J Plant Res (2017) 130:809–826
DOI 10.1007/s10265-017-0945-1

REGULAR PAPER

Two early eudicot fossil flowers from the Kamikitaba assemblage (Coniacian, Late Cretaceous) in northeastern Japan

Masamichi Takahashi[1] · **Patrick S. Herendeen**[2] · **Xianghui Xiao**[3]

Received: 7 December 2016 / Accepted: 3 April 2017 / Published online: 11 May 2017

Abstract Two new fossil taxa referable to the basal eudicot grade are described from the Kamikitaba locality (ca. 89 MYBP, early Coniacian: Late Cretaceous) of the Futaba Group in Japan. These charcoalified mesofossils exhibit well-preserved three-dimensional structure and were analyzed using synchrotron-radiation X-ray microtomography to document their composition and internal structure. *Cathiaria japonica* sp. nov. is represented by infructescence segments that consist of an axis bearing three to four fruits. The capsular fruits are sessile and dehiscent and consist of a gynoecium subtended by a bract. No perianth parts are present. The gynoecium is monocarpellate containing two pendulous seeds. The carpel is ascidiate in the lower half and conduplicate in the upper part, and the style is deflected abaxially with a large, obliquely decurrent stigma. Pollen grains are tricolpate with a reticulate exine. The morphological features of *Cathiaria* are consistent with an assignment to the Buxaceae *s. l.* (including Didymelaceae). *Archaestella verticillatus* gen. et sp. nov. is represented by flowers that are small, actinomorphic, pedicellate, bisexual, semi-inferior, and multicarpellate. The floral receptacle is cup shaped with a perigynous perianth consisting of several tepals inserted around the rim. The gynoecium consists of a whorl of ten conduplicate, laterally connate but distally distinct carpels with a conspicuous dorsal bulge, including a central cavity. The styles are short, becoming recurved with a ventrally decurrent stigma. Seeds are ca. 10 per carpel, marginal, pendulous from the broad, oblique summit of the locule. Pollen grains are tricolpate with a reticulate exine pattern, suggesting a relationship to eudicots. The morphological features of *Archaestella* indicate a possible relationship to Trochodendraceae in the basal grade of eudicots. The fossil currently provides the earliest record of the family and documents the presence of Trochodendraceae in eastern Eurasia during the middle part of the Late Cretaceous.

Keywords Angiosperms · *Archaestella verticillatus* · *Cathiaria japonica* · Futaba group · Japan · Kamikitaba assemblage · Coniacian · Cretaceous · Buxaceae *s. l.* · Mesofossil · Synchrotoron-radiation X-ray microtomography (SRXTM) · Trochodendraceae

Introduction

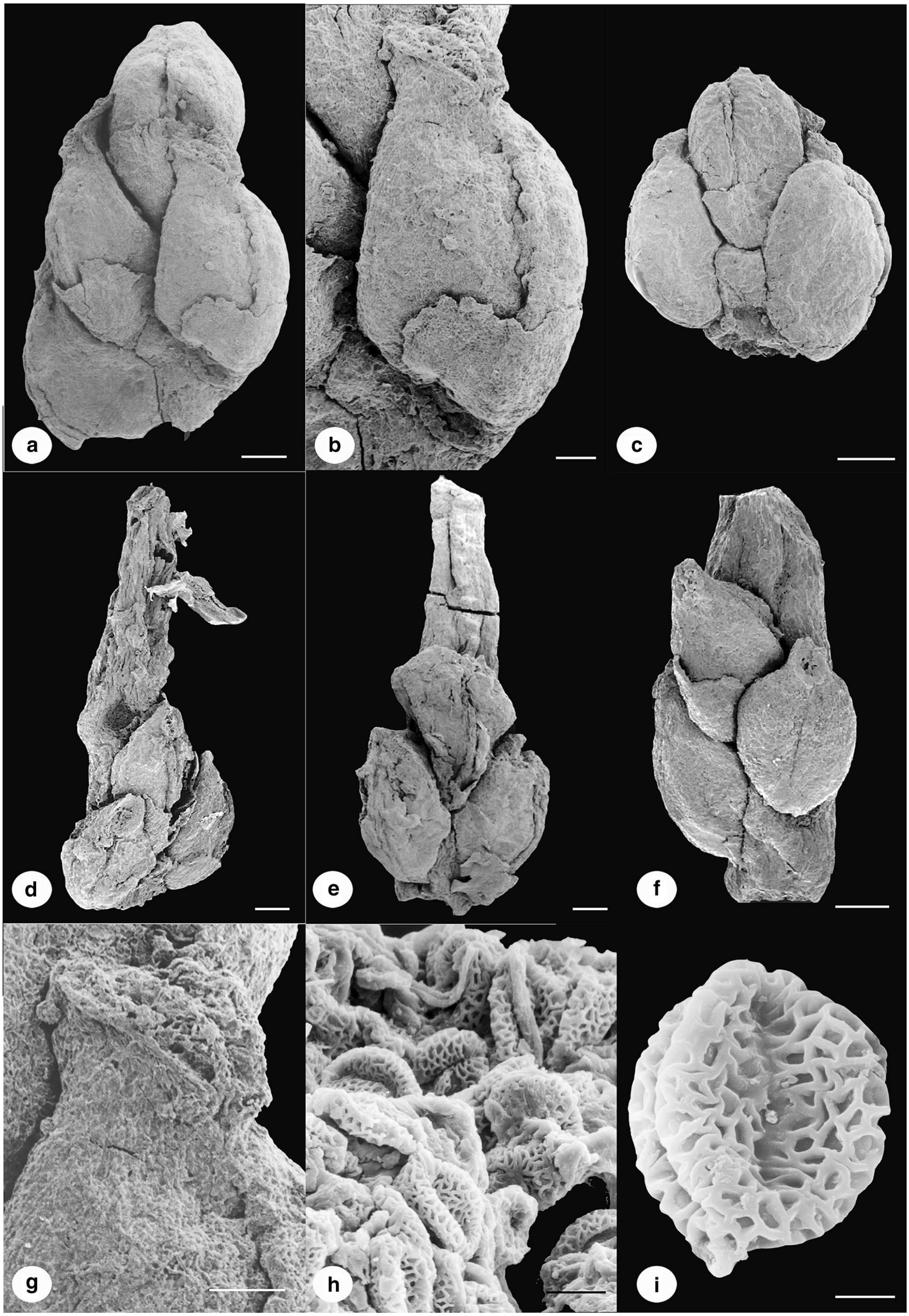
Paleobotanical studies of Cretaceous mesofossils over the last 25 years have demonstrated that the major lineages of early angiosperms were already differentiated by the early Late Cretaceous (Crane et al. 1994, 2004; Friis et al. 1994, 2006, 2011). In recent years the study of mesofossils with scanning electron microscopy (SEM) has been augmented by the application of synchrotron-radiation X-ray microtomography (SRXTM) to provide a more complete understanding of the complex internal structure of the Cretaceous fossils without the need to dissect or section the fossil specimens (e.g., Friis et al. 2007, 2009; Herendeen et al. 2016; Schönenberger et al. 2012; Takahashi et al. 2008a, b, 2014; von Balthazar et al. 2007).

✉ Masamichi Takahashi
masamichi@env.sc.niigata-u.ac.jp

[1] Department of Environmental Sciences, Faculty of Science, Niigata University, Ikarashi, Nishi-ku, Niigata 950-2181, Japan

[2] Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022, USA

[3] Advanced Photon Source, 9700 S Cass Avenue, Argonne, IL 60439, USA


a
b
c
d
e
f
g
h
i

◂**Fig. 1** SEM images of *Cathiaria japonica* infructescence pieces with attached fruits and associated pollen grains. **a** Infructescence segment with four attached fruits. PP56480. *Scale bar* 180 µm. **b** Closeup of one fruit from **a**. Note nearly sessile stigma, abaxial suture, and subtending bract. PP56480. *Scale bar* 100 µm. **c** Infructescence segment with three attached fruits. PP56481. *Scale bar* 300 µm. Infructescence segments with attached fruits. **d** PP56482, **e** PP56483. **f** PP56484. *Scale bars* 200 µm. **g** Enlargement of stigmatic surface of fruit shown in **b**. PP56480 *Scale bar* 100 µm. **h** Pollen grains on the stigmatic surface of the fruit shown in **a, b**. PP56480 *Scale bar* 5 µm. **i** Enlargement of single pollen grain found on stigmatic surface. PP56480 *Scale bar* 2 µm

The Kamikitaba flora (Coniacian; Late Cretaceous) is a unique assemblage from northeastern Japan. The mesofossil assemblage was isolated from a poorly sorted carbonaceous, black, sandy siltstone from the lower sediments of the Asamigawa Member of the Ashizawa Formation in the Futaba Group that extends from Iwaki city to Hirono-machi in Fukushima Prefecture. The mesofossils comprising the Kamikitaba assemblage are small, three-dimensional, and charcoalified or mummified/lignitized (mesofossils), including well-preserved angiosperm flowers, fruits, seeds, leaf fragments and wood, as well as shoots, leaves, pollen cones, cone scales and seeds of conifers (Takahashi et al. 1999a). Some of the angiosperm mesofossils have been described as *Esgueiria* (Combretaceae; Takahashi et al. 1999b), *Hironoia* (Cornaceae; Takahashi et al. 2002), *Lauranthus*, *Microlaurus* (Lauraceae; Takahashi et al. 2001, 2014), *Symphaenale* (Nymphaeales; Takahashi et al. 2007), *Archaefagacea* (Fagales; Takahashi et al. 2008a), and *Futabanthus* (Annonaceae; Takahashi et al. 2008b).

