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Fossil Flowers and Associated Plant Fossils from the Kamikitaba Locality (Ashizawa Formation, Futaba Group, Lower Coniacian, Upper Cretaceous) of Northeast Japan

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A preliminary description is provided of a new assemblage of plant fossils (the Kamikitaba mesofossil flora) from the Asamigawa Member of the Ashizawa Formation, Futaba Group (lower Coniacian, Upper Cretaceous) exposed in Kamikitaba, Fukushima Prefecture, northeastern Honshu, Japan. The fossils are small, three-dimensional and charcoalified or lignitized (mesofossils) and yield exquisite structural details when studied with scanning electron microscopy. The Kamikitaba assemblage comprises the first record of this style of fossil plant preservation from the Cretaceous of eastern Asia. The flora complements and extends current knowledge of Cretaceous fossil plants from Japan and provides a basis for comparison with similar mesofossil assemblages from eastern North America and Europe. The fossil assemblage contains well-preserved angiosperm flowers, fruits, seeds, leaf fragments and wood, as well as shoots, leaves, pollen cones, cone scales and seeds of conifers. Extant taxa that can be recognized provisionally include: Lauraceae, Hamamelidaceae, Fagaceae, Cornales, Combretaceae, and probably Ericales, Magnoliaceae, Nymphaeales and Taxodiaceae. Leaf and rachis fragments of ferns, sporangia with *in situ* spores, and megaspores also document the presence of Selaginellaceae and Schizaeaceae.

Key words: Ashizawa Formation (Futaba Group)—Cretaceous—Fossil flowers—Fossil plants—Japan—Kamikitaba assemblage

Plant fossils from Upper Cretaceous sediments in Northeast Japan have been studied for many decades, and have provided important data on the flora and vegetation of eastern Asia during the pre-Tertiary phase of angiosperm evolution (Stopes and Fujii 1910, Miki 1977, Tanai 1979, Nishida 1991). Especially significant for the study of angiosperm reproductive structures is a rich assemblage of fossil plants from marine deposits of the Yezo Group (Tur-

onian-Santonian) in Hokkaido (Nishida 1991) that are permineralized in calcium carbonate, and have yielded excellent details of anatomical structure (Stopes and Fujii 1910, Nishida 1991). In this paper we provide a preliminary report on a newly discovered assemblage of Late Cretaceous fossil plants (the Kamikitaba assemblage) of similar age to that from the Yezo Group. The new assemblage, from the Asamigawa Member of the Ashizawa Formation (Futaba Group), is of early Coniacian age (ca. 89 million years before present, Gradstein *et al.* 1995) and substantially extends current knowledge of Cretaceous angiosperms from eastern Asia. The flora includes well-preserved angiosperm flowers, fruits, seeds, leaf fragments and wood. Shoots, leaves, pollen cones, cone scales and seeds of conifers, and remains of ferns and lycopods are also present. Detailed treatments of selected taxa from the Kamikitaba assemblage are currently in preparation (Takahashi *et al.* in press).

In contrast to previously described fossil floras from the Upper Cretaceous of Japan, the plant remains comprising the Kamikitaba assemblage are small, three-dimensional, and charcoalified or mummified/lignitized (mesofossils). Over the last fifteen years similar Cretaceous mesofossil floras have been described from Europe (e.g., Friis and Skarby 1982, Friis 1983, 1984, Knobloch and Mai 1984, 1986, Friis *et al.* 1994), eastern North America (e.g., Crane *et al.* 1994, 1995), and most recently from Kazakhstan in central Asia (Frumina *et al.* 1995, Frumina and Friis 1996, 1999). Research on these floras has revolutionized our understanding of the Cretaceous history of angiosperm diversity (Crane *et al.* 1995). The Kamikitaba assemblage is the first record of mesofossil preservation from eastern Asia and provides a basis for comparison with mesofossil floras from elsewhere. Recognition of the Kamikitaba flora also suggests that the application of bulk sieving techniques to other samples from eastern Asia, is likely to yield additional mesofossil assemblages that will further elucidate the early evolution of flowering plants in this region.

Material and Methods

The Kamikitaba plant mesofossil assemblage was isolated

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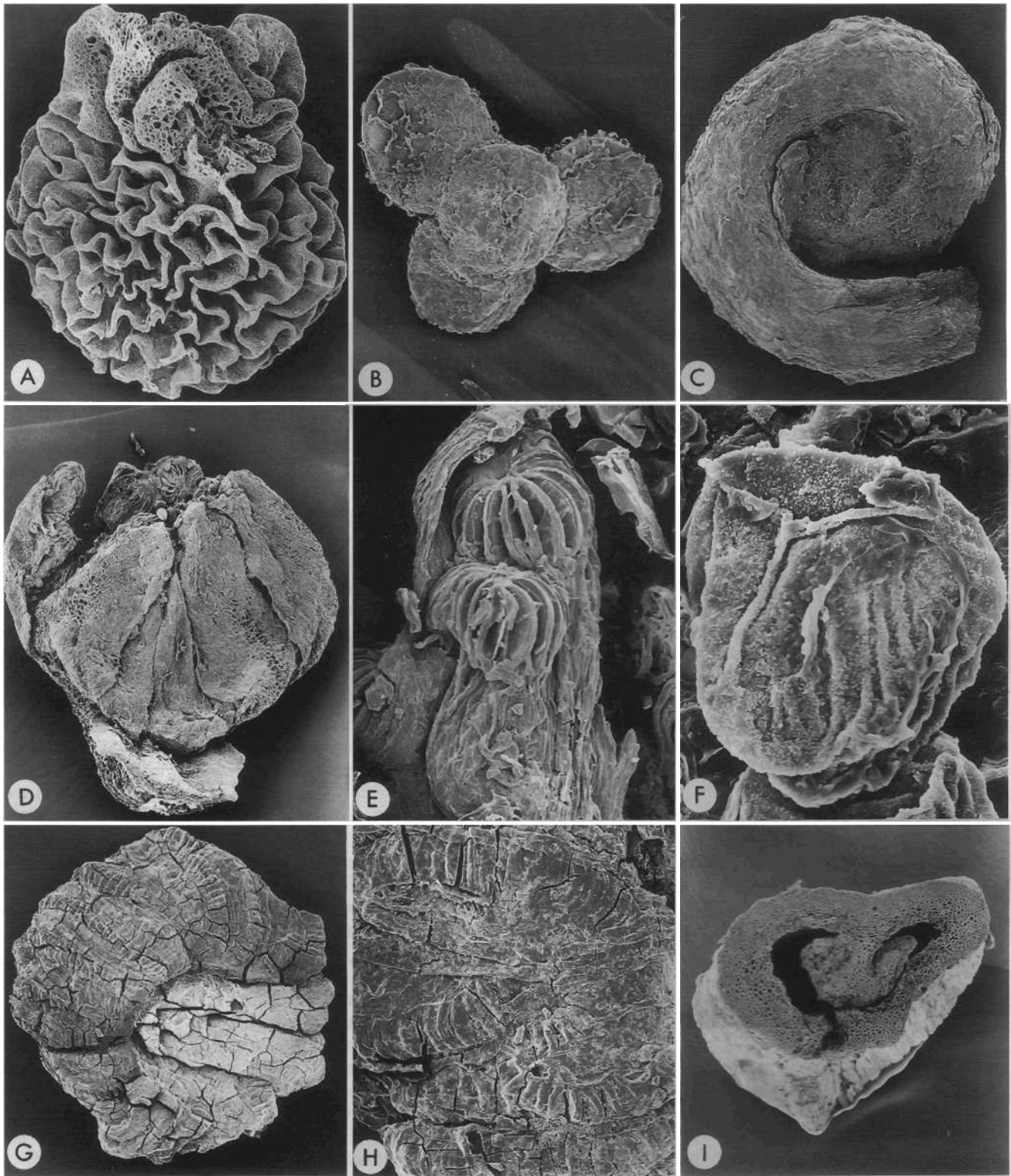


Fig. 1. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, lower Coniacian, Upper Cretaceous), Fukushima Prefecture, Honshu. Pteridophytes. A. Megaspore type 1, probable selaginellaceous megaspore similar to *Erlansonisporites erlansonii* (Miner) Potonie, equatorial view showing spongy mass of exospore at the proximal pole, PP45426, $\times 85$. B. Megaspore type 2, possible aborted megaspore tetrad of megaspore type 1, PP45427, $\times 55$. C. Circinate fern rachis, PP45428, $\times 20$. D. Fertile fern type 1, probable Schizaeaceae, cluster of pinnules enclosing sporangia with apical annulus, PP45429, $\times 35$. E. Fertile fern type 1, probable Schizaeaceae, detail of two elongated sporangia each with an apical annulus, PP45430, $\times 150$. F. Fertile fern type 1, probable Schizaeaceae, isolated *Appendicisporites/Cicatricosisporites* spore from specimen in Fig. 1E showing trilete mark on proximal

from about 500 kg of carbonaceous, black, poorly-sorted sandy siltstone (sample F16) collected by MT and HA in March 1998 at the Kamikitaba locality along a tributary of the Kitaba River in Kamikitaba, Hirono-machi, Fukushima Prefecture, northeastern Honshu (Study Route B of Ando *et al.* 1995; 37°12'N, 140°57'E). Samples were from the Asamigawa Member of the Ashizawa Formation, which is the lowermost sedimentary unit in the Futaba Group.

The Futaba Group comprises a sequence of sandy, to subordinately silty, clastics deposited in fluvial to shallow marine environments on the western margin of a matured forearc basin (Ando 1997). The sediments outcrop in the southern Abukuma Belt in Northeast Japan close to the Pacific Coast of Honshu (Ando *et al.* 1995). In the north the Futaba Group unconformably overlies the Lower Cretaceous Abukuma granite, while in the south it rests unconformably on the shales of the Permian Takakurayama Group. The Futaba Group is itself overlain by the Lower Oligocene Shiramizu Group (Ando 1997).

The Ashizawa Formation is the lowermost of three formations that comprise the Futaba Group. The Asamigawa Member of the Ashizawa Formation is interpreted as an alluvial fan deposit comprising poorly-sorted mid to lower fan sandstones and siltstones, some of which contain abundant plant debris. Above the Asamigawa Member, the Obisagawa Member of the Ashizawa Formation is interpreted as shallow marine, inner shelf to upper to lower shoreface sediments. The overlying Kasamatsu Formation is interpreted to reflect meandering to braided river sediments with lagoonal facies. The uppermost sedimentary unit in the Futaba Group, the Tamayama Formation, is interpreted as braided river flood plain sediments with a return to lagoonal and shallow marine facies in the uppermost part. Samples from the Tamayama Formation have also yielded mesofossil assemblages that are not considered in this paper (Takahashi *et al.* in press.).

Based on the occurrence of Lower Coniacian ammonites and inoceramids in the middle of the Ashizawa Formation, and a species of lower Santonian inoceramid (*Inoceramus amakusensis*) in the upper part of the Tamayama Formation, the Futaba Group is thought to range in age from early Coniacian to early Santonian. The age of the plant-bearing sediments in the Asamigawa Member is probably (and certainly not younger than) early Coniacian (ca. 89 million years before present, Gradstein *et al.* 1995).

After drying in the laboratory, the samples were disaggregated in water and sieved through a 0.3 mm mesh. The carbonaceous debris recovered was then cleaned of adhering mineral material by treatment with hydrofluoric and hydrochloric acids, thoroughly rinsed in water, and dried in air. Individual specimens were then separated by visual identification and picking under the dissecting microscope.

