus* (Singh, 1964) Singh, 1971.

Distaltriangulisporites sp. (Fig. 12B, C)

Distaltriangulisporites sp. B, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 169, pl. XIV, fig. 10 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Cingulate trilete microspore. Amb rounded triangular. The laesurae are slightly raised and extend to the cingulum. Proximal face scabrate. The distal face shows flat muri forming a coarse reticulum with wide rounded lumina. Equatorial diameter = 28-32 μ m.

BOTANICAL AFFINITIES

Schizaeales, Anemiaceae (Dettmann & Clifford 1992).

Genus *Patellasporites*
Groot & Groot, 1962 emend. Kemp, 1970

TYPE SPECIES. — *Patellasporites tavadensis* Groot & Groot, 1962.

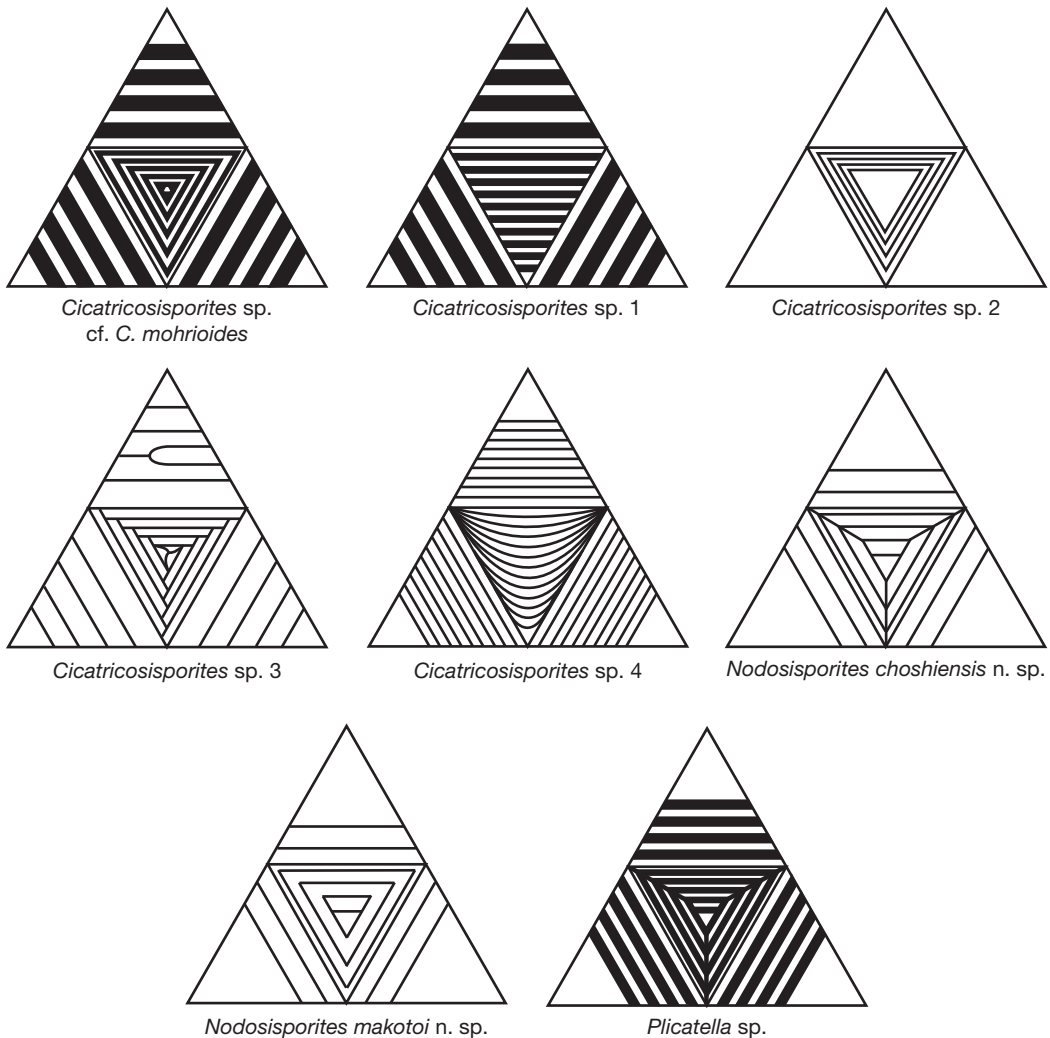


FIG. 11. — Ornamentation of the schizaealean forms corresponding to new species or taxa placed in open nomenclature.

Patellasporites sp.

Patellasporites sp. A, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 172, pl. XV, fig. 2 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Trilete microspore. Amb circular. The laesurae are straight, slightly raised, thicken, and extend

to the inner side of the patella. Proximal face psilate. Verrucae merge at the equator, forming a patella, but are separated by thin radial canals. The distal face is covered by verrucae of various sizes, bigger near the equator than at the pole, which merge and let only very small irregular spaces between them. Equatorial diameter = 30 μ m.

BOTANICAL AFFINITIES
Filicopsida.

Genus *Aequitriradites* Delcourt & Sprumont, 1955 emend. Dettmann, 1963

TYPE SPECIES. — *Aequitriradites dubius* Delcourt & Sprumont, 1955.

Aequitriradites sp.
(Fig. 12E)

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Zonate trilete microspore. Amb rounded subtriangular. Central body subcircular. Laesurae are not visible. Central body verrucate; verrucae are very small and contiguous (about 1-2 µm in diameter). The exine thickens near the periphery of the central body (about 3-3.5 µm). The zona is thin, granulate, radially folded, with irregular and more or less transparent margins. It is wider in three areas (about five times wider), which gives to the spore a subtriangular shape. No hilum is visible. Equatorial diameter = 45-70 µm; zona width = 2-12 µm.

BOTANICAL AFFINITIES

Bryophyta, Marchantiopsida.

Genus *Laevigatosporites*
Ibrahim, 1933
emend. Schopf, Wilson & Bentall, 1944

TYPE SPECIES. — *Laevigatosporites vulgaris* (Ibrahim, 1932) Ibrahim, 1933.

Laevigatosporites sp. (Fig. 12J)

Laevigatosporites sp. A, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 177, pl. XVI, fig. 11 (2009).

OCCURRENCE. — Ashikajima Fm (rare).

DESCRIPTION

Psilate monolete microspore. Amb broadly elliptical in lateral view. The proximal face is slightly concave. The laesura is straight and runs longitudinally on 1/3 of the proximal face. Exine about 2 µm thick. Equatorial diameter = 60 µm; polar diameter = 40 µm.

BOTANICAL AFFINITIES

Polypodiales (Polypodiaceae, Pteridaceae or Dennstaedtiaceae).

Incertae sedis

Incertae sedis in Hasenboehler (1981)
(Fig. 5E)

OCCURRENCE. — Ashikajima Fm.

DISTRIBUTION. — Albian-Cenomanian of Portugal (Hasenboehler 1981).

DESCRIPTION

Psilate trilete microspore. Amb triangular. The laesurae are straight, bordered by lips about 3 µm wide, and extend to the equator of the spore. Equatorial diameter = 45-50 µm.

BOTANICAL AFFINITIES

Filicopsida.

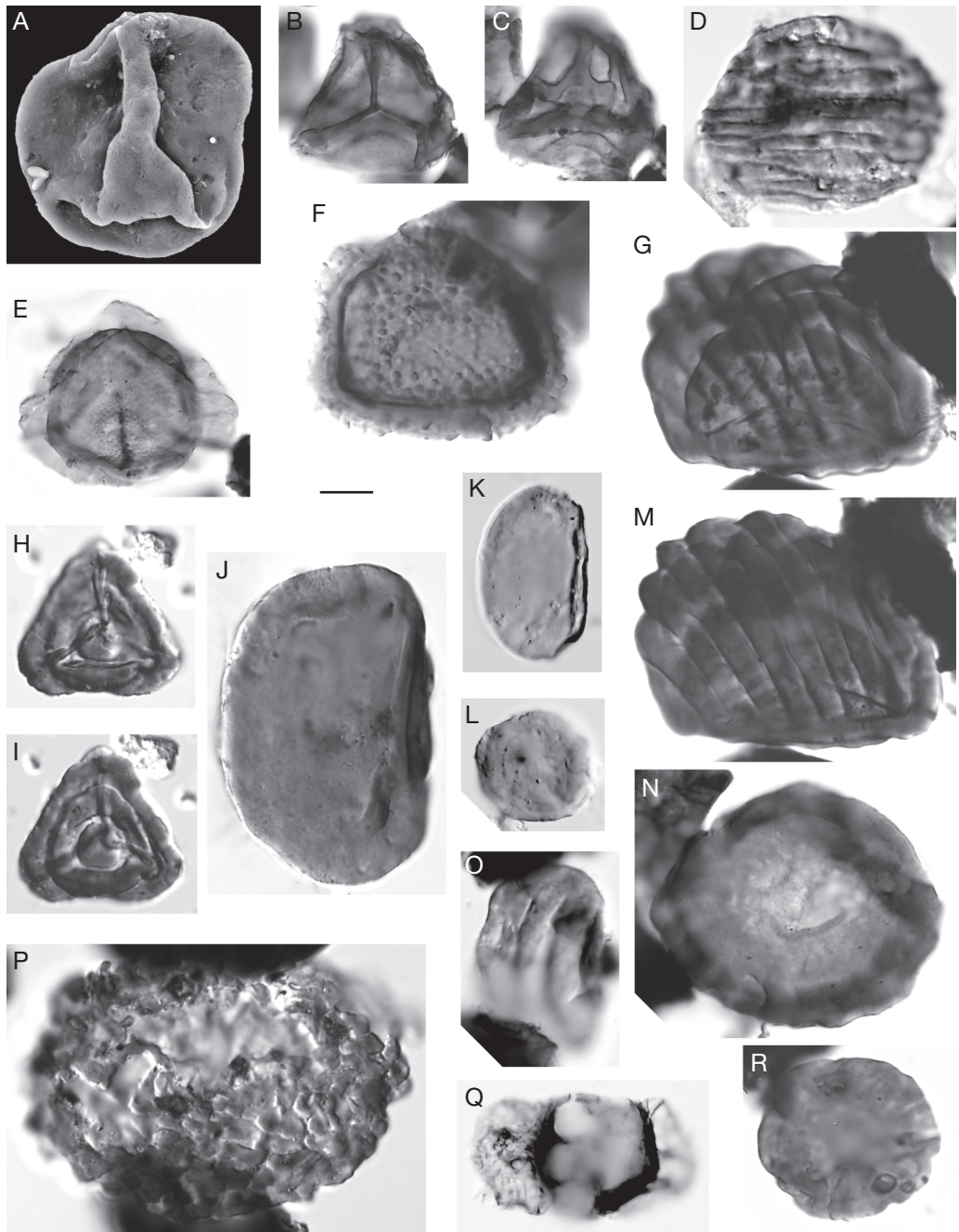
Incertae sedis sp. 1
(Fig. 13N, O)