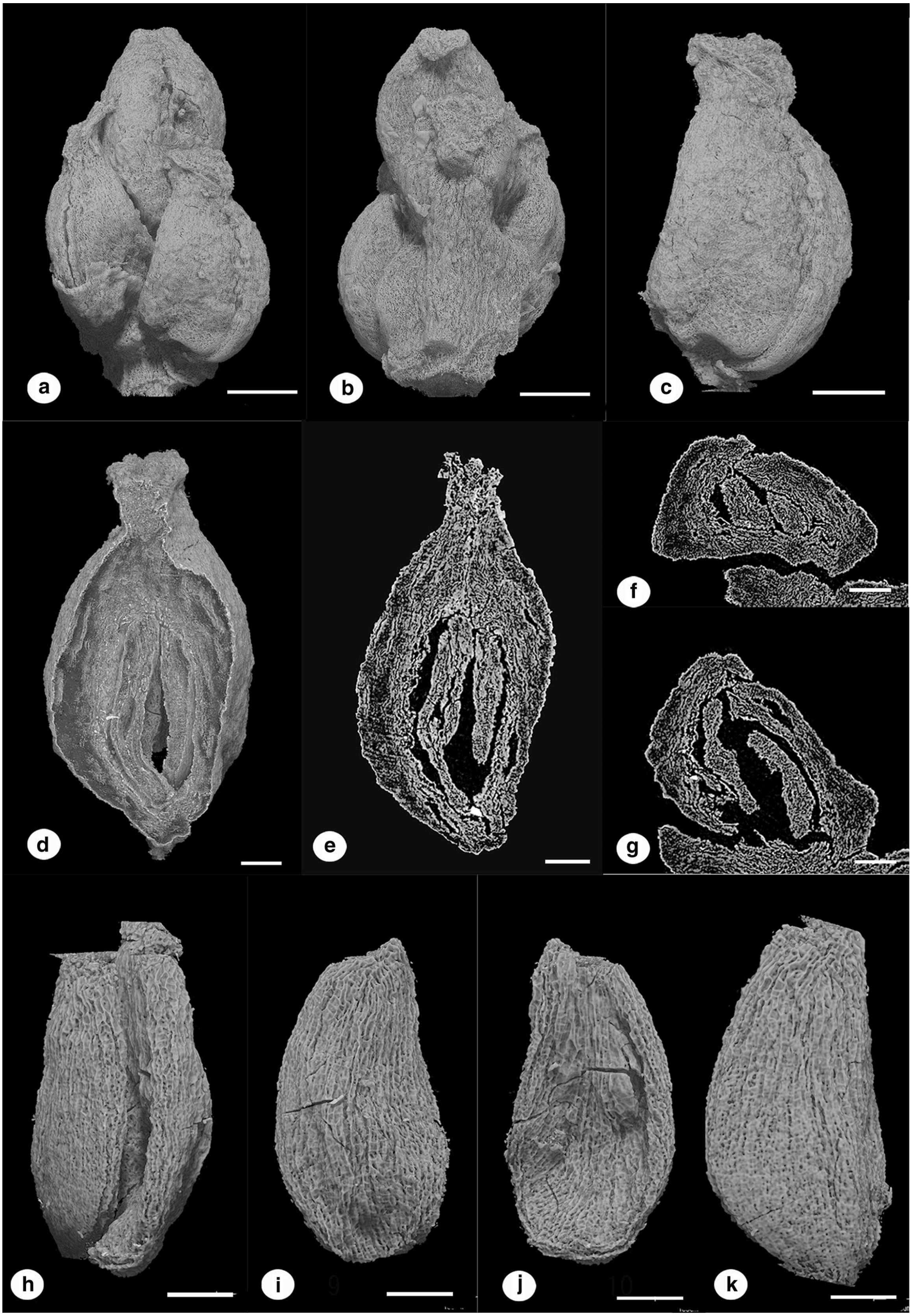
In this paper, we describe two new fossil taxa that are referable to the early-branching lineages of the large eudicot clade. The eudicot clade consists of the core eudicots plus several additional lineages that collectively form a paraphyletic basal grade. These early branching eudicot groups include the Ranunculales (Berberidaceae, Circaesteraceae, Eupteleaceae, Lardizabalaceae, Menispermaceae, Papaveraceae, Ranunculaceae), Sabiaceae, Proteales (Nelumbonaceae, Platanaceae, Proteaceae), Trochodendrales (Trochodendraceae) and Buxales (Buxaceae *s. l.*) (APG IV 2016). One of the new fossil taxa, *Cathiaria japonica* is described as a new species. We provide new morphological details for *Cathiaria* Golovneva et Oskolski based on well-preserved charcoalified fossil fruits. Based on the new information, we suggest a close relationship to the Buxaceae *s. l.* (including Didymelaceae). The second new fossil taxon, *Archaestella verticillatus*, is described as a new genus and species that is referable to the Trochodendraceae. The fossil flower and fruits of *Archaestella* extend the fossil record of Trochodendraceae into significantly earlier Cretaceous rocks than those from which it has been recorded previously. This new discovery helps to bring the fossil history of the Trochodendraceae into line with the long fossil history of other basal eudicot lineages. The description of these mesofossils from the Late Cretaceous of eastern Eurasia documents additional diversity in floral morphology among the Cretaceous angiosperms and represent important additions to our understanding of the history of the early lineages within the eudicots.

Materials and methods

Plant mesofossils were isolated from bulk matrix samples of the Kamikitaba locality. The fossil bearing sediments are a poorly sorted, carbonaceous, sandy siltstone. Samples were collected during 1998–2008 from the Asamigawa Member of Ashizawa Formation (Futaba Group), exposed along a tributary of the Kitaba River in Kamikitaba, Hirono-machi, Fukushima Prefecture, northeastern Japan. Sample F16 has yielded diverse mesofossils (Kamikitaba mesofossil flora) that include a range of pteridophytes, conifers, and angiosperms (Takahashi et al. 1999b). Several of these mesofossils have now been studied in detail, along with material recovered from other levels in the Futaba Group (Takahashi et al. 1999a, b, 2002, 2007, 2008a, b). The Asamigawa Member is the lowermost member of the Ashizawa Formation, which itself is the lowermost formation of the Futaba Group. The plant-bearing sediments are probably of lower Coniacian age (ca. 89Myr BP; Cohen et al. 2016) based on ammonites and inoceramids from the middle of the Ashizawa Formation (see Takahashi et al. 1999b for details).

Material collected in the field was dried, disaggregated in water, and sieved through a 125-µm mesh screen to separate the organic debris from the sediment. Residual mineral matter remaining attached to the carbonaceous material was removed by bulk cleaning in hydrofluoric and hydrochloric acids. Samples were then thoroughly rinsed in water and air dried. The mesofossil specimens were examined with a Hitachi S-800 field emission SEM.

The specimens were also imaged with microtomography using the X-ray microscope at the 2-BM-B beamline of Advanced Photon Source (APS) at the US Department of Energy's Argonne National Laboratory. The measurements were done with X-rays of 15 keV. The exposure time was 600 ms, and 1,800 projections were acquired equi-angularly over 180°. The specimens' 3-dimensional structures were reconstructed from the projection images with gridrec algorithm (Dowd et al. 1999). Isotropic voxel is 0.74 µm along each dimension. The specimens illustrated in this article are deposited in the paleobotanical collections of the Field Museum, Chicago.


a
b
c
d
e
f
g
h
i
9
j
10
k

◂**Fig. 2** SRXTM renderings of *Cathiaria japonica* infructescence pieces and fruits. PP56480. **a** Infructescence segment shown in Fig. 1a. *Scale bar* 300 µm. **b** Reverse side of infructescence segment shown in **a**. *Scale bar* 300 µm. **c** Single fruit isolated from specimen shown in Fig. 1b. *Scale bar* 200 µm. **d** Three dimensional rendering of longitudinal section of single fruit showing two ovules attached at apex of single locule. *Scale bar* 100 µm. **e** Two dimensional rendering of longitudinal section of fruit shown in **d** showing two ovules attached at apex of single locule. *Scale bar* 100 µm. **f** Two dimensional rendering of transverse section of fruit shown in **d** showing two ovules in single locule. *Scale bar* 100 µm. **g** Two dimensional rendering of transverse section of fruit shown in **d** showing two ovules in single locule. *Scale bar* 100 µm. **h–k** Three dimensional rendering of a single seed isolated from fruit shown in **d–g**. *Scale bar* 100 µm

Systematic description

Angiosperms
Eudicots
Order: Buxales
Family: Buxaceae *s. l.* (including Didymelaceae)
Genus: *Cathiaria Golovneva* et Oskolski, here emended
Type: *Cathiaria zhilinii* Golovneva et Oskolski

Emended generic diagnosis: Infructescence compound, consisting of two orders of axes, bearing sessile fruits on the adaxial side. Pistillate flowers alternately or spirally arranged on the spike-like inflorescence. Flower consisting of a single unilocular pistil with distinct stigma and a scale-like bract at the base. No evidence of scars for perianth or stamens. Fruit wall composed of sclerenchyma. Seed coat consisting of lignified hard cells; surface verrucate. Pollen grains tricolpate with reticulate exine.

Cathiaria japonica Takahashi, Herendeen, et Xiao sp. nov. (Figs. 1, 2).

Holotype: Field Museum PP56480. Figures 1a–b, g–i, 2a–k

Paratypes: Field Museum PP56481 (Fig. 1c), PP56482 (Fig. 1d), PP56483 (Fig. 1e), PP56484 (Fig. 1f),

Locality and horizon: The specimens are from the Asamigawa Member of the Ashizawa Formation, Futaba Group. Samples were collected at the Kamikitaba locality, Hirono-machi, Fukushima Prefecture, northeastern Japan (37°12′N, 140°57′E).

Age: early Coniacian (Late Cretaceous)

Derivation of specific epithet: The specific epithet, "*japonica*", refers to the source country for these fossils.

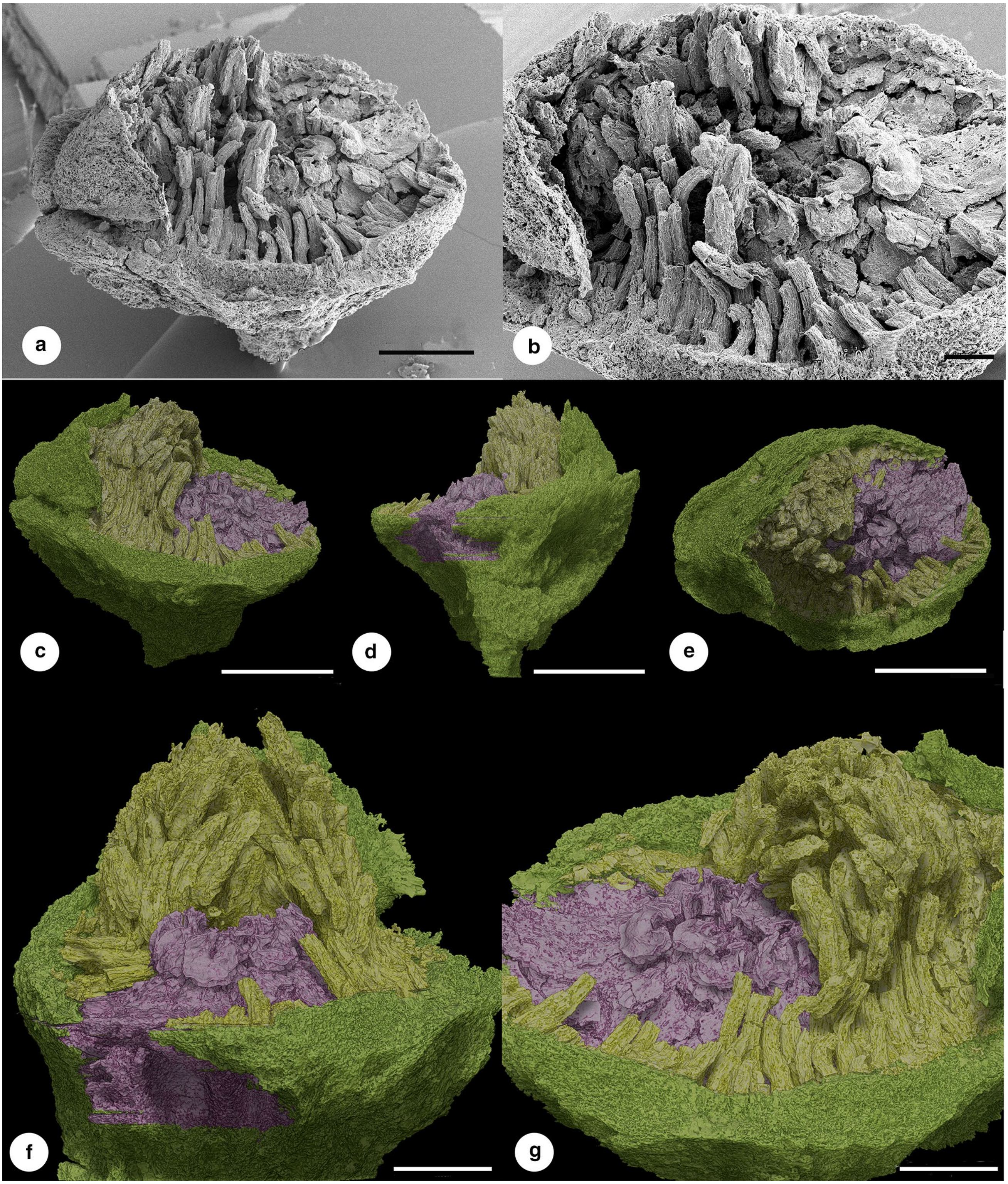
Specific diagnosis: Infructescence bearing sessile fruits on the adaxial side (Figs. 1a, c–f, 2a–b). Pistillate flower lacking perianth and is subtended by a scale-like bract (Figs. 1b, 2a–c). No evidence of scars for perianth or stamens (Figs. 1b–c, 2a–c). Gynoecium composed of one carpel with a short style and sessile stigma (Figs. 1b, g, 2c–g). Stigma obliquely decurrent, extending to form a flattened, papillate surface (Fig. 1g). Fruit ellipsoid with a longitudinal suture on the distal (abaxial) side; two seeds are borne in the single locule (Figs. 1b, 2d–g). Fruit wall composed of sclerenchyma. Seed coat consisting of lignified hard cells and having a verrucate surface (Fig. 2h–k). Pollen grains tricolpate with reticulate exine (Fig. 1h –i).