Specimens selected for scanning electron microscopy were mounted on polished aluminum scanning electron microscope stubs, sputter coated with platinum-palladium, and examined in a Hitachi S-800 field emission scanning electron microscope (FE-SEM).

All specimens illustrated in the present work are deposited in the paleobotanical collections of the Field Museum of Natural History, Chicago (PP).

Composition of the Plant Fossil Assemblage

Lycopods

Lycopods comprise a minor component of the Kamikitaba mesofossil assemblage and are represented by two kinds of dispersed megaspores (Fig. 1A, B).

Megaspore type 1 (Fig. 1A) is the more abundant of the two megaspores and is represented in the collection by more than 50 specimens. The megaspores vary considerably in size (0.75–1.3 mm in diameter) and also in the extent to which the ornamentation has been abraded. In unabraded specimens (Fig. 1A), the wall ornament (perispore) is comprised of spongy sporopollenin that forms a reticulate pattern in which the mura are often more or less undulating. At the proximal pole the exine is elaborated into a spongy mass and the trilete mark itself is not clearly visible. In abraded specimens the remaining spore wall (exospore) is opaline in appearance, and the trilete mark is raised and clearly visible at the proximal pole. Megaspores of this type are thought to have produced by selaginellaceous lycopods and are similar to *Erlansonisporites erlansonii* (Miner) Potonie, which ranges in age from Barremian–Aptian to Santonian–Campanian (Kovach and Dilcher 1988, Kovach and Batten 1989).

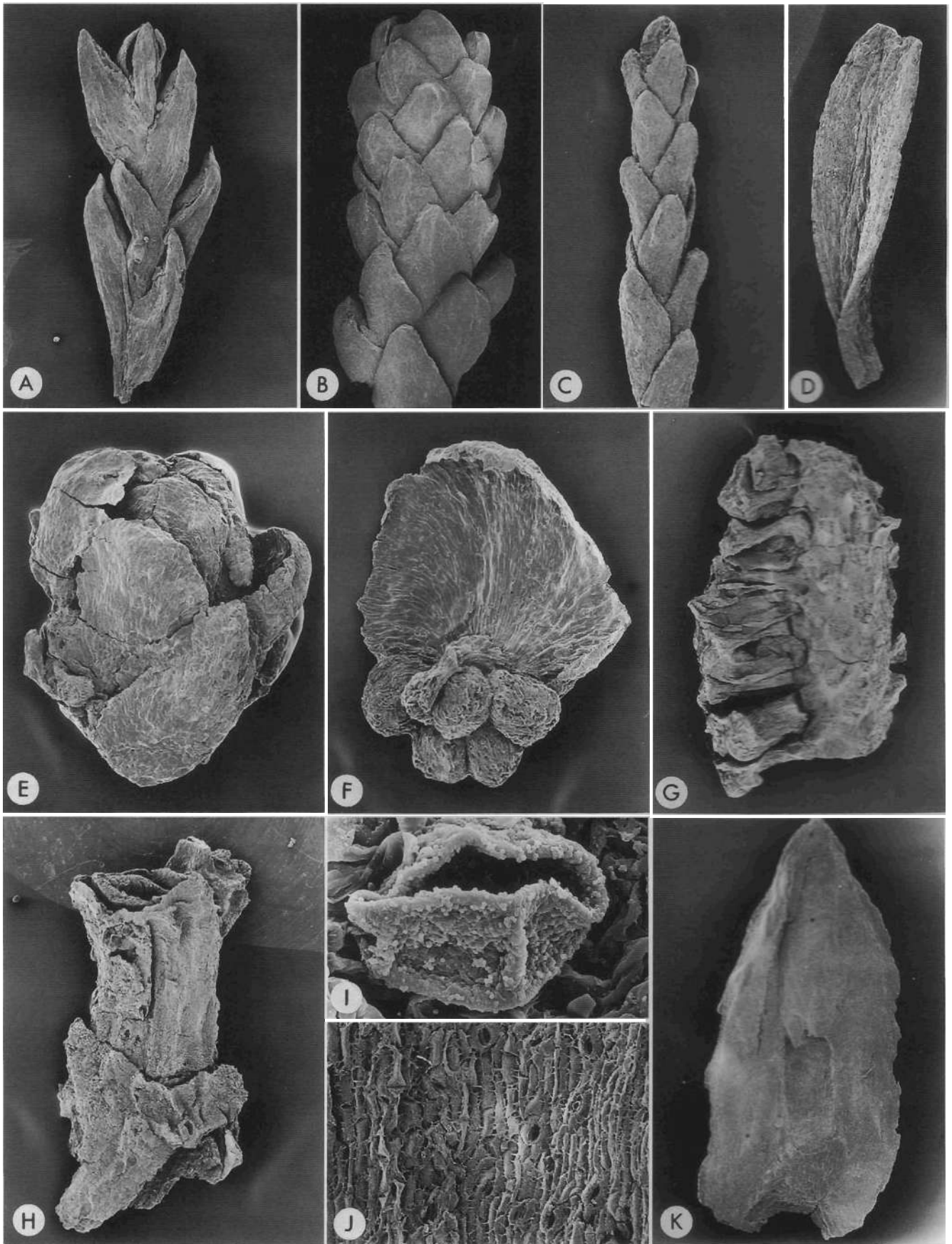
Megaspore type 2 (Fig. 1B) is represented in the collection by less than 20 specimens. In all cases four megaspores occur together in a tetrad. The individual spores are ca. 0.4 mm in diameter with a poorly-developed fibrous exospore arranged in more or less reticulate pattern. These tetrads may be an aborted form of the more common *Erlansonisporites* megaspores.

Ferns

Ferns are represented in the Kamikitaba mesofossil assemblage by fragments of leaves and rachides, occasional leaf fragments bearing sporangia, dispersed sori and dispersed sporangia (Fig. 1C–I). Two types of fertile fern material have been recovered.

Fertile fern type 1 is represented in the collection by about 15 specimens that typically show groups of sporangia enclosed by clusters of adpressed pinnules (Fig. 1D). Sporangia are elongated, ca. 0.3 mm long, and have a terminal annulus (Fig. 1E). Spores are trilete, ca. 40 μ m in diameter

surface, exospore ribs in the distal hemisphere and thin covering of perine, PP45430, $\times 1,500$. G. Fertile fern type 2, circular sporangial cluster from a single sorus showing a mass of sporangia with longitudinal annuli surrounding a central cavity, PP45431, $\times 50$. H. Fertile fern type 2, detail of three sporangia from specimen in Fig. 1G showing longitudinal annuli, PP45431, $\times 110$. I. Transverse section through a fern rachis showing thick-walled cortical cells and cavity from which soft tissues have decayed, PP45432, $\times 40$.



with a clear trilete mark and numerous prominent ribs on their distal hemisphere (Fig. 1F). The ribs are partly obscured by a granular perispore. Dispersed spores of this type from the Futaba Group have been referred to the genera *Appendicisporites* and *Cicatricosisporites* (Takahashi 1988). The combination of the apical annulus and trilete ribbed spores strongly suggests a relationship to the extant fern family Schizaeaceae. Pemineralized schizaeaceous fern sporangia, similar to fertile fern type 1, have been described from the Upper Yezo Group (Coniacian-Santonian) of Hokkaido as *Schizaeopteris mesozoica* (Stopes and Fujii 1910, Yoshida *et al.* 1996b).

Fertile fern type 2 is represented in the collection by two dispersed sori, ca. 1.1 mm in diameter (Fig. 1G). Each sorus is composed of numerous sporangia surrounding a central sterile region that possibly indicates the position of the stalk. No indusium is preserved in either specimen. Sporangia have a longitudinal annulus. Spores have not been identified unequivocally. Spores in similar, but more fragmentary, specimens from the Kamikitaba locality are trilete with a psilate wall.

Other fern material in the Kamikitaba assemblage includes charcoalified fern rachides with well-preserved anatomy (Fig. 1I), some of which exhibit circinate vernation (Fig. 1C), and a variety of leaf fragments.

Conifers

Conifers are abundant in the Kamikitaba mesofossil assemblage and are represented by leaves and shoots, as well as a variety of reproductive structures that include ovulate cone scales, seeds, pollen cones and pollen cone scales (Figs. 2, 3).

Conifer leaves and shoots. Three different types of conifer shoots have been recognized provisionally in the Kamikitaba mesofossil assemblage.

Conifer leaf type 1 (Fig. 2A-C) is represented in the collection by several hundred shoots with attached leaves. The shoots range from 0.8-1.5 mm in width, while the leaves range from 0.8-1.5 mm in length. Leaves vary considerably in shape from more or less elliptical in lateral view with a bluntly rounded apex (Fig. 2C), to shorter, broader forms with an obtuse apex (Fig. 2B), to longer, narrower, acicular forms in which the apex is acute (Fig. 2A). Stomata are not visible on the abaxial leaf surface, although this surface of the leaf

often shows characteristic perforations in the cuticle with SEM. It is possible that more than one species is represented among the fragments of leafy shoots grouped together here as conifer leaf type 1. In particular, it is possible that the shoots with acicular leaves may belong to a different species than those with a more rounded apex. The systematic affinities of these kinds of leaves from the Jurassic and Cretaceous are generally taken to be with extant Araucariaceae or Taxodiaceae (e.g., Harris 1979, Srinivasan and Friis 1989), or extinct Cheirolepidiaceae (e.g., Watson 1988). We consider a taxodiaceous affinity most likely for the Kamikitaba material.

Conifer leaf type 2 (Fig. 2D, J) is represented in the collection by more than 80 leaf fragments, none of which is attached to a shoot. The leaves are linear, parallel-sided and dorsiventrally flattened. They are up to 2 mm broad, with an estimated length of up to 8.0 mm. At the base, the leaves narrow to a short, poorly defined petiole and are distinctly twisted, probably indicating that they were helically-attached to the shoot, but planated into a dorsiventral arrangement. At the apex the leaves taper to a sharp point. Stomata are rare on the adaxial leaf surface, but abundant abaxially where they are arranged in two broad bands on either side of the midrib. Stomata are mainly oriented with their axes parallel or oblique to the long axis of the leaf (Fig. 2J). The systematic affinities of conifer leaf type 2 are uncertain.

Conifer leaf type 3 (Fig. 2H) is represented in the collection by more than 70 fragments of shoots that have long internodes (up to 9.0 mm long and 2.5 mm wide) and leaves arranged in whorls of three. Occasional shoot fragments in which more than one internode is preserved show that the leaves of successive nodes alternate (Fig. 2H). The cuticle of the shoots is thick and featureless. Stomata have not been observed. The systematic affinities of conifer leaf type 3 are uncertain. While it is similar to shoots of some cheirolepidiaceae conifers, it is also possible that it is incorrectly assigned as to major group. These shoots may perhaps be of angiosperm or gnetalean affinity. One poorly preserved specimen shows a shoot of this kind connected to a reproductive structure resembling hypogynous flower type 3.