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Microspore? Amb circular. The proximal face is not seen. The exine is reticulated with a mesh polygonal, of various shapes and sizes (lumina 1-5 µm in

FIG. 12. — Spores and pollen grains from the Barremian of south-west Japan: **A**, *Cingulatisporites* sp. 2, proximal face, Ashikajima Fm, SEM-II2c; **B, C**, *Distaltriangulisporites* sp., proximal and distal faces, Ashikajima Fm, II2c-N53; **D**, *Contignisporites cooksonii* (Balme, 1957) Dettmann, 1963, distal face, Kimigahama Fm, I1a-O51/1; **E**, *Aequitriradites* sp., Ashikajima Fm, II2c-Y59/2; **F**, *Aequitriradites verrucosus* (Cookson & Dettmann, 1958) Cookson & Dettmann, 1961, Ashikajima Fm, II2h-J66/4; **G, M**, *Contignisporites burgeri* Filatoff, McKellar & Price in Filatoff & Price, 1988, proximal and distal faces, Ashikajima Fm, II2d-P47/4; **H, I**, *Polycingulatisporites reduncus*



(Bolkhovitina, 1953) Playford & Dettmann, 1965, proximal and distal faces, Kimigahama Fm, I1a-Z52; **J**, *Laevigatosporites* sp., lateral view, Ashikajima Fm, I12e-Y60; **K**, *Laevigatosporites ovatus* Wilson & Webster, 1946, lateral view, Kimigahama Fm, I1c-P35/3; **L**, *Exesipollenites tumulus* Balme, 1957, distal view, Kimigahama Fm, I1a-R60/3; **N**, *Callialasporites* sp. cf. *C. ugensis* Takahashi & Sugiyama, 1990, Ashikajima Fm, I12f-Y42/3; **O**, *Eucommiidites troedssonii* (Erdtman, 1948) Potonié, 1958, Kimigahama Fm, I1b-R39; **P**, *Cerebropollenites mesozoicus* (Couper, 1958) Nilsson, 1958, lateral view, Ashikajima Fm, I12a-J61/1d; **Q**, *Alisporites* sp., polar view, Ashikajima Fm, I12d-Q59/2; **R**, *Callialasporites dampieri* (Balme, 1957) Sukh-Dev, 1961, Ashikajima Fm, I12b-T46/4m. Scale bar: 10 μ m.

diameter). The exine is about 1.5 µm thick. Equatorial diameter = 20-25 µm.

REMARKS

Only a group of these elements was observed, and isolated ones must be found to permit an observation of the two faces and propose an identification.

BOTANICAL AFFINITIES

Unknown.

Anteturma

VARIEGERMINANTES = POLLENITES

Genus *Callialasporites*

Sukh-Dev, 1961 emend. Potonié, 1966

TYPE SPECIES. — *Callialasporites trilobatus* (Balme, 1957) Sukh-Dev, 1961.

Callialasporites sp. cf. *C. ugensis*

Takahashi & Sugiyama, 1990

(Fig. 12N)

OCCURRENCE. — Ashikajima Fm (rare).

DESCRIPTION

Monosaccate pollen grain. Amb oval to subcircular. The central body is surrounded by a narrow and undulating equatorial saccus (5-8 µm). The exine is punctate on the thinned distal pole area. Equatorial diameter = 35-55 µm.

REMARKS

Two morphologically similar but larger species have been reported by Takahashi & Sugiyama (1990) from the Santonian of the Taneichi Formation, north-east Honshu, Japan (70-84 µm): *Callialasporites ugensis* Takahashi & Sugiyama, and by Kumar (1973) from the Lower Cretaceous of

India (55-68 µm): *Callialasporites doringii* Kumar (previously named *C. lenticularis* (Döring, 1961) Venkatachala & Kar, 1969 by Singh & Kumar (1969): pl. 1, figs 15, 16). Deák (1962) reported a grain also showing similarities to ours: *Inaperturopollenites undulatus* Weyland & Greifeld, 1953 (pl. 12, figs 10, 13).

BOTANICAL AFFINITIES

Pinales. Archangelsky & Gamero (1967) and Gamero (1965, 1968) suggested similarities of grains of the genus *Callialasporites* with those observed in cones of *Apterocladus lanceolatus* Archangelsky (Podocarpaceae) from the Lower Cretaceous of Patagonia. Van Konijnenburg-Van Cittert (1971) reported abnormal grains of the same morphology in an Araucariaceae.

Genus *Alisporites*

Daugherty, 1941 emend. Rouse, 1959

TYPE SPECIES. — *Alisporites opii* Daugherty, 1941.

Alisporites sp. cf. *A. australis*

de Jersey, 1962

OCCURRENCE. — Ashikajima Fm.

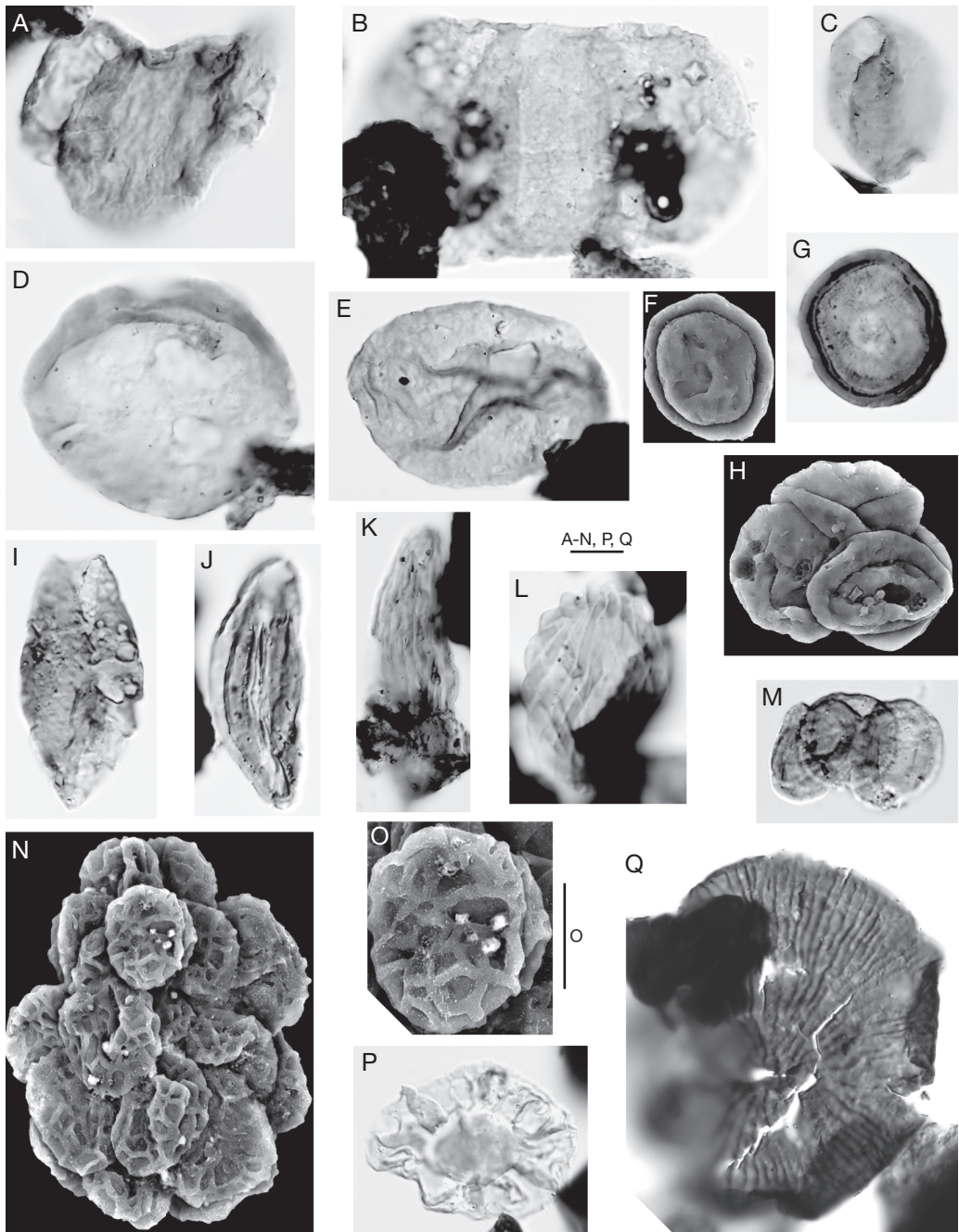
DESCRIPTION

Bisaccate pollen grain. Central body spherical, scabrate. The sacci are reticulate and a little longer than the central body, probably hanging. Total width = 50 µm. Central body diameter = 25 µm. Saccates (length × width) = 40 × 10 µm.