Dimensions: Length of fragmentary axis 2.5 mm, diameter of axis 0.30–0.43 mm, length of scale-like bract 0.25 mm, width 0.47 mm, length of fruit 0.65–1.0 mm, diameter of fruit, 0.44–0.57 mm, length of stigma, 0.30–0.35 mm, width of stigma 0.20–0.25 mm, length of seed 0.55 mm, width of seed 0.26 mm. Polar axis of pollen grains 10 µm, equatorial diameter of pollen grains, 8 µm, diameter of lumina 0.5 µm, width of muri, 0.3–0.4 µm.

Description and remarks: The fossil specimens are found as fruits borne on a fragmentary spike (Figs. 1a–f, 2a–b). Fruits are alternately or spirally arranged on the short segments of the infructescence axis and are subtended by a persistent floral bract (Figs. 1a–f, 2a–b). The length of the complete infructescence is not clear. The floral bract is long and distinctly acuminate with a narrow apex and irregularly serrate margins and it is almost completely fused basally to enclose the ovary (Figs. 1a–b, 2a–c). There is no evidence of an androecium, and no attached remains of perianth have been observed. The gynoecium is monocarpellate with apical placentation, bearing two pendulous seeds in the single locule (Fig. 2d–g). The carpel is ascidiate in the lower half, conduplicate above, distally deflected abaxially with a dorsiventral suture and a large, obliquely decurrent stigma (Figs. 1b, g, 2c). The fruit is ellipsoid with a longitudinal suture on the distal (abaxial) side. In transverse section the fruits are semicircular in outline, slightly flattened laterally, with a straight ventral (adaxial) margin; the dorsal (abaxial) margin is strongly convex (Figs. 1a–c, 2a–c). The fruit is dehiscent, having a suture at the dorsal margin. The fruit surface consists of elongated epidermal cells (Fig. 1b). The base of the fruit is usually rounded, and the apex is slightly pointed and extends adaxially to form a lip-like stigma (Figs. 1a, b, 2a–c). The papillate stigma is almost sessile (Fig. 1b, g). The seed surface is striate (Fig. 2h–k). Pollen grains are small, 10 µm in polar axis, 8 µm in equatorial axis, and tricolpate with a reticulate exine sculpture pattern (Fig. 1h, i). Colpus is elongated toward the poles of grain (Fig. 1i).

Order: Trochodendrales
Family: Trochodendraceae
Genus: *Archaestella* Takahashi, Herendeen, et Xiao gen. nov. (Figs. 3, 4, 5, 6, 7)
Type species: *Archaestella verticillatus* Takahashi, Herendeen, et Xiao sp. nov.

Generic diagnosis: Flower actinomorphic, bisexual, semi-inferior, and multi-carpellate. Floral receptacle concave, with a perigynous perianth consisting of several tepals, borne around the rim. Androecium consisting of ca. 120 stamens with clear differentiation into anther and filament.



Gynoecium consisting of a whorl of 10 conduplicate, laterally connate but distally distinct carpels with a conspicuous dorsal bulge, including a small central cavity. Styles recurved with papillate and ventrally decurrent stigma. Ovules ca. 10 per carpel, marginal, pendulous from the broad, concrescent oblique summit of the locule. Seeds with chalazal, apical and lateral wing-like extensions. Pollen grains, tricolpate, with reticulate exine pattern.

Derivation of generic name: *Archaestella* refers to the meanings of "ancient" and "star".

◂**Fig. 3** SEM and SRXTM images of flower of *Archaestella verticillatus* gen. et sp. nov. Ashizawa Foramtion, Lower Coniacian, Upper Cretaceous. Holotype, PP56485. **a** SEM image, oblique lateral view showing stout peduncle, expanded flattened receptacle extending into base of the tepals and partially-preserved cavity of the gynoecium. *Scale bar* 300 µm. **b** SEM image, oblique apical view showing remains of several carpels, numerous filaments of stamens and expanded receptacle. *Scale bar* 100 µm. **c** Three dimensional rendering of oblique lateral view of flower. Artificially colored to show hypanthium and pedicel (*green*), androecium (*yellow*), and gynoecium (*pink*). **d** Reverse side of flower shown in **c. e** Three dimensional rendering of apical view of flower shown I **c, d. c–e** *Scale bar* 500 µm. **f** Three dimensional rendering of oblique view of flower showing broad hypanthium cup (*green*), stamens (*yellow*) and carpels (*pink*). **g** Three dimensional rendering of oblique view of flower showing broad hypanthium cup (*green*), stamens (*yellow*) and carpels (*pink*). **f, g** *scale bar* 200 µm

Archaestella verticillatus Takahashi, Herendeen, et Xiao sp. nov. (Figs. 3, 4, 5, 6, 7).

Holotype: Field Museum PP56485. Figures 3, 4 and 5.

Paratypes: Field Museum PP56486 (Figs. 6, 7a–c), PP56487 (Fig. 7d–f).

Locality and horizon: The specimens are from the Asamigawa Member of the Ashizawa Formation, Futaba Group. Samples were collected at the Kamikitaba locality, Hirono-machi, Fukushima Prefecture, northeastern Japan (37°12′N, 140°57′E).

Age: early Coniacian (Late Cretaceous)

Derivation of specific epithet: The specific epithet, "*verticillatus*", is from the meaning of "whorl".

Specific diagnosis: Flower pedicellate, actinomorphic, bisexual, half-inferior, and multi-carpellate (Figs. 3a–g, 4a–f, 5a–h, 6a–b, f). Floral receptacle concave with a perigynous perianth consisting of several tepals, borne in two cycles, around the rim (Figs. 4c–f, 5a–h, 6f, 7a). Androecium consisting of ca. 120 stamens with clear differentiation into anther and filament (Figs. 3a–g, 4b–f, 5a, c, e, g, 7b). Gynoecium is syncarpous and consisting of a whorl of 10 conduplicate carpels that are laterally connate basally but distinct distally, with a conspicuous dorsal bulge, including a central cavity (Figs. 3c–g, 4a, c–f, 5a–h, 6a–e). Styles recurved with a papillate and ventrally decurrent stigma (Figs. 3f, g, 4a, c, d, 5a, c). Ovules ca. 10 per carpel, marginal, pendulous from the broad, concrescent oblique summit of the locule (Fig. 7d–f). Seeds with chalazal, apical and lateral wing-like extensions (Fig. 7d–f). Pollen grains, tricolpate, with reticulate exine pattern (Fig. 7c).

Dimensions: Pedicel of flower, 0.1 mm in diameter, developed to 1.0 mm in diameter in fruit. Flower, 1.2 mm in diameter and 1.2 mm high, developed to 4.2 mm in diameter and 4.0 mm high in fruit. Tepals ca. 0.8 mm wide, length unknown (incomplete). Stamens, 0.2–0.3 mm in length; anthers 0.1 mm in length; filaments, 0.1–0.2 mm. Pollen grains 9.3 µm in equatorial diameter, no data on polar axis. Gynoecium, 0.8 mm in diameter, 0.6 mm high, developed to 3.9 mm in diameter, 1.7 mm high in fruit. Stigma 0.1 mm wide, 0.1 mm high.

Description and remarks: The fossil material consists of three charcoalified specimens (Figs. 3, 4, 5, 6, 7). One of them is a flower in the stage of anthesis with perianth, androecium and gynoecium preserved in a good condition (Figs. 3, 4, 5). The other specimens are young fruits after anthesis (Figs. 6, 7).

Flower The flowers are pedicellate, actinomorphic, bisexual with a broad receptacle and a semi-inferior ovary (Figs. 3, 4, 5, 6, 7). Whorls of perianth parts and stamens are borne along the rim of the receptacle and surround a ring of carpels (Figs. 3a–g, 4c–f). The pedicel is slender at the stage of flower anthesis and becomes stout at fruiting stage (Figs. 1c, e, 6f).