Conifer reproductive structures. Several kinds of conifer ovulate and pollen-producing reproductive structures occur

Fig. 2. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, lower Coniacian, Upper Cretaceous), Fukushima Prefecture, Honshu. Conifers. A. Conifer leaf type 1, fragment of leafy shoot showing acicular leaves with acute apices, PP45433, $\times 20$. B. Conifer leaf type 1, fragment of a broad leafy shoot showing leaves with broad bases and rounded apices, PP45434, $\times 20$. C. Conifer leaf type 1, fragment of slender leafy shoot showing leaves with broad bases and rounded apices, PP45435, $\times 20$. D. Conifer leaf type 2, almost complete isolated leaf, note twisted base and more or less parallel-sided lamina (leaf apex broken), PP45436, $\times 15$. E. Conifer pollen cone type 1 showing helically-arranged, overlapping microsporophylls, PP45437, $\times 40$. F. Conifer pollen cone type 1, microsporophyll showing peltate cone scale, five sporangia and short stalk, PP45438, $\times 60$. G. Conifer pollen cone type 2, cone fragment showing thick central axis and attached microsporophylls on one side, PP45439, $\times 30$. H. Conifer leaf type 3 (possible gnetalean or angiosperm?), shoot showing one complete internode (above) and one fragmentary internode (below), note leaves borne in alternating whorls of three, PP45440, $\times 30$. I. Conifer pollen cone type 1, pollen grain from surface of specimen in Fig. 2F showing verrucate wall, irregular aperture and orbicules on surface, PP45438, $\times 2,200$. J. Conifer leaf type 2, detail of abaxial surface showing longitudinal to obliquely-oriented stomata between the midrib and the leaf margin, PP45441, $\times 120$. K. Conifer seed type 1, specimen with poorly-developed wing, note cordate base and depression in the proximal part of the seed surface, PP45442, $\times 150$.

in the Kamikitaba mesofossil assemblage (Figs. 2E-G, I, K, 3A-C).

Conifer pollen cone type 1 is represented in the collection by more than 50 specimens that include isolated microsporophylls (Fig. 2F), as well as cones with attached microsporophylls (Fig. 2E). Cones are ca. 1.4 mm long and ca. 1.2 mm wide, and consist of about 12 helically attached microsporophylls (Fig. 2E). Microsporophylls are peltate with a short stalk attached to the adaxial surface of a shield-shaped head. Several pollen sacs (at least five in the most complete specimens) are attached laterally and beneath the stalk. The microsporophyll head is smooth with radiating cells and often has a fimbriate margin. Stomata have not been observed on the microsporophylls. The abaxial surface of the microsporophylls often shows characteristic perforations in the cuticle similar to those seen in conifer leaf type 1, suggesting that they may have been produced by the same plant species. Pollen on the surface of the microsporophylls is more or less spherical, ca. 20 μm in diameter, with verrucate surface. Grains have an irregular opening (Fig. 2I) and were probably inaperturate. Some specimens have orbicules adhering to the pollen wall. Similar cones and microsporophylls from the late Santonian-early Campanian of Sweden have been compared with pollen cones of extant *Sequoia*, *Sequoiadendron* and *Taxodium*, and assigned to the Taxodiaceae (Srinivasan and Friis 1989, see also Aulenback and LePage 1998).

Conifer pollen cone type 2 is represented in the collection by a single specimen ca. 1.9 mm long, which shows about 20 microsporophylls attached along one side of a stout central cone axis (Fig. 2G). Each microsporophyll has a long stalk bearing several elongated pollen sacs (number unknown).

Distally, the microsporophylls are expanded into a small upturned head. Pollen grains have not been observed. Pollen cones of this type are produced by a variety of conifers but are especially common among extant Pinaceae.

Conifer seed type 1 (Fig. 2K) is represented in the collection by more than 100 specimens. Each seed is ovate, ca. 3.4 mm long and ca. 1.9 mm wide with an acute apex and an obtuse or cordate base. Often there is a narrow wing that varies in its development in different specimens. Seeds are dorsiventrally flattened with a marked, small, linear-oblong depression over the seed body on each surface. The depressions on either side of the seed are very similar. One is the seed attachment scar, while the other may be a feature associated with germination. Similar winged seeds are produced by a variety of extant taxodiaceous conifers (Aulenback and LePage 1998).

Conifer ovulate cone scale type 1 (Fig. 3A) is represented in the collection by three specimens. Cone scales are ca. 1.9 mm long, ca. 1.5 mm wide, obovate with a narrow base and rounded apex. They are not massive and woody. The bract scale is not visible. In several specimens two or three immature ovules are present on the abaxial surface of the cone scale close to the base with their micropyles directed toward the cone axis. The systematic affinities of conifer cone scale type 1 are uncertain.

Conifer ovulate cone scale type 2 (Fig. 3B) is represented in the collection by five specimens. The scales are ca. 4.7 mm long and 4.2 mm wide and rhomboidal in shape. Distally, they have a more or less diamond-shaped to square head with a distinct umbo. Proximally they narrow toward their attachment to the cone axis. They are more massive and woody than conifer ovulate cone scale type 1 and do not

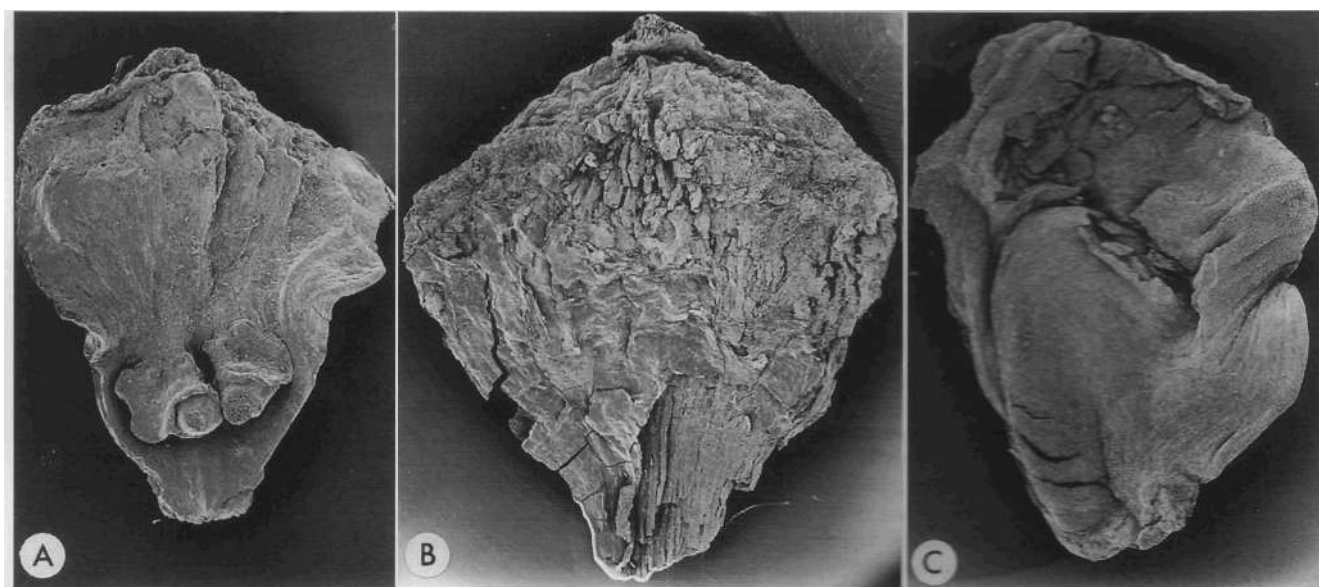


Fig. 3. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, lower Cretaceous, Upper Cretaceous) Fukushima Prefecture, Honshu. Conifer ovulate cone scales. A. Conifer ovulate cone scale type 1, note two immature ovules attached near the base with their micropyles pointed toward the cone axis, PP45443, $\times 30$. B. Conifer ovulate cone scale type 2, note the thick woody texture and distinct apical umbo, PP45444, $\times 15$. C. Conifer ovulate cone scale type 3, showing broken point of attachment and seed embedded obliquely in the cone scale near the base, PP45445, $\times 15$.

show ovules or obvious scars of seeds. The bract scale is presumed fused to the ovuliferous scale. The systematic affinities of conifer cone scale type 2 are uncertain. However, similar cone scales occur among extant Taxodiaceae and these fossils may have been produced by the same species as conifer leaf type 1 and conifer pollen cone type 1 (see above).

Conifer ovulate cone scale type 3 (Fig. 3C) is represented in the collection by about 15 specimens. These fossils are provisionally interpreted as cone scales, but as additional material becomes available it is possible that they may be reinterpreted as isolated seeds. Generally they are more or less flattened, and broadly obovate and rounded. However, they vary considerably in shape, and are frequently more or less irregular in all dimensions. They give the appearance that their growth was influenced, sometimes in a partly spiral fashion, by other structures, presumably as a result of packing in a cone. Each has a narrow attachment to the presumed cone axis and a thicker region (the seed or seed body) embedded in it oblique to the longitudinal axis close to its base. The systematic affinities of conifer cone scale type 3 are unknown.

Angiosperms

Angiosperms are represented in the Kamikitaba mesofossil assemblage by a variety of small flowers, fruits and seeds. Well-preserved fragments of angiosperm wood and leaves are also present but have not yet been studied. The angiosperm remains are considered here under three headings; hypogynous flowers, epigynous flowers and miscellaneous seeds.

Hypogynous flowers. Several different kinds of hypogynous flowers, or fruits clearly developed from hypogynous flowers, are present in the Kamikitaba mesofossil assemblage and eight types are recognized here.

Hypogynous flower type 1 (Fig. 4A) is known from a single specimen consisting of a thick, ribbed pedicel that terminates in a broad flat receptacle about 2.5 mm in diameter. The receptacle has broad imbricate petals attached around the rim. On one side the petals have separated from the rim of the receptacle to reveal numerous short elongated structures, some of which have longitudinally-oriented lateral sacs and resemble staminodes or immature stamens. Other details of this flower (e.g., pollen, carpels) are unknown and until these become available its systematic affinities will remain uncertain.

Hypogynous flower type 2 (Fig. 4B-D) is represented in the collection by about 15 specimens. Flowers are pedicellate, trimerous, about 1.2 mm long and 1.2 mm broad. The perianth consists of three outer tepals and three inner tepals, both borne on a short cup-like receptacle. The number of stamens is uncertain but is at least six, and perhaps as many as nine. Stamens dehisce through flap-like valves (Fig. 4C). Stamens have four valves per anther (Fig. 4C). The gynoecium is not clearly seen in the specimen with unequivocal stamens (Fig. 4B), perhaps indicating that the flowers were unisexual. The fruit developed from a single carpel and is borne in a shallow cup-like receptacle with persistent

perianth parts (Fig. 4D). The characters of this flower clearly indicate a relationship to extant Lauraceae. Fossil flowers of Lauraceae have been recorded from several other Cretaceous mesofossil floras (e.g., Drinnan *et al.* 1990, Herendeen *et al.* 1994, Crane *et al.* 1994, Eklund and Kvacek 1998).

Hypogynous flower type 3 (Fig. 4E, F) is represented in the collection by about nine specimens. Flowers are pedicellate, trimerous, ca. 1.5–2.3 mm long. The perianth consists of three small outer tepals, extending about one fifth to one quarter the length of the ovary (Fig. 4E, F). The tepals are placed at the corners of the triangular ovary and alternate with what appear to be three large valves of the fruit (Fig. 4F). Stamens have not been observed. The fruit is triangular in cross-section with no evidence of styles at the apex. At maturity the fruit splits into three valves along the three angles of its triangular cross-section (Fig. 4E). The surface of the pedicel, tepals and fruit wall have scattered, distinct, small holes that perhaps indicate the position of ruptured secretory structures (Fig. 4E). Stomata are present and superficial (not sunken). The systematic relationships of hypogynous flower type 3 are uncertain. It is possible that it is incorrectly assigned as to major group and may be part of the same species as conifer leaf type 3. It is perhaps of gnetalean or possibly coniferous affinity.