REMARKS

This grain is morphologically very similar to *Alisporites australis* de Jersey, 1962 previously reported from the Triassic of Australia (de Jersey 1962).

FIG. 13. — Pollen grains, alga and fungus from the Barremian of south-west Japan: **A**, *Pityosporites* sp. cf. *P. constrictus* Singh, 1964, lateral view, Ashikajima Fm, I12b-J34/1; **B**, *Alisporites thomasii* (Couper, 1958) Pocock, 1962, polar view, Ashikajima Fm, I12b-O42/3; **C**, *Incertae sedis* sp. 2, Ashikajima Fm, I12c-W65/4; **D**, *Balmeiopsis limbatus* (Balme, 1957) Archangelsky, 1977, Ashikajima Fm, I12d-N41/2; **E**, *Inaperturopollenites* sp., Kimigahama Fm, I1b-U64/4; **F-H**, *Classopollis torosus* (Reissinger, 1950) Couper, 1958 emend.



Burger, 1965 (F, distal polar view, Ashikajima Fm, SEM-II2a; G, distal polar view, Ashikajima Fm, II2c-H32/1; H, tetrad, Ashikajima Fm, SEM-II2a); I, *Cycadopites minimus* (Cookson, 1947) Pocock, 1970, Ashikajima Fm, II2e-U64; J, *Cycadopites* sp., Kimigahama Fm, I1a-X30; K, *Ephedripites montanaensis* Brenner, 1968, Ashikajima Fm, II2c-N35/4h; L, *Gnetaceapollenites* sp., Ashikajima Fm, II2a-S47/1a; M, *Corollina* sp., tetrad, Kimigahama Fm, I1a-X42; N, O, *Incertae sedis* sp. 1, group with detail, Ashikajima Fm, SEM-II2a; P, *Pterospermella* sp., Ashikajima Fm, II2b-O65; Q, *Microthyriacites* sp., Ashikajima Fm, II2e-R63/4. Scale bars: 10 μ m.

BOTANICAL AFFINITIES

Gymnosperms, Pteridospermales?

Alisporites sp.
(Fig. 12Q)

Alisporites sp. A, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 183, pl. XVIII, figs 4, 7, 8 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Bisaccate pollen grain. Central body spherical. The sacci are semi-circular, about as high as the central body, and wrap the proximal face. The exine is about 1.5 µm thick. Total width = 43 µm. Central body diameter = 25 µm. Sacci (length × width) = 15 × 28 µm.

BOTANICAL AFFINITIES

Gymnosperms, Pteridospermales?

Genus *Pityosporites* Seward, 1914

TYPE SPECIES. — *Pityosporites antarcticus* Seward, 1914.

Pityosporites sp. cf. *P. constrictus* Singh, 1964
(Fig. 13A)

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Bisaccate pollen grain. Central body more or less spherical, granulate. The sacci are reticulate; they are small, hanging, narrower at their base, letting a space of about 12 µm between them. The exine is thin (about 1 µm). Total width = 50 µm. Central body diameter = 30 µm. Sacci (length × width) = 25 × 17-20 µm.

REMARKS

This grain is morphologically very similar to *Pityosporites constrictus* Singh, 1964 previously

reported from the Aptian-Albian of Korea (Yi *et al.* 1993), Albian of Canada (Singh 1964), and Santonian of the Kuji Group in north-east Honshu, Japan (Miki 1972; Takahashi & Sugiyama 1990).

BOTANICAL AFFINITIES

Pinales.

Pityosporites sp. cf. *P. piniformis*
(Zaklinskaya, 1957) Takahashi & Sugiyama,
1990

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Bisaccate pollen grain. Central body oval, psilate to finely scabrate. Two small sacci are distally hanging. Proximal crest 1 to 1.5 µm thick. Total width = 50-55 µm; grain height = 15-20 µm. Sacci (length × width) = 20 × 15 µm.

REMARKS

This grain, firstly described in the Eocene-Oligocene of the Pavlodar Irtysh Basin (western Siberia) by Zaklinskaya (1957), was found by Takahashi & Sugiyama (1990) in the Santonian (Taneichi Formation) of north-east Honshu, Japan. Zaklinskaya (1957) had previously placed it in the genus *Cedrus* Trew.

BOTANICAL AFFINITIES

Pinales, probably Pinaceae.

Genus *Inaperturopollenites*
Pflug & Thomson *in* Thomson & Pflug, 1953

TYPE SPECIES. — *Inaperturopollenites dubius* (Potonié & Venitz, 1934) Pflug & Thomson *in* Thomson & Pflug, 1953.

Inaperturopollenites sp.
(Fig. 13E)

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Inaperturate pollen grain. Amb subcircular. The exine is psilate, very folded and thin (about 1 μm thick). Equatorial diameter = 25-45 μm .

BOTANICAL AFFINITIES

Pinales.

Genus *Corollina* Maljavkina, 1949

TYPE SPECIES. — *Corollina compacta* Maljavkina, 1949.

Corollina sp.
(Fig. 13M)

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Pollen grain. Amb subspherical with poles flattened. At the proximal pole, a trilete mark is seen. At the distal pole, a pseudopore 3-7 μm in diameter is present. The rimula delimits a cap about 17-24 μm in diameter. No equatorial ridge is seen. The exine is psilate to slightly punctate. Equatorial diameter = 22-30 μm .

REMARKS

The genus *Corollina* gathers species from the Keuper without ridge, but it still remains used for the Cretaceous of southeastern Asia.

BOTANICAL AFFINITIES

Pinales, Cheirolepidiaceae (Couper 1958). Tekleva & Krassilov (2009) suggested an affinity with the Gnetales.

Genus *Gnetaceapollenites* Thiergart, 1938

TYPE SPECIES. — *Gnetaceapollenites ellipticus* Thiergart, 1938.

Gnetaceapollenites sp.
(Fig. 13L)

Gnetaceapollenites sp. B, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et*

provinces paléofloristiques du sud-est asiatique: 191, pl. XX, fig. 15 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Polyplicate pollen grain. Amb ellipsoidal. The exine is constituted of about 15 ribs running through the grain, and describing a senestral "helix" of 180°. The ribs are 1.8-3 μm wide, separated by furrows less than 0.5 μm wide. The ends of the ribs closely gather at each end of the long axis of the grain without joining. Length = 38 μm ; width = 27 μm .

BOTANICAL AFFINITIES

Gymnosperms, Gnetales.

Genus *Cycadopites*

Wodehouse, 1933 ex Wilson & Webster, 1946

TYPE SPECIES. — *Cycadopites follicularis* Wilson & Webster, 1946.

Cycadopites sp.
(Fig. 13J)

Cycadopites sp. A, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 192, pl. XXI, fig. 2 (2009).

OCCURRENCE. — Kimigahama Fm.

DESCRIPTION

Monosulcate pollen grain. Amb ellipsoidal fusiform. A narrow furrow runs longitudinally through the grain, slightly widening at the ends; it can be bordered by folds of the exine (4 to 5 μm wide). The exine is thin (about 1 μm thick) and psilate. Length = 45-50 μm ; width = 20-25 μm .

BOTANICAL AFFINITIES

Cycadales or Bennettiales (Balme 1995). The present Cycadales are distributed in the tropical to subtropical arid regions. The genus *Cycadopites* is often found associated with coal strata, and the habitat of this group is supposed to have been

much more diversified than now (Singh 1964). Nevertheless, grains of the genus *Cycadopites* were found *in situ* in *Sabnia* Puri (Pentoxylales, Pentoxylaceae) (Sukh-Dev 1980) and *Lepidopteris* Schimper emend. Townrow (Peltaspermales) (Anderson & Anderson 1983).

Incertae sedis

Incertae sedis sp. 2
(Fig. 13C)

Incertae sedis sp. G, Legrand, *Palynologie des dépôts Jurassique supérieur et Crétacé inférieur du Japon, et provinces paléofloristiques du sud-est asiatique*: 195, pl. XXI, fig. 7 (2009).

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Pollen grain. Amb oval in polar view. An eight shape wide median sulcus with rounded ends, runs through the grain. In the middle part of the grain, the edges of the sulcus strongly widen (until 10-12 µm), and can fold one over the other. This thickening can widen progressively or quite abruptly. The exine is psilate (about 1.5 µm thick). Length × width = 40-50 × 30-35 µm; longitudinal thickenings (length × width) = 25 × 10-12 µm.

REMARKS

These grains have similarities with *Cycadopites*, but the folded lips that can be observed here on some grains are much more developed. The genus *Entylissa* Naumova ex Ischenko, shows developed lips, but slenderer and more ornamented than in *Incertae sedis* sp. 2. McGregor (1965) figured a pollen grain similar to our species: cf. *Ginkgocycadophytus caperatus* (Luber, 1941) Samoilovich, 1953 (pl. 5, fig. 25), from the Upper Jurassic of Canada. *Monosulcites scaber* Kimyai, 1966 reported from the Cretaceous of New Jersey, USA (Kimai 1966), also shows great similarities to our species.

BOTANICAL AFFINITIES
Gymnosperms.

Algae chlorophyta
CHLOROPHYCEAE

Genus *Botryococcus* Kützing, 1849

TYPE SPECIES. — *Botryococcus braunii* Kützing, 1849.

Botryococcus sp. cf. *B. braunii* Kützing, 1849

OCCURRENCE. — Ashikajima Fm (rare).

DISTRIBUTION. — This genus is known from the Precambrian.