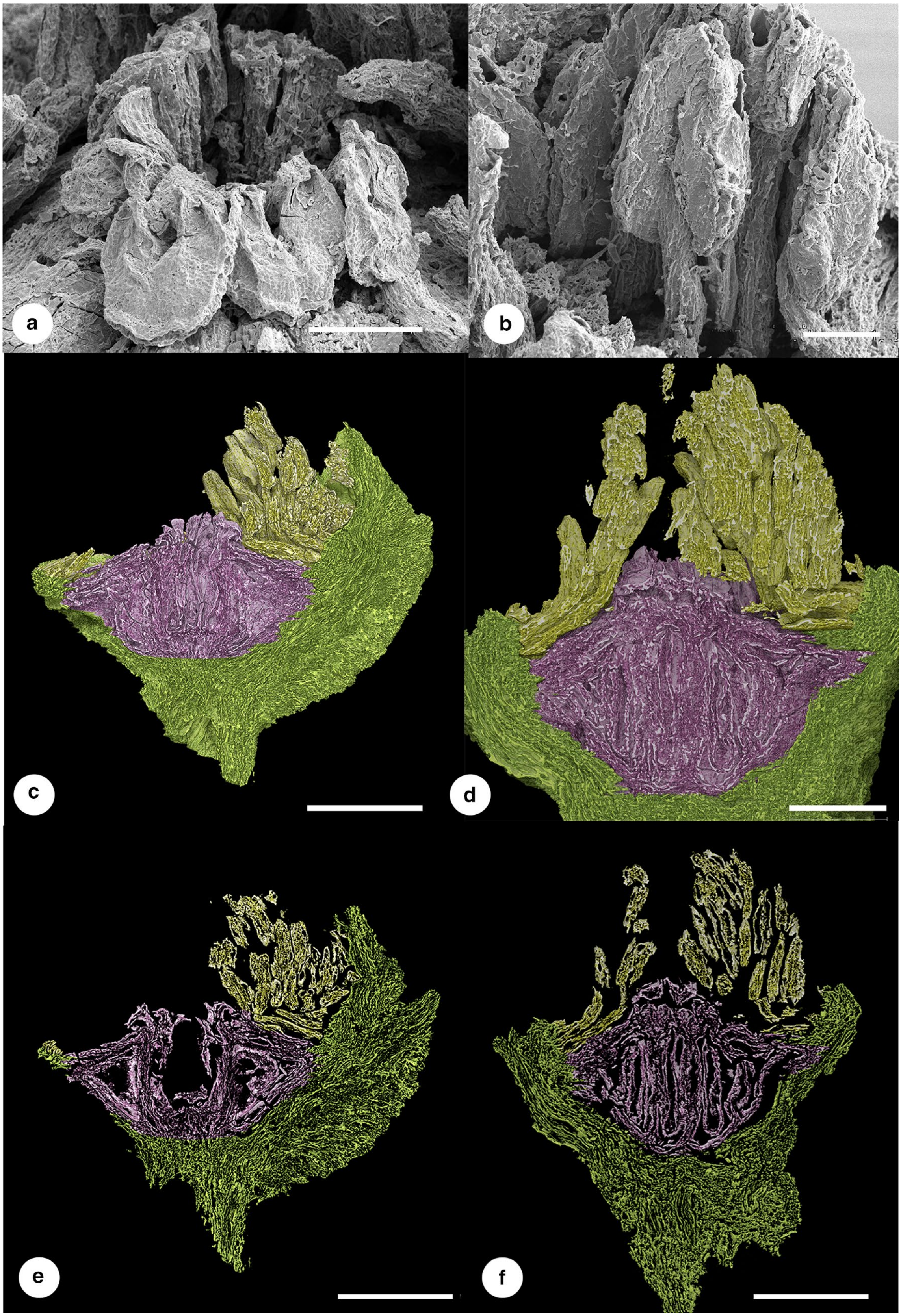
Perianth Elongated scars along the outer margin of the receptacle indicate that the flowers had a perianth of stout and free parts; each perianth part with a thick base. The number and shape of perianth parts are unknown (Figs. 3a–g, 4d–f).

Androecium Numerous, closely spaced stamens are preserved inside the perianth, showing that the androecium is composed of approximately 120 free stamens (Figs. 3a–g, 4b–f, 5a–h). Filaments of outer stamens are long and curve centripetally into the center of flower (Figs. 3a–g, 4b–f). Anthers are basifixed, tetrasporangiate with an acute apex (Figs. 3a, b, f, g, 4b). The dehiscence type is not clear. Pollen grains are tricolpate with fine reticulate exine (Fig. 7c).

Gynoecium The gynoecium is radially symmetrical and consists of one whorl of approximately 10 carpels that form a shallow cavity in the center of the flower (Figs. 3f, g, 4c–f, 6a–f). The carpels are falcate in lateral view and semicircular in transverse view, borne on a short stipe (Figs. 4c, e, 5a–h, 6a, c–e). The ventral margin of the carpel is more or less concave and leaves a small central cavity (Figs. 6c, 7e). The dorsal margin is convex tapering toward the center of flower axis (Figs. 4c–f, 5a–h). The exposed margins of the carpels are free, but it is unclear whether the carpels are completely free (Figs. 4c–f, 5a–h). The styles are short, becoming recurved and ventrally decurrent with a U-shaped stigma (Figs. 3a, f, g, 4a).

Fruits Fruits are small follicles dehiscent along the adaxial margin (Fig. 5a–f). The stigma is not present at the stage of fruit (Fig. 5a–e).

Seed Seeds are small, spindle-shaped, with chalazal slender pointed extension (Fig. 7d–f).


a
b
c
d
e
f

◂**Fig. 4** SEM and SRXTM images of flower of *Archaestella verticillatus*. PP56485. **a** SEM image of stigmas in center of flower. *Scale bar* 100 µm. **b** SEM image of stamens showing well differentiated filaments and basifixed anther. *Scale bar* 50 µm. **c** Three dimensional rendering of longitudinal section of flower shown in Fig. 3 showing broad hypanthium cup (*green*), stamens (*yellow*) and carpels (*pink*). *Scale bar* 400 µm. **d** Three dimensional rendering of longitudinal section of flower shown in Fig. 3 showing broad hypanthium cup (*green*), stamens (*yellow*) and carpels (*pink*). *Scale bar* 200 µm. **e** Two dimensional rendering of longitudinal section of flower shown in Fig. 3 showing broad hypanthium cup (*green*), stamens (*yellow*) and carpels (*pink*). *Scale bar* 400 µm. **f** Two dimensional rendering of longitudinal section of flower shown in Fig. 3 showing broad hypanthium cup (*green*), stamens (*yellow*) and carpels (*pink*). *Scale bar* 400 µm

Discussion

Cathiaria: structure

The genus *Cathiaria* Golovneva and Oskolski was established based on three-dimensionally preserved mesofossils of compound infructescences consisting of two orders of axes bearing sessile fruits from the Novosozyrevsky Formation (Cenomanian—early Turonian) in northern Kazakhstan and Siberia. Golovneva and Oskolski (2007) described two species, *C. zhilinii* and *C. tyensis*, which differ in the number of fruits on the lateral axes and in their arrangement. The gynoecium was interpreted to be unilocular bearing a single sub-basal or basal seed. However, the specified seed number should be viewed as uncertain because the interpretation was based on only one side of a fractured specimen. The fruits were described as being subtended by remnants of a bract or perianth at the base and they found no evidence of an androecium. According to Golovneva and Oskolski (2007), the infructescences consist of a main axis and alternate or sub-opposite lateral axes. The main axis is straight and irregularly finely ribbed. The lateral axes in immature condition are short, flattened and bear sessile fruits on the adaxial side; in maturity lateral axes are elongated, more or less cylindrical, and straight or curved. The type species, *Cathiaria zhilinii*, is characterized by lateral axes of mature infructescences that bear 5–12 sessile fruits, on the adaxial and lateral sides of the axis. There are no fruits on the abaxial surface.

The mesofossil specimens from the Kamikitaba locality share the same diagnostic features as seen in *Cathiaria zhilinii* and *C. tyensis*, but the excellent preservation of the Japanese material, and visualization using SRXTM, allows for the clarification of several important morphological details. The specimens from the Kamikitaba assemblage are recovered as fragments of axes bearing three or four fruits, which are interpreted to be the lateral axes of Cathiaria. Although the main axis has not been recovered from the Kamikitaba assemblage, most of features of the specimens from Kamikitaba agree with those of *Cathiaria zhilinii* from Kazakhstan, except for the small size of fruits, stout style and the number of seeds in the fruit. The flower consists of a single unilocular pistil, subtended by a scale-like bract. The style is extremely short and the stigma appears to be sessile. SRXTM does not indicate any perianth scars to be present, thus we conclude that the flower lacks perianth. Although the subtending scale-like structure was interpreted as either a bract or a reduced perianth by Golovneva and Oskloski (2007), SRXTM shows that each fruit is subtended by a single abaxial structure and therefore we interpret it as a persistent bract. The present study using SRXTM shows that *Cathiaria* is a unisexual female infructescence. No evidence of filaments or stamen scars was observed and we conclude that the flowers were unisexual. No staminate inflorescence specimens have not been recovered. It is unknown whether *Cathiaria* was monoecious or dioecious.

The fruit has a dorsiventral suture on the distal (abaxial) side. The suture is also observed in the specimens from Kazakhstan (Golovneva and Oskolski 2007, Pl. 3 Figs. 3, 4; Pl. 6, Fig. 2). Whereas Golovneva and Oskolski (2007) found evidence for only a single seed attached sub-basally or basally within a fruit based on SEM observations of a longitudinally fractured fruit, SRXTM of whole fruits demonstrates that the monocarpellate fruit includes two pendulous seeds from an apical placenta in a single locule (Fig. 2d–g). Determining the number of seeds and their attachment might not be so easy to confirm by SEM. The single seed borne in half of a longitudinally fractured fruit (Golovneva and Oskolski 2007, Pl. 4, Fig. 1) would imply the possible presence of two seeds in complete fruits of *Cathiaria* from Kazakhstan. However, it is still uncertain whether the number of seeds differs between the specimens of *Cathiaria* from Japan and Kazakhstan. The number of seeds and placentation in a fruit of *Cathiaria* from Kazakhstan would need to be examined in detail. Given these differences, the specimens from the Kamikitaba locality are described as a new species, *Cathiaria japonica*.