Hypogynous flower type 4 (Fig. 4G, H) is represented in the collection by two specimens. Flowers are sessile on an elongated inflorescence and consist of a single carpel (or possibly immature stamen?) in the axil of a short bract (Fig. 4G, H). Each carpel is ca. 0.75–1.1 mm long and ca. 0.3–0.5 mm wide. A shallow groove extends from the base to the apex of the carpel on the adaxial side. At the apex of each carpel there is an oblique, oval surface. It is unclear whether this is the stigmatic surface or the broken style base. The systematic relationships of hypogynous flower type 4 are uncertain.

Hypogynous flower type 5 (Fig. 4I) is known from a single specimen. The flower is 0.9 mm wide with five sepals and two carpels. The sepals extend about half the length of the carpels and are rounded at their apices. The two carpels are free for most of their length and have their ventral sutures facing one another (Fig. 4I). At the apex each carpel shows the point of attachment of a stout style (both broken). Stamens and pollen have not been observed. The systematic relationships of hypogynous flower type 5 are unknown, but are possibly with the Hamamelidoideae (represented in the Kamikitaba assemblage by seed type 2) and almost certainly with some group within the core eudicots *sensu* Magallón *et al.* (1999).

Hypogynous flower type 6 is represented in the collection by about ten specimens (Fig. 5A–C). The flower is pentamerous, actinomorphic, with an estimated diameter of about 1.8 mm (including the sepals). The diameter of the receptacle is ca. 1.0 mm. The perianth consists of five broad membranous tepals, and five petals of which only the narrow petal bases are preserved (Fig. 5A). The androecium consists of 10 stamens in two whorls. The outer whorl of five stamens opposite the sepals have broad, laterally

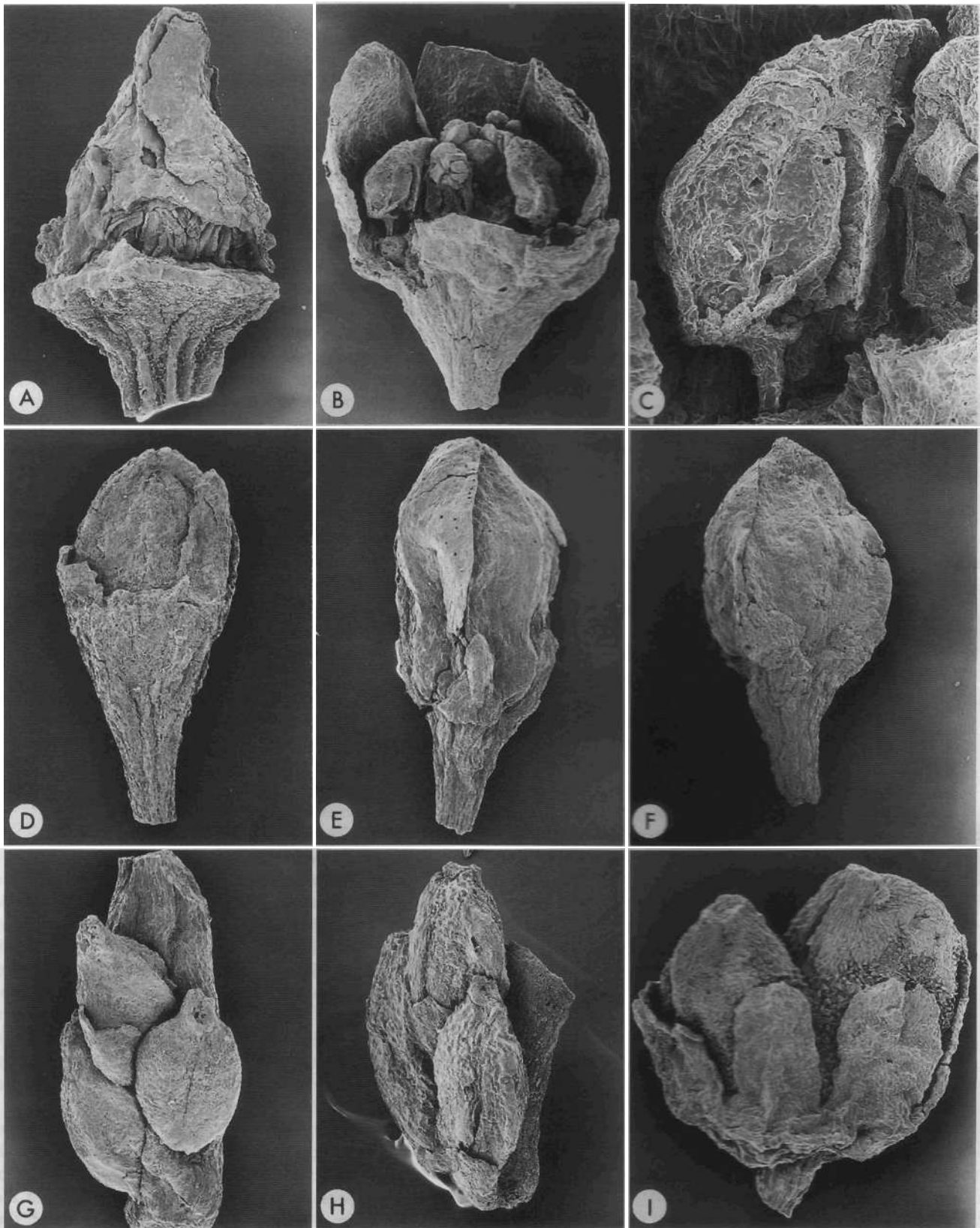


Fig. 4. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, lower Cretaceous, Upper Cretaceous) Fukushima Prefecture, Honshu. Angiosperm hypogynous flowers, types 1-5. A. Hypogynous flower type 1, showing broad receptacle, petals and elongated structures (? staminodes or immature stamens), PP45446, $\times 20$. B. Hypogynous flower type 2, Lauraceae, showing six tepals (three broken) and stamens with valvate dehiscence, PP45447, $\times 45$. C. Hypogynous flower type 2, Lauraceae,

expanded bases (Fig. 5A). The inner whorl of five stamens have narrower bases and are attached close to the base of the petals (Fig. 5A). Anthers and pollen have not been observed. The ovary is low, dome-shaped and composed of five carpels (Fig. 5A, B). The apex of the ovary is pleated into five lobes, which presumably reflect a five-lobed style (Fig. 5A-C), but details of the stigmatic surface are unknown. Hypogynous flower type 6 is one of the most distinctive fossils in the Kamikitaba mesofossil assemblage. Its systematic affinity is clearly among some group within the core eudicots *sensu* Magallón *et al.* (1999).

Hypogynous flower type 7 is represented in the collection by about seven specimens. The flower is pentamerous, actinomorphic and ca. 2.5 mm in diameter. The perianth consists of five, broad thick (fleshy?) tepals, which are persistent and enclose the fruit (Fig. 5D, E, F). Petals have not been observed. At least five stamens are present opposite the sepals and alternating with the carpels, but details of anthers and pollen are not preserved. The gynoecium is syncarpous consisting of five carpels alternating with the sepals and stamens. At maturity the ovary is a capsular fruit with loculicidal dehiscence (Fig. 5E). The capsule contains elongated seeds (Fig. 5F) with a prominently ribbed seed coat that resemble seed type 5 (Fig. 9H). The systematic affinity of hypogynous flower type 7 is clearly with some group within the core eudicots *sensu* Magallón *et al.* (1999). Both the capsular fruit and the ribbed seeds are similar to those of some Ericales.

Hypogynous flower type 8 is represented in the collection by about five specimens. The flower is pentamerous, actinomorphic and ca. 1.2 mm in diameter (Fig. 5G, H). The perianth consists of five sepals fused at the base to form a shallow cup. Corolla and androecium are unknown. The gynoecium is syncarpous consisting of three fused carpels each of which is divided apically and has a bifid tip (Fig. 5G, H). Details of styles and stigmatic surfaces are not well preserved. At maturity the ovary develops into a dry capsular fruit with septicidal dehiscence. Each of three valves of the mature fruit has a prominent two-pronged apex. Specimens from other localities in the Futaba Group show that two elongated seeds were produced in each valve. The systematic affinity of hypogynous flower type 8 is clearly with some group within the core eudicots *sensu* Magallón *et al.* (1999).

In addition to the eight flowers described above several other types of hypogynous flowers (possibly three or four additional types) occur in the Kamikitaba mesofossil assem-

blage but remain to be characterized (e.g., Figs. 5I, 6A, B).

Epigynous flowers. Epigynous flowers, or fruits clearly developed from epigynous flowers, are common in the Kamikitaba mesofossil assemblage. Five types have been recognized, of which epigynous flower types 2, 3, 4 and 5 are much more abundant than any of the hypogynous forms.

Epigynous flower type 1 (Fig. 6C) is known from one specimen of a young fruit. In lateral view the fruit is diamond-shaped, 2.0 mm long and 1.5 mm broad at the widest point. The fruit developed from an epigynous flower and the perianth is attached at its broadest point. Tepals are prominent, leathery and hairy, but the number and arrangement of perianth parts, and the androecium are unknown. The ovary is tricarpellate with the three carpels probably fused below the insertion of the perianth. Above the insertion of the perianth the carpels are free. Like the sepals, the carpels and hypanthium are densely hairy. The systematic affinity of epigynous flower type 1 is unknown.

Epigynous flower type 2 (Fig. 7A-C) is represented in the collection by about 50 fruits. The fruits are typically 1.1-1.9 mm long and 1.0-1.8 mm broad. Each consists of a cup-shaped hypanthium bearing an almost hemispherical, tricarpellate syncarpous ovary. The ovary has three separate, short, recurved styles at the apex (Fig. 7B). The ovary is rounded triangular in transverse section (Fig. 7A) and internally has three locules. The hypanthium tapers to a truncate base and has three major ribs that run from the base to the rim and that are aligned with three rounded corners of the ovary. Between the three major ribs are two subsidiary ribs that are also well-developed. Epidermal cells of the ovary wall each bear a single short papilla (Fig. 7B). Close to the style bases, and in other scattered locations on the fruit surface, the papillae are sometimes elongated into a long, apparently unicellular, trichomes (Fig. 7C). Details of perianth, stamens and pollen are currently unknown. The systematic affinity of epigynous flower type 2 is unknown.

Epigynous flower type 3 (Fig. 7D-G) is represented in the collection by about 90 fruits, many of which are heavily abraded. The fruit is fusiform, typically 3.25-7.25 mm long and 1.5-3.0 mm broad, with the basal two-thirds covered by the hypanthium. Above the hypanthium projects the elongated, tapering apex of the ovary (Fig. 7D). The hypanthium bears about six prominent, broadly-triangular to ovate tepals (Fig. 7F). Prominent longitudinal vascular bundles occur in the tissues of the hypanthium. In many specimens the hypanthium and epidermis of the ovary is abraded away and the woody tissue of the mesocarp is exposed. These

—
lateral view of single stamen showing apical extension of the connective and two pollen sacs with valvate dehiscence, PP45447, $\times 170$. D. Hypogynous flower type 2, probable Lauraceae, mature fruit borne in a shallow cup-like receptacle, note remains of persistent perianth, PP45448, $\times 30$. E. Hypogynous flower type 3, lateral view showing three outer tepals/bracts and two valves of the presumed ovary wall, PP45449, $\times 30$. F. Hypogynous flower type 3, lateral view showing two outer tepals/bracts and one large inner tepal/bract (left), PP45450, $\times 30$. G. Hypogynous flower type 4, showing three uncarpellate flowers attached to an inflorescence axis, note single bract subtending upper flower and impressions of bracts that subtended the lower two flowers, PP45451, $\times 40$. H. Hypogynous flower type 4, showing three uncarpellate flowers attached to an inflorescence axis, note the single bract subtending each flower, PP45452, $\times 30$. I. Hypogynous flower type 5, showing pentamerous calyx and bicarpellate ovary, note broken style bases and tepals with rounded apices, PP45453, $\times 70$.