DESCRIPTION

Algae grouped in small bulb-like colonies, very altered. Colony diameter = 20-25 µm.

BOTANICAL AFFINITIES

Chlorococcales, Botryococcaceae. Freshwater green algae.

PRASINOPHYCEAE

Genus *Pterospermella* Eisenack, 1972

TYPE SPECIES. — *Pterospermella aureolata* (Cookson & Eisenack, 1958) Eisenack, 1972.

Pterospermella sp.
(Fig. 13P)

OCCURRENCE. — Ashikajima Fm (rare).

DISTRIBUTION. — This genus is known from the Precambrian to possibly Holocene.

DESCRIPTION

Flattened lenticular body. The central body is biconvex and darker than the folded equatorial membrane that surrounds it. Length = 38 µm; width = 30 µm; central body (length × width) = 15 × 10 µm; equatorial membrane width = 10 µm.

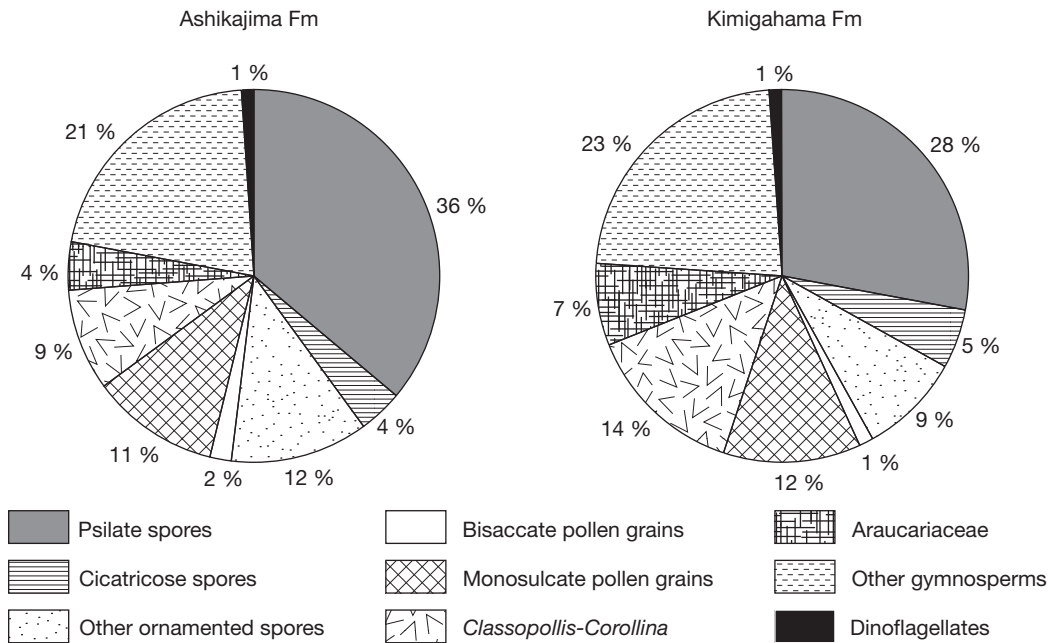


FIG. 14. — Percentages of nine palynomorph groups: **A**, Ashikajima Formation; **B**, Kimigahama Formation, south-west Japan.

BOTANICAL AFFINITIES

Pterospermatales, Pterospermellaceae of marine environment.

Genus *Tasmanites* Newton, 1875

TYPE SPECIES. — *Tasmanites punctatus* Newton, 1875.

Tasmanites sp.

OCCURRENCE. — Ashikajima Fm (rare).

DISTRIBUTION. — This genus is known from the Precambrian to possibly Holocene.

DESCRIPTION

Cyst with a circular equatorial shape. The wall is thick (about 10 μm), pierced by many distinct small pores about 1 μm in diameter. A slit can be seen at the center of the cyst, suggesting an empty phycoma. Equatorial diameter = 83-93 μm .

BOTANICAL AFFINITIES

Pterospermatales, Tasmanitaceae of marine environment.

FUNGI ASCOMYCOTA

Genus *Microthyriacites* Cookson, 1947

TYPE SPECIES. — *Microthyriacites grandis* Cookson, 1947

Microthyriacites sp.

(Fig. 13Q)

OCCURRENCE. — Ashikajima and Kimigahama Fm.

DESCRIPTION

Disc-like body, brown-colored, with radially arranged cell rows; the margins of the body are thin and irregular. The "ostiole" is not distinct, but a hole in the center of the disc is present, formed by dissolving of the central cells. Cells are square to

elongated, without pore, 3-10 μm long and 2.5 μm wide. Cells of the central part of the disc are thicker. Equatorial diameter = 65-70 μm .

BOTANICAL AFFINITIES

Dothideomycetes, Microthyriales. Epiphyllous fungi.

Genus *Phragmothyrites* Edward, 1922

TYPE SPECIES. — *Phragmothyrites eocaenicus* Edward, 1922.

Phragmothyrites sp.

OCCURRENCE. — Ashikajima Fm.

DESCRIPTION

Disc-like body, brown-colored, with radially arranged cell rows; the margins of the body are irregular. No ostiole is present, and the central area is continuous. Cells are square to elongated, 5-10 μm long and 4-6 μm wide. Cells of the central part of the disc are thicker. Equatorial diameter = 75-85 μm .

BOTANICAL AFFINITIES

Dothideomycetes, Microthyriales. Epiphyllous fungi.

RESULTS

The palynomorphs recovered from the Ashikajima and Kimigahama formations of the Choshi Group show a generally good state of preservation and considerable diversity. They are dominated by spores, mainly represented by species with affinities to the Anemiaceae, Matoniaceae or Cyatheaceae (Table 2). *Matoniasporites* (Matoniaceae) is represented by three species, some large (90 μm). *Cicatricosisporites* (Anemiaceae) spores are abundant and diverse in the assemblages, but may not reflect a diversity of the source plants (several studies have shown the presence, inside the same sporangium, of variously ornamented spores that

can belong to different “morphographic” species). *Ruffordiaspora australiensis*, *Plicatella* are common, and two new species of *Nodosisporites* have been described: *N. choshiensis* and *N. makotoi*. Several species of *Cyathidites* (Cyatheaceae or Dicksoniaceae), which had a world-wide distribution during this period, and spores having affinities with the Osmundaceae (*Biretisporites potoniaei*, *Baculatisporites*, *Todisporites*, *Osmundacidites*) are present. *Deltoidospora* (Cyatheales), *Undulatisporites* and *Cingulatisporites* (Filicopsida) are common. *Contignisporites* (Pteridaceae) was observed, but is rare in the assemblages.

Densely echinate spores, with echinae of various shapes and sizes, are common. We observed *Distaltriangulisporites*, verrucate spores referable to *Verrucosisporites*, *Converrucosisporites*, *Leptolepidites*, reticulate spores of *Klukisporites* and *Ischyosporites*, and *Pilosisporites*. A new species of *Manumia*: *M. japonica* (Pteridaceae), with verrucae and ridges more or less randomly distributed, has been described. This genus is reported here for the first time in Asia. Monolete spores of the genus *Laevigatosporites* are common.

Spores with lycopsid affinities are common. We note the presence of *Lycopodiumsporites dentimuratus* in both formations. This species was described by Brenner (1963) from the Barremian-Albian of Maryland (USA), but has never been reported from any other area. *Retitriletes austroclavatidites*, *Echinatisporis varispinosus*, various species of *Neoraistrickia* and a new species of *Foveosporites*: *F. ryosekiensis*, are present. *Triporoletes reticulatus*, *Aequitriradites verrucosus* and *A. spinulosus*, which have affinities with the Marchantiopsida (Hepatica), are also recorded.

Gymnosperm pollen grains are mainly represented by *Classopollis* (Cheirolepidiaceae), *Araucariacites australis* and *Balmeiopsis limbatus* (Araucariaceae), and monosulcate grains of *Cycadopites*. However, proportions of *Classopollis* are quite low (9-14%) compared to the 70% reported by Takahashi (1974) in the Aptian-Albian of the Miyako Group (north-east Honshu, Japan). Bisacate pollen grains are few but quite diverse, being represented by *Alisporites*, *Abietinaepollenites*, *Cedripites* and *Pityosporites*. We also recorded