Cathiaria: systematic relationships

Golovneva and Oskolski (2007) evaluated possible systematic relationships of *Cathiaria* based on their structural interpretation: unisexual flowers, single unilocular pistil, reduced perianth, nut-like indehiscent one-seeded fruits, and compound infructescences with dorsiventral arrangement of fruits on flattened lateral axes. Golovneva and Oskolski (2007) concluded that there is not any extant taxon that is closely similar to Cathiaria, but they suggested that the infructescence of *Cathiaria* shares most traits with the Moraceae and partially with the Urticaceae. Although *Cathiaria* shares a number of features with the Urticales

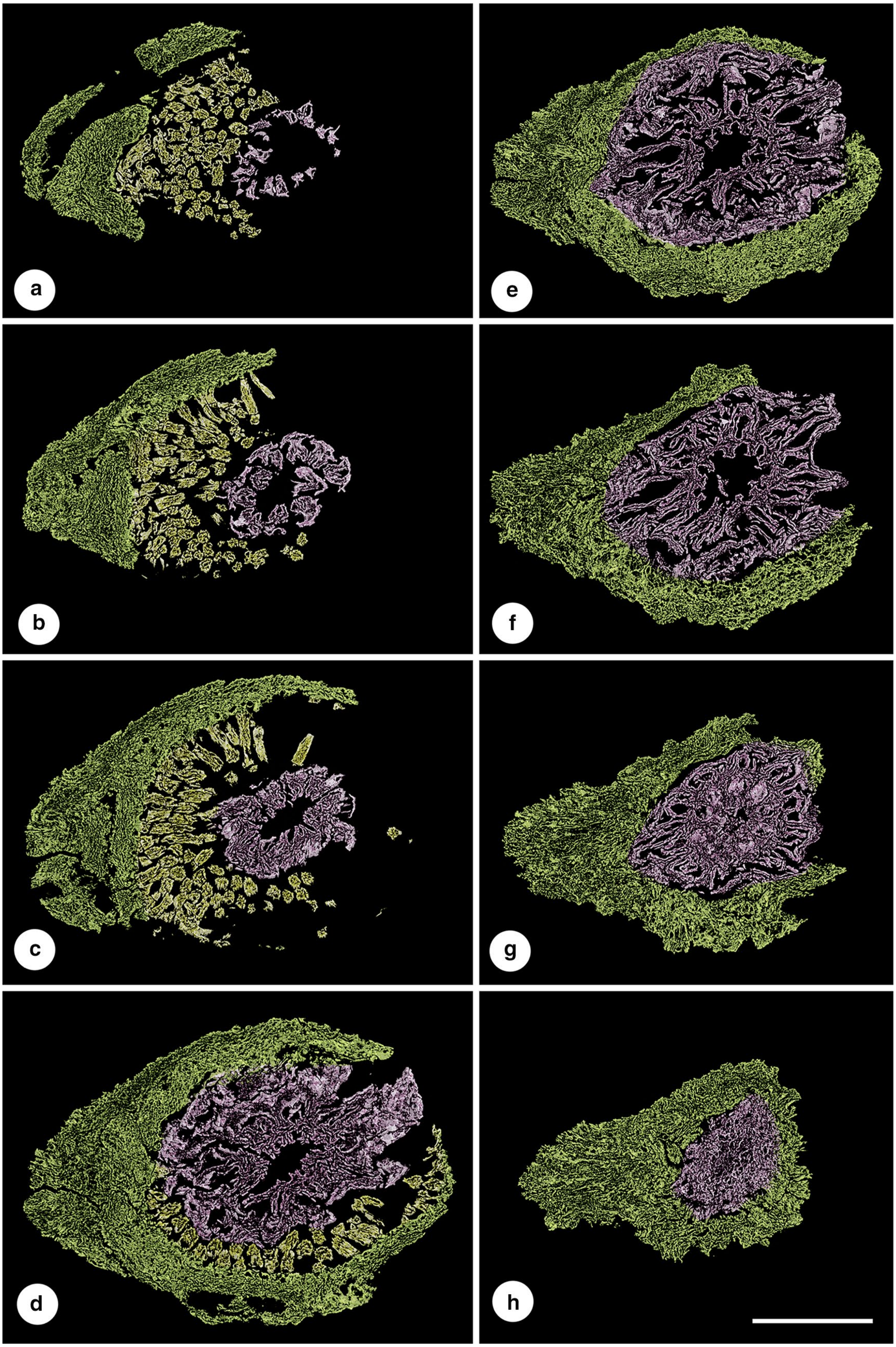


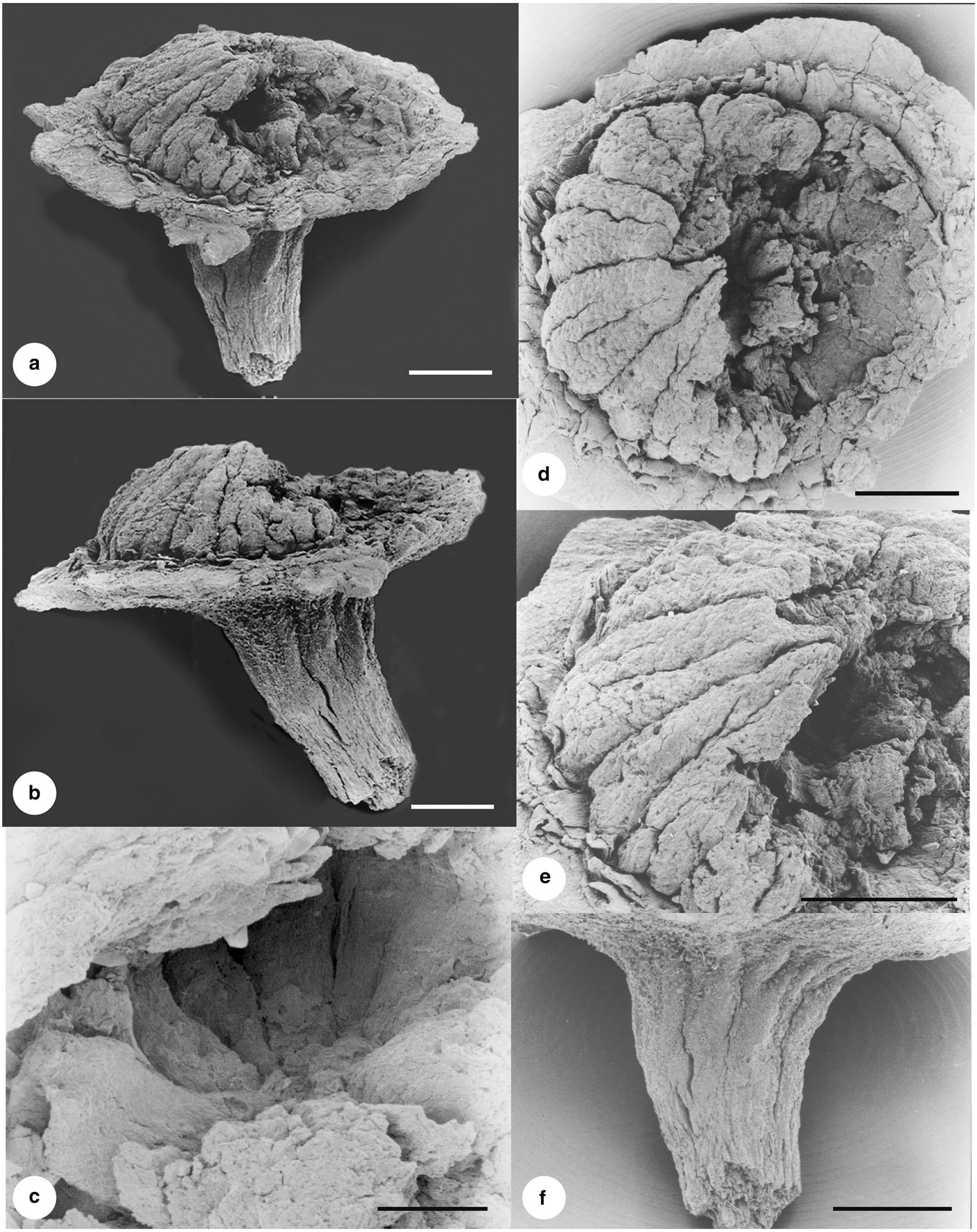
Fig. 5 SRXTM two dimensional rendering images of flower of *Archaestella verticillatus*. Same specimen as shown in Figs. 3, 4. 1**a**–**h** PP56485. Series of transverse sections from near top of specimen (**a**) to near base (**h**). All *scale bars* 400 µm

(e.g., compound branched unisexual inflorescences, dorsiventral arrangement of flowers and fruits, flowers with a single unilocular pistil, reduced perianth), the new structural details documented in this study call these conclusions into question. The fruits of *Cathiaria japonica* contain two seeds, not one as interpreted by Golovneva and Oskolski (2007). The tricolpate reticulate pollen grains of *Cathiaria* are also different from the porate (2–6 pores) or forate pollen of Moraceae and Urticaceae. These differences may indicate that *Cathiaria* is not closely related to Moraceae–Urticaceae. Golovneva and Oskolski (2007) also compared *Cathiaria* with the Chloranthaceae because they share branched unisexual inflorescences, flowers with a single unilocular pistil and reduced perianth, and a one-seeded fruit. Flowers in Chloranthaceae are bisexual or unisexual with a single pendulous ovule in the fruit and the pollen grains are polyforate, 4-colpate, monosulcate, or 5–6-tomosulcate. Golovneva and Oskolski (2007) suggested that *Cathiaria* differs from extant Chloranthaceae by the adaxial arrangement of flowers and fruits on flattened lateral axes of infructescences and by non-fleshly fruits. However, mesofossils are often influenced by compression and do not necessarily retain their original shape. In addition, it could be difficult to determine whether the fruits were fleshy or not by the condition of mesofossils. *Cathiaria* differs from extant Chloranthaceae by the dorsiventral suture and a large, obliquely decurrent stigma suture, twin seeds in the locule and the tricolpate pollen grains. We conclude that *Cathiaria* is not closely related to Chloranthaceae.

Based on the new structural details described here we suggest that *Cathiaria* is most closely related to the Buxaceae s.l., which are placed among the early-diverging groups of eudicots, often close to the Trochodendraceae (Chase et al. 1993; von Balthazar et al. 2000, APG III 2009, APG IV 2016). The Buxaceae s.l. is now recognized to include the Didymelaceae and Haptanthaceae (APG 2009, 2016; Shipunov and Shipunova 2011). The Buxaceae s.l. are a small family of about 70 species in seven genera (*Didymeles*, *Haptanthus*, *Buxus*, *Notobuxus*, *Sarcococca*, *Styloceras* and *Pachysandra*), that are characterized by monoecious evergreen herbs to small trees and rather small flowers with an inconspicuous perianth or just a subtending bract (von Balthazar and Endress 2002). Pollen morphology includes tricolpate grains in *Didymeles* and *Notobuxus*, 3–7-colporate, 5–12-pantocolporate and 12–40 pantoporate in Buxus, and pantoporate in *Sarcococca*, *Pachysandra* and *Styloceras* (Table 1). Shipunov and Shipunova (2011) suggested that *Didymeles* is placed as sister to the other genera in the Buxaceae s.l. Golovneva and Oskolski (2007) noted that *Cathiaria* is similar to *Didymeles* in the branched unisexual inflorescences, flowers with single unilocular pistil and reduced perianth, but they distinguished *Cathiaria* from *Didymeles* by the structure of its female inflorescence consisting of two orders of axes with flattened secondary axes bearing up to 20 flowers, whereas *Didymeles* have three orders of axes and secondary axes bear paired flowers and fleshy fruits (Sutton 1989; Golovnea and; Oskolski 2007). Pistillate flowers of *Cathiaria* and *Didymeles* lack perianth, are subtended by a bract, have a unicarpellate gynoecium with an adaxial suture and a large, truncate or obliquely decurrent bilobate stigma, short style, and tricolpate pollen. *Cathiaria* and *Didymeles* differ in the size of the ovary and the number of seeds. *Cathiaria japonica* has two ovules in the monocarpellate ovary. A single fertile ovule is included in a single locule in *Didymeles*, and an additional rudimentary ovule is occasionally present in the locule (von Balthazar et al. 2003). The degree of branching of the inflorescence axis is difficult to document in the fossil material due to fragmentation of the charcoalified material. Flowers of *Didymeles* differ from those of the other five genera of Buxaceae s.l. (*Buxus*, *Notobuxus*, *Sarcococca*, *Styloceras* and *Pachysandra*), which are characterized by the presence of 4–6 tepals, 3-carpellate gynoecium with two ovules per carpel, and divergent styles. The rare genus *Haptanthus*, which is endemic to Honduras, has an unusual inflorescence morphology with a central pistillate flower and two subtending clusters of staminate flowers. The staminate and pistillate flowers are practically naked with minute basal bracts or vestigial perianth. The morphological details have not been made clear for *Haptanthus*, but the available information clearly distinguishes the genus from Cathiaria.