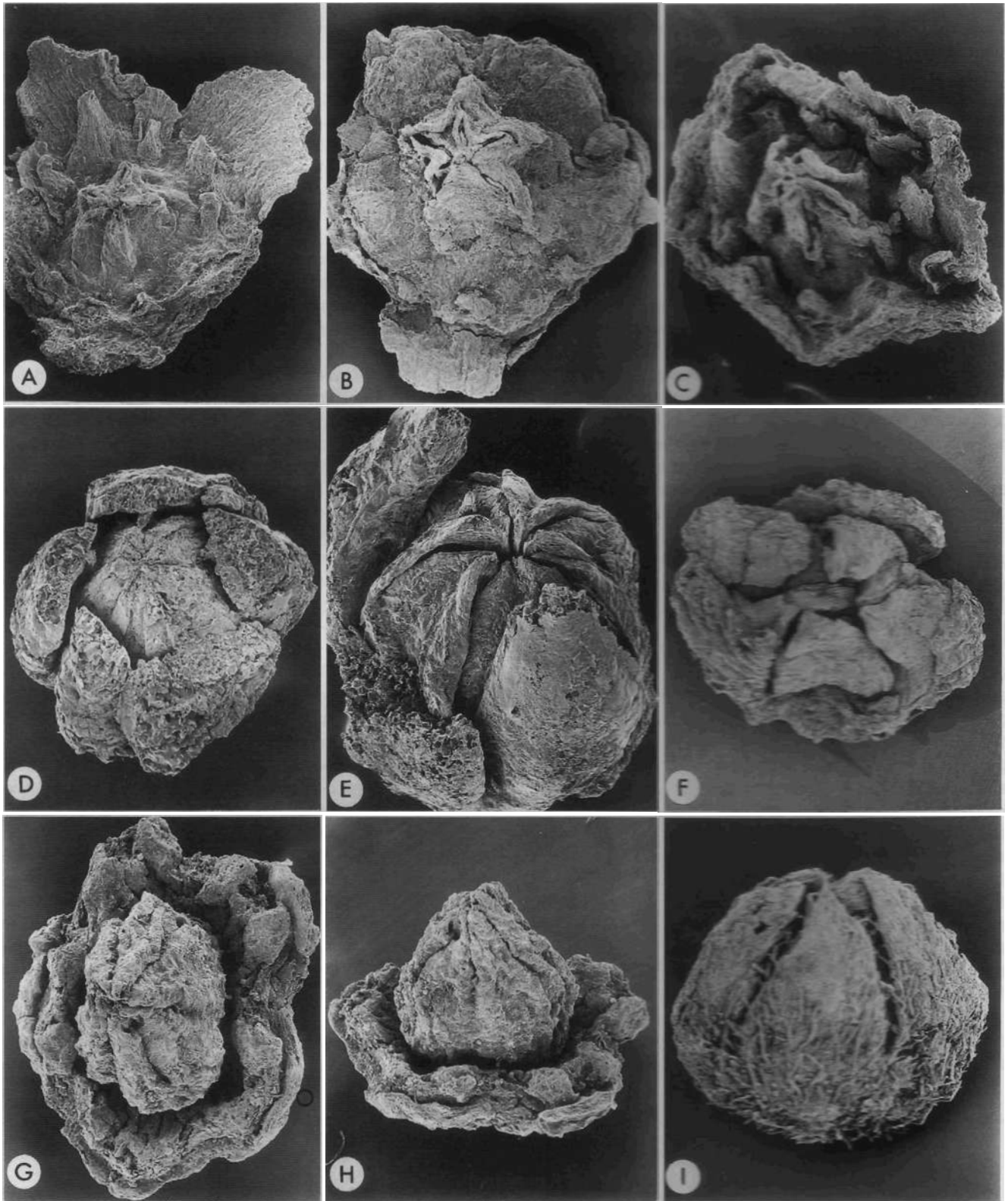


Fig. 5. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, lower Cretaceous or 'Upper Cretaceous', Fukushima Prefecture, Honshu). Angiosperm hypogynous flowers, types 6–8. A. Hypogynous flower type 8, apical view, showing five sepals, the points of attachment of four petals, and two whorls of five stamens surrounding a five-carpellate, syncarpous ovary, PP45454, $\times 50$. B. Hypogynous flower type 6, apical view of flower showing remains of sepals and stamen bases surrounding a five-carpellate, syncarpous ovary, PP45455, $\times 35$. C. Hypogynous flower type 6, apical view of flower showing remains of perianth and stamens surrounding a five-carpellate, syncarpous ovary, PP45456, $\times 70$. D. Hypogynous flower type 7 (possible Ericales?), apical

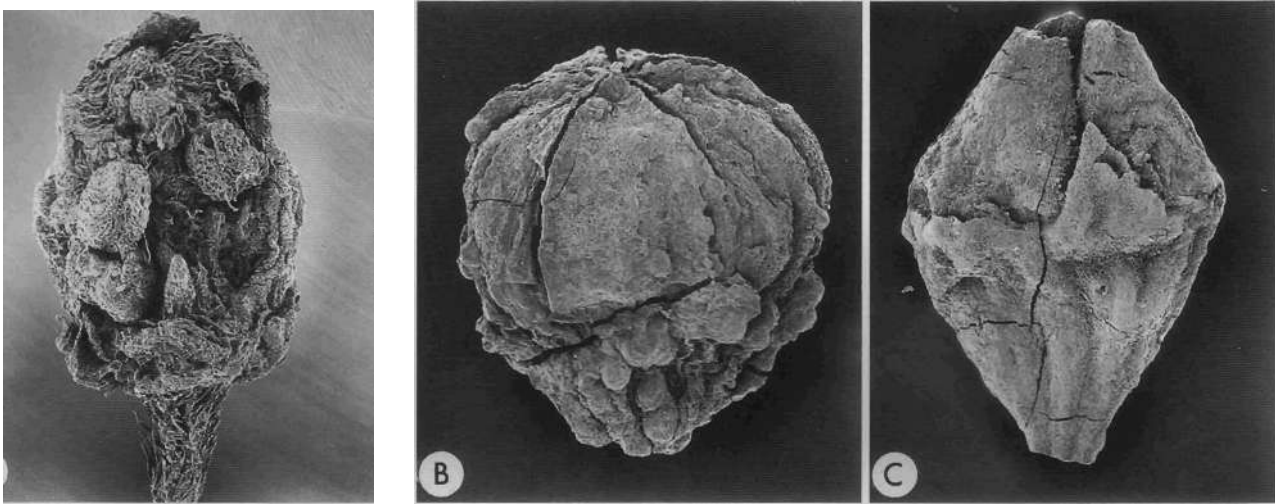


Fig. 6. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, lower Coniacian, Upper Cretaceous), Fukushima Prefecture, Honshu. Miscellaneous angiosperm hypogynous flowers and epigynous flower type 1. A. Miscellaneous hypogynous flower, lateral view of a transversely fractured flower showing probable stamen filament, anthers and well-developed hairs (possible staminate flower of Fagaceae), PP45463, $\times 50$. B. Miscellaneous hypogynous flower, lateral view showing five carpels and pustulose apex of the pedicel, PP45464, $\times 40$. C. Epigynous flower type 1, lateral view showing remains of a sepal and tricarpellate ovary with the carpels free in their upper parts, PP45465, $\times 27$.

specimens are often more ovoid in shape rather than fusiform (Fig. 7E). The ovary contains three to four locules (Fig. 7G), which open from the apex by broad valves at maturity (Fig. 7E). Each locule appears to contain a single elongated seed that is released when the valves open. In the fossil material the valves are frequently broken off at the base and the locule is empty. Details of stamens and pollen are currently unknown. The distinctive valvate fruit dehiscence suggests that the systematic affinity of epigynous flower type 3 is with the Cornales.

Epigynous flower type 4 (Fig. 8A-C) is represented in the collection by about 60 specimens. Each consists of an inferior ovary that is broadly elliptical to broadly obovate in lateral view. The ovary is distinctly triangular to three-lobed when viewed from above or in transverse section (Fig. 8C), and about 1.3–2.2 mm long and 1.0–2.0 mm in maximum diameter. At the apex of the ovary there are three separate, short, slightly recurved styles surrounded by the bases of at least three stamens and three or more tepals (Fig. 8B, C). The epidermis of the ovary is smooth (Fig. 8A) but is often abraded to expose the mesocarp (Fig. 8B, C). Three prominent longitudinal vascular bundles extend from the base of the ovary along the three main ribs and converge on the

corresponding styles. Three less prominent longitudinal vascular bundles are present between the primary bundles. The ovary contains three locules. One specimen shows that each locule probably contained two ovules that were borne close to the apex on the innermost locule wall below the styles. Details of stamens and seeds are currently unknown. Small tricolporate pollen grains (ca. 7–8 μm in polar length) occur near the style bases of some of the fruits. Clarification of the systematic affinity of epigynous flower type 4 will require additional structural details, but the form of the ovary, the presence of two ovules per locule, and the size and sculpture of the pollen grains are suggestive of a possible affinity with the Fagaceae.

Epigynous flower type 5 (Fig. 8D-F) is represented in the collection by 29 specimens. Each consists of a narrow, elongated inferior ovary, typically 2.8 mm long and 1.1 mm broad, that has three styles at the apex (Fig. 8D). The calyx consists of five free sepals (Fig. 8D, E). The corolla is poorly preserved. Stamen filaments are present opposite to, and alternating with, the sepals suggesting an androecium of up to ten stamens (Fig. 8D). The gynoecium is tricarpellate, syncarpous and unilocular. Distinctive peltate, glandular trichomes occur on the style bases and in rows in grooves in

view showing five (broken) fleshy tepals surrounding the five-carpellate, syncarpous ovary, PP45457, $\times 22$. E. Hypogynous flower type 7 (possible Ericales?), oblique lateral view showing five fleshy tepals surrounding the septidial, five-loculed capsule, PP45458, $\times 24$. F. Hypogynous flower type 7 (possible Ericales?), apical view of mature capsule showing five sepals and five valves of the capsule, note elongated seeds with a prominently ribbed seed coat, compare with seed type 7 (Fig. 9H), PP45459, $\times 18$. G. Hypogynous flower type 8, apical lateral view showing tricarpellate syncarpous ovary borne in a shallow five-lobed receptacle, note remains of sepals and petals around the periphery and the bifid apex of each carpel, PP45460, $\times 50$. H. Hypogynous flower type 8, oblique lateral view of specimen in Fig. 5G, showing tricarpellate ovary, note the bifid apex of the carpel with the lobes separated by a suture extending for half the length of the ovary, PP45461, $\times 40$. I. Miscellaneous hypogynous flower, lateral view showing sepals with well-developed hairs, PP45462, $\times 50$.