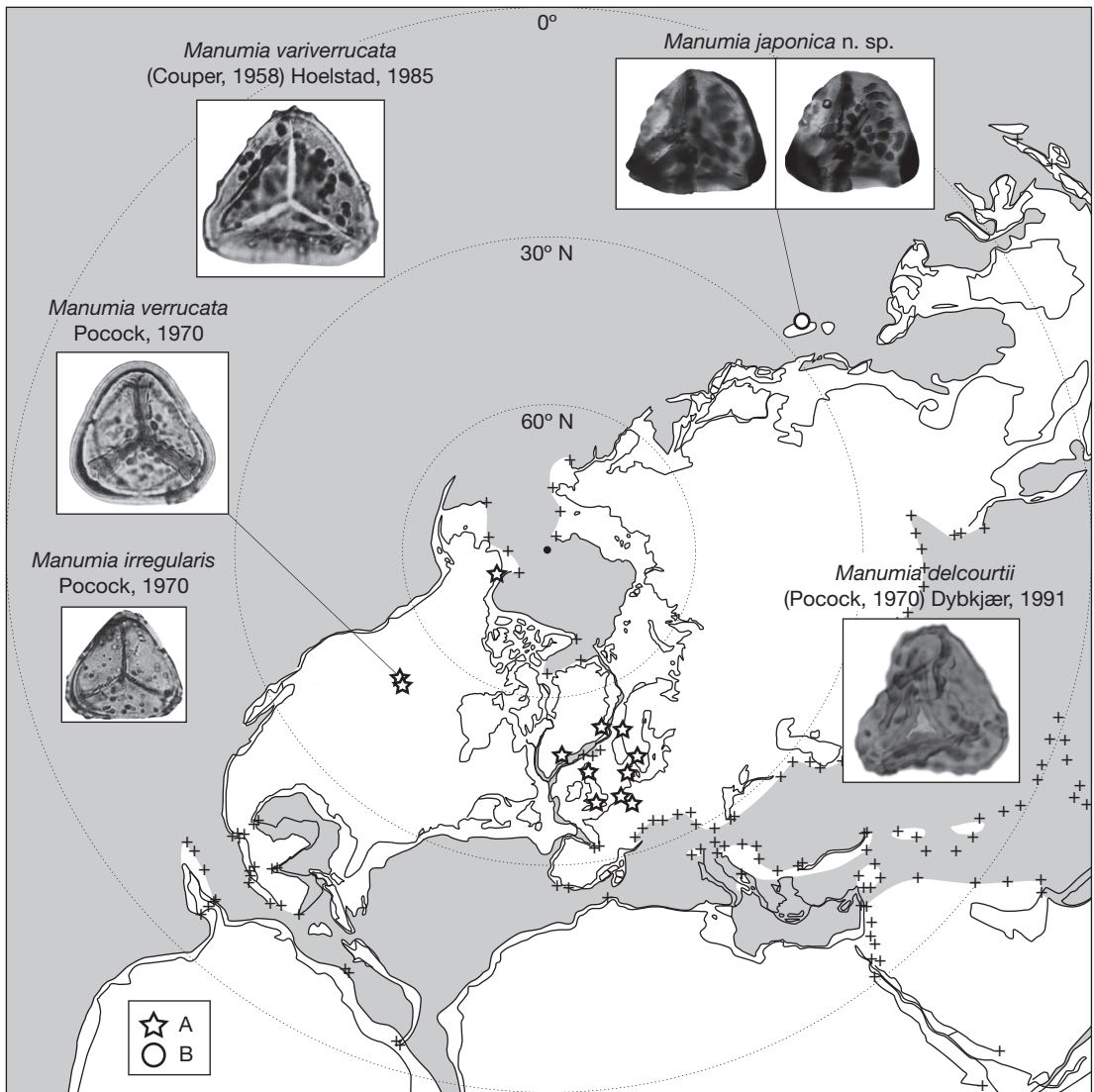


Fig. 15. — Spatio-temporal distribution of genus *Manumia*. This genus had a wide distribution across the South-Laurasian Province (= Euro-Sinian Region): **A**, during Jurassic time; **B**, during Early Cretaceous time. Paleogeographical map during the Hauterivian (120 My) in North polar stereographic projection, modified from Smith & Briden (1977) and Masse *et al.* (1993). Figures of *Manumia irregularis* Pocock, 1970 and *M. verrucata* Pocock, 1970 are from Pocock 1970 (source: www.schweizerbart.de); figure of *M. variverrucata* (Couper, 1958) Hoelstad, 1985 is from Hoelstad 1985 (source: 2dggf.dk); figure of *M. delcourtii* (Pocock, 1970) Dybkjær, 1991 is from Koppelhus & Batten 1996 (source: www.palynology.org).

rare *Callialasporites* (Podocarpaceae) and some *Eucommiidites*, *Ephedripites* and *Gnetaceaepollenites* (Gnetophyta). *Callialasporites* is rare in Japan, whereas this genus is generally abundant world-wide.

Several types of dinoflagellates and some foraminiferal linings were also observed in the two formations, and will be reported elsewhere. The composition of the palynofloras is summarized in two diagrams (Fig. 14).

DISCUSSION

Most of the species we identified are distributed world-wide, and of long stratigraphic range. However, some species may be specific to the Ryoseki-type Province in Japan (*Foveosporites ryosekiensis*, *Nodosisporites choshiensis*, *N. makotoi*, *Lycopodiumsporites dentimuratus*) or show different proportions from what is generally observed for the same period in the adjacent regions, for example the scarcity of *Classopollis* or *Callialasporites*, and the absence of *Appendicisporites* and *Gleicheniidites* often reported from China and Russia. Spores of the genus *Manumia*, reported for the first time in Asia (Fig. 15), are common in the two formations. Four species have been described in this genus: *Manumia delcourtii* (Pocock, 1970) Dybkjær, 1991 was reported from the Lower to Middle Jurassic of Denmark (Dybkjær 1991; Koppelhus 1992; Seidenkrantz *et al.* 1993; Koppelhus & Nielsen 1994; Koppelhus & Dam 2003), East Greenland (Koppelhus & Hansen 2003) and Sweden (Lindström & Erlström 2007), and the Middle Jurassic of Scotland (Stefanowicz 2008); *Manumia irregularis* Pocock, 1970 was reported from the Lower to Middle Jurassic of East Greenland (Lund & Pedersen 1984) and Afghanistan (Schweitzer *et al.* 1987), and the Middle Jurassic of Germany (Schweitzer *et al.* 1987) and Canada (Pocock 1970); *Manumia variverrucata* (Couper, 1958) Hoelstad, 1985 was reported from the Lower to Middle Jurassic of Germany (Schulz 1967) and Holland (Herngreen & de Boer 1974), the Middle Jurassic of Denmark (Hoelstad 1985), Sweden (Guy 1971) and Alaska (Bjærke 1993), and the Middle to Upper Jurassic of England (Couper 1958); *Manumia verrucata* Pocock, 1970 was reported from the Middle Jurassic of Canada (Pocock 1970). Bøe *et al.* (2005) also reported *Manumia* sp. from the Upper Jurassic to Lower Cretaceous (Barremian) of Norway.

We identified *Cicatricosisporites sinuosus* in both formations. This species was reported for the first time by Hunt (1985) from the Purbeck Limestone Group of southern England. It has been reported from the Hauterivian-Barremian of Japan (Legrand 2009). It seems to have crossed

the Tethys and reached North Africa via Lebanon (Dejax, personal communication), Israel (de Haan 1997) and Libya (Batten & Uwins 1985; Uwins & Batten 1988) during the Barremian, and then spread through Egypt (Saad 1978; Omran *et al.* 1990; Schrank & Ibrahim 1995; Ibrahim 1996; Ibrahim *et al.* 2001; Mahmoud & Deaf 2007; Mahmoud *et al.* 2007), Tunisia (Pons, personal communication) and Iraq (Al-Ameri *et al.* 2001) during the Albian-early Cenomanian. It was recorded from the early Aptian of France (Masure *et al.* 1998) and Colombia (Mejia Velasquez 2007), the late Aptian of Brazil (Pons *et al.* 1996), the late Aptian-early Albian of Spain (Peyrot *et al.* 2007), and the Aptian-Albian of north-east Japan (Umetsu & Sato 2007). We plot these reports of *Cicatricosisporites sinuosus* on a paleogeographical map (Fig. 16), where we note that its distribution is between 0° and 50° in the Northern Hemisphere. This species seems to have disappeared during the Cenomanian transgression. In Africa, it lived in swamps (Al-Ameri *et al.* 2001) or near the coast, in warm and humid areas (Mahmoud *et al.* 2007). It seems not to have lived in dry and arid areas further in the south, and may have reached eastern Asia by water or by following coastal areas from the Tethysian regions.

Bisaccate pollen grains are poorly represented and badly preserved in the assemblages, but we encountered grains of the genera *Abietinaepollenites*, *Alisporites*, *Cedripites* and *Pityosporites*.

Cycadopites is also common in the assemblages. This type of pollen grain was produced by Bennettitales, Cycadales, Ginkgoales or Czekanowskiales. The different species we observed may represent different origins. Kimura (2000) considered that Ginkgoales characterize the Tetori-type Province. The grains we observed were most probably produced by Bennettitales or Cycadales, but only a TEM study can enable more precise identification than the four orders known from the macroflora.

We reported *Eucommiidites troedssonii* in our assemblages. This species has previously been observed in Japan by Umetsu & Sato (2007) from the late Aptian-early Albian sediments of the Hiraiga