Drinnan et al. (1991) described *Spanomera* from eastern North American deposits of 113–98 m.y. age (Albian), which may be a member of stem group Buxaceae s.s. (see also Crepet et al. 2004; Doyle and Endress 2010; Doyle and Upchurch 2014). The pistillate flowers are dimerous, but in the staminate flowers there may be five stamens opposite five tepals, the pollen is tricolpate, and the fruit is follicular (Drinnan et al. 1991). *Lusistemon*, also with striate, tricolpate pollen (but with different anther insertion and arrangement), from deposits in Portugal of about the same age, seems to be related (Pedersen et al. 2007).

Thus, based on comparison of the available morphological features we conclude that *Cathiaria* is closely related to *Didymeles* in the Buxaceae s. l.. The discovery of *Cathiaria* from North Kazakhstan, Siberia, and Japan suggests that the extinct genus was widely distributed in eastern Laurasia during the Late Cretaceous, and the extant *Didymeles* is an endemic genus restricted in Madagascar at present.


a
b
c
d
e
f

◂**Fig. 6** SEM images of fruiting specimen of *Archaestella verticillatus*. PP56486. **a** Oblique view of specimen showing broad hypanthium, stout pedicel, and single whorl of fruits. *Scale bar* 1000 µm. **b** Lateral view of specimen showing broad hypanthium, stout pedicel, and single whorl of fruits. *Scale bar* 1000 µm. **c** View of small cavity in the flower center formed by ring of carpels. *Scale bar* 250 µm. **d** Apical view of single whorl of fruits. *Scale bar* 1000 µm. **e** Oblique view of single whorl of fruits. *Scale bar* 1000 µm. **f** Stout pedicel of flower. *Scale bar* 1000 µm

Archaestella: structure

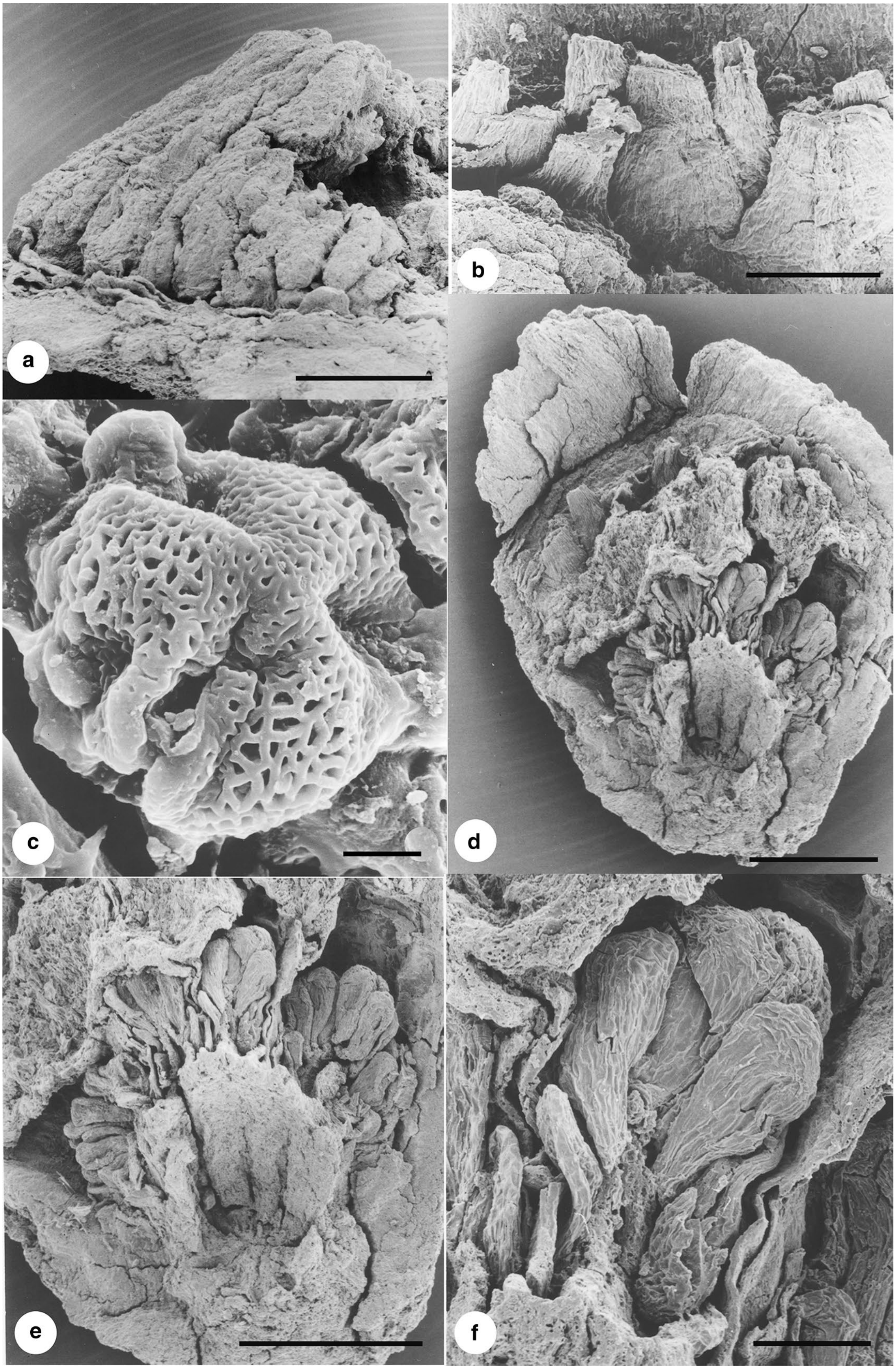
The genus *Archaestella* is established based on three-dimensionally preserved mesofossil specimens of a flower and fruits from the lower part of Ashizawa Formation of the Futaba Group (early Coniacian) in northeastern Japan. *Archaestella verticillatus*, is characterized by an actinomorphic, bisexual and multicarpellate flower. The gynoecium consists of a whorl of 10 conduplicate carpels that are laterally connate basally but distally distinct, with a conspicuous dorsal bulge. In the center of the flower there is a cavity. The styles are recurved with a papillate and ventrally decurrent stigma. There are ca. 10 ovules per carpel, marginal, pendulous from the broad, concrescent oblique summit of the locule. The pollen grains are tricolpate, with a reticulate exine pattern. The central cavity in the gynoecium is preserved until the stage of fruit. The characteristic stigma observed in the flower is absent in the fruiting specimens.

Archaestella: systematic relationships

The overall form of the fossil flowers, with numerous stamens that are clearly differentiated into anther and filament, laterally coherent carpels in a single whorl, and tricolpate pollen, narrows the range of likely systematic relationships and points toward affinities with members of the basal grade of the eudicots. A characteristic gynoecium with more than 10 laterally coherent carpels arranged in a single whorl is present in Menispermaceae, Papaveraceae and Trochodendraceae of the basal eudicot grade (Endress 1990). Among these families, the affinity of *Archaestella* is clearly with Trochodendraceae. Only Trochodendraceae have an androecium and stamens similar to those of the fossils. In Menispermaceae, the plants are dioecious with unisexual flowers composed of united stamens or free carpels with two ovules. In Papaveraceae the gynoecium is unilocular composed of a syncarpous ovary with sessile stigma or with indistinct to distinct style.

The Trochodendraceae are endemic to eastern Asia, from northeastern India to Japan, and comprise only two monospecific genera, *Trochodendron* and *Tetracentron* (Endress 1986). The systematic position of the Trochodendraceae was controversial until relatively recently. Li et al. (2011) and Ren et al. (2007) recently documented the presence of both of perforate vessel elements and tracheary elements in the xylem of Trochodendraceae, which was previously thought to lack vessels. Phylogenetic analyses based on molecular data (APG 2016) have placed the family in the basal eudicot grade close to Buxaceae s.l., along with Ranunculales (Berberidaceae, Circaesteraceae, Eupteleaceae, Lardizabalaceae, Menispermaceae, Papaveraceae, Ranunculaceae), Sabiaceae, and Proteales (Nelumbonaceae, Platanaceae, Proteaceae).

Flowers of the extant Trochodendraceae are hypogynous, bisexual, and actinomorphic or dissymmetric. The perianth consists of four sepals (*Tetracentron*) or is rudimentary (*Trochodendron*). The stamens have well differentiated filaments and anthers, which are basifixed, tetrasporangiate, apiculate, and latrose with each theca opening by pair of lateral valves. The semi-inferior carpels are syncarpous basally with free styles. In the stylar region the carpels are free and slightly recurved. The carpel flanks are congenitally fused. In the upper part of the ovary a compitum is formed by post genital fusion of the carpels in the center, while in the lower portion of the gynoecium the carpels do not meet in the center, but form a central dome (Chen et al. 2007; Endress 1986, Hsu et al. 2017). The pollen grains are spheroidal and tricolpate with striate-reticulate exine. The flowers of *Tetracentron* are sessile, small, about 2 mm in diameter, and hypogynous with 4 tepals and 4 stamens in decussate pairs and a whorl of 4 carpels. In fruit the follicles are laterally coherent and distally distinct. *Archaestella* is similar to *Tetracentron* in the presence of tepals, but differs in the presence of a pedicel and the larger number of floral parts. The flowers of *Trochodendron* are pedicellate, about 10 mm in diameter, with 40–70 spirally arranged stamens and one whorl of 4–(6)–17 semi-inferior carpels with free styles. *Trochodendron* is generally described as lacking a perianth, although variable numbers of rudimentary tepals are recognizable in early ontogenetic stages of flower development, but they are ephemeral and are lost at anthesis (Endress 1986). Wu et al. (2007) confirmed that extant *Trochodendron* has numerous perianth-like structures in young flowers, suggesting that the perianth of *Trochodendron* has been secondarily lost, and that both protandrous and protogynous flowers are present. The perianth of Cretaceous *Archaestella* could represent the ancestral form in Trochodendraceae, although this hypothesis would require testing with phylogenetic analyses. In post-anthetic flowers and fruits of Trochodendraceae the styles are recurved towards the outside of the flower, but in young flowers the tips are close to the center of the flower as also observed in the fossil flowers. The fruits of *Trochodendron* are follicles that are laterally coherent with distally distinct short recurved styles. The dorsal part of the ovary is horizontally extended at anthesis. *Trochodendron* and *Archaestella*


a
b
c
d
e
f

◂**Fig. 7** SEM images of fruiting specimens of *Archaestella verticillatus*. **a** Lateral view of fruits shown in Fig. 6. PP56486. *Scale bar* 500 µm. **b** Close up showing filament bases. PP56486. *Scale bar* 300 µm. **c** Tricolpate pollen grain found on PP56486. *Scale bar* 2 µm. **d** Oblique view of young fruit. More than half part of fruit has been removed. PP56487. *Scale bar* 500 µm. **e** Close up showing seeds in each locule. PP56487. *Scale bar* 500 µm. **f** Close up showing seeds. PP56487. *Scale bar* 100 µm

share a number of distinctive floral features, including an extensively developed hypanthium and a stout pedicel. These two genera also share a whorl of carpels that form a small cavity of well-developed gynoecium. The features of young flowers of *Trochodendron* particularly resemble those of *Archaestella*. The fossil genus *Archaestella* shares most of the morphological features with the extant Trochodendraceae, particularly in the recurved styles and the small cavity at the cener of the whorl of carpels, although it is uncertain whether anthers dehisce by longitudinal slits or by lateral valves as in *Trochodendron*. The most striking feature of the *Archaestella* flowers, compared to flowers of extant Trochodendraceae, is their very small size and the corresponding small size of the stamens, carpels and pollen grains. The small size of *Archaestella* fits the common pattern seen when many other Late Cretaceous flowers are compared with flowers of their extant relatives (Friis et al. 2011).