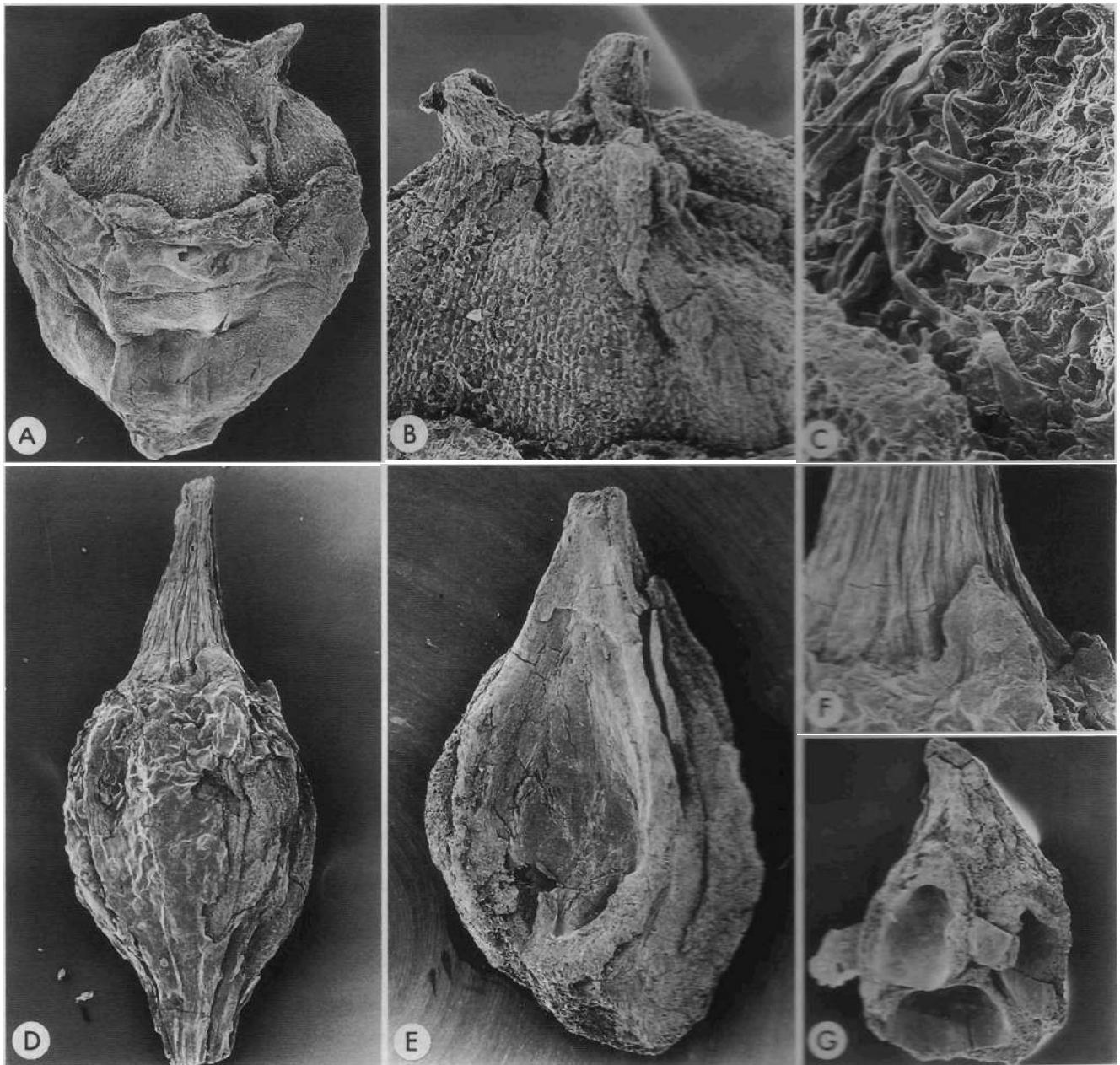


Fig. 7. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, Upper Danian, Upper Cretaceous), Fukushima Prefecture, Honshu. Angiosperm epigynous flowers, types 2 and 3. A. Epigynous flower type 2, lateral view showing hypanthium and ovary with three short styles (one broken), PP45466, $\times 45$. B. Epigynous flower type 2, oblique lateral view showing three styles at apex of the ovary, PP45467, $\times 80$. C. Epigynous flower type 2, detail of tepal surface showing papillae and hairs, PP45468, $\times 300$. D. Epigynous flower type 3, probable *Comales*, lateral view showing long style and elongated apex of ovary, PP45469, $\times 18$. E. Epigynous flower type 3, probable *Comales*, lateral view of an abraded specimen showing valve opening from the apex (right), PP45470, $\times 20$. F. Epigynous flower type 3, probable *Comales*, detail of tepal, PP45471, $\times 300$. G. Epigynous flower type 3, probable *Comales*, oblique view of fractured specimen showing three locules surrounded by massive floral wall, PP45472, $\times 25$.

the ovary wall (Fig. 8E, F). Simple trichomes occur all over the surface of well preserved specimens (Fig. 8D, F). Epigynous flower type 5 can be assigned to the genus *Esgueiria* Friis, Pedersen and Crane (1992). Two species of *Esgueiria* (*E. adenocarpa*, *E. miraensis*) were established based on fusainized (charcoalified) flowers from two localities (Esgueira and Mira) of Campanian-Maastrichtian age (Late

Cretaceous) in the Beira Litoral region of Portugal (Friis *et al.* 1992). The flowers from the Kamikitaba assemblage are a new species, but are the first record of *Esgueiria* from outside Portugal (Takahashi *et al.*, in press). The affinities of *Esgueiria* are thought to be with extant Combretaceae (Friis *et al.* 1992).

Miscellaneous seeds. A variety of dispersed seeds and

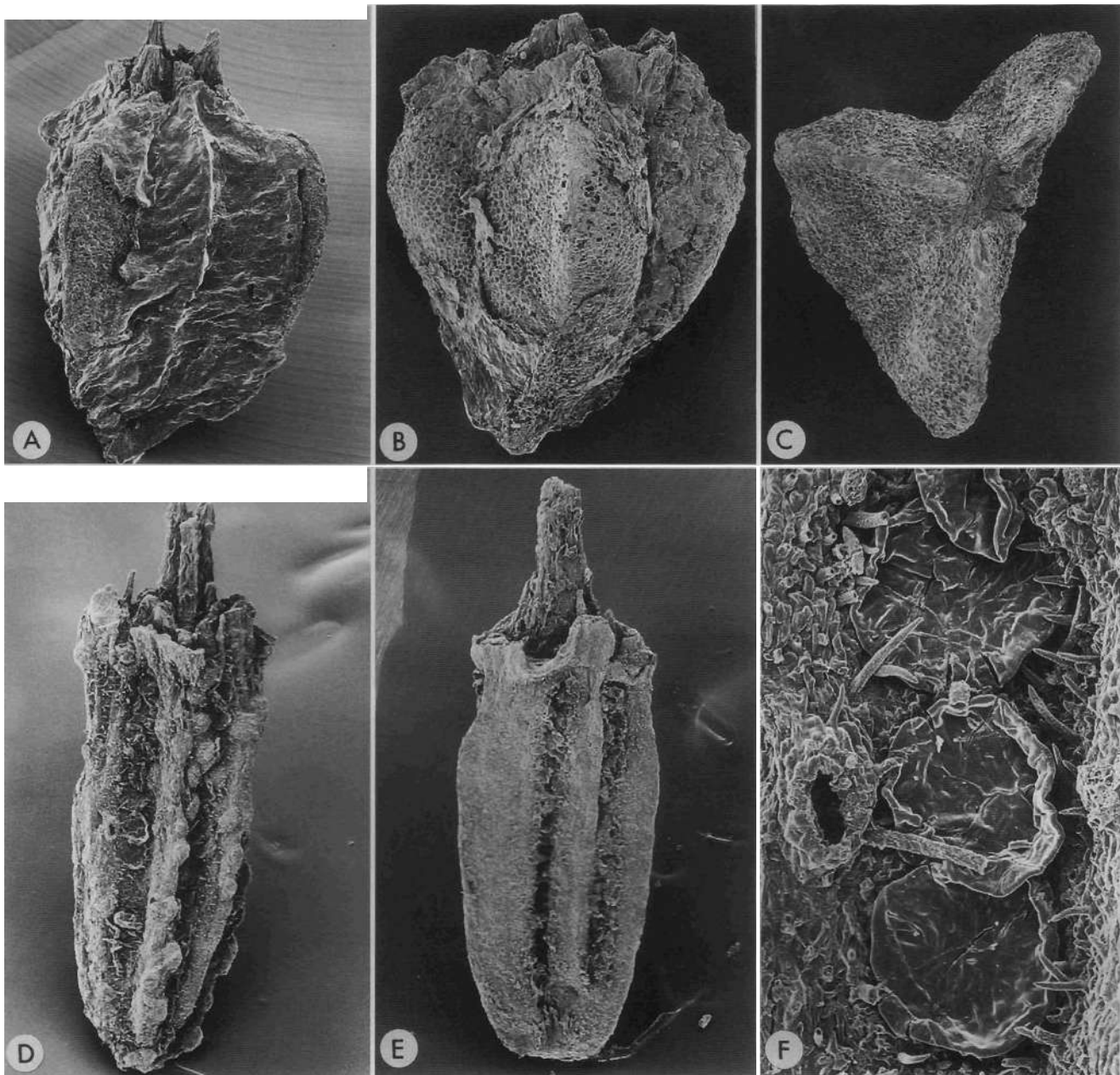
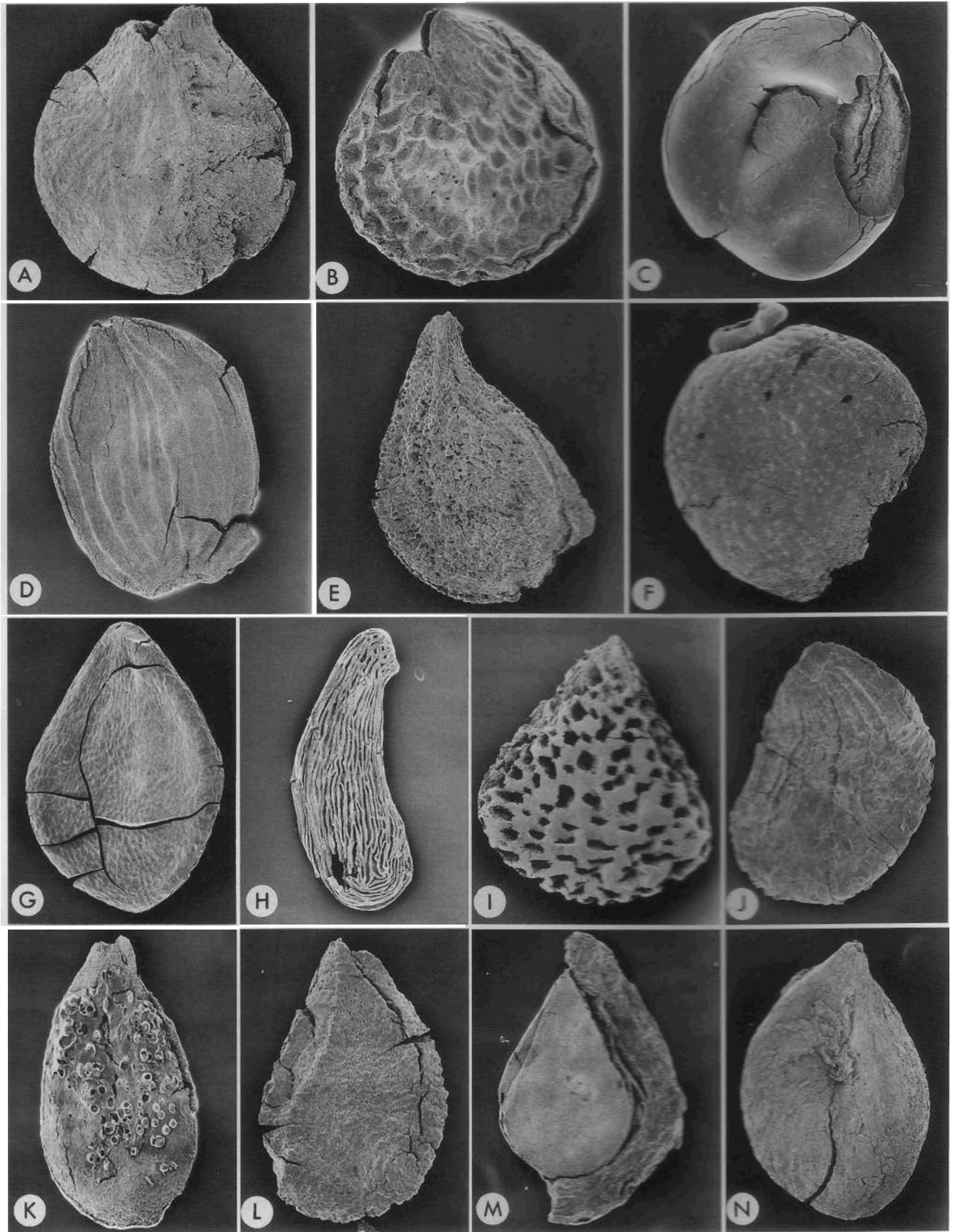