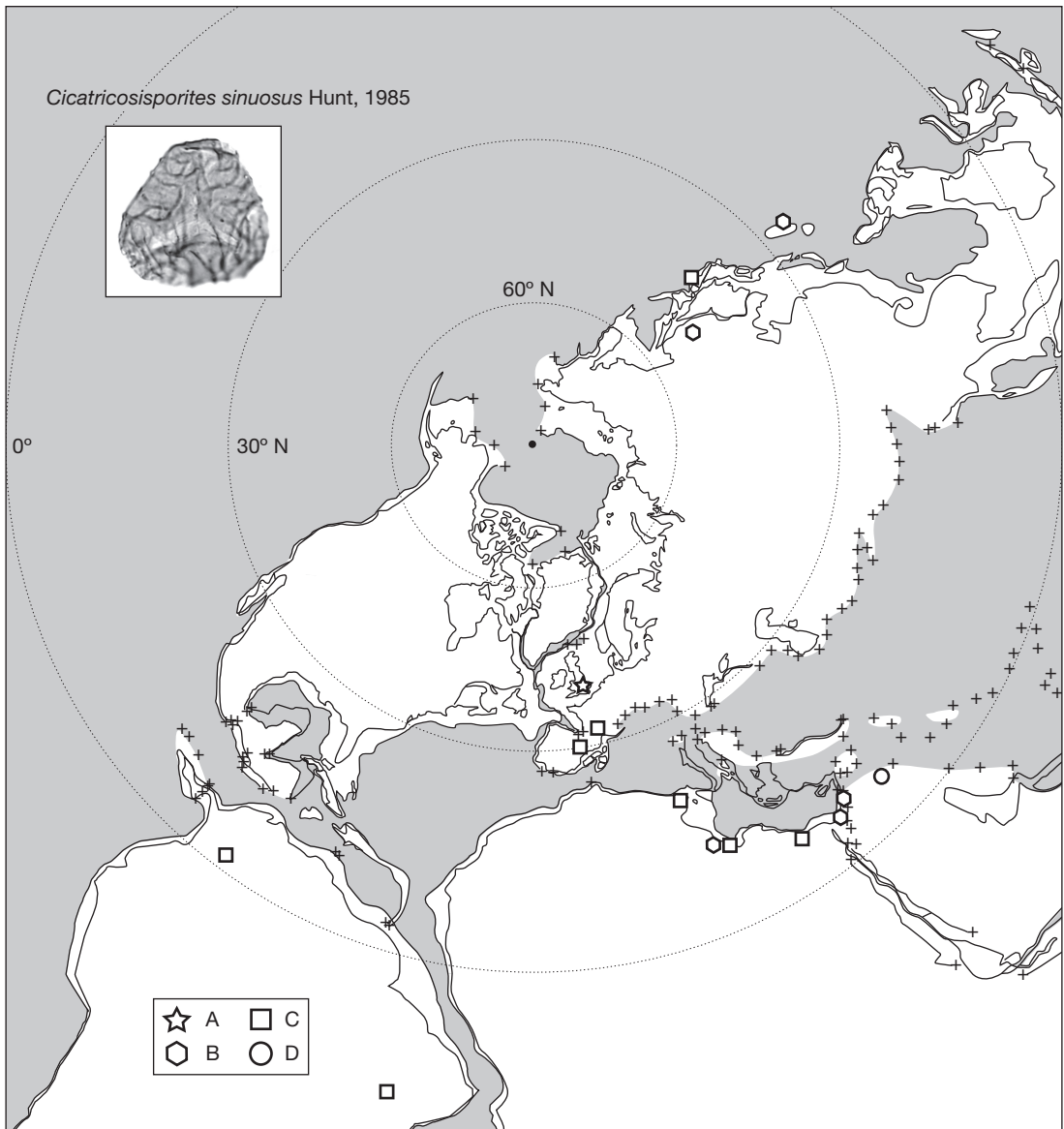


FIG. 16. — Spatio-temporal distribution of *Cicatricosisporites sinuosus* Hunt, 1985: **A**, Purbeckian of England; **B**, pre-Aptian of Lebanon, Israel, Libya, China, south-west Honshu (Japan); **C**, Aptian of France, Colombia and Brazil, Aptian-Albian of Spain, Egypt and north-east Honshu (Japan), Albian of Libya and Tunisia; **D**, Albian-early Cenomanian of Iraq. Paleogeographical map during the Hauterivian (120 My) in North polar stereographic projection, modified from Smith & Briden (1977) and Masse *et al.* (1993).

Formation (Miyako Group in north-east Honshu), by Takahashi (1988) and Takahashi & Sugiyama (1990) from the Upper Cretaceous sediments of the Kuji and Futaba groups (north-east Honshu)

under the name *Cupuliferoidaepollenites* sp. The latter, however, is a Tertiary angiospermous tricolpate pollen grain, and cannot be compared to our species, which has a smooth exine.

COMPARISON WITH OTHER PALYNOFLORISTIC DOMAINS

Brenner (1976) did not consider eastern Asia in his model of palynological provinces, but by extension of his latitudinally defined provinces, we can suppose that Japan would be included in the South-Laurasian Province of temperate to humid subtropical climate. We noted in our assemblages a dominance of spores, with schizaeaceous spores particularly diversified. *Classopollis*, bisaccate pollen grains, monosulcate (*Cycadopites*) or polylicate (*Ephedripites* and *Gneatceapollenites*) grains are also present. These observations are in accordance with the characteristics Brenner defined for the South-Laurasian Province.

Vakhrameev (1991) placed Japan in the East Asia Province of his Euro-Sinian Region, but we did not observe in our assemblages the abundance of cheirolepidiaceus pollen grains which generally characterizes this region. We note that Vakhrameev (1991) defined the East Asia Province based on studies on macrofloras of Kimura (1987) and those on palynofloras of Takahashi (1974) and Miki (1972) (Aptian-Albian of the Miyako Group), who reported, for example, 70% of *Classopollis* in their assemblages (Takahashi 1974). This difference in age between the Choshi and Miyako groups can explain the percentage gap (9-14% in our assemblages). However, it should be noted that climatic change would not be a result of the migration of the Outer Zone terranes, because cheirolepidiaceus macrofossils are abundant in the Aptian Sasayama Group of the Inner Zone (Yamada 2009).

Li (1980, 1983), Chen *et al.* (1982) and Li & Liu (1994) noted the abundance and diversity of bisaccate pollen grains and schizaeaceous spores, and scarcity of *Classopollis* in the North China Province they defined. The South China Province is characterized by an abundance of *Classopollis* (up to 50%) and cicatricose spores (about 10%) with common *Exesipollenites* in the assemblages. The palynofloras we have described from the Choshi Group cannot be linked with those from China.

Cerebropollenites mesozoicus is rare in our assemblages, whereas some authors (Herngreen *et al.* 1996; Nichols 2003) consider this genus to be a common and distinctive element constituting the

Cerebropollenites Province where Japan has been included. The scarcity of *Cerebropollenites* in both formations can be attributed either to a taphonomic bias or to local climatic effects, but further studies are needed to test these possibilities.

In short, the palynofloras of the Ashikajima and Kimigahama formations can be included in the South-Laurasian Province of Brenner (1976). For a period of Upper Jurassic to Lower Cretaceous time, Japan can also be placed in the East Asia Province of the Euro-Sinian Region as Vakhrameev (1991) suggested based on the micro- and macrofossils. However, even though the macrofloral data from Choshi are consistent with the definition of this province, our palynological data suggest that there could be climatic differences on a finer scale than previously considered.

PALEOECOLOGY

A shallow marine environment for the succession has been suggested from sedimentological studies and the abundance of molluscs in the Choshi area (Obata *et al.* 1975; Katsura *et al.* 1984). Green algae of the genera *Tasmanites* and *Pterospermella* (Prasinophyceae), which lived in marine environments, confirm the interpreted sedimentary environments of the Ashikajima and Kimigahama formations from the palynological point of view.

In association with these marine elements, we observed various terrestrial and freshwater palynomorphs: *Chomotriletes minor*, *Ovoidites parvus* (Zygnemataceae) and *Botryococcus* sp. cf. *B. braunii* (Botryococcaceae), which lived in shallow freshwater environments (Grenfell 1995). The composition of the marine sediments, which contain abundant organic matter of continental origin, is consistent with a deposit in a coastal environment as previously suggested. Terrestrial elements may have been carried and dispersed by water or wind more or less far from their habitat, what can explain the rare occurrence of bisaccate pollen grains, for example.

Pollen grains of the genus *Classopollis*, related to the extinct conifer family Cheirolepidiaceae, are common (9-14%) in the assemblages. Cheirolepidiaceus plants have been generally reported to have lived near or along coastal areas. They have

been considered to have formed mangroves, and also been adapted to arid or semi-arid environments (Srivastava 1976; Upchurch & Doyle 1981; Pons & Koeniguer 1985). *Classopollis* grains are often observed in tetrads in our assemblages, suggesting the proximity of the producing plants. Cheirolepidiaceae twigs of *Cupressinocladus obatae* (Okubo & Kimura 1991) and *Frenelopsis choshiensis* (Kimura *et al.* 1985) have been reported from the Choshi Group. Among the elements associated with the palynomorphs, we observed fragments of tracheids with araucarioid cross-fields and mixed radial pitting which suggest the presence of this family.

The landscape reconstructed thanks to the palynofloral results is in accordance with that previously suggested by the macroremains. However, many of the species we identified are rare (less than 1% in the assemblage), and may indicate a diversity of source areas. For example, the large number of psilate trilete spores indicates a provenance not only from coastal areas.

PALEOCLIMATE

In some paleoclimatic reconstitutions for the mid-Cretaceous period, the Outer Zone of Japan has been located in a humid tropical climatic belt, with an arid zone in the south (Chumakov *et al.* 1995). Kimura (1987) also suggested a tropical to subtropical and arid climate from the macrofloral data.

The relative abundance of *Classopollis* in the Choshi area and the presence of inaperturate pollen grains (for example, Araucariaceae) and Gnetales, associated with low percentages of bisaccate pollen grains and schizaeaceous spores (even if diversified) suggest a tropical to subtropical warm climate. Spores of the genera *Cyathidites* and *Deltoidospora* are common to abundant, epiphyllous fungi of the genera *Microthyriacites* and *Phragmothyrites* are present, and parasitic epiphyllous fungi (hyphopodia) are observed on thin cuticle fragments in the Ashikajima Formation. These observations suggest locally humid climatic conditions in a lacustrine environment. We suggest that the climate indicated had marked dry and more humid seasons. Our results probably correspond to para-autochthonous and allochthonous elements derived from a variety of habitats.

Haggart *et al.* (2006) suggested the existence of a warm current on the eastern coastal areas of the Outer Zone. This current may have influenced the climate of these areas, and our results are consistent with the hypothesis of an unusually warm oceanic climate instead of a "real" tropical to subtropical climate. However, while Haggart *et al.* (2006) simply focused on the action of marine currents to explain the floral differences observed in Japan, we think these currents were not enough to create the two distinct floristic provinces, even though they may have influenced them (Legrand 2009). Our results are in accordance with the hypothesis of a moderate migration of the terranes constituting the Outer Zone, or moderate climatic change during the Early Cretaceous in Japan.