Archaestella: comparison with fossil taxa

Although some fossils of the Trochodendraceae are reported from Cretaceous sediments in the Northern Hemisphere, most of these fossils are questioned and reliable data are sparse on the Trochodendraceae during Cretaceous (Friis et al. 2011). "Trochodendrophyll" leaves that are characterized with actinodromous venation and chlorantoid teeth occur in the middle Cretaceous of North America and Eurasia (Crabtree 1987; Crane 1989; Upchurch and Wolfe 1987), but these leaves have been assigned to Cercidiphyllaceae or a variety of extant families including Menispermaceae, Piperaceae, Rhamnaceae and Salicaceae (Crane et al. 1991). A fossil wood, *Tetracentronites japonica* Nishida, from the Lower Cretaceous of Japan is regarded to a member of *Phoroxylon* in Bennettitales (Suzuki et al. 1991).

An impression fossil of a pluricarpellate structure was recovered from the Aptian or Albian Crato Formation in Brazil, which appears to be a syncarpous and multilocular gynoecium borne on stout axis. There are eight (or nine?) carpels, laterally fused to from a capsule-like fruit (Mohr and Friis 2000). Mohr and Friis (2000) suggested that the syncarpous capsule-like fossil is a potential basal member of the eudicots, showing some resemblance to the fruits of *Trochodendron*, although the fossil is much larger, ca. 3 cm in diameter, and differs from extant *Trochodendron* in the position of styles. *Archaestella* is much smaller than the pluricarpellate structure from Brazil. The inner structure of the Brazilian specimen is not clear because of the impression fossil.

The fossil genus *Nordenskioeldia* is widespread from Late Cretaceous to Miocene of the Northern Hemisphere (Crane et al. 1991; Pigg et al. 2001; Wang et al. 2009). The fossil record of *Nordenskioeldia* has been reviewed by Crane (1989), Crane et al. (1990, 1991), Manchester et al. (1991), Pigg et al. (2001, 2007) and Wang et al. (2009). The fruit of *Nordenskioeldia* is described as schizocarpic, consisting of 10–20 fruitlets arranged in a whorl around a parenchymatous central column. Each fruitlet has a laterally concrescent single-seed. The central column tapers apically and is bilaterally symmetrical, with regular longitudinal ridges developed between each of the adjacent fruitlets. In *Nordenskioeldia*, remains of the receptacle and exocarp persist on the infructescence axis after dehiscence as a shallow cup with a central column. Dispersed fruitlets are D-shaped in outline, dehiscent and contain a single small ovate seed (Crane et al. 1991). Doweld (1998) suggested that the fruits of the extant Trochodendraceae are syncarpous, lack a central colum, and contain many seeds in the locules, unlike the "one-seeded" fruitlets of *Nordenskioeldia*. The extinct Cretaceous genus *Archaestella* differs from *Nordenskioeldia* in the syncarpous fruits, presence of a central cavity and lack of a central column, and presence of many seeds in each locule.

There are many reports of fossil infructescence and fruits of *Trochodendron*, such as from the Miocene of Clarkia and Emerald Creek, Idaho (Manchester et al. 1991), the Eocene McAbee and One Mile Creek sites of British Columbia, Canada, and the Eocene Republic flora of Washington, USA (Pigg et al. 2001, 2007). The fossil fruits of *Trochodendron* from the middle Eocene of Washington State, 2.0–3.7 mm wide, supported by peduncles that are very similar to the extant T. aralioides (Pigg et al. 2001). *Trochodendron drachukii* are from the Early to Middle Eocene of McAbee near Cache Creek, Columbia, Canada, is a well-preserved paniculater infructescence that has a woody axis and fruits, 3–4 mm long × 3–4 mm wide consisting of six or more fused carpels. Fossil fruits of *Trochodendron* are also known from the late Miocene of Iwate Prefecture, Japan (Uemura 1988).

The fossil record of *Tetracentron* was reviewed by Grímsson et al. (2008). Fossil fruits of *Tetracentron remberi* were described from the Middle Miocene Clarkia locality, Idaho, United States (Manchester and Chen 2006), and *T. atlanticum* was recovered from the Middle Eocene of Iceland and Middle Miocene of western North America (Grímsson et al. 2008). Fruits of *T. atlanticum* are slightly narrower, more elliptical, and longer than the

Table 1 Comparison of *Cathiaria* and other fossil taxa with major lineages of Buxaceae sens. lat

Taxa	Inflorescence	Flower	Perianth	Carpel number	Ovules/carpel	Fruits	Style and stigma	Pollen
Didymeles (Didymelaceae)	Simple or compound botryoid spike	Unisexual	None	1	1 functional, 1 vestigial	Indehiscent drupe	Style very short or absent; stigma bilobed, truncate or oblique decurrent	Tricolpate
Stylocerateae (=Pachysandraceae, Styloceraceae)	Botryoid spike	Unisexual	None	2–3, ovaries connate	2	Dry, indehiscent	Style long, slender, recurved; stigma long decurrent	Pantoporate
Haptanthus (=Haptanthaceae)	Compound botryoid	Unisexual	None	3, ovaries connate	8–15, parietal	Unknown	Styles long, broad, recurved; stigma decurrent	Tricolpate
Buxeae	Botryoid spike	Unisexual	4–6 tepals	3, ovaries connate	2	Dehiscent capsule	Styles short, divergent; stigma bilobed, decurrent	3–12 colporate
Cathiaria	Spike-like segments (apex not preserved)	Unisexual	None	1	2	Indehiscent drupe	Style very short or absent; stigma oblique, decurrent	Tricolpate
Spanomera	Botryoid raceme (staminate flowers pedicillate; terminal pistillate flower sessile)	Unisexual	4–5 tepals	2, connate at base only	Unknown	Follicles	Style absent, sessile stigma decurrent	Tricolpate
Lusistemon	Unknown	Unisexual (staminate)	6 tepals	n.a	n.a	n.a	n.a	Tricolpate, striate
Lusicarpus	Unknown	Unisexual (pistillate)	Unknown	2, ovaries connate	Unknown	Unknown	Styles two, short, stout, recurved; stigma double-crested	Tricolpate, striate

Comparative data from Hutchinson (1964); Cronquist (1981); Drinnan et al. (1991); Stevens (2001 onwards); von Balthazar and Endress (2002); von Balthazar et al. (2003); Golovneva and Oskolski (2007); Pedersen et al. (2007); Shipunov and Shipunova (2011)

fruits of *T. remberi*. The fossil fruits of *Tetracentron* are quite similar to the extant *T. sinense*, which are tetralocular capsules with four styles. The general organization of the fossil and extant fruits is identical (Grímsson et al. 2008). *Tetracentron* is different from *Archaestella* by the fruits of four carpels.

Conclusion

Cathiaria and *Archaestella* provide important new information about the early history of the eudicot clade. The first evidence of the group comes from tricolpate pollen grains in the late Barremian or Aptian of South America, Africa, and the Middle East (Northern Gondwana), as reviewed by Doyle (2012). The main radiation of the basal eudicots is considered to have occurred during the Albian (Early Cretaceous) (Crane 1989; Doyle 2012; Doyle and Hickey 1976). The new fossil genus *Archaestella* provides the earliest record of the Trochodendraceae. The new species *Cathiaria japonica* provides structural details that help to clarify the systematic relationships of this previously described fossil genus, The presence of *Cathiaria* and *Archaestella* in the Kamikitaba assemblage suggests that the two basal eudicot families, Trochodendraceae and Buxaceae (including Didymelaceae), had differentiated by the Coniacian (Late Cretaceous) in eastern Eurasia. The two families were members of the late Cretaceous paleoflora in eastern Eurasia, with the other Angiosperm families including Annonaceae, Nymphaeaceae, Lauraceae, Combretaceae, Cornales and Fagales, with Conifers and Pteridophytes.

Acknowledgements The authors thank Peter R Crane and Stephen R Manchester for constructive and helpful comments on the manuscript. The study was funded by Grants-in-Aid for Scientific Research (21570092, 24570097 and 16K07477) from Japan Society for the Promotion of Science to M. T. and NSF Grant DEB-1348456 to P.S.H. Use of the Advanced Photon Source, an Office of Science User Facility operated for the US Department of Energy (DOE) Office of Science by Argonne National Laboratory, was supported by the US DOE under Contract No. DE-AC02-06CH11357.

References

APG III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants:APG III. Bot Linn Soc 161:105–121

APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc 181:1–20

Chase MW, Soltis DE, Olmstead RG, Morgan D, Les DH, Mishler BD, Duvall MR, Price RA, Hills HG, Qiu Y-L, Kron KA, Rettig JH, Conti E, Palmer JD, Manhart JR, Sytsma KJ, Michaels HJ, Kress WJ, Karol KG, Clark WD, Hedren M, Gaut BS, Jansen RK, Kim K-J, Wimpee CF, Smith JF, Furnier GR, Strauss SH, Xiang Q-Y, Plunkett GM, Soltis PS, Swensen SM, Williams SE, Gadek PA, Quinn CJ, Eguiarte LE, Golenberg E, Learn GH Jr, Sean W, Graham SW, Barrett SCH, Dayanandan S, Albert VA (1993) Phylogenetics of seed plants; an analysis of nucleotide sequences from the plastid gene *rbc*L. Ann Missouri Bot Gard 80:528–580

Chen L, Ren Y, Endress PK, Tian XH, Zhang XH (2007) Floral organogenesis in *Tetracentron sinense* (Trochodendraceae) and its systematic significance. Pl Syst Evol 264:183–193

Cohen KM, Finney SC, Gibbard PL, Fan J-X (2013) The ICS International Chronostratigraphic Chart. Episodes 36:199–204 **(updated 2016)**

Crabtree DR (1987) Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras. Ann Missouri Bot Gard 74:707–747

Crane PR (1989) Paleobotanical evidence on the early radiation of nonmagnoliid dicotyledons. Plant Syst Evol 162:165–191

Crane PR, Manchester SR, Dilcher DL (1990) A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. Fieldiana Geol NS 20:1–63

Crane PR, Manchester SR, Dilcher DL (1991) Reproductive and vegetative structure of *Nordenskioldia* (Trochodendraceae), a vesselless dicotyledon from the Early Tertiary of the Northern Hemisphere. Am J Bot 78:1311–1334

Crane PR, Friis EM, Pedersen KR (1994) Paleobotanical evidence on the early radiation of magnoliid angiosperms. Plant Syst Evol 8(Suppl.):51–72

Crane PR, Friis EM, Pedersen KR (2004) Fossils and plant phylogeny. Am J Bot 91:1683–1699

Crepet WL, Nixon KC, Gandolfo MA (2004) Fossil evidence and phylogeny: the age of major angiosperm clades based on mesofossil and macrofossil evidence from Cretaceous deposits. Am J Bot 91:1666–1682.