Fig. 8. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, lower Coniacian, Upper Cretaceous), Fukushima Prefecture, Honshu. Angiosperm epigynous flowers, types 4 and 5. A. Epigynous flower type 4, probable Fagaceae, lateral view showing inferior, three-lobed ovary with three styles at apex, note smooth surface in unabraded parts of the ovary, PP45473, $\times 30$. B. Epigynous flower type 4, probable Fagaceae, lateral view showing inferior, three-lobed ovary with three styles and remains of perianth parts at the apex, note abraded surface of ovary, PP45474, $\times 37$. C. Epigynous flower type 4, probable Fagaceae, apical view of abraded ovary showing three-lobed ovary and remains of three vascular strands converging toward the apex, PP45475, $\times 45$. D. Epigynous flower type 5, *Esgueiria* sp., aff. Combretaceae, lateral view showing inferior ovary, remains of perianth, filaments and three styles, PP45389, $\times 32$. E. Epigynous flower type 5, *Esgueiria* sp., aff. Combretaceae, lateral view showing inferior ovary, remains of perianth and base of styles, note remains of peltate glands in rows within grooves in the ovary wall, PP45393, $\times 28$. F. Epigynous flower type 5, *Esgueiria* sp., aff. Combretaceae, detail of ovary wall showing simple and peltate glandular trichomes, PP45389, $\times 200$.

fruits are present in the Kamikitaba assemblage. Only some of the more distinctive forms are illustrated (Fig. 9) and described briefly below.

Seed type 1 is represented in the collection by about 190 specimens (Fig. 9A, B). It consists of flattened woody struc-

tures that vary in size from ca. 1.0–2.5 mm in diameter. In some specimens the outer layer of the seed (? exotesta) is more or less smooth with an apparently leathery texture (Fig. 9A). More commonly, this outer layer is missing and exposes a inner sclerotic layer (endotesta) with a distinctive



reticulate surface (Fig. 9B). We interpret these structures as seeds, but it is possible that they are fruits. Their systematic affinity is unknown, but although smaller, they are similar in general form to specimens described as *Carpolithes kujienis* from the macroflora of the Kuji Group (Tanai 1979). Other specimens of seed type 1 from other mesofloras in the Futaba Group approach *C. kujienis* in size.

Seed type 2 is represented in the collection by about 40 specimens. Seeds are broadly elliptical to more or less circular in outline and ca. 1.5 mm in maximum diameter (Fig. 9C). The seeds are flattened in cross-section. The exotesta is black, shiny, hard and brittle. It is almost always fractured in the Kamikitaba material. On the seed margin there is a distinct elliptical hilar scar with a longitudinal slit running along the center (Fig. 9C). The structure of these seeds is very similar to those of the subfamily Hamamelidoideae (Hamamelidaceae).

Seed type 3 is represented in the collection by about 4 specimens. The seed is broadly elliptical in shape, ca. 1.7 mm in maximum dimension, and flattened with about 10 weakly delimited longitudinal ribs on each surface (Fig. 9D). The seed surface is covered by numerous fine closely-spaced, perforations formed by small thick-walled cells each of which contains the outline of a single crystal (Fig. 9D). The systematic affinity of seed type 3 is unknown but some Chloranthaceae have seeds of this type (Friis pers. comm.).

Seed type 4 is represented in the collection by about five specimens. The seed (possibly a fruit) is asymmetrically ovate, ca. 1.7 mm long. At one end it is distinctly tapered, while at the other it is rounded (Fig. 9E). The seed is flattened in transverse section with a distinctive surface of bulging, more or less equiaxial, cells (Fig. 9E). The systematic affinity of seed type 4 is unknown.

Seed type 5 is represented in the collection by three specimens. The seed is spherical to ellipsoidal in shape, ca. 1.2 mm in diameter (Fig. 9F). At one end there is a distinctive cap that is connected to the seed body by a narrow zone of attachment. The seed surface is composed of thick-walled palisade cells with interdigitating sinuous outlines. The structure of seed type 5 is very similar to the seeds described *in situ* within follicles of *Protomonimia*

kasai-nakajhongii from the Turonian of Hokkaido (Nishida and Nishida 1988). Based on this comparison the affinities of seed type 5 are probably with some group at the magnoliid grade. A relationship to Monimiaceae is unlikely. The digitate palisade cells and germinal cap are reminiscent of seeds of Nymphaeales.

Seed type 6 is represented in the collection by about three specimens. The seed is ovoid in shape ca. 1.6 mm long and ca. 1.1 mm broad (Fig. 9G). The seed coat is composed of equiaxial to elliptical cells with periclinal walls that are slightly impressed to form a smoothly reticulate surface (Fig. 9G). The systematic affinity of seed type 6 is unknown.

Seed type 7 is represented in the collection by two dispersed specimens. The seed is narrowly ovate, ca. 1.8 mm long, ca. 0.7 mm broad with the apex (presumed hilum) turned to one side (Fig. 9H). The seeds are flattened and have a distinctive surface of narrowly elongated cells with raised anticlinal cells walls that give the seed coat a prominently ribbed appearance (Fig. 9H). These dispersed seeds resemble those that occur *in situ* within the fruits of hypogynous flower type 7 (Fig. 5F). The systematic affinity of seed type 7 is possibly with Ericales.

Seed type 8 is represented in the collection by four specimens. The seeds are ovoid in shape ca. 3.1 mm long and ca. 2.3 mm broad (Fig. 9I). The seed surface is smooth, but perforated by numerous large, and distinctive, pits of variable size. The systematic affinity of seed type 8 is unknown.

Seed type 9 is represented in the collection by more than 700 specimens. Seeds are elliptical in outline, ca. 1.3 mm long and ca. 0.9 mm broad (Fig. 9J). The seed surface has cells arranged in rows, with the rows radiating from a point (the presumed hilum) generally positioned near one end of the seed (Fig. 9J). Frequently the seeds are found adhering together in groups (generally pairs, rarely threes) and are often associated with cuticular layers that may represent the remains of outer seed tissues. The systematic affinity of seed type 9 is unknown.

Seed type 10 is represented in the collection by about 20 specimens (Fig. 9K). Seeds are narrowly ovate in shape, ca. 2.0 mm long and ca. 1.2 mm wide. At one end they show a clear attachment scar. The seed surface is smooth but

Fig. 9. Mesofossils from the Kamikitaba locality (Asamigawa Member, Ashizawa Formation, lower Coniacian, Upper Cretaceous), Fukushima Prefecture, Honshu. Angiosperm seeds. A. Seed type 1, lateral view of specimen with leathery outer layer of the seed coat intact, PP45476, $\times 20$. B. Seed type 1, lateral view of specimen with outer layer of seed coat missing, showing reticulate surface of the inner sclerotic layer, PP45477, $\times 46$. C. Seed type 2, lateral view showing fractured exotesta, note elliptical hilar scar on the margin with a median longitudinal slit, PP45478, $\times 30$. D. Seed type 3, lateral view showing weakly delimited longitudinal ribs and seed surface perforated by numerous fine, closely-spaced, pores, PP45479, $\times 30$. E. Seed type 4, lateral view showing characteristic shape and surface ornamentation of bulging equiaxial cells, PP45480, $\times 30$. F. Seed type 5 (cf. seeds of *Protomonimia kasai-nakajhongii*, possible Nymphaeales), lateral view showing cap and partly abraded seed surface, PP45481, $\times 40$. G. Seed type 6, lateral view showing ovate outline and smooth, faintly reticulate surface, PP45482, $\times 36$. H. Seed type 7, possible Ericales lateral view showing the distinctive, ribbed seed coat composed of narrow, elongated cells with raised anticlinal cells; compare with seeds *in situ* within hypogynous flower type 7 (Fig. 5F), PP45483, $\times 28$. I. Seed type 8, lateral view showing smooth seed surface perforated by distinctive pits of variable size, PP45484, $\times 15$. J. Seed type 9, lateral view showing rows of raised cells converging at one end, PP45485, $\times 45$. K. Seed type 10, lateral view of specimen with outer surface (extotesta) partially preserved and showing distinctive blisters, PP45486, $\times 24$. L. Seed type 11, lateral view of specimen with exotesta missing showing characteristic "finger print" cell pattern of the inner mesotesta, PP45487, $\times 28$. M. Seed type 12, lateral view of specimen with exotesta and mesotesta missing, showing incompletely preserved wing and distinctive crystal cells of the endotesta over the seed body, PP45488, $\times 30$. N. Miscellaneous seed, lateral view showing ovoid shape and partially abraded testa, PP45489, $\times 20$.

often blistered into prominent, shiny hemispherical projections (probable resin bodies). Some conifer seeds show similar resin bodies, but the systematic affinity of seed type 10 is uncertain.

Seed type 11 is represented in the collection by about 10 specimens (Fig. 9H). The seeds are variable in shape, but are generally ovate ca. 1.8 mm long and ca. 1.2 mm wide, often with one margin straight and the other convex. The outer layer of the seed coat is missing and exposes a mesotesta composed of thin-walled cells that often leave a weakly developed "finger print" pattern on the endotesta. The systematic affinity of seed type 11 is uncertain, but seeds with similar anatomical features have often been compared to extant Magnoliaceae (Frumin and Friis 1996).

Seed type 12 is represented in the collection by about 7 specimens (Fig. 9M). Seeds are ca. 1.7 mm long and 1.0 mm wide. The outer layers of the seed coat are missing, revealing an ovate seed body, surrounded along one side by the remains of a distinct wing. The cells of the seed body are very distinctive, cuboidal and show the outline of a single, more or less square, crystal inside. The exposed cells of the wing are smooth. The systematic affinity of seed type 12 is uncertain. It may represent an abraded form of seed type 11.

In addition to the 12 types described above about five to ten other types of seeds occur in the Kamikitaba mesofossil assemblage but remain to be characterized (e.g., Fig. 9N).

Discussion

The fossil flora of the Futaba Group

The Kamikitaba plant assemblage is the first macrofossil or mesofossil flora to be described from the Futaba Group. Previous paleobotanical studies have focused solely on the dispersed palynoflora, mainly from the Kasamatsu and Tamayama Formations (Miki 1972a, 1977, Takahashi 1988). Three samples from the Ashizawa Formation (Obisagawa Member) were studied by Miki (1977) and are broadly representative of the palynoflora of the Futaba Group as a whole (Miki 1972a, 1977).