CONCLUSION

The Ashikajima and Kimigahama formations yield rich assemblages, characterized by a predominance of terrestrial palynomorphs associated with dinoflagellates and foraminiferal linings. The associated particles are mainly woody fragments and altered cuticles. The assemblages can be attributed to the East Asia Province of the Euro-Sinian Region or the South-Laurasian Province. However, they cannot be linked to any adjacent palynological area in Asia, and appear to be unique to the region. Many of the species identified have been reported previously from Europe, and we report for the first time the genus *Manumia* in Asia. The genera *Callialasporites* and *Eucommiidites*, generally common in the European palynofloras, are rare in both Ashikajima and Kimigahama formations.

Many of the species encountered were originally described in the palynofloras of Canada and the USA. *Lycopodiumsporites dentimuratus* previously reported only from the Barremian-Albian of the Potomac Group by Brenner (1963) is common in Japan, and the genus *Manumia* reported from the Jurassic of Canada and northern Europe is present. These North-American elements were most probably carried by marine currents or wind up to the Outer Zone of Japan.

This first report of Barremian palynofloras from the Outer Zone of Japan confirms the composition of the vegetation described by Kimura (1987), but not the arid climate that he suggested. We bring new data to the knowledge of the Ryoseki Floras, but other palynological studies are needed in Japan to define characteristics for those floras that appear to be unique to Asia.

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APPENDICES

TABLE 1. — List of all the taxa encountered during our investigation, in nomenclatural order, with their occurrence in the Ashikajima Formation (**A**) and in the Kimigahama Formation (**K**) and their figurative position. Abbreviations: –, one grain; **C**, common; **P**, present; **R**, rare.

	Figures	Occurrence	
		A	K
PROXIMEGERMINANTES			
Triletes Azonales			
Acavatriletes			
Azonotriletes			
Laevigati, Quasilaevigati			
<i>Biretisporites potoniaei</i> (Delcourt & Sprumont, 1955) Delcourt, Dettmann & Hughes, 1963	5A, B	P	P
<i>Cibotiumspora paradoxa</i> (Maljavkina, 1949) Chang, 1965	5P	R	R
<i>Cyathidites australis</i> Couper, 1953	5G	P	P
<i>Cyathidites minor</i> Couper, 1953	5F	P	P
<i>Cyathidites rarus</i> (Bolkhovitina, 1953) Deák, 1964	5H	–	–
<i>Deltoidospora hallii</i> Miner, 1935		P	P
<i>Todisporites major</i> Couper, 1958	5D	–	–
<i>Todisporites miser</i> Takahashi, 1988	5C	–	–
<i>Undulatisporites undulapolus</i> Brenner, 1963		R	–
<i>Undulatisporites sinuosus</i> Groot & Groot, 1962		–	–
Apiculati			
Granulati, Scabrati			
<i>Concavissimisporites punctatus</i> (Delcourt & Sprumont, 1955) Brenner, 1963	5Q	R	–
<i>Concavissimisporites variverrucatus</i> (Couper, 1958) Brenner, 1963	5K	R	R
<i>Osmundacidites wellmanii</i> Couper, 1953	5L	P	R
Verrucati			
<i>Convrrucosporites</i> sp.	5N, O	–	–
<i>Manumia japonica</i> n. sp.	5A-F, I, J	P	P
<i>Trilites bossus</i> Couper, 1958	5M	–	–
<i>Uvaesporites</i> sp.		–	–
<i>Verrucosporites densus</i> (Bolkhovitina, 1956) Pocock, 1970	5I, J	–	–
Baculati			
<i>Baculatisporites comaumensis</i> (Cookson, 1953) Potonié, 1956		R	R
<i>Baculatisporites</i> sp.	6N	R	–
<i>Neoraistrickia</i> sp. 1	7A, B	–	–
<i>Neoraistrickia</i> sp. 2	7C, D	–	–
<i>Neoraistrickia</i> sp. 3	7G, J	R	R
<i>Pilososporites verus</i> Delcourt & Sprumont, 1955	6G	R	–
<i>Pilososporites brevis</i> Delcourt & Sprumont, 1955	6K	R	–
<i>Tuberositriletes</i> sp.	6H, L, M	–	–
Nodati			
<i>Echinatisporis varispinosus</i> (Pocock, 1962) Srivastava, 1975		P	P
Murornati			
<i>Cicatricosisporites annulatus</i> Archangelsky & Gamero, 1966		R	–
<i>Cicatricosisporites hughesi</i> Dettmann, 1963	8Q, R	R	R
<i>Cicatricosisporites mohrioides</i> Delcourt & Sprumont, 1955	9I, J	–	R
<i>Cicatricosisporites sinuosus</i> Hunt, 1985	8K, L, S, T	P	P
<i>Cicatricosisporites</i> sp. 1	9A, B	R	–
<i>Cicatricosisporites</i> sp. 2	9C, D	R	–
<i>Cicatricosisporites</i> sp. 3	9E, F	R	–
<i>Cicatricosisporites</i> sp. 4	9G, H	R	–
<i>Foveosporites ryosekiensis</i> n. sp.	8D, E, H-J	P	P
<i>Klukisporites variegatus</i> Couper, 1958	7E, F, I, L, M	P	P
<i>Lycopodiumsporites crassimacerius</i> Hedlund, 1966		–	–
<i>Lycopodiumsporites dentimuratus</i> Brenner, 1963	7H, K, N-P	C	C
<i>Microreticulatisporites</i> sp. 1	8M, P	–	R

TABLE 1. — Continuation.

	Figures	Occurrence	
		A	K
<i>Microreticulatisporites</i> sp. 2	8N, O	R	
<i>Retitriletes austroclavatidites</i> (Cookson, 1953) Döring, Krutzsch, Mai & Schulz <i>in</i> Krutzsch, 1963	8F, G	R	R
<i>Retitriletes</i> sp.	8A-C		R
<i>Ruffordiaspora australiensis</i> (Cookson, 1953) Dettmann & Clifford, 1992	9K-M, P	P	P
Triletes Zonales			
Auritotriletes			
Auriculati			
<i>Matonisporites</i> sp. 1			–
<i>Matonisporites</i> sp. 2	9O	P	P
Appendiciferi			
<i>Nodosisporites makotoi</i> n. sp.	10A-F	P	P
<i>Nodosisporites choshiensis</i> n. sp.	10G-K	P	P
<i>Plicatella</i> sp.	9N, Q	R	
Zonotriletes			
Cingulati			
<i>Cingulatisporites psilatus</i> Groot & Penny, 1960	10O, P		R
<i>Cingulatisporites</i> sp. 1	10L-N	P	P
<i>Cingulatisporites</i> sp. 2	12A	R	R
<i>Cingutriletes</i> sp.	10Q	R	
<i>Contignisporites burgeri</i> Filatoff, McKellar & Price <i>in</i> Filatoff & Price, 1988	12G, M	R	
<i>Contignisporites cooksonii</i> (Balme, 1957) Dettmann, 1963	12D	R	R
<i>Distaltriangulisporites</i> sp.	12B, C	R	
<i>Polycingulatisporites reduncus</i> (Bolikhovitina, 1953) Playford & Dettmann, 1965	12H, I	R	R
<i>Patellasporites</i> sp.		–	
Tricrassati			
<i>Coronatispora valdensis</i> (Couper, 1958) Dettmann, 1963		–	
Zonolaminatitriletes			
Zonati			
<i>Aequitriradites spinulosus</i> (Cookson & Dettmann, 1958) Cookson & Dettmann, 1961			–
<i>Aequitriradites verrucosus</i> (Cookson & Dettmann, 1958) Cookson & Dettmann, 1961	12F	R	
<i>Aequitriradites</i> sp.	12E	R	
<i>Triporoletes reticulatus</i> (Pocock, 1962) Playford, 1971		R	R
Monoletes			
Acavatomonoletes			
Azonomonoletes			
Laevigatomonoleti			
<i>Laevigatosporites ovatus</i> Wilson & Webster, 1946	12K	R	R
<i>Laevigatosporites</i> sp.	12J	–	
Incertae sedis			
<i>Incertae sedis in</i> Hasenboehler (1981)	5E	–	
<i>Incertae sedis</i> sp. 1	13N, O	R	
VARIEGERMINANTES			
Saccites			
Monosaccites			
Inaperturati (= Saccizonati)			
<i>Callialasporites dampieri</i> (Balme, 1957) Sukh-Dev, 1961	12R	R	
<i>Callialasporites</i> sp. cf. <i>C. ugensis</i> Takahashi & Sugiyama, 1990	12N	–	
<i>Cerebropollenites mesozoicus</i> (Couper, 1958) Nilsson, 1958	12P	–	

TABLE 1. — Continuation.

	Figures	Occurrence	
		A	K
Disaccites			
Disacciatrileti			
<i>Alisporites thomasi</i> (Couper, 1958) Pocock, 1962	13B	R	
<i>Alisporites</i> sp. cf. <i>A. australis</i> de Jersey, 1962		–	
<i>Alisporites</i> sp.	12Q	–	
<i>Pityosporites</i> sp. cf. <i>P. constrictus</i> Singh, 1964	13A	–	–
<i>Pityosporites</i> sp. cf. <i>P. piniformis</i> (Zaklinskaya, 1957) Takahashi & Sugiyama, 1990		–	–
Aletes and Kryptoaperturates			
Azonaletes			
Pilonapiti			
<i>Inaperturopollenites</i> sp.	13E	P	P
Granulonapiti			
<i>Araucariacites australis</i> Cookson, 1947 ex Couper, 1953		P	P
<i>Balmeiopsis limbatus</i> (Balme, 1957) Archangelsky, 1977	13D	P	P
<i>Spheripollenites psilatus</i> Couper, 1958		R	R
Circumpollini			
<i>Classopollis torosus</i> (Reissinger, 1950) Couper, 1958 emend. Burger, 1965	13F-H	C	C
<i>Corollina</i> sp.	13M	R	R
Plicates			
Costates (= Polyplicates)			
Costati			
<i>Ephedripites montanaensis</i> Brenner, 1968	13K	R	
<i>Gnetaceapollenites</i> sp.	13L	–	
Monocolpates (Monosulcites) and Zonocolpates			
Quasilaevigati and Microsculptati			
<i>Cycadopites minimus</i> (Cookson, 1947) Pocock, 1970	13I	R	R
<i>Cycadopites</i> sp.	13J		R
Tricolpates, Triptyches			
Heterotricolpati, Praecolpati			
<i>Eucommiidites minor</i> Groot & Penny, 1960		–	–
<i>Eucommiidites troedssonii</i> (Erdtman, 1948) Potonié, 1958	12O	R	R
Poroses			
Monoporines			
<i>Exesipollenites tumulus</i> Balme, 1957	12L		–
Incertae sedis			
<i>Incertae sedis</i> sp. 2	13C	–	
ALGAE CHLOROPHYTA			
Charophyceae			
<i>Chomotriletes minor</i> (Kedves, 1961) Pocock, 1970		R	
<i>Ovoidites parvus</i> (Cookson & Dettmann, 1959) Nakoman, 1966		R	
Chlorophyceae			
<i>Botryococcus</i> sp. cf. <i>B. braunii</i> Kützing, 1849		–	
Prasinophyceae			
<i>Pterospermella</i> sp.	13P	–	
<i>Tasmanites</i> sp.		–	
FUNGI ASCOMYCOTA			
<i>Microthyriacites</i> sp.	13Q	R	P
<i>Phragmothyrites</i> sp.		R	
<i>Pluricellaesporites</i> spp.			R
Parasite fungus with hyphopodia		R	

TABLE 2. — Botanical affinities of all the taxa encountered during our investigation. Macrofloral remains of only Lignophyta (Spermatophyta) were previously studied. Abbreviations: **A**, Ashikajima Formation; **K**, Kimigahama Formation; –, unknown.

BOTANICAL AFFINITY				FOSSIL		
Phylum	Class	Order	Family	Microflora		
Bryophyta	Marchantiopsida	–	–	<i>Aequitriradites spinulosus</i> , <i>Aequitriradites verrucosus</i> , <i>Aequitriradites</i> sp., <i>Triporoletes reticulatus</i>		
	–	–	–	<i>Neoraistrickia</i> sp. 1, <i>Neoraistrickia</i> sp. 2, <i>Neoraistrickia</i> sp. 3		
Lycophyta	Lycopsida	Lycopodiales	Lycopodiaceae	<i>Foveosporites ryosekiensis</i> n. sp., <i>Lycopodiumsporites crassimacerius</i> , <i>Lycopodiumsporites dentimuratus</i> , <i>Retitriletes austroclavitudites</i>		
		Selaginellales	Selaginellaceae	<i>Cingutriletes</i> sp., <i>Echinatisporis varispinosus</i> , <i>Neoraistrickia</i> sp. 1, <i>Neoraistrickia</i> sp. 2, <i>Neoraistrickia</i> sp. 3, <i>Uvaesporites</i> sp.		
		–	–	<i>Retitriletes</i> sp.		
Monilophyta	Equisetopsida (= Sphenopsida)	Noeggerathiales	–	<i>Microreticulatisporites</i> sp. 1, <i>Microreticulatisporites</i> sp. 2		
			Cyatheales	Cyatheaceae or Dicksoniaceae	<i>Cibotiumspora paradoxa</i> , <i>Concavissimisporites punctatus</i> , <i>Concavissimisporites variverrucatus</i> , <i>Cyathidites australis</i> , <i>Cyathidites minor</i> , <i>Cyathidites rarus</i> , <i>Deltoidospora hallii</i> , <i>Uvaesporites</i> sp.	
				?	<i>Converrucosisporites</i> sp., <i>Verrucosisporites densus</i>	
				Gleicheniales	Matoniaceae	<i>Cyathidites rarus</i> , <i>Matonisporites</i> sp. 1, <i>Matonisporites</i> sp. 2
			Osmundales	Osmundaceae	<i>Baculatisporites comaumensis</i> , <i>Baculatisporites</i> sp., <i>Biretisporites potoniaei</i> , <i>Osmundacidites wellmanii</i> , <i>Todisporites major</i> , <i>Todisporites miser</i>	
					<i>Biretisporites potoniaei</i> , <i>Laevigatosporites</i> sp., <i>Microreticulatisporites</i> sp. 1, <i>Microreticulatisporites</i> sp. 2	
			Polypodiopsida (= Filicopsida)	Polypodiales	Polypodiaceae	<i>Baculatisporites comaumensis</i> , <i>Laevigatosporites</i> sp.
					Pteridaceae	<i>Contignisporites burgeri</i> , <i>Contignisporites cooksonii</i> , <i>Laevigatosporites</i> sp., <i>Manumia japonica</i> n. sp.
					Saccolomataceae	<i>Cicatricosisporites sinuosus</i>
					Schizaeales	Anemiaceae
Lygodiaceae	<i>Concavissimisporites punctatus</i>					
Schizaeaceae	<i>Klukisporites variegatus</i> , <i>Plicatella</i> sp.					

TABLE 2. — Continuation.

BOTANICAL AFFINITY				FOSSIL
Phylum	Class	Order	Family	Microflora
Monilophyta	Polypodiopsida (= Filicopsida)	—	—	<i>Cingulatisporites psilatus</i> , <i>C. sp. 1</i> , <i>C. sp. 2</i> , <i>Cingutriletes sp.</i> , <i>Coronatispora valdensis</i> , <i>Incertae sedis in Hasenboehler</i> (1981), <i>Laevigatosporites ovatus</i> , <i>Patellasporites</i> <i>sp.</i> , <i>Pilosisorites brevis</i> , <i>P. verus</i> , <i>Polycingulatisporites reduncus</i> , <i>Trilites</i> <i>bossus</i> , <i>Tuberositriletes sp.</i> , <i>Undulatisporites</i> <i>undulapolus</i> , <i>U. sinuosis</i>
				—

BOTANICAL AFFINITY				FOSSIL			
Phylum	Class	Order	Family	Microflora	Macroflora		
Lignophyta (Spermatophyta)	Gymnosperms	Bennettitales, Cycadales or Pentoxylales	—	<i>Cycadopites minimus</i> , <i>Cycadopites sp.</i>	Bennettitales: <i>Ptilophyllum acinacifolium</i> Kimura & Okubo (K), <i>P. choshiense</i> Kimura, Okubo & Miyahashi (K), <i>P. elongatum</i> Kimura & Ohana (non Douglas) emend. Kimura, Okubo & Miyahashi (K), <i>P. subulatum</i> Kimura & Okubo (K), <i>P. sp. A in</i> Kimura (1997) (K), <i>P. sp. B in</i> Kimura (1997) (K), <i>Zamites choshiensis</i> Kimura & Ohana (K)		
				Caytoniales	—		<i>Sagenopteris inequilateralis</i> Oishi (K)
				Erdtmani- thecales	Erdtmanitheceae	<i>Eucommiidites minor</i> , <i>Eucommiidites troedssonii</i>	
		Gnetales	Ephedraceae	<i>Ephedripites montanaensis</i>			
			Gnetaceae	<i>Gnetaceapollenites sp.</i>			
			—	<i>Classopollis torosus</i> , <i>Corollina sp.</i>			
			Araucariaceae and/or Podocarpaceae	<i>Araucariacites australis</i> , <i>Balmeiopsis limbatus</i> , <i>Callialasporites dampieri</i> , <i>Callialasporites sp. cf. C. ugensis</i>			
		Coniferales	Cheirolepidiaceae or Voltziaceae	<i>Classopollis torosus</i> , <i>Corollina sp.</i>	Cheirolepidiaceae: <i>Cupressinocladus</i> <i>obatae</i> Okubo & Kimura (K), <i>Frenelopsis choshiensis</i> Kimura, Saiki & Arai (K)		
				Cupressaceae or Taxaceae	<i>Exesipollenites tumulus</i> , <i>Spheripollenites psilatus</i>		
			Pinaceae	<i>Cerebropollenites mesozoicus</i> , <i>Pityosporites sp. cf. P. piniformis</i>			
Sciadopityaceae	<i>Cerebropollenites mesozoicus</i>						
—	<i>Inaperturopollenites sp.</i> , <i>Pityosporites sp. cf.</i> <i>P. constrictus</i>						
Pterido- spermales	—	<i>Alisporites thomasii</i>	<i>Stenopteris cyclostoma</i> Saiki, Kimura & Horiuchi (A)				
—	—	<i>Alisporites sp. cf. A. australis</i> , <i>A. sp.</i> , <i>Incertae sedis sp. 2</i>					

TABLE 2. — Continuation.

Phylum	BOTANICAL AFFINITY			FOSSIL
	Class	Order	Family	Microflora
Algae Chlorophyta	Charophyceae	Zygnematales	Zygnemataceae	<i>Chomotriletes minor</i> , <i>Ovoidites parvus</i>
	Chlorophyceae	Chlorococcales	Botryococcaceae	<i>Botryococcus</i> sp. cf. <i>B. braunii</i>
	Prasinophyceae	Pterospermatales	Pterospermellaceae Tasmanitaceae	<i>Pterospermella</i> sp.
Fungi Ascomycota	Dothideomycetes	Asterinales	Asterinaceae	Parasite fungus with hyphopodia
		Microthyriales	–	<i>Microthyriacites</i> sp., <i>Phragmothyrites</i> sp.
	–	–	–	<i>Pluricellaesporites</i> spp.