Cronquist A (1981) An integrated system of classification of flowering plants. Columbia Univeristy Press, New York

Dowd BA, Campbell GH, Marr RB, Nagarkar VV, Tipnis SV, Axe L, Siddons DP (1999) Developments in synchrotron X-ray computed microtomography at the National Synchrotron Light Source. In: Bonse U (ed) Developments in X-Ray Tomography II, vol 3772. Proc SPIE, pp 224–236

Doweld AB (1998) Carpology, seed anatomy and taxonomic relationships of *Tetracentron* (Tetracentraceae) and *Trochodendron* (Trochodendraceae). Ann Bot 82:413–443

Doyle JA (2012) Molecular and fossil evidence on the origin of angiopserms. Ann Rev Earth Planet Sci 40:301–326

Doyle JA, Endress PK (2010) Integrating early Cretaceous fossils into the phylogeny of living angiosperms: Magnoliidae and eudicots. J Syst Evol 48:1–35

Doyle JA, Upchurch GR (2014) Angiosperm clades in the Potomac Group: what have we learned since 1977? Bull Peabody Musem Nat Hist 55:111–134

Drinnan AN, Crane PR, Friis EM, Pedersen KR (1991) Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (mid-Cretaceous) of eastern North America. Am J Bot 78:153–176

Endress PK (1986) Floral structure, systematics, and phylogeny in Trochodendrales. Ann Missouri Bot Gard 73:297–324

Endress PK (1990) Patterns of floral construction in ontogeny and phylogeny. Biol J Linn Soc 39:153–175

Friis EM, Pedersen KR, Crane, PR (1994) Angiosperm floral structures from the Early Cretaceous of Portugal. Pl Syst Evol 8:31–49 **(Suppl)**

Friis EM, Pedersen KR, Crane PR (2006) Cretaceous angiopserm flowers: innovation and evolution in plant reproduction. Palaeogeogr Palaeoclimatol Palaeoecol 232:251–293

Friis EM, Crane PR, Pedersen KR, Bengtson S, Donoghue PCJ, Grimm GW, Stampanoni M (2007) Phase contrast enhanced synchrotron-radiation X-ray analyses of Cretaceous seeds link Gnetales to extinct Bennettitales. Nature 450:549–552

Friis EM, Pedersen KR, von Balthazar M, Grimm GW, Crane PR (2009) *Monetianthus mirus* gen. et sp. nov., a Nymphaealean flower from the Early Cretaceous of Portugal. Int J Plant Sci 10:1086–1101

Friis EM, Pedersen KR, Crane PR (2011) Early flowers and angiosperm evolution. Cambridge University Press, Cambridge

Golovneva IB, Oskolski AA (2007) Infructescences of *Cathiaria* gen n. from the late Cretaceous of North Kazakhstan and Siberia (Russia). Acta Paleobot 47:57–87

Grímsson F, Denk T, Zetter R (2008) Pollen, fruits, and leaves of *Tetracentron* (Trochodendraceae) from the Cainozoic of Iceland and western North America and their palaeobiogeographic implications. Grana 47:1–14

Herendeen PS, Doyle JA, Endress PK, Takahashi M (2016) *Cecilanthus polymerus*, a novel multiparted flower from the mid-Cretaceous Rocky Point locality, Maryland. Botany 94:787–803

Hsu Y-C, Jane W-N, Chen S-H (2017) Infrorescence and floral development in *Trochodendron aralioides* (Trochodendraceae). Plant Syst Evol 303:403–412

Hutchinson J (1964) The genera of flowering plants (Angiospermae), vol 1. Clarendon Press, Oxford

Li H-F, Chaw S-M, Du C-M, Ren Y (2011) Vessel elements present in the secondary xylem of *Trochodendron* and *Tetracentron* (Trochodendraceae). Flora 206:595–600

Manchester SR, Chen I (2006) *Tetracentron* fruits from the Miocene of western North America. Int J Plant Sci 167:601–660

Manchester SR, Crane PR, Dilcher DL (1991) *Nordenskioldia* and *Trochodendron* (Trochodendraceae) from the Miocene of northwestern North America. Bot Gaz 152:357–368

Mohr BAR, Friis EM (2000) Early angiosperms from the Aptian Crato Formation (Brazil), a preliminary report. Int J Plant Sci 161(6 Suppl.):S155–S167

Pedersen KR, von Balthazar M, Crane PR, Friis EM (2007) Early Cretaceous floral structures and in situ tricolpate-striate pollen: new early eudicots from Portugal. Grana 46:176–196

Pigg KB, Wehr WC, Ickert-Bond SM (2001) *Trochodendron* and *Nordenskioeldia* (Trochodendraceae) from the Middle Eocene of Washington State, USA. Int J Plant Sci 162:1187–1198

Pigg KB, Dillhoff RM, DeVore ML, Wehr WC (2007) New diversity among the Trochodendraceae from the Early/Middle Eocene Okanogan Highlands of British Columbia, Canada, and northeastern Washington State, United States. Int J Plant Sci 168:521–532

Ren Y, Chen L, Tian XH, Zhang XH, Lu AM (2007) Discovery of vessels in *Tetracentron* (Trochodendraceae) and its systematic significance. Pl Syst Evol 267:155–161

Schönenberger J, von Balthazar M, Takahashi M, Xiao X, Crane PR, Herendeen PS (2012) *Glandulocalyx upatoiensis*, a fossil flower of Ericales (Actinidiaceae/Clethraceae) from the Late Cretaceous (Santonian) of Georgia, USA. Ann Bot 109:921–936

Shipunov AB, Shipunova E (2011) *Haptanthus* story: rediscovery of enigmatic flowering plant from Honduras. Am J Bot 98:761–763

Stevens PF (2001) Angiosperm Phylogeny Website. Version 12, July 2012 [and more or less continuously updated since]. http://www.mobot.org/MOBOT/research/APweb/. Accessed 1 Dec 2016

Sutton DA (1989) The *Didymelales*: a systematic review. In: Crane PR, Blackmore S (eds) Evolution, systematics, and fossil history of the Hamamelidae, vol 1. Clarendon Press, Oxford, pp 279–284

Suzuki M, Joshi L, Fujii T, Noshiro S (1991) The anatomy of unusual tracheids in *Tetracentron* wood. IAWA J 12:23–33

Takahashi M, Crane PR, Ando H (1999a) Fossil flowers and associated plant fossils from the Kamikitaba locality (Ashizawa Formation, lower Coniacian, Upper Cretaceous) Northeast Japan. J Plant Res 112:187–206

Takahashi M, Crane PR, Ando H (1999b) *Esgueiria futabaensis* sp. nov.; a new angiosperm flower from the upper Cretaceous (lower Coniacian) of northeastern Honshu, Japan. Paleontol Res 3:81–87

Takahashi M, Herendeen PS, Crane PR (2001) Lauraceous fossil flowers from the Kamikitaba locality (Lower Coniacian; Upper Cretaceous) on northeastern Japan. J Plant Res 114:429–434

Takahashi M, Crane PR, Manchester SR (2002) *Hironoia fusiformis* gen. et sp. nov.; a cornalean fruit from the Kamikitaba locality (upper Cretaceous, lower Coniacian) in northeastern Japan. J Plant Res 115:463–473

Takahashi M, Friis EM, Crane PR (2007) Fossil seeds of *Nymphaeales* from the Tamayama Foramtion (Futaba Group), upper Cretaceous (early Santonian) of Northeastern Honshu, Japan. Int J Plant Sci 168:341–350

Takahashi M, Friis EM, Herendeen PS, Crane PR (2008a) Fossil flowers of Fagales from the Kamikitaba Locality (Early Coniacian; Late Cretaceous) of Northeastern Japan. Int J Plant Sci 169:899–907

Takahashi M, Friis EM, Uesugi K, Suzuki Y, Crane PR (2008b) Floral evidence of Annonaceae from the Late Cretaceous of Japan. Int J Plant Sci 169:908–917

Takahashi M, Herendeen PS, Xiao X, Crane PR (2014) Lauraceous fossil flowers from the Kamikitaba assemblage (Coniacian, Late Cretaceous) of northeastern Japan. Syst Bot 39:715–724

Uemura K (1988). Late Miocene Floras in Northeast Honshu, Japan. National Science Museum, Tokyo

Upchurch GR, Wolfe JA (1987) Mid-Cretaceous to Early Tertiary vegetation and climate: evidence from fossil leaves and woods. In: Friis EM, Chaloner WG, Crane PR (eds) The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge, pp 75–105

von Balthazar M, Endress PK (2002) Development of inflorescences and flowers in Buxaceae and the problem of perianth interretation. Int J Plant Sci 163:847–876

von Balthazar M, Endress PK, Qiu U-L (2000) Pylogenetic relaltionships in Buxaceae based on nuclear internal transcribed spacers and plastid *ndh*F sequences. Int J Plant Sci 161:785–792

von Balthazar M, Schatz GE, Endress PK (2003) Female flowers and inflorescences of Didymelaceae. Plant Syst Evol 237:199–208

von Balthazar M, Pedersen KR, Crane PR, Stampanoni M, Friis EM (2007) *Potomacanthus lobatus* gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of Eastern North America. Am J Bot 94:2041–2053

Wang YH, Ferguson DK, Feng GP, Wang YF, Zhilin SG, Li CS, Svetlana PT, Yang J, Ablaev AG (2009) The phytogeography of the extinct angiosperm *Nordenskioeldia* (Trochodendraceae) and its response to climate changes. Palaeogeog Palaeoclimatol Palaeoecol 280:183–192

Wu H-C, Su H-J, Hu J-M (2007) The identification of A-, B-, C-, and E-class MADS-box genes and implications for perianth evolution in the basal eudicot *Trochodendron aralioides* (Trochodendraceae). Int J Plant Sci 168:775–799