All three palynological samples from the Ashizawa Formation were dominated (ca. 60–90% of the 200 spores/pollen counted) by about 13 species of gymnosperm pollen. Saccate podocarpaceous-pinaceous grains and inaperturate probable taxodiaceous grains were especially prominent, with pollen of putative Araucariaceae also present in some samples. *Classopollis* (pollen of extinct cheirolepidiaceus conifers) was consistently present (ca. 5–7%), while monosaccate pollen of presumed non-conifer gymnosperms (e.g., cycads, Bennettitales, *Ginkgo*, Gnetales and extinct groups) were also significant in some samples (ca. 3–16%).

Angiosperms were the next most abundant group in the Ashizawa palynoflora, with about 8–20 species accounting for ca. 7–25% of the spores/pollen counted. Monosaccate grains were significant in some samples, but especially prominent were a variety of small tricolpate and tricolporate grains. Porate angiosperm pollen types were relatively rare. In all three palynofloras from the Ashizawa Formation scores

of pteridophytes were both less diverse (about 6–13 species) and less abundant (ca. 3–13.5%) than either angiosperm or gymnosperm pollen.

Qualitative comparison of the diversity and abundance of different elements in the Kamikitaba mesoflora, with their representation in the Ashizawa palynoflora gives a similar impression of the relative importance of angiosperms, gymnosperms and pteridophytes. Conifers are well-represented in the mesoflora, and fragments of probable taxodiaceous leafy shoots (conifer leaf type 1) are especially abundant. The most abundant palynomorph in the Futaba Group samples studied by Miki (*hapetropollenites laevigatus*) is also of probable taxodiaceous affinity (Miki 1977). Further studies of pollen associated with conifer pollen cone type 1 (Fig. 2f) are needed to establish whether they are identical to those included by Miki (1972a, 1977) in *I. laevigatus*.

Angiosperms are well represented in the Kamikitaba mesofossil assemblage and, as in two of the three palynological samples from the Ashizawa Formation (Miki 1977), they appear to be represented by more species than the gymnosperms. Three species of epigynous flowers (epigynous flower types 2–4) are especially abundant in the mesoflora, as are several of the angiosperm seed type (seed types 1–2, 9–10). There are also indications that some angiosperm taxa present in the mesoflora may not have been recognized in the Ashizawa palynoflora. The very small pollen grains associated with epigynous flower type 4 (ca. 7–8 μm polar length) suggests that they might be lost during standard palynological processing. As in other Cretaceous mesofloras it is also clear that the presumed cellulosic pollen wall of epigynous flower type 2 (Lauraceae) would not have survived fossilization or oxidative preparation.

In the numerous palynological samples from the Ashizawa Formation and in the Kamikitaba mesofossil assemblage, pteridophytes are often more poorly represented in terms of both species diversity and abundance than gymnosperms or angiosperms. However, when different palynological samples are aggregated into a single palynoflora for the Futaba Group as a whole, pteridophyte spores comprise the most diverse floral element (Miki 1977). Schizaeaceae spores are one of the most distinctive components of the Futaba Group palynoflora, and schizaeaceae mesofossils (fertile fern fronds) are the most abundant of the generally sparse fern remains in the Kamikitaba mesofossil assemblage.

We conclude from the combined evidence of the mesoflora and palynoflora that the early Coniacian vegetation in the environments represented by the Futaba Group was dominated, in terms of abundance, by both conifers and angiosperms, with angiosperms probably more diverse in terms of species. The predominant conifers were probably Taxodiaceae, while angiosperms were represented by a range of modern groups that probably included Nymphaeales, Magnoliales, Lauraceae, Hamamelidaceae, Comales, Papaveraceae, Compositaceae and Ericales, as well as many others not yet identified. Non-conifer gymnosperms may also have been significant in some areas. Ferns were probably only locally abundant, but were nevertheless re-

presented by diverse species in the regional vegetation. Schizaeaceae were especially prominent. The charcoalified preservation of many of the plant fossils also indicates that the vegetation was periodically subjected to fire.

Comparison with other Late Cretaceous floras in Northeast Japan

In addition to the plant fossils from the Futaba Group, several other Upper Cretaceous fossil floras are known from Northeast Japan. Leaf macrofossils and pollen have been described from the Kuji Group (Santonian–Campanian, Ando 1997) of northern Honshu (Sasa 1932a, b, c, Ogura 1933, Tokunaga and Takase 1968, Sohma 1969, Miki 1972b, 1977, Tanai 1979), and from the Hakobuchi Group (Campanian–Maastrichtian; Endo 1925, Oishi 1940, Takahashi 1964, Miki 1977, Ando 1997) and Yezo Group (mainly Turonian–Santonian; Stopes and Fujii 1910, Nishida 1991) of Hokkaido.

The Kuji Group of northeastern Honshu is of early Santonian to early Campanian age (Ando 1997), and has yielded a similar palynoflora to that from the Futaba Group, except for the presence of *Aquilapollenites* pollen in the Kuji assemblages (Miki 1972b, 1977). Fossil leaf compressions have been recovered from the both the Tamagawa and Sawayama Formations, the lowermost and uppermost of the three formations that comprise the Kuji Group (Tanai 1979). The flora of the Tamagawa Formation consists of 17 species of pteridophyte, six species of conifer and ten species of angiosperm, while the flora of the Sawayama Formation comprises 12 species of pteridophyte, two species of cycadophyte, eight species of conifer and 20 species of angiosperm (Tanai 1979). Among the taxa recorded in the macroflora that may also be represented in the Kamikitaba assemblage, are Schizaeaceae (fertile fern type 1), Taxodiaceae (conifer leaf type 1), Lauraceae (hypogynous flower type 2), Fagaceae (epigynous flower type 4), and possibly Magnoliaceae (seed type 10). Seed type 1 from the Kamikitaba assemblage may also be similar to *Carpolithes kujiensis* known as compressions from the Sawayama flora (Tanai 1979). Interestingly, fossil Platanaceae, which are well known in mesofloras from Europe and eastern North America, and represented by several species in the Kuji leaf flora, have not yet been detected in the Kamikitaba assemblage.

The Hakobuchi Group of Hokkaido (Campanian–Maastrichtian, Ando 1997) has yielded a diverse macroflora composed of ferns, abundant *Nilssonia* (extinct cycad foliage) and diverse angiosperm leaves (Endo 1925, Oishi 1940). Palynofloras from the Hakobuchi Group contain more diverse and abundant angiosperm pollen than the older palynofloras from the Futaba and Kuji Groups (Miki 1977), and fewer schizaeaceous spores. Triporate pollen and *Aquilapollenites* are also more prominent among the angiosperm grains. Taken as a whole, palynofloras from the Hakobuchi Group are more modern in aspect than those from the Futaba and Kuji Groups (Miki 1977).

Plant fossils from the middle and upper parts of the Yezo Group of Hokkaido occur in calcareous nodules from offshore marine deposits of Albian to early Campanian (mainly Turonian–Santonian) age. They preserve exceptional ana-

tomical details and have been studied intensively for almost one hundred years (Stopes and Fujii 1910, Ogura 1930, 1932, Nishida 1991). Ferns currently recognized in this flora include a variety of extinct taxa, as well as representatives of the extant families Cyatheaceae, Dennstaedtiaceae, Gleicheniaceae, Loxomataceae, Matoniaceae and Schizaeaceae (e.g., Stopes and Fujii 1910, Kershaw 1910, Ogura 1927, 1930, 1933, Nishida 1981a, 1981b, 1984, 1989, 1991, Nishida and Nishida 1979, 1982, Yoshida *et al.* 1996a, b). Conifers include Araucariaceae (e.g., Nishida 1981, Stockey *et al.* 1986, 1990, 1993, 1994, Ohsawa *et al.* 1991) Pinaceae (e.g., Stopes and Kershaw 1910, Ogura 1932, Stockey and Nishida 1986, Stockey and Ueda 1986, Ueda and Nishida 1982) and a variety of Taxodiaceae, as well as other conifers that are extinct or unassignable to modern groups (e.g., Suzuki 1910, Ogura 1944, Ohana and Kimura 1993, 1995, Nishida and Nishida 1984, 1985, 1986, Ohsawa *et al.* 1991, 1992a, 1992b, 1993, Nishida 1991, 1994, Nishida *et al.* 1991, 1992, Nishida, M. Nishida, H. and Ohsawa, T. 1991, Saiki 1992, Saiki and Kimura 1993).

Other seed plants in the permineralized flora from the Yezo Group include *Ginkgo* (Nishida 1991), cycads (Ogura 1930, Nishida 1991), Bennettitales (Ogura 1930, Tanai 1960, Nishida 1991, Ohana and Kimura 1991, Ohana *et al.* 1998), several enigmatic gymnosperms (Nishida 1974, 1991), and a variety of angiosperms based on stems, wood, and fructifications (Nishida 1985, 1991, 1994, Nishida and Nishida 1988, Nishida *et al.* 1996, Ohana and Kimura 1987).

Different styles of preservation make the fossil assemblage from the Yezo Group difficult to compare with the Upper Cretaceous floras from the Kuji and Hakobuchi Groups (Tanai 1979). However, as further studies are completed comparisons with the Kamikitaba flora, and other mesofloras from the Futaba Group, are likely to be more straightforward because of the preservation of anatomical details. For example, fertile fern type 1 is similar to *Schizaeopteris mesozoica* (Stopes and Fujii 1910, Yoshida, Nishida and Nishida 1996b), while seed type 5 shares significant similarities with seeds described inside the follicles of *Protomonimia kasai-nakajhongii* (Nishida and Nishida 1988). Fossil floras from the Yezo Group and Futaba Group might also be expected to share fossil plant taxa in view of their geographical proximity, comparable age and similar palynofloras (Miki 1977). Given the frequent occurrence of angiosperm reproductive structures in both floras (Nishida 1991), comparisons focusing on this component of the fossil assemblages will be of particular interest.

Comparison with mesofossil floras from Europe and North America

The Kamikitaba assemblage is the first mesofossil flora to be described from the Cretaceous of eastern Asia, and together with the recently described Sarbay flora from Kazakhstan (Frumina *et al.* 1995, Frumina and Friis 1996, 1999) provides new insights into the flora and vegetation of Asia during the Late Cretaceous. The Kamikitaba assemblage is also very comparable to the Upper Cretaceous mesofossil assemblages from Europe and eastern North America, in the

style of fossil preservation and in its overall composition. In particular, as in other mesofossil floras of this age, the size of the angiosperm flowers and fruits is small and epigynous flowers are especially common, suggesting that these phenomena are basic features of angiosperm floral evolution during the Cretaceous.

Systematically, the occurrence of such diverse groups as magnoliids (Lauraceae, possible Magnoliaceae, Nymphaeales), saxifragoids (Hamamelidaceae), core rosids (Fagaceae), Myrtales (Combretaceae), and asterids (Cornales, Ericales) in the Kamikitaba assemblage is consistent with evidence from Europe and eastern North America that angiosperms were diverse, and had already undergone considerable systematic differentiation at an early Late Cretaceous age (Magallón *et al.* 1999). The occurrence of *Esgueiria* in Europe and Japan (Takahashi *et al.* in press), and *Liriodendroidea* in Kazakhstan, North America and Europe (Frumin and Friis 1996), also establishes that at least some angiosperms were geographically widespread at this time, in spite of evidence for floristic differentiation based on palynofloras (Hemgreen *et al.* 1996). Additional studies of mesofossil assemblages from Asia will be critical to further resolving the history of angiosperm diversification, and clarifying its relation to pre-Tertiary biogeographic patterns.